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Paleobiogeography of Latest Cretaceous and Early Paleocene Mammals from North America

by

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Abstract

Nearly all of what is known of the patterns of latest Cretaceous and early Paleogene mammalian evolution (from approximately 69 to 57 million years ago) is documented in stratigraphic sequences from the Western Interior of North America. Throughout much of the latest Cretaceous and early Paleogene this region was tectonically active, with the emergence of the Rocky Mountains and Western Interior foreland basin. Several major marine transgressions also occurred during this interval and, at times, the Western Interior epicontinental seaway bisected the continent. Moreover, the latest Cretaceous and early Paleogene is marked by episodes of rapid climatic warming and cooling, and intensive volcanism. That mammals were affected by these changes is without question; however, the extent to which these factors helped shape the evolutionary patterns of this group is less obvious. To better comprehend the evolutionary dynamics between mammals and their environments across this interval, this dissertation focuses on the paleobiogeography of latest Cretaceous through the early Paleogene mammals from the Western Interior of North America. A number of statistical analyses (e.g., ordination, clustering, linear regression) were employed to assess mammalian faunal provinciality within North America during this interval, differences in the relative abundances of fossil mammals during the latest Cretaceous assemblages, and, finally, the latitudinal diversity gradient in latest Cretaceous and early Paleogene mammals. Notable discoveries include the absence of faunal provinciality and little variation in mammalian taxonomic richness across latitude, but considerable differences in the relative abundance of mammals within assemblages from the latest Cretaceous, with eutherians more diverse and abundant in some of the northerly assemblages. These findings suggest that the paleogeographic and climatic changes that characterized the latest Cretaceous and early Paleogene resulted in intricate biogeographic patterns among mammals from this interval. These studies additionally emphasize the importance of quantitatively assessing these patterns to understand the interactions between mammals and their environments.

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Dedication

This dissertation is dedicated to my parents, Larry and Brenda.

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Institutional Abbreviations

AMNH	American Museum of Natural History
DMNH	Denver Museum of Natural History
KU	Kansas University
LSUMG	Louisiana State University Museum of Geology
NMMNH	New Mexico Museum of Natural History
PTRM	Pioneer Trails Regional Museum
TMM	Texas Memorial Museum
UW	University of Wyoming

Statistical abbreviations

MST	Minimum spanning tree
NMDS	Non-metric multidimensional scaling
SD	Standard deviation

North American Land Mammal Ages

Cf	Clarkforkian
Pu	Puercan
Ti	Tiffanian
To	Torrejonian

1 General Introduction, Paleogeography and Climatic Setting, and Chapters and Objectives

1.1 General Introduction

Continental strata of the latest Cretaceous and early Paleogene of North America (from approximately 69 to 57 million years ago [mya]) document the densest and most complete record of late Mesozoic and early Cenozoic mammalian evolution in the world (Cifelli et al., 2004; Lofgren et al., 2004). Current evidence, based largely on this North American record, points to this interval of time as one of the most important in the evolutionary history of mammals. More specifically, following the catastrophic mass extinction events that marked the Cretaceous/Paleogene (K/Pg) boundary (approximately 65.6 mya) (see Renne et al., 2013), many lineages of mammals underwent a remarkable evolutionary radiation (see e.g., Alroy, 1999; Novacek, 1999; Rose and Archibald, 2006; Rose, 2006).

Through the same interval of time, North America underwent remarkable geophysical and climatic changes. Beginning in the Middle Jurassic and continuing to the early Eocene (from roughly 170 to 45 mya), the North American Cordilleran orogenic fold-thrust belt (i.e., the emerging Rocky Mountains) and the Western Interior foreland basin were tectonically active, and underwent episodes of convergence, subduction, rifting, faulting, uplift, erosion, volcanism, and subsidence (Miall et al., 2008). In addition, eustatic sea levels were fluctuating and at multiple times during the Late Cretaceous and early Paleogene the Western Interior foreland basin was inundated with marine waters (Kauffman, 1984, 1977). Climate fluctuations through this interval further compounded events, with generally warm temperatures during the latest Cretaceous and Paleocene, followed by even warmer temperatures at the Paleocene/Eocene boundary and into the early Eocene (e.g., Zachos et al., 2001).

That mammals were affected by these environment changes is without question; however, the extent to which these factors helped shaped the diversity and evolutionary patterns of this group is less obvious. On that account, and because these mammals lived during a crucial interval during the Earth's history, the paleobiogeography of mammals from the latest Cretaceous and early Paleogene of the Western Interior of North America is the focus of this dissertation. To begin to this discussion, I review the paleogeography and climate of North America during the Late Cretaceous and early Paleogene.

1.2 Paleogeography and Climatic Setting of North America during the latest Cretaceous and early Paleogene

1.2.1 Latest Cretaceous and early Paleogene Paleogeography of North America

The North American Cordilleran orogenic fold-thrust belt and Western Interior foreland basin evolved together for over 100 million years, from the Middle Jurassic to the early Eocene (DeCelles, 2004; Miall et al., 2008). The earliest development of these geologic features is conventionally associated with the rapid sea-floor spreading in the North Atlantic Ocean. This spreading initiated the westward drift of the North American continent relative to Europe and, consequently, the subduction of several Pacific oceanic plates beneath the western margin of the North American continental plate (Miall et al., 2008; Ricketts, 2008). The asymmetrical Western Interior foreland basin developed to the east of the Cordillera orogenic fold-thrust belt and west of the North American craton, and tapers to the east.

In the Canadian portion of the Cordillera, the change from regional extension to contraction was coupled with the collision of a series of terranes that drifted into the Cordilleran subduction zone throughout the Middle Jurassic and early Eocene. The accretion of these successive terranes to the North American plate, rather than their subduction beneath it, resulted in major crustal deformation and, ultimately, the expansion of the western margin in Canada by several hundred kilometers (i.e., much of British Columbia is comprised of these terranes) (Ricketts, 2008). As older terranes were displaced eastward with the successive arrival of each new terrane, a new cycle of fold-thrust belt tectonism, uplift, erosion and clastic wedge generation was initiated (Miall et al., 2008).

The American Cordillera was largely not influenced by the accretion of these offshore terranes (Ingersoll, 2008); instead, changes in the angle of the subducting Pacific plate resulted in episodes of deformation and volcanism (Miall et al., 2008). Additionally, the latest Cretaceous to early Eocene Laramide Orogeny, likely driven by the shallow subduction of the Farallon Plate beneath the western margin of North America (Bird, 1988), fractured and partitioned the foreland basin into a mosaic of smaller basins and uplifts (Decelles, 2004; Miall et al., 2008; Lawton, 2008). Laramide-style tectonism largely did not occur in Canada although regional fold-thrust tectonism did continue in this area until the early Eocene, as noted earlier (Hildenbrand, 2009).

1.2.2 Marine Transgressions and Epicontinental Seaways

During the uplift of the North American Cordillera, several major marine transgressions occurred in the Western Interior Basin. Towards the end of the Early Cretaceous, most of the Western Interior Basin was occupied by easterly flowing fluvial and estuarine systems (Miall et al., 2008). However, following a brief sea level fall, a major transgression occurred in the early Late Cretaceous and marine waters from the ancestral Gulf of Mexico in the south and the ancient Arctic Ocean in the north inundated the foreland basin, giving rise to the Western Interior Seaway. At its maximum coverage, this seaway extended roughly 4800 kilometers in length and to a maximum width of 1600 kilometers (Kauffman, 1984). The presence of the Western Interior Seaway is generally thought to have led to more humid and equable climates in the Late Cretaceous (Valdes et al., 1996) and is also suggested to have acted as a geographic barrier to terrestrial organisms (e.g., Sampson et al., 2010).

Pulses of the Laramide orogeny coupled with the fall of eustatic sea levels eventually led to the rapid regression of the Western Interior Seaway beginning in the latest Cretaceous (Miall et al., 2008). Here in western Canada, the Bearpaw and Pierre formations represent the last vestiges of this receding seaway, with the shorelines quickly migrating south towards the Gulf of Mexico (Lillegraven and Ostresh, 1990). As this seaway regressed, Archibald (1996; in Archibald and Fastovsky, 2004) contends that this would have led to habitat fragmentation and contemporaneous reduction in mammalian (and, notably, dinosaurian) diversity that culminated at the K/Pg boundary extinction event.

Finally, the last major marine transgression, and the last known epicontinental seaway in North America, occurred briefly from the early Paleocene to the middle Paleocene (Hartman and Hunter, 1998). The Cannonball Seaway, unlike its predecessor, extended from the southernmost parts of Canada to the Gulf of Mexico (Lund et al., 2002). And, while notably smaller in geographic scale when compared to the Western Interior Seaway, the Cannonball Seaway is also thought to have led to more temperate conditions and similarly acted as a barrier.

1.2.3 Latest Cretaceous and early Paleogene Climate of North America

Oxygen isotope records from benthic foraminifera indicate a general long-term trend of global warming extending from the latest Cretaceous through the early Paleogene. This was followed by an interval of cooler, more temperate conditions during the late Paleocene, and then a gradual rise in temperature to a climatic optimum in the early Eocene, interrupted briefly by an abrupt warming event at the Paleocene/Eocene boundary (i.e., the Paleocene/Eocene Thermal Maximum [PETM]) (Zachos et al., 2001)

Climate trends from the continental record are no less profound. The warm global climates in the latest Cretaceous and early Paleogene are generally corroborated by fossil floral composition and leaf margin data (e.g., Wolfe and Upchurch, 1987; Johnson and Ellis, 2002), although a slight cooling is reported immediately preceding the K/Pg boundary (Wilf, 2003). Fossil flora from early Paleogene sediments at mid-latitudes in the Western Interior Basin are indicative of warm climates, with estimates of mean annual temperature typically exceeding 15°C (Hickey, 1980; Wing et al., 1991; Wilf, 2000) and, based on an exceptionally preserved assemblage from Castle

Rock in Colorado, even thought to reach as high as 22°C (Johnson and Ellis, 2002). Mean annual temperatures during the late Paleocene cooled to as low as 10°C but approached 20°C at the end of the epoch, and reached as high as 23°C at the PETM and again at the climatic optimum of the early Eocene (Wilf, 2000). Non-mammalian faunal data add further support for these trends (Markwick, 1998).

1.3 Chapters and Objectives

This dissertation is comprised of three quantitative studies on the paleobiogeography of latest Cretaceous and early Paleogene mammals, each with the aim of improving the understanding of mammalian evolution across the dramatic geologic and climatic events that marked this interval. The first study within this dissertation (Chapter Two) examines mammalian faunal provinciality within North America during the latest Cretaceous and earliest Paleocene. A number of previous studies (e.g., Sloan, 1969; Anthony and Maas, 1990; Weil, 1999; Donohue et al., 2013) have suggested that the northern and southern parts of the Western Interior of North America represented distinct biogeographic provinces during parts of the Late Cretaceous and early Paleogene. I developed a newly constructed dataset documenting mammalian taxonomic richness and occurrences, and employed non-hierarchical cluster analyses, non-metric multidimensional scaling, minimum spanning trees, and simple chi-squared analyses to assess claims of provinciality. This research represents the first comprehensive study of mammalian faunal provinciality immediately before and after the dramatic events that characterized the Cretaceous/Paleogene boundary.

Recognizing some of the limitations with occurrence data (see e.g., Nicholls and Russell, 1990), Chapter Three assesses the relative abundances of fossil mammals and focuses on latest Cretaceous assemblages from across North America. A standardized resampling approach was employed to generate assemblage-specific abundance estimates for each mammal, based on the faunal composition from the well-studied Type Lance local fauna from the Lance Formation of northeastern Wyoming (e.g., Clemens, 1964, 1966, 1973). Using these estimates, the faunal similarity between latest Cretaceous assemblages was quantitatively assessed and genera that were unusually abundant or rare compared to the Type Lance local fauna were identified. A discussion on the timing and patterns of the evolutionary radiation of certain mammalian groups near the K/Pg boundary is also provided.

In Chapter Four, I examine the latitudinal diversity gradient within latest Cretaceous and early Paleogene mammals from North America. The modern latitudinal diversity gradient (i.e., the increase in taxonomic richness from the poles to the equator) is often suggested to have been in place through most of the last 544 million years (see e.g., Crame, 2001; Hillebrand, 2004; Leighton, 2005); yet, several recent studies have demonstrated that the taxonomic richness of certain groups was higher in temperate paleolatitudes than in more tropical paleolatitudes (e.g., Eocene insects [Archibald et al., 2010] and Mesozoic non-avian dinosaurs [Mannion et al., 2012]). Expanding on the dataset presented in Chapter One and applying regression analyses, the latitudinal diversity gradient within latest Cretaceous and early Paleogene mammalian assemblages from North America is reconstructed. In addition, several of the mechanisms that have previously been proposed to determine patterns of latitudinal diversity, including differential sampling and climate, are also assessed and reviewed in this study.

The final chapter (Chapter Five) provides a summary of the central findings within this research, and presents some of the broader implications and areas for further research.

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2 Faunal Provinciality within Latest Cretaceous and Earliest Paleocene Mammalian Assemblages from the Western Interior of North America

2.1 Abstract

Although the presence of mammalian provinciality within North America during the latest Cretaceous and earliest Paleocene (from approximately 69 to 64 million years ago) is commonly cited, few quantitative analyses have actually centered on mammalian occurrences from this interval. In fact, the vast majority of these studies have inferred that the geographic distributions of mammals during the latest Cretaceous and Paleocene were likely similar to those during the Late Cretaceous (i.e., Campanian [from roughly 83 to 72 million years ago]), an interval in which faunal provinciality is better established. However, there are no reasons to suspect that the distribution of these animals remained the same across these intervals, particularly with the dramatic events that characterize the Cretaceous/Paleogene boundary, including the impact of a large bolide, intensive volcanism, and changes in the global sea level. In this study, I assembled information on the occurrences of over 100 latest Cretaceous and earliest Paleocene mammalian genera from 30 localities across North America. To identify mammalian provinciality, non-hierarchical cluster analyses, non-metric multidimensional scaling, and minimum spanning trees were employed. A biogeographic province was also explicitly defined as containing at least 25% endemic taxa and suggestions of the presence of faunal barriers near a paleolatitude 50° N were assessed. Despite the disparity among the approaches, the findings provide little quantitative support for mammalian provinciality during the latest Cretaceous or

earliest Paleocene. The vast majority of the recovered clusters are weakly supported and the geographic position of these clusters is inconsistent with previous suggestions of provinciality. Taxa endemic to localities north or south of the proposed barrier comprise a comparatively small proportion of the dataset and the pattern of occurrences cannot be differentiated from gradual change across a latitudinal range. These results suggest that latest Cretaceous and earliest Paleocene mammalian faunas were markedly different than those from stratigraphically older time intervals and undergoing remarkable changes.

2.2 Introduction

The latest Cretaceous and earliest Paleogene of North America (from approximately 69 to 64 million years ago [mya]) documents the densest and most intensely sampled record of late Mesozoic and early Cenozoic mammalian evolution in the world (Cifelli et al., 2004; Lofgren et al., 2004). Current evidence, based largely on this North American record, points to this interval of time as one of the most important in the evolutionary history of mammals. In particular, following the catastrophic mass extinction events that marked the Cretaceous/Paleogene (K/Pg) boundary (approximately 65.6 mya) (Renne et al., 2013; Sprain et al., 2014), many lineages of mammals underwent remarkable adaptive radiations (Alroy, 1999; Novacek, 1999; Archibald and Deutschman, 2001; Rose and Archibald, 2006; Rose, 2006).

In western Canada, latest Cretaceous and early Paleogene mammals were first described by Simpson (1927). Since that time, numerous localities yielding fossil mammals have been discovered in the region, ranging in age from the Aquilan to latest Tiffanian (Woodburne, 2004 and references therein) (the terms “Aquilan” and “Tiffanian” refer to North American Land Mammal Ages [NALMAs] that are approximately equivalent to the middle Upper Cretaceous and early late Paleocene; see discussion below). Intriguingly, while many taxa recovered from these assemblages occur in the U. S., many others are new and apparently confined to more northerly latitudes. These taxa include the plesiadapiform primate *Saxonella* (Fox, 1991) and the adapisoricid insectivoran *Adapisorex* (Fox, Scott, and Rankin, in prep.), two mammals otherwise known only from northern Europe, and the stylinodontid taeniodont *Schowalteria* (Fox and Naylor, 2003), the enigmatic eutherian *Horolodectes* (Scott et al., 2006), the epoicotheriid pholidotan *Melaniella* (Fox, 1984) and the last surviving non-mammalian synapsid *Chronoperates* (Fox et al., 1992), taxa known from nowhere else.

Based on these observations, some researchers (e.g., Sloan, 1969, 1987; Lillegraven, 1969; Anthony and Maas, 1990; Rowe et al., 1992; Weil, 1999; Williamson and Weil, 2008; Donohue et al., 2013) have suggested that the northern part of the Western Interior of North America represented a distinct biogeographic province during parts of the Late Cretaceous and early Paleogene, separate from that in the south. Weil (1999), in her study on the biogeographic distribution of Late Cretaceous and earliest Paleocene North American mammals (from approximately 85 to 64 mya), and one of the few quantitative studies on the subject, reported that distinct biogeographic provinces, characterized by northern and southern provinces, were present during parts of the Late Cretaceous and during the earliest Paleocene. Similarly, Donohue et al. (2013) noted faunal provinciality in the latest Cretaceous, and Anthony and Maas (1990) recognized faunal distinctions in the middle and late earliest Paleocene, but also in parts of the early late Paleocene. Although widely accepted, these views are not universal. Lillegraven and McKenna (1986), Williamson (1996), and Hunter and Archibald (2002) argue that there is little differentiation between northern and southern faunas during the Late Cretaceous and earliest Paleocene, and maintain that the composition of these North American faunas was relatively homogeneous.

The possibility that distinct faunal provinces were present during parts of the Late Cretaceous and early Paleogene has notable implications for the patterns of mammalian evolution in North America. Changes in the number of biogeographic provinces, for instance, can have considerable effects on taxonomic diversity, with the establishment of more provinces generally leading to increases in richness (Valentine, 1970; Valentine et al. 1978; Jablonski et al., 1985; Gaston, 2000). Moreover, different macroevolutionary processes would likely be operating in separate provinces (Jablonski et al., 1985; Flessa and Thomas, 1985; Jackson and D'Croz, 1997; Sampson and Loewen, 2010; Sampson, 2013), leading to the suggestion that properly identifying faunal provinces in the past would permit a more accurate understanding of the evolutionary history of mammals.

Within this study, I quantitatively analyze the biogeographic distribution of latest Cretaceous and earliest Paleocene North American mammals. To test previous hypotheses of mammalian biogeographic provinciality in North America, I compiled information on latest Cretaceous and earliest Paleocene mammalian fossil occurrences in a newly constructed dataset. By utilizing clustering and ordination methods, and simple chi-squared analyses with biogeographic provinces quantitatively defined, I examine the possibility that the northern and southern parts of the Western Interior of North America represented unique faunal regions during the latest Cretaceous and earliest Paleocene.

2.3 Methods and Materials

2.3.1 Stratigraphic framework

The age and correlation of late Mesozoic and early Cenozoic mammal assemblages in North America is principally based on the system of North American

Land Mammal Ages (NALMAs) and their subdivisions (Lillegraven and McKenna, 1986; Archibald et al., 1987; Cifelli et al., 2004; Lofgren et al., 2004). Most NALMAs are biochronological units and "recognize distinct intervals of time based on the evolution of fossil mammals" (Woodburne, 2004b, p. 15). For example, the Puercan NALMA is conventionally described as the interval between the first appearance of the arctocyonid condylarth *Protungulatum* and the first appearance of the periptychid condylarth *Periptychus carinidens* (Lofgren et al., 2004). The Late Cretaceous of North America is divided into four Land Mammal Ages: from oldest to youngest, these are the Aquilan, Judithian, "Edmontonian", and Lancian (Cifelli et al., 2004). Within the Paleocene, the first epoch in the Paleogene, four NALMAs are also recognized: the Puercan, Torrejonian, Tiffanian, and Clarkforkian, with each further divided into subzones (e.g., the Puercan is divided into three subzones: Pu1, Pu2, and Pu3) (Lofgren et al., 2004). I examined the Lancian and the three subzones of the Puercan, comprising roughly the last two million years of the Cretaceous and first million years of the Paleocene epoch (e.g., Cifelli et al., 2004; Wilson et al., 2010; Sprain et al. 2014; Wilson, 2014).

The Lancian/Puercan NALMA boundary has conventionally been correlated with the Cretaceous/Paleogene boundary (Archibald et al. 1987); however, several authors (Archibald and Lofgren 1990; Lofgren et al. 2004; Archibald et al., 2011; Kelly, 2014) have recently suggested that the Puercan should be extended into the latest Cretaceous. These authors have generally based this extension on the first appearance of *Protungulatum* (or, more precisely, *P. donnae* [see Archibald et al., 2011]), marking the advent of a dramatic shift in mammalian assemblages in North America. As noted by Lofgren et al. (2004), there are no conceptual reasons why the two boundaries must coincide and, following the opinion of these authors, I recognize that the Puercan straddles the K/Pg boundary. As a result, assemblages that are considered to document a "transitional" latest Cretaceous mammalian fauna (i.e., Long Fall horizon, Spigot-Bottle, and Lane's Little Jaw Site) are compared with earliest Puercan (Pu1) assemblages.

In addition to this distinction, the age assignments of several important latest Cretaceous and earliest Paleocene localities have also been somewhat contentious. The Rav W-1 horizon of southwestern Saskatchewan, for instance, has more conventionally been assigned to the latest Puercan (Pu3) (see e.g., Lofgren et al., 2004) but Fox and Scott (2011) provide a different opinion. In their recent assessment of the age of the Rav W-1 locality, Fox and Scott (2011) noted that the specimens initially identified as the index taxon *Taeniolabis* sp. by Johnston and Fox (1984) are more appropriately assigned to *Catopsalis* sp., cf. *C. waddleae*, and can no longer be thought of as evidence of a latest Puercan age for the Rav W-1 horizon. In addition, these authors recognized that the Rav W-1 horizon occurred within magnetostratigraphic chron 29R (Lerbekmo, 1985) and, importantly, that most North American assemblages occurring within this magnetostratigraphic chron are assigned to the earliest Puercan (Pu1). Despite these findings, the composition of the fauna recovered from the site is more similar to middle Puercan (Pu2) faunas from the Western Interior of North America than with earliest Puercan faunas. Under these considerations, Fox and Scott (2011) suggest that the Pu1 and Pu2 interval zones are coeval and that the Rav W-1, as well as the Hiatt local fauna from the Ludlow Member of the Fort Union Formation of

Montana (Hunter et al., 1997; Hunter and Archibald, 2002) and PITA Flats local fauna from the Ludlow Member of the Fort Union Formation of North Dakota (Hunter 1999; Hunter and Hartman, 2003), occur within this interval of overlap. Although I agree with Fox and Scott (2011) and recognize that there are limitations in the biochronologic scheme outlined by Lofgren et al. (2004), rather than establishing a new provincial age that is intermediate in age between the early and middle Puercan, I compare the Rav W-1 and Hiatt local faunas with Pu2 faunas.

Additionally, although the Gas Tank local fauna from North Horn Formation of central Utah has been included within the present analyses, several issues with the assigned age for this fauna should be addressed. Robison (1986) tentatively referred the local fauna to the middle Puercan (Pu2) based on its stratigraphic position below the likely late Puercan (Pu3) Wagonroad local fauna; however, Robison (1986) also assigned a fragmentary incisor from Ferron Mountain locality of the Gas Tank local fauna to cf. *Taeniolabis taoensis*. If confirmed, the presence of this taxon would suggest a late Puercan age for, at least, the Ferron locality and possibly the entire local fauna. In addition, Williamson (1996; also see Eberle, 1996) recognized that only one of the five ungulates identified from the local fauna are restricted to Pu2, and Archibald et al. (1987) and Lofgren et al. (2004) noted that the sites that comprise the local fauna (i.e., Gas Tank Hill, Dairy Creek, Jason Spring, Ferron Mountain, Blue Lake, and Flat Sage) are relatively geographically separated from each other and that it is possible that the three sites represent different stratigraphic intervals or depositional settings. Similar to my assessment of the Rav W-1 and Hiatt local faunas, although I acknowledge these various issues, the Gas Tank local fauna is compared with middle Puercan assemblages; the Wagonroad local fauna is compared with latest Puercan assemblages.

2.3.2 Data

To test previous hypotheses of North American mammalian biogeographic provinciality during the Late Cretaceous and early Paleogene, information on North American mammalian fossil occurrences was integrated into a newly developed dataset. A total of 30 Lancian and Puercan local faunas were included in the resulting dataset, with information on the presence/absence of 101 mammalian genera. Generic-level data are studied here since confident taxonomic identification of many latest Cretaceous and early Paleocene mammalian species is difficult, owing to dental similarities shared between species (e.g., condylarths); only local faunas containing eight or more genera were analyzed here. Published literature was the principal resource for retrieving the appropriate data; however, unpublished literature that was deemed especially critical (e.g., unpublished doctoral dissertations) was also used, as well as information that might be garnered from personal observations during visits to select institutional collections (e.g., University of California Museum of Paleontology, University of Alberta Laboratory for Vertebrate Paleontology). To ensure that all geographically and temporally significant specimens and assemblages are accurately recorded, the constructed dataset was compared with the locality and taxonomic lists gathered by Janis et al. (1998, 2008) and Kielan-Jaworowska et al. (2004), as well as those compiled within the Paleobiology Database using the Fossilworks Gateway [http://www.fossilworks.org].

2.3.3 Assemblages

Twelve Lancian assemblages were analyzed, including: the Scollard local fauna from the Scollard Formation of Kneehill County, southcentral Alberta (Lillegraven, 1969; Lillegraven and McKenna, 1986; Fox, 1989, 1994, 1997; Fox and Naylor, 2003), Gryde local fauna from the Frenchman Formation of Val Marie Rural Municipality, southwestern Saskatchewan (Storer, 1991), Hell Creek Montana (including Tuma, Just Past Celeste, Hauso 1, and Flat Creek) from the Hell Creek Formation of Garfield and McCone counties, Montana (Archibald, 1982, Lillegraven and McKenna, 1986; Johansen, 1996; Wilson, 2005, 2014; Donohue et al. 2013; pers. obs.), Claw Butte Anthills local fauna from the Hell Creek Formation of Carter County, southeastern Montana (Hunter and Archibald, 2002), Hell Creek North Dakota (including Marmath, and Pretty, Sunset, and Mud buttes) from the Hell Creek Formation of Slope and Bowman counties, North Dakota (Hunter and Archibald, 2002), Hell Creek South Dakota (including the Joe Painter and Eureka quarries) from the Hell Creek Formation of Harding County, South Dakota (Wilson, 1983), Red Owl Quarry from the Fox Hills Formation of Meade County, South Dakota (Wilson, 1983, 1987), the Type Lance local fauna (including General Lance locality) from the Lance Formation of Niobrara County, eastern Wyoming (Clemens, 1964, 1966, 1973; Krause, 1992; Case et al., 2005; Wilson and Riedel, 2010), Hewett's Foresight local fauna from the Lance Formation of Park County, northwestern Wyoming (Webb, 2001), Black Butte Station local fauna from the Lance Formation of Sweetwater County, southwestern Wyoming (Breithaupt, 1982; Donohue et al. 2010), and Pawnee local fauna (including Dog Pond Area, Natural Fort, and Ingrid's Jaw localities, and excluding the geologically older

Ken’s Site) from the ?Laramie Formation of Weld County, northeastern Colorado (Carpenter, 1979; Diem, 1999; Wilson et al., 2010) (Table 2.1).

Seven earliest Puercan (Pu1) assemblages were examined (Table 2.2). These include: the Long Fall horizon from the Ravenscrag Formation of Reno Rural Municipality, southwestern Saskatchewan (Johnston and Fox 1984; Fox, 1989, 1997), Hell’s Hollow local fauna of the Tullock Member of the Fort Union Formation of Garfield and McCone counties, northeastern Montana (Archibald, 1981, 1982), Lane’s Little Jaw Site local fauna from the Hell Creek Formation of Powder River County, southeastern Montana (Kelly, 2014), Spigot-Bottle local fauna from the Hell Creek Formation of Carter County, southeastern Montana (Hunter and Archibald, 2002; Zhang 2009; Archibald et al. 2011), Mantua Lentil local fauna of the Polecat Bench Formation of Park County, northeastern Wyoming (Jepsen, 1930, 1940, Van Valen, 1978), Ferris Formation Pu1 local fauna from the Ferris Formation of Carbon County, southcentral Wyoming (Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), and Littleton local fauna from the Denver Formation of Arapahoe County, central Colorado (Middleton, 1982, 1983; Eberle and Lillegraven, 1998b; Middleton and Dewar, 2004).

The analyses included seven middle Puercan (Pu2) assemblages: the Rav W-1 horizon from the Ravenscrag Formation of Reno Rural Municipality, southwestern Saskatchewan (Johnston and Fox 1984; Fox, 1989, 1997), Hiatt local fauna from the Ludlow Member of the Fort Union Formation of Dawson County, southeastern Montana (Hunter et al., 1997), Ferris Formation Pu2 local fauna from the Ferris Formation of Carbon County, southcentral Wyoming (Eberle and Lillegraven, 1998a, 1998b; Eberle, 1999; Lillegraven and Eberle, 1999), Gas Tank local fauna of the North Horn Formation of Emery and Sanpete counties, central Utah (Gazin, 1938, 1939, 1941; Spieker 1960; Van Valen, 1978; Robison, 1986; Cifelli et al., 1995, 1999; Lofgren et al., 2005, 2012), and East Flank Kimbeto Wash, West Flank Kimbeto Wash, and Betonnie Tsosie Wash from the Nacimiento Formation of San Juan County, northwestern New Mexico (Lucas and Williamson, 1993; Williamson, 1996; Williamson et al., 2011; Lucas, 2011; Williamson and Brusatte, 2013) (Table 2.3).

Five latest Puercan (Pu3) assemblages were examined: the Croc Pot local fauna from the Ravenscrag Formation of southwestern Alberta (Fox, 1990, 1997), Garbani and Purgatory Hill local faunas (including the Garbani Channel deposits and Purgatory Hill locality) from the Tullock Member of the Fort Union Formation of Garfield County, northwestern Montana (Van Valen and Sloan, 1965; Clemens, 1974; 2002, 2013; 2015; Novacek and Clemens, 1977; Van Valen, 1978; Archibald et al., 1983; Simmons, 1987; Weil, 1998), Ferris Formation Pu3 local fauna from the Ferris Formation of Carbon County, southcentral Wyoming (Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), Wagonroad local fauna of the North Horn Formation of Emery and Sanpete counties, central Utah (Gazin, 1941; Tomida and Butler, 1980; Robison, 1986; Cifelli et al., 1995, 1999; Williamson, 1996), De-na-zin Wash local fauna from the Arroyo Chijuillita Member of the Nacimiento Formation of San Juan County, New Mexico (Williamson, 1996; Williamson and Brusatte, 2013) (Table 2.4).

2.3.4 Taxonomic issues

Attempts have been made to incorporate the most recent taxonomic opinions of the mammalian genera within the dataset, including the taxonomic revisions presented by Davis (2007) and Williamson et al. (2012) in their studies on latest Cretaceous metatherians, and those reported by Williamson and Carr (2007) on early Paleocene oxyclaenid condylarths. Unsurprisingly, however, a number of subjective taxonomic decisions were also required. These opinions are not intended to reflect any authoritative views but are informed choices. For instance, Reynolds (1936) initially identified and described *Puercolestes simpsoni* based on material recovered from the Betonnie-Tsosie Wash from the Nacimiento Formation of New Mexico. Clemens (1973) later suggested that Reynolds' species is more appropriately assigned to *Cimolestes*. Subsequently, Williamson et al. (2011) described new material from Betonnie-Tsosie Wash and from the newly discovered Willow Wash local fauna, also from the Nacimiento Formation of New Mexico, and recognized *Puercolestes* as a distinct and valid taxon. For the purposes of this study, Fox (1989, 1997) assigned specimens from the Rav W-1 horizon to "*Cimolestes* sp., cf. *C. simpsoni*" and Clemens (2002) similarly identified specimens from the Garbani Channel local fauna as "*Cimolestes* sp., cf. *C. simpsoni*". Although I follow Williamson et al. (2011) in recognizing *Puercolestes* as a valid taxon, given the limited geographic range of specimens confidently assigned to this genus, specimens referred to "*Cimolestes* sp., cf. *C. simpsoni*" from the localities outside of the San Juan Basin of New Mexico are referred to *Cimolestes*.

Aside from adopting these revisions, all tentative taxonomic assignments, including references with “cf.” or “?”, are also discarded within the dataset and the taxon is simply assigned to the designated genus. Similar approaches are used by Weil (1999), Hunter and Archibald (2002), and Donohue et al. (2013), with Weil (1999) suggesting that this technique increases similarity among faunas and, hence, is more conservative for these types of biogeographic analyses.

2.3.5 Statistical Methods

To quantitatively test the validity of mammalian biogeographic provinciality within different time intervals (i.e., NALMAs and their subdivisions), several complementary analytical approaches were examined. The first of these approaches followed the non-hierarchical clustering methods outlined by Vavrek (2010), in his unpublished doctoral dissertation on patterns of species diversity through time. This non-hierarchical, non-Euclidean relational clustering method is based on an iterative process, with random initialization points and a branch-and-bound heuristic search, and can use non-Euclidean distances based on relational data (e.g., Jaccard’s, Sørenson) as the measure of similarity between assemblages. Simpson’s Index (Simpson, 1943, 1960) is often suggested to be less sensitive to differences in sampling intensity and this index is used for the clustering analysis and all other pairwise comparisons (see below). Within this clustering approach, the mean pairwise distance among the assemblages within a cluster is used as the measure of the within-cluster dissimilarity (i.e., the lower the within-cluster dissimilarity the more likely the assemblages form a true cluster). It should be noted that the “best” number of clusters is not known *a priori*; rather, the number of clusters being tested must be specified by the researcher in advance. Under these considerations, the number of clusters was limited to two to assess previous claims of a north-south division within latest Cretaceous and earliest Paleocene mammalian faunas. To assess the robustness of the recovered clusters, the assemblages within each cluster were resampled 1000 times to measure the mean within-cluster pairwise distance of randomly sampled clusters and generate standard deviations (Table 2.5).

For the second approach, non-metric multidimensional scaling (NMDS), an ordination method commonly employed to visualize multivariate data in community ecology (e.g., Gotelli and Ellison, 2013), is used. NMDS is an iterative approach that attempts to best fit a set of data points within a predetermined number of dimensions to a given matrix of distances (Minchin, 1987). NMDS shares a number of similarities with other frequently used ordination methods, such as Principal Component Analysis or Principal Coordinates Analysis; however, unlike these other methods, NMDS does not assume a Euclidean structure to the data, an approach that can emphasize absences between samples (Shi, 1993; Magurran, 2004). This difference is particularly important for studies that attempt to analyze incomplete samples (i.e., occurrence data), as the absence of a taxon within a sample may represent a true absence or simply the lack of sampling. In particular, Euclidean distance measures can lead to erroneous results when a large number of taxa are absent from two samples, and the lack of a taxon between samples is equally informative as the presence of a taxon within the two samples.

Minimum spanning trees (MSTs) join all the data points in a sample with the minimum number of connections. The approach begins with a single random data point and connects to the next closest point that is not already incorporated within the tree; if two points are equally close, the approach will randomly select one. MSTs are used here with NMDS to visually display the relationships of the assemblages.

Finally, to evaluate the presence of biogeographic provinces during the latest Cretaceous and earliest Paleocene, I employed simple chi-squared analyses. Before providing a full description of this method, a definition of a biogeographic province is required and a short discussion of this term is provided here. Following Dice (1943, p. 3), a biogeographic province can be defined as "a considerable and continuous geographic area … characterized by the occurrence of one or more ecological associations that differ, at least in proportional area covered, from the associations of adjacent provinces". Other authors (Woodward, 1856; Coomans, 1962; Kaufman, 1973; Briggs 1974; 1995; Rosenzweig, 1995; Briggs and Bowen, 2012), however, have favoured definitions that are more quantitative and that emphasized a certain threshold of endemism within an area, albeit with an astonishingly wide range of suggested values. Woodward (1856), Hedgpeth (1957), and Coomans (1962), for instance, recommend that at least 50% of taxa must be endemic for a distinct biogeographic province to be recognized, whereas Kaufman (1973) suggests a minimum of 25% of endemics, and Briggs (1974, 1995) and Briggs and Bowen (2012) reports that 10% of endemics is sufficient. Alternatively, because plants and animals are obviously influenced by their surroundings, Spalding et al. (2007) proposed that the recognition of a biogeographic province should not only include information on endemism and shared evolutionary history of the taxa, but also information on the abiotic factors that help to delimit the biogeographic distributions of these organisms. While such a definition is intuitively appealing, it is difficult to obtain these types of data for extant ecosystems, let alone for fossil ecosystems. For simplicity and to quantitatively assess hypotheses on the presence or absence of biogeographic provinces, I follow the definition and threshold of endemism outlined by Kaufman (1973) (i.e., 25%).

With a biogeographic province explicitly defined, I assessed Lehman's (1987, 1997) suggestion that a faunal barrier existed during the Lancian near a paleolatitude of 50°N, as well as Weil's (1999) report that a similar barrier occurred between paleolatitudes 48° and 51°N during the early Paleocene with chi-squared analyses. Under this approach, taxa that only occur within a single local fauna are removed (see discussion below) and each taxon that occurs in two or more local faunas is categorized as a northern endemic, southern endemic, or cosmopolitan genus. Northern endemic are restricted to latitudes north of the proposed faunal barrier, and southern endemic taxa are restricted to latitudes south of this barrier. Cosmopolitan mammalian genera occur in both of these regions. These groups are summarized for each time interval (Table 2.6). I tested against a null hypothesis that biogeographic provinces contain a minimum of 25% of endemic taxa (i.e., 25% of mammalian genera are restricted to the north, 25% of genera are restricted to the south, and the remaining 50% of the mammalian genera extend across the proposed barrier); the alternative hypothesis states that biogeographic provinces, as quantitatively defined here, are not recovered based on the distribution of these taxa (for a further explanation of this approach see Zar, 1999). Where the probability of the chi-square analysis is less than 0.05 (p value ≤ 0.05), the null hypothesis is rejected and no distinct biogeographic provinces are detected (i.e., distribution of mammals significantly differs from that expected).

All analyses were conducted in R version 3.0.2 (R Development Core Team, 2015), with the clustering and ordination methods performed using the fossil package version 0.3.7 (Vavrek, 2011).

2.4 Results

2.4.1 Clustering Analyses

The results of the non-hierarchical clustering analysis reveal several interesting features of latest Cretaceous and earliest Paleocene mammalian biogeography. With regards to the Lancian faunas, the clustering analysis unites the Scollard, Gryde, Wounded Knee, Hell Creek Montana, and Black Butte Station local faunas within a distinct cluster, and suggests that the second cluster is comprised of the Claw Butte Anthills, Hell Creek North Dakota, Hell Creek South Dakota, Red Owl, Hewett's Foresight, Type Lance, and Pawnee local faunas (Figure 2.5). Support for both clusters was rather weak, however, with the mean within-cluster distance of each well inside the standard deviation of the resampled clusters (Table 2.5).

Among earliest Puercan local faunas, the first cluster contains the Hell's Hollow, Mantua Lentil, Ferris Formation Pu1, and Littleton local faunas, with the second cluster comprised of the Spigot-Bottle and Lane's Little Jaw Site local faunas (Figure 2.6). The within-cluster distance for the first of these clusters is within the range of the standard deviation, whereas that of the second cluster is outside, providing some support for the recognition of this latter grouping (Table 2.5). The middle Puercan Rav W-1, Hiatt, Ferris Formation Pu2, and the Gas Tank local faunas are suggested to form a cluster that is distinct from the cluster that contains the three New

Mexico local faunas (West Flank Kimbeto Wash, East Flank Kimbeto Wash, and Betonnie-Tsosie Wash) (Figure 2.7). In contrast to the earliest Puercan, the first of these clusters is better supported than the second (Table 2.5). Finally, within the latest Puercan, the Croc Pot and Garbani Channel deposits and Purgatory Hill local faunas are recognized as a cluster, and the second cluster is comprised of the Ferris Formation Pu3, Wagonroad, and De-na-zin Wash local faunas (Figure 2.8). The within-cluster distance of the first cluster is within the range of the standard deviation, whereas that of the second cluster is outside, similar to the results for the earliest Puercan (Table 2.5).

2.4.2 Non-Metric Multidimensional Scaling and Minimum Spanning Trees

The results of the non-metric multidimensional scaling (NMDS) and Minimum Spanning Tree (MST) methods also present some interesting aspects of mammalian biogeography from these time intervals. The NMDS and MST analyses of the Lancian faunas are similar to the results recovered from the clustering analysis (Figures 2.9). In fact, the only difference between the two analyses is the placement of the Claw Butte Anthills local fauna of southeastern Montana (i.e., grouped with more southerly localities based on the clustering analysis or recovered with several of the more northerly localities based on the NMDS and MST results). These results provide some evidence for the presence of two biogeographic provinces during the Lancian; yet, with the placement of the Black Butte Station local fauna with those from western Canada and Montana, these provinces are not along a north-south transect (Figure 2.10).

The remaining results of the NDMS and MST analyses, based on the occurrence of Puercan mammals, are somewhat less revealing. For instance, the earliest Puercan

Lane's Little Jaw Site local fauna and Spigot-Bottle local fauna from the Hell Creek Formation of southeastern Montana are closely positioned and could represent a group; however, these two assemblages are within the latitudinal range of the other assemblages (Figure 2.11). Also, perhaps unsurprisingly, the three middle Puercan local faunas from the Nacimiento Formation of San Juan County, northwestern New Mexico (i.e., West Flank Kimbeto Wash, East Flank Kimbeto Wash, and Betonnie-Tsosie Wash) form a grouping that is separate from the larger grouping that contains the other local faunas (Figure 2.12). No distinct groups are recognized among the latest Puercan assemblages but, similar to the cluster analysis, the Croc Pot and Garbani Channel deposits and Purgatory Hill local faunas are closely positioned (Figure 2.13).

2.4.3 Chi-Squared Analyses

The chi-squared analysis on the latitudinal ranges of Lancian mammalian genera reveals that the ranges of these mammals differs significantly from that expected if northern and southern biogeographic provinces were present (χ^2 value = 8.769, p-value = 0.0125). In particular, only five taxa were restricted to assemblages north of paleolatitude 50°N and just a single taxon was restricted to assemblages south of this paleolatitude, with the remaining twenty genera known from this interval ranging across the proposed barrier (Table 2.6). Similar results are recovered for the distribution of mammalian genera from the earliest Puercan (χ^2 value = 10.250, p-value = 0.0059) and middle Puercan (χ^2 value = 11.909, p-value = 0.0026), although the suggested barrier during these intervals was placed at paleolatitude 49.5°N. Interestingly, during the earliest Puercan, 11 genera are endemic to the northern region, whereas, zero genera are restricted to assemblages south of the suggested barrier; 13 mammalian genera extend across paleolatitude 49.5°N (Table 2.6). Conversely, within the middle Puercan, just one taxon is restricted to assemblages north of paleolatitude 49.5°N and 15 genera are restricted to the southern region; 17 genera are cosmopolitan.

In contrast to these other intervals, during the latest Puercan eight genera are restricted to the north and eight genera are restricted to the south, with the remaining 13 taxa occurring within localities on both sides of the suggested barrier (Table 2.6). The distributions of mammals from this interval do not differ significantly from the expected and the presence of northern and southern biogeographic provinces cannot be rejected (χ^2 value = 0.310, p-value = 0.8563).

2.5 Discussion

2.5.1 Mammalian Faunal Provinciality

The presence of mammalian provinciality within North America during the Late Cretaceous and early Paleogene has been a relatively common statement in the literature. Russell (1967) and Lillegraven (1969) were some of the first to cite the presence of provinciality, characterized by northern and southern biogeographic provinces, with both authors noting differences in the taxonomic composition between the latest Cretaceous Scollard local fauna from southcentral Alberta and the Type Lance local fauna from southcentral Wyoming. Sloan (1969; also see Sloan, 1987), reviewing the structure of Late Cretaceous and Paleocene mammalian faunas across North America, supported these earlier suggestions and additionally stated the presence of northern and southern provinces in the Paleocene, with the boundary between these provinces likely occurring in southern Wyoming. Fox (1990, 1997, 2005; Fox and Naylor, 2003) reported the presence of endemic mammals in the latest Cretaceous and Paleocene of western Canada and suggested that aspects influencing changes in mammalian evolution in the region were not exerted elsewhere in North America during this time. In one of the first quantitative analyses on the topic, Anthony and Maas (1990) reported the presence of mammalian faunal provinciality during the middle and late Puercan, and, similar to Sloan (1969, 1987), suggested the occurrence of a barrier in southern Wyoming separating the northern and southern biogeographic provinces.

Although not explicitly addressing faunal provinciality, in their discussion of latest Cretaceous and earliest Paleocene mammals from the Ferris Formation of the Hanna Basin, southcentral Wyoming, Eberle and Lillegraven (1998b; also see Eberle, 1996) noted closer similarities between assemblages from the Ferris Formation with those south of the Hanna Basin rather than more northern faunas. Based on a quantitative analysis, Weil (1999) suggested that mammalian faunal provinciality was established during the late Campanian and earliest Paleocene, with the separation between northern and southern provinces occurring in central Wyoming (i.e., between the "Mesaverde" Formation of Wyoming and Kaiparowits Formation of Utah during the late Campanian, and the Polecat Bench Formation of northeastern Wyoming and Ferris Formation of southcentral Wyoming during the Puercan). Within his comprehensive study of Late Cretaceous metatherians, Davis (2007) recognized the absence of pediomyids from more southerly assemblages and suggested that these faunal differences could indicate provinciality. More recently, Donohue et al. (2013)

examined provinciality and heterogeneity among latest Cretaceous multituberculate faunas from across North America, and concluded that variations among the composition of these faunas most closely correspond to differences in latitude.

Provinciality has also been suggested within other Late Cretaceous and early Paleocene organisms recovered from terrestrial deposits of the Western Interior of North America. Nichols (1984, 1994; Nichols et al., 1990), for instance, noted the presence of distinctive floral provinces during parts of the Late Cretaceous and Paleocene on the basis of palynomorphs; Wolfe and Upchurch (1987) and Wheeler and Lehman (2005) also reported regional differences between plant macrofossils across the same interval. Differences among the latitudinal distributions of Late Cretaceous dinosaurs have also been noted by a number of authors (e.g., Russell, 1967; Lehman, 1987, 1997, 2001). More recently, Sampson and colleagues, in a series of papers (e.g., Sampson and Loewen, 2010; Sampson et al., 2010; Sampson et al., 2013), have indicated that dinosaurian faunas from the late Campanian of Laramidia (i.e., the landmass west of the Late Cretaceous Western Interior epicontinental seaway) were divided into southern and northern biogeographic provinces, with distinctive patterns of dinosaurian evolution within these regions. Gates et al. (2010), examining the distributions of all terrestrial vertebrates across North America during the late Campanian, similarly reported differences in faunas from the northern and southern regions of Laramidia.

Despite these findings, the establishment of Late Cretaceous and early Paleocene faunal provinciality has not been supported by all studies. For example, Lillegraven and McKenna (1986) and Eaton and Scott (2011), respectively, suggested that the composition of late Campanian mammalian assemblages between southern Alberta and northern Wyoming, and between southern Alberta and southern Utah were relatively homogeneous (although more southerly late Campanian localities might still reveal some differences with these northerly faunas [see e.g., Flynn, 1986; Rowe et al., 1992; Gates et al., 2010]). Williamson (1996) calculated heterogeneity indices for earliest Paleocene North American assemblages based on the composition of therian mammals and reported that a clear distinction between northern and southern faunas did not exist. Hunter and Archibald (2002), in one of the few quantitative studies to examine mammalian occurrences during the latest Cretaceous (i.e., Lancian), indicated that taxonomic differences among assemblages did not reveal provinciality but more strongly reflected differences in the geographic distances between assemblages. Moreover, some authors (e.g., Sullivan, 2003; Sullivan and Lucas, 2006) also contend that many of the observed taxonomic differences among Late Cretaceous vertebrate assemblages are in fact attributable to differences in stratigraphic age or small sample sizes. Vavrek and Larsson (2010), more recently, suggested that differences in sampling approaches could also have influenced previous studies and were unable to support multiple dinosaurian biogeographic provinces within the latest Cretaceous.

Within this study, several different analytical methods were applied, including non-hierarchical, non-Euclidean relational cluster analyses, non-metric multidimensional scaling (NMDS), minimum spanning trees (MSTs), and chi-squared analyses. The results provide little quantitative support for the presence of mammalian faunal provinciality within North America during the latest Cretaceous and earliest Paleocene. The strongest evidence for mammalian faunal provinciality is recovered among Lancian assemblages. The cluster analysis reveals the presence of two large groupings: the first comprised of the Scollard, Gryde, Wounded Knee, Hell Creek Montana, and Black Butte Station local faunas and the second containing the Claw Butte Anthills, Hell Creek North Dakota, Hell Creek South Dakota, Red Owl, Hewett's Foresight, Type Lance, and Pawnee local faunas (Figure 2.5). The NMDS and MST reveal similar groupings, with only the placement of the Claw Butte local fauna of southeastern Montana differing between the analyses (Figure 2.9).

Although the recognition of these divergent groups does provide some evidence for the presence of mammalian faunal provinciality, the support for the clusters is rather weak (Table 2.5), and the assemblages included within these distinct groups and the spatial location of these groups is inconsistent with previous suggestions of provinciality. For instance, the inclusion of the Black Butte Station local fauna from southwestern Wyoming with assemblages from western Canada (Scollard, Gryde, and Wounded Knee) and several from Montana (Hell Creek of Montana and Claw Butte Anthills) indicates that these groupings do not correspond to northern and southern biogeographic provinces. Moreover, if the Black Butte Station local fauna is removed from the more northerly province, the boundary between the two regional groupings is not in northern Wyoming, as previously suggested in the literature (e.g., Sloan, 1969), but in southern Montana (Figure 2.5).

In addition to these ambiguities, very few Lancian mammalian genera are restricted to northern or southern assemblages; rather, the latitudinal ranges of the vast majority of these mammals (i.e., 20 of 26 genera) extend across the proposed barrier at paleolatitude 50°N (Table 2.7; Figure 2.10). Based on these numbers and the threshold of endemism (i.e., 25%) suggested by Kaufman (1973) to define a distinct biogeographic province, distinct northern and southern provinces are not supported by the chi-squared analysis. These findings are comparable to those presented by Hunter and Archibald (2002) but notably differ from those of Donohue et al. (2013). Within their study, Donohue et al. (2013) reported that the newly described multituberculate fauna from the Black Butte Station was statistically distinct from that of other assemblages and that differences among latest Cretaceous multituberculate faunas reflected latitudinal differences. It should be mentioned, however, that these authors included mammals that are endemic to a single assemblage within their clustering and ordination analyses (e.g., *Parikimys*). As noted by Nicholls and Russell (1990), taxa that are rare and restricted to a single assemblage can skew biogeographic analyses, as the absence of these taxa within other assemblages may be due to sampling rather than representing a real absence. Moreover, based on the present data, the true geographic distribution between latest Cretaceous assemblages is strongly correlated with composition of these faunas (Spearman's rank correlation = 0.45; p-value < 0.001); hence, taxa are more likely to be shared between assemblages that are geographically closer. Therefore, for the purposes of this study, endemic mammals were classified as taxa that are restricted to latitudes north or south of the proposed barrier and, importantly, also co-occurred in at least two faunal assemblages.

With regards to the earliest and middle Puercan, the non-Euclidean relational clustering analyses, NMDS, and MST provide little support for the recognition of distinctive faunal groups. The clustering analysis of the earliest Puercan assemblages, for instance, separates Lane's Little Jaw Site local fauna and Spigot-Bottle local fauna from the Hell Creek Formation of southeastern Montana into one cluster and the Long Fall local fauna of southwestern Saskatchewan, Hell's Hollow of northeastern Montana, the Mantua Lentil of northeastern Wyoming, the Ferris Formation Pu1 local fauna of southcentral Wyoming, and Littleton local fauna of central Colorado into another (Figure 2.6). Yet, the cluster containing Lane's Little Jaw Site and Spigot-Bottle is poorly supported (Table 2.5) and fully encompassed within the latitudinal range of the assemblages within the other cluster. Furthermore, the NMDS and MST of these earliest Puercan faunas indicate that no groupings are recognized (Figure 2.11).

The clustering analysis additionally places the middle Puercan Rav W-1 local fauna of southwestern Saskatchewan, Hiatt local fauna of southeastern Montana, the Ferris Formation Pu2 local fauna of southcentral Wyoming, and the Gas Tank local fauna of Utah into the first cluster and the three assemblages from the Nacimiento Formation of northwestern New Mexico (i.e., West Flank Kimbeto Wash, East Flank Kimbeto Wash, and Betonnie-Tsosie Wash) into the second cluster (Figure 2.7). The NMDS and MST recovered similar groups (Figure 2.13). Here again, the recognition of these divergent groups provides some support for the presence of mammalian faunal provinciality; however, given the geographic proximity of the assemblages from New Mexico, the clustering of these localities is unsurprising. In addition, similar to the Lancian assemblages, the boundary between the two faunal groupings is not in northern Wyoming, as previously suggested in the literature, but near southern Utah and Colorado.

Unlike the distribution of mammalian genera during the Lancian, a number of earliest and middle Puercan mammals are endemic to assemblages north or south of the proposed barrier (Table 2.6; Figures 2.12 and 2.14). The number of endemics, however, differs considerably between the northern and southern regions, and between the two time intervals. More specifically, eleven earliest Puercan genera are endemic to the northern region, whereas zero genera are restricted to southern assemblages. In contrast, just one taxon is restricted to northern assemblages and fifteen genera are restricted to the southern region during the middle Puercan. Despite the increase in the number of endemics, the distributions of mammals during the earliest and middle Puercan are significantly different from the expected distributions and, based on the chi-squared analyses, distinct biogeographic provinces are not recognized from these intervals.

With regards to the latest Puercan, the clustering analysis, NDMS, and MST recover similar groupings, with the Croc Pot local fauna of southeastern Saskatchewan and the Garbani Channel deposits and Purgatory Hill local faunas of northeastern Montana forming the first group and the local faunas from the latest Puercan assemblages of the Ferris Formation from southcentral Wyoming, Wagonroad of Utah, and the De-na-zin Wash of northwestern New Mexico forming the second group (Figure 2.8). Moreover, eight genera are restricted to the north and eight genera are restricted to the south, with the remaining thirteen taxa occurring in localities on both sides of the suggested barrier. In contrast to the other intervals, these distributions do not differ significantly from those expected and the presence of northern and southern biogeographic provinces cannot be rejected (Table 2.6). These findings provide evidence for the recognition of divergent faunas and distinct biogeographic provinces but, since only five latest Puercan assemblages are included in the analyses, it is difficult to confidently state the establishment of mammalian faunal provinciality during this interval.

Although the general lack of support for the establishment of mammalian provinciality within North America during the latest Cretaceous and early Paleocene differs from the findings and suggestions of many previous authors (e.g., Weil, 1999; Donohue et al., 2013), the absence of provinciality should be considered unsurprising. This interval is characterized by a number of dramatic events, including the impact of a large bolide, intensive volcanism, and changes in the global sea level. These events, and their subsequent consequences (i.e., the Late Maastrichtian Event [see, e.g., Li and Keller 1998a, 1998b; Wilf et al., 2003, Tobin et al., 2012; Wilson, 2014]), could have perturbed these mammalian communities and impacted the biogeography of these animals. In fact, a number of studies have already suggested that communities from this interval were unstable (e.g., Wilson, 2005, 2013, 2014; Rose et al., 2011; Mitchell et al. 2012; Clemens, 2013; Sprain et al., 2014; Wilson et al., 2014). For example, in their study on trophic networks among Late Cretaceous terrestrial communities, Mitchell et al. (2012) reported that latest Cretaceous (Maastrichtian) communities were less stable than those within the Late Cretaceous (Campanian), with a distinct decline in β-diversity (i.e., taxonomic differences between assemblages) among some taxonomic groups across this interval. Wilson (2005, 2013, 2014) indicated that changes in mammalian evenness and richness occurred in the Hell Creek local faunas of Montana through the last 500 000 years of the latest Cretaceous. Puercan assemblages from Montana were also suggested by Wilson (2013, 2014) to be comprised of some latest

Cretaceous lineages that persisted through the boundary but largely dominated by a number of immigrants previously unknown from the area.

Based on these reports, and the results presented here, instability within mammalian communities during the latest Cretaceous and early Paleogene, principally related to the stresses related to the K/Pg extinction event, could have driven changes in the geographic distributions of mammals from this interval. Moreover, it is doubtful that the faunal barriers that might have separated biogeographic provinces within the early parts of the Late Cretaceous (e.g., Sampson et al., 2010; Gates et al., 2012) persisted into the latest Cretaceous and early Paleocene. Hence, during the Late Cretaceous and early Paleogene mammalian faunal provinciality was likely not established.

2.5.2 Provinciality and Biochronology

Discussing mammalian faunal provinciality within North America during the Late Cretaceous and early Paleocene, Weil (1999) noted that the identification of separate biogeographic regions could reveal limitations in biochronological correlations between northern and southern faunas. For instance, Weil (1999) cautiously suggested that use of the "Judithian" North American Land Mammal Age should be restricted to assemblages that include mammals more typical of the "Mesaverde" Formation of Wyoming, with contemporaneous assemblages south of this formation (e.g., assemblages from the Kaiparowits Formation of Utah) likely requiring another term. Although grouping the three subzones of Puercan into a single analysis, Weil (1999) further indicated that issues assigning assemblages from either northern or southern provinces to distinct Puercan subzones might further support the presence of mammalian provinciality during the earliest Paleocene.

A number of authors have identified additional issues with the biochronologic succession and correlation of latest Cretaceous and earliest Paleocene mammalian assemblages in North America (e.g., Williamson, 1996; Fox and Scott, 2011; Archibald et al., 2011; Kelly, 2014; and see discussion above). Most of these objections have focused on the use of a single taxon to characterize a faunal zone, principally relating to the poor understanding on the rarity or commonness of the index taxon, and diachronous appearances of index taxa in different sedimentary basins. As noted earlier, although limitations in the biochronologic scheme outlined by Cifelli et al. (2004) and Lofgren et al. (2004) can be clearly recognized, based on the limited support for the presence of faunal provinciality during these intervals, biogeographic provinciality does not appear to be a principal concern for latest Cretaceous and earliest Paleocene biochronologic correlations.

2.6 Conclusions

The patterns of Late Cretaceous and early Paleogene mammalian evolution have become an important focus of study as a consequence of interest in the dramatic adaptive radiation that mammals underwent shortly after the catastrophic events near the K/Pg boundary (see e.g., Matthew, 1914, 1921; Simpson, 1937; Van Valen, 1978; Archibald, 1982; Lofgren, 1995; Foote et al., 1999; Alroy, 1999; Wible et al., 2009; Fox et al., 2010). The world's richest discovered succession of mammals from this time interval, offering direct evidence of these patterns, is preserved in continental strata of

North America (Cifelli et al., 2004; Lofgren et al., 2004). This study entailed an intensive investigation of the biogeographic distributions of Late Cretaceous and early Paleogene mammals from North America, with the aim of contributing to the understanding of mammalian diversity and evolution during this important time interval.

Previous studies have indicated that the northern and southern regions of the Western Interior of North America represented distinct biogeographic provinces during parts of the Late Cretaceous and early Paleocene (e.g., Sloan, 1969, 1987; Anthony and Maas, 1990; Rowe et al. 1992; Weil, 1999; Donohue et al., 2013); however, based on non-Euclidean relational cluster analyses, non-metric multidimensional scaling, minimum spanning trees, and simple chi-squared analyses, my findings reveal that there is little quantitative support for mammalian provinciality during this interval. Although differing from many other authors, these results suggest that the catastrophic events that occurred across the latest Cretaceous and early Paleocene, including the impact of a large bolide, intensive volcanism, and changes in the global sea level, likely contributed to unstable mammalian communities and biogeographic distributions unlike those from the earlier parts of the Late Cretaceous.

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Table 2.1.—Occurrences of mammalian genera within earliest Puercan (Pu1) local faunas from the Western Interior of North America. Presence = 1; Absence = 0. Locality abbreviations are: SC = Scollard, WK = Wounded Knee, GR = Gryde, HCM = Hell Creek Montana, CB = Claw Butte, HCN = Hell Creek North Dakota, HCS = Hell Creek South Dakota, RO = Red Owl, TL = Type Lance, BBS = Black Butte Station, HF = Hewett's Foresight, and PA = Pawnee

Genera	SCL	WK	GR	HCM	CB	HCN	HCS	RO	TL	BBS	HF	PA
Alostera	1	1	1	1	0	0	0	0	0	0	0	0
Alphadon	1	0	0	1	1	1	1	1	1	1	1	0
Batodon	1	0	1	1	1	0	0	0	1	0	0	0
Bubodens	0	0	0	0	0	0	0	1	0	0	0	0
Cimexomys	0	0	0	1	0	0	0	1	1	1	1	0
Cimolestes	1	1	1	1	0	1	0	0	1	0	1	0
Cimolodon	1	1	1	1	1	1	1	1	1	1	1	0
Cimolomys	1	0	1	1	0	0	1	0	1	0	1	0
Clemensodon	0	0	0	0	0	0	0	0	1	0	0	0

Didelphodon	1	1	1	1	0	1	1	1	1	0	1	0
Essonodon	0	1	0	1	1	0	0	0	1	1	0	0
Glasbius	0	1	0	1	1	0	0	0	1	0	1	0
Gypsonictops	1	1	1	1	1	1	1	1	1	1	1	1
Hatchertherium	0	0	0	0	0	0	0	0	1	0	0	0
?*Leptalestes*	0	0	0	1	1	0	0	1	1	0	1	1
Leptalestes	1	0	1	1	1	0	1	1	0	0	1	0
Meniscoessus	0	1	0	0	1	1	1	1	1	0	1	1
Mesodma	1	1	1	1	1	1	1	1	1	1	1	1
Nanocuris	1	0	0	0	0	0	0	0	1	0	0	0
?*Neoplagiaulax*	0	0	0	1	0	0	0	0	0	0	1	0
Nortedelphys	1	1	1	1	0	0	1	0	1	0	1	1
Paracimexomys	1	1	1	1	0	0	0	0	0	1	0	0
Parectypodus	0	0	1	1	0	0	0	0	0	0	0	0
Paressonodon	0	0	0	1	0	0	0	0	0	1	0	1

Parikimys	0	0	0	0	0	0	0	0	0	1	0	1
Pediomys	0	1	0	1	1	0	0	0	0	0	0	0
Protalphadon	0	0	0	1	1	0	0	1	1	0	1	1
Protolambda	1	0	1	1	1	1	1	0	1	0	1	1
Schowalteria	1	0	0	0	0	0	0	0	0	0	0	0
Telacodon	0	0	0	0	0	0	0	0	1	0	0	0
Turgidodon	1	0	1	1	1	0	0	0	1	0	1	0

Table 2.2.—Occurrences of mammalian genera within earliest Puercan (Pu1) local faunas from the Western Interior of North America. Presence = 1; Absence = 0. Locality abbreviations are: LF = Long Fall horizon, HH = Hell's Hollow, LLJS = Lane's Little Jaw Site, ML = Mantua Lentil, FF1 = Ferris Formation Pu1, and LIT = Littleton.

Genera	LF	HH	LLJS	SB	ML	FF1	LIT
Albertatherium	0	0	0	1	0	0	0
Acheronodon	0	1	0	0	0	0	0
Alphadon	1	0	0	1	0	0	0
Alticonus	0	0	0	0	0	0	1
Ampliconus	0	0	0	0	0	0	1
Auraia	0	0	0	0	0	0	1
Baioconodon	1	1	1	0	1	1	1
Batodon	0	0	0	1	0	0	0
Catopsalis	1	1	0	0	1	0	1
Carcinodon	0	0	0	0	0	0	1

Cimexomys	1	1	0	0	1	0	1
Cimolestes	1	1	1	1	0	0	0
Cimolodon	1	0	1	1	0	0	0
Cimolomys	1	0	0	1	0	0	0
Conacodon	0	0	0	0	0	0	1
Didelphodon	0	0	1	1	0	0	0
Earendil	0	0	0	0	1	0	0
Eoconodon	0	0	0	0	1	1	0
Glasbius	0	0	1	1	0	0	0
Gypsonictops	1	0	0	1	0	0	0
?*Kimbetohia*	0	0	0	0	0	0	1
?*Leptalestes*	0	0	1	1	0	0	0
Leptalestes	0	0	0	1	0	0	0
Maiorana	0	0	0	0	1	1	0
Meniscoessus	1	0	1	1	0	0	0

Mesodma	1	1	1	1	1	1	1
Microcosmodon	0	1	0	0	0	0	0
Mimatuta	1	1	0	0	1	1	0
Nortedelphys	0	0	0	1	0	0	0
Oxyacodon	0	0	0	0	1	0	1
"*Oxyclaenus*"	0	0	0	0	0	0	1
Oxyprimus	1	1	0	0	1	1	1
Palaeoungulatum	0	0	1	0	0	0	0
Paracimexomys	1	0	0	0	0	0	0
Paranyctoides	0	0	0	1	0	0	0
Pediomys	0	0	1	0	0	0	0
Peradectes	0	1	0	0	0	1	1
Procerberus	1	1	1	0	0	0	1
Prodiacodon	0	1	0	0	0	0	0
Protalphadon	0	0	0	1	0	0	0

Protolambda	0	0	1	1	0	0	0
Protungulatum	1	1	0	1	0	1	0
Stygimys	1	1	0	0	0	1	0
Turgidodon	0	0	1	1	0	0	0
Xyronomys	0	0	0	0	0	0	1

Table 2.3.—Occurrences of mammalian genera within middle Puercan (Pu2) local faunas from the Western Interior of North America. Presence = 1; Absence = 0. Locality abbreviations are: RAV = Rav W-1 horizon, PITA = PITA Flats, GAT = Gas Tank, FF2 = Ferris Formation Pu2, WFK = West Flank Kimbeto Wash, EFK = West Flank Kimbeto Wash, and BTW = Betonnie-Tsosie Wash.

Genera	RAV	PITA	GAT	FF2	WFK	EFK	BTW
Alticonus	0	0	0	1	0	0	0
Alveugna	0	0	0	1	0	0	0
Ampliconus	0	0	0	1	0	0	0
Anisonchus	1	0	1	0	0	0	0
Baioconodon	1	1	0	1	0	0	0
Betonnia	0	0	0	0	1	0	1
Bomburodon	0	0	0	0	0	1	1
Bubogonia	1	0	0	0	0	0	1
Carcinodon	1	1	0	0	0	1	1
"*Carcinodon*"	1	0	0	0	0	1	1

Catopsalis	1	0	0	1	0	0	0
Chacopterygus	0	0	0	0	1	0	0
Cimexomys	1	0	0	0	0	0	0
Cimolestes	1	0	0	0	0	0	0
Choeroclaenus	0	0	0	0	1	1	0
Conacodon	0	0	1	1	1	1	1
Desmatoclaenus	0	0	1	0	0	1	0
Dissacus	0	0	0	0	0	1	0
Ectoconus	0	0	1	1	1	1	1
Ectypodus	1	0	0	1	0	0	0
Eoconodon	1	1	0	1	1	1	1
Escatepos	0	0	0	0	0	0	1
Gillisonchus	0	0	0	0	1	1	1
Haploconus	0	0	1	0	0	0	0
Hemithlaeus	0	0	0	0	1	1	1

Kimbetohia	0	0	1	0	0	0	1
Litalestes	1	0	1	0	0	0	0
Litomylus	1	0	0	0	0	0	0
Loxolophus	1	1	1	1	1	1	1
Mesodma	1	0	0	1	0	0	0
Microcosmodon	1	0	0	0	0	0	0
Mimatuta	0	0	0	1	0	0	0
Mithrandir	0	0	0	1	0	0	0
Neoplagiaulax	1	1	0	0	0	0	0
Onychodectes	0	1	0	0	1	0	0
Oxyacodon	1	1	1	1	0	0	1
"*Oxyclaenus*"	0	1	1	0	0	0	0
Parectypodus	1	0	0	0	0	0	0
Peradectes	0	0	0	0	1	0	1
Periptychus	0	0	1	1	1	1	1

Platymastus	0	0	0	0	0	0	1
Procerberus	1	0	0	0	0	0	0
Prodiacodon	1	0	0	0	0	0	0
Promioclaenus	0	0	1	1	0	0	0
Protungulatum	0	0	0	1	0	0	0
Ptilodus	1	0	1	1	0	0	0
Puercolestes	0	0	0	0	1	0	1
Purgatorius	1	0	0	0	0	0	0
Ravenictis	1	0	0	0	0	0	0
Robertschochia	0	0	0	0	0	1	0
Stygimys	1	1	1	0	0	0	0
Taeniolabis	0	0	1	0	0	0	0
Tinuviel	0	1	0	0	0	0	0
Tiznatzinia	0	0	0	0	0	0	1
Wortmania	0	0	0	0	1	0	1

Xyronomys	1	0	0	0	0	0	0

Table 2.4.—Occurrences of mammalian genera within late Puercan (Pu3) local faunas from the Western Interior of North America. Presence = 1; Absence = 0. Locality abbreviations are: CP = Croc Pot, GAR = Garbani Channels and Purgatory Hill, FF3 = Ferris Formation Pu3, WAG = Wagonroad, and DNZ = De-na-zin Wash.

Genera	CP	GAR	FF3	WAG	DNZ
Anisonchus	1	1	0	1	0
Baioconodon	1	1	1	0	0
Besseocetor	0	0	0	1	0
Bomburodon	0	0	0	0	1
Bubogonia	0	1	0	0	1
“*Carcinodon*”	1	1	1	0	1
Catopsalis	1	1	0	0	0
Choeroclaenus	0	0	0	0	1
Cimexomys	1	1	0	0	0
Cimolestes	1	1	0	0	0

Conacodon	0	0	1	1	1
Desmatoclaenus	1	0	0	1	0
Ectoconus	0	0	1	1	1
Ectypodus	0	1	1	0	0
Ellipsodon	0	0	0	1	0
Eoconodon	0	1	0	0	1
Eucosmodon	0	1	0	0	0
Gillisonchus	0	0	0	0	1
Haploconus	0	0	0	1	0
Litomylus	0	1	0	0	0
Loxolophus	1	1	1	1	1
Mesodma	1	1	0	0	0
Microcosmodon	0	1	0	0	0
Mithrandir	0	0	1	0	0
Neoplagiaulax	0	1	0	0	0

Onychodectes	0	0	0	1	1
Oxyacodon	0	1	1	0	1
Oxycleanus	0	0	1	1	0
Oxyprimus	1	0	0	0	0
Pandemonium	0	1	0	0	0
Parectypodus	1	1	0	0	0
Peradectes	0	1	1	0	1
Periptychus	0	0	0	1	1
Procerberus	1	1	0	0	0
Prochetodon	1	0	0	0	0
Prodiacodon	1	1	0	0	0
Promioclaenus	0	0	1	0	1
Protoselene	0	0	1	0	0
Protungulatum	0	0	1	0	0
Ptilodus	0	1	1	0	0

Puercolestes	0	0	0	0	1
Purgatorius	0	1	0	0	0
Stygimys	1	1	0	0	0
Taeniolabis	1	1	1	1	0
Tiznatzinia	0	0	0	0	1
Wortmania	0	1	0	0	1
Xyronomys	1	1	0	0	0

Table 2.5.—Observed and resampled average within- and between-cluster pairwise distance of two clusters based on latest Cretaceous and early Paleocene mammalian assemblages from North America, using non-hierarchical, non-Euclidean relational clustering analyses and a two cluster arrangement. Note that 'Cluster 1' refers to the more northerly (i.e., mean latitude) of the two generated cluster and 'Cluster 2' to the more southerly cluster (see Figures 2.5-2.8). SD = Standard deviation of resampled clusters.

Faunal Zone		Within-cluster distance Cluster 1 ("northern")	 Cluster 2 ("southern")	Between-cluster distance
Lancian	Observed	0.250	0.215	0.339
	Resampled	0.286	0.286	
	SD	0.077	0.053	
Early Puercan	Observed	0.406	0.308	0.748
	Resampled	0.564	0.569	
	SD	0.057	0.215	
Middle Puercan	Observed	0.531	0.310	0.679
	Resampled	0.584	0.583	
	SD	0.044	0.077	
Late Puercan	Observed	0.176	0.567	0.691
	Resampled	0.601	0.603	
	SD	0.179	0.079	

Table 2.6.—Observed and expected number of northern endemics, southern endemics, and cosmopolitan taxa within latest Cretaceous and earliest Paleocene of North America. Northern endemics are mammalian genera known from more than one local fauna and that are restricted to latitudes north of the proposed faunal barrier (i.e., paleolatitude 50°N [Lehman, 1987] during the Lancian, and between paleolatitudes 48° and 51°N during the early Paleocene [Weil, 1999]); whereas, southern endemics are also known from at least two local faunas but restricted to latitudes south of this barrier. Cosmopolitan mammalian genera known are not restricted to one of these regions. The expected values are based on the threshold of endemism outlined by Kaufman (1973), with 25% of the mammalian genera restricted to northern assemblages, 25% of genera are restricted to the south, and the remaining 50% of the mammalian genera extending across the proposed barrier. Where the probability of the chi-square analysis is less than 0.05 (p value ≤ 0.05), the distribution of mammals significantly differs from that expected (i.e., no distinct biogeographic provinces).

Faunal Zone		Latitudinal Range		
		Northern	Southern	Cosmopolitan
Lancian	Observed	5	1	20
	Expected	6.5	6.5	13
p-value = 0.0125	χ^2	8.769		
Early Puercan	Observed	11	0	13
	Expected	6	6	12
p-value = 0.0059	χ^2	10.250		
Middle Puercan	Observed	1	15	17
	Expected	8.25	8.25	16.5
p-value = 0.0026	χ^2	11.909		
Late Puercan	Observed	8	8	13
	Expected	7.25	7.25	14.5
p-value = 0.8563	χ^2	0.310		

Figure 2.1.—Outline map of the Western Interior of North America with location of Lancian mammalian local faunas, with respective sources of faunal data are: Scollard (Lillegraven, 1969; Lillegraven and McKenna, 1986; Fox, 1989, 1994, 1997; Fox and Naylor, 2003), Wounded Knee (Fox, 1989, 1997), Gryde (Storer, 1991), Hell Creek Montana (Archibald, 1982; Lillegraven and McKenna, 1986; Johansen, 1996; Wilson, 2005, 2014; Donohue et al. 2013; pers. obs.), Claw Butte Anthills (Hunter and Archibald, 2002), Hell Creek North Dakota (Hunter and Archibald, 2002), Hell Creek South Dakota (Wilson, 1983), Red Owl (Wilson, 1983, 1987), Type Lance (Clemens, 1964, 1966, 1973; Krause, 1992; Case et al., 2005; Wilson and Riedel, 2010), Hewett's Foresight (Webb, 2001), Black Butte Station (Breithaupt, 1982; Donohue et al. 2012), and (12) Pawnee (Carpenter, 1979; Diem, 1999; Wilson et al., 2010).

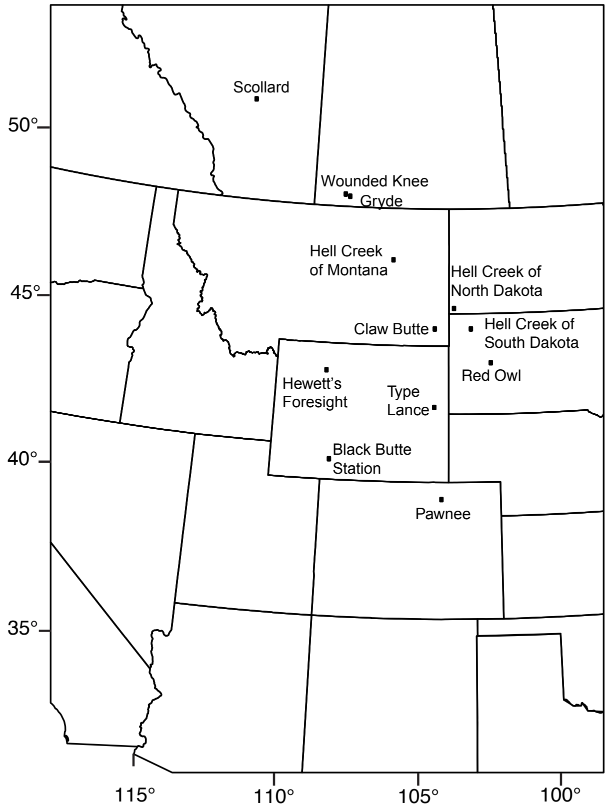

Scollard
Wounded Knee
Gryde
Hell Creek of Montana
Hell Creek of North Dakota
Claw Butte
Hell Creek of South Dakota
Red Owl
Hewett's Foresight
Type Lance
Black Butte Station
Pawnee
50°
45°
40°
35°
115°
110°
105°
100°

Figure 2.2.—Outline map of the Western Interior of North America with location of early Puercan (Pu1) mammalian local faunas, with respective sources of faunal data are: Long Fall (Johnston and Fox, 1984; Fox, 1988, 1990a, 1997; Fox and Youzwyshyn, 1994), Hell's Hollow (Archibald, 1981, 1982), Spigot-Bottle (Hunter and Archibald, 2002; Zhang 2009; Archibald et al. 2011), Lane's Little Jaw Site (Kelly, 2014), Mantua Lentil (Jepsen, 1930, 1940, Van Valen, 1978), Ferris Formation (Pu1 level) (Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), and Littleton (Middleton, 1983; Eberle and Lillegraven, 1998b; Middleton and Dewar, 2004).

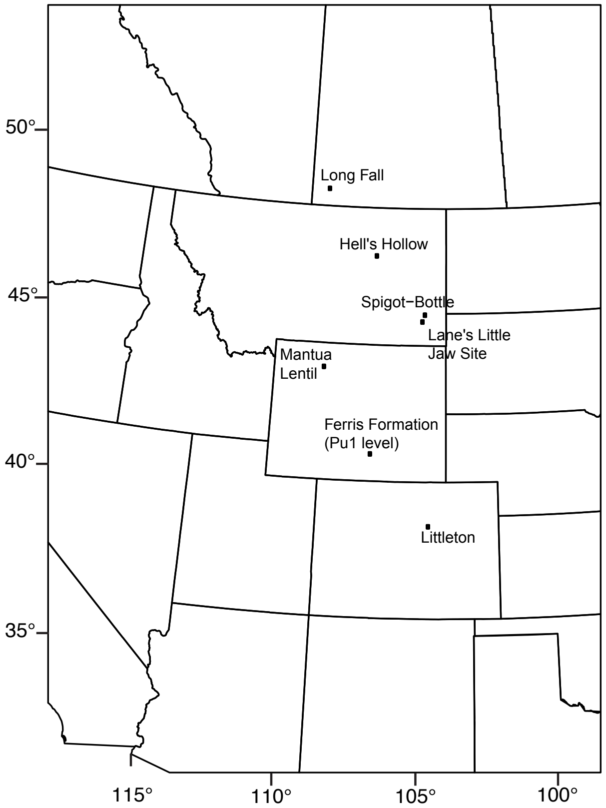

50°
45°
40°
35°
115°
110°
105°
100°
Long Fall
Hell's Hollow
Spigot−Bottle
Lane's Little Jaw Site
Mantua Lentil
Ferris Formation (Pu1 level)
Littleton

Figure 2.3.—Outline map of the Western Interior of North America with location of middle Puercan (Pu2) mammalian local faunas, with respective sources of faunal data are: Rav W-1 (Johnston and Fox 1984; Fox, 1989, 1997), (20) Hiatt (Hunter et al., 1997), Ferris Formation (Pu2 level) (Eberle and Lillegraven, 1998a, 1998b; Eberle, 1999; Lillegraven and Eberle, 1999), Gas Tank (Spieker 1960; Van Valen, 1978; Robison, 1986; Eberle, 1996; Lofgren et al., 2005, 2012), West Flank Kimbeto Wash and East Flank Kimbeto Wash (Williamson, 1996; Williamson and Brusatte, 2013), and Betonnie-Tsosie Wash (Williamson, 1996; Williamson and Brusatte, 2013).

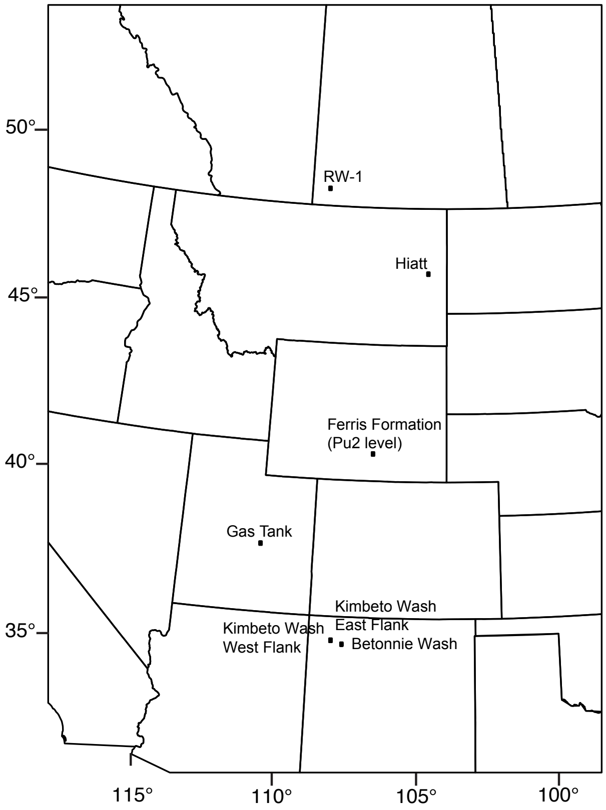
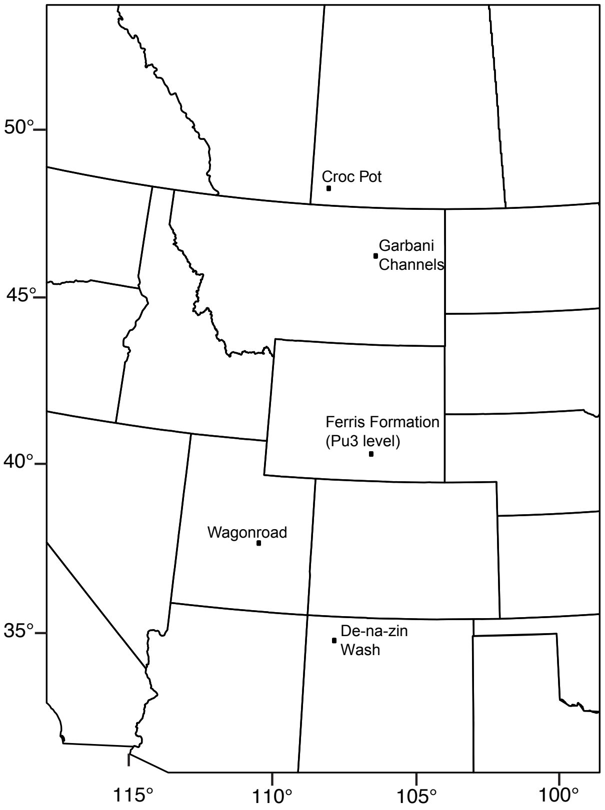

50°
45°
40°
35°
115°
110°
105°
100°
RW-1
Hiatt
Ferris Formation
(Pu2 level)
Gas Tank
Kimbeto Wash
East Flank
Kimbeto Wash
West Flank
Betonnie Wash

Figure 2.4.—Outline map of the Western Interior of North America with location of late Puercan (Pu3) mammalian local faunas, with respective sources of faunal data are: Croc Pot (Fox, 1990; 1997), Garbani Channel deposits and Purgatory Hill (Van Valen and Sloan, 1965; Clemens, 1974; 2002, 2013; 2015; Novacek, 1977 and Clemens, 1977; Van Valen, 1978; Archibald et al., 1983; Simons, 1987; Weil, 1998), Ferris Formation (Pu3 level) (Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), Wagonroad (Gazin, 1941; Tomida and Butler, 1980; Robison, 1986; Cifelli et al., 1995; Williamson, 1996), and De-na-zin Wash (Williamson, 1996; Williamson and Brusatte, 2013).



50°
45°
40°
35°
115°
110°
105°
100°
Croc Pot
Garbani Channels
Ferris Formation (Pu3 level)
Wagonroad
De-na-zin Wash

Figure 2.5.—Non-hierarchical, non-Euclidean clustering analysis of Lancian local faunas from across North America, with two cluster arrangement. The first cluster (black convex hull) is comprised of the Scollard, Gryde, Wounded Knee, Hell Creek Montana, and Black Butte Station local faunas; whereas, the second cluster (red convex hull) contains the Claw Butte Anthills, Hell Creek North Dakota, Hell Creek South Dakota, Red Owl, Hewett's Foresight, Type Lance, and Pawnee local faunas.

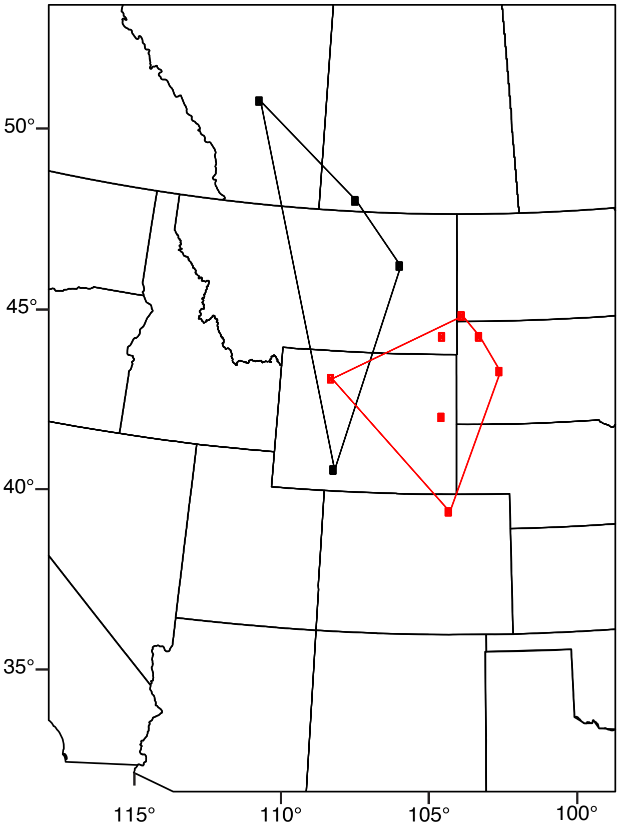


Figure 2.6.—Non-hierarchical, non-Euclidean clustering analysis of early Puercan (Pu1) local faunas from across North America, with two cluster arrangement. The first cluster (black convex hull) is comprised of the Long Fall, Hell's Hollow, Mantua Lentil, Ferris Formation Pu1, and Littleton local faunas; whereas, the second cluster (red convex hull) contains the Spigot-Bottle and Lane's Little Jaw Site local faunas.

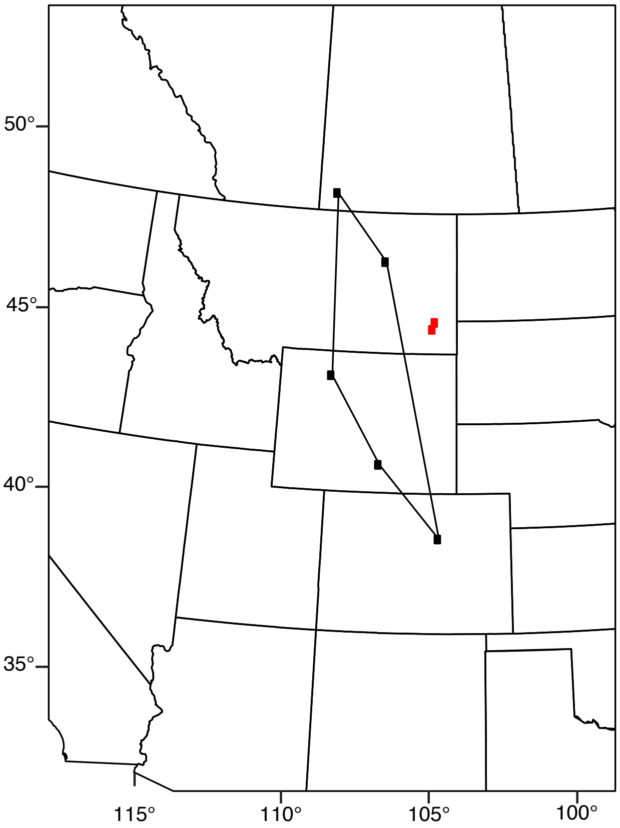


Figure 2.7.—Non-hierarchical, non-euclidean clustering analysis of middle Puercan (Pu2) local faunas from across North America, with two cluster arrangement. The first cluster (black convex hull) is comprised of the Rav W-1, Hiatt, Ferris Formation Pu2, and the Gas Tank local faunas; whereas, the second cluster (red convex hull) contains the West Flank Kimbeto Wash, East Flank Kimbeto Wash, and Betonnie-Tsosie Wash local faunas.

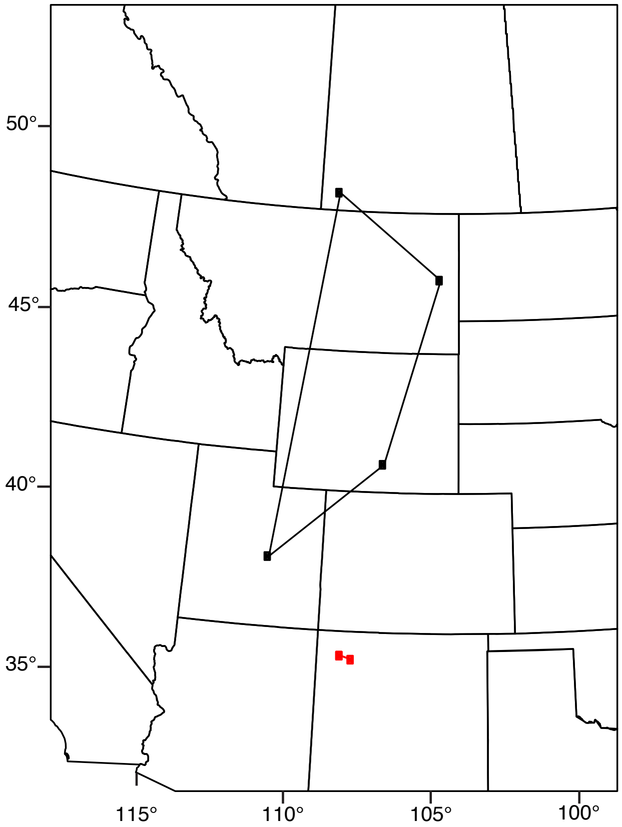


Figure 2.8.—Non-hierarchical, non-Euclidean clustering analysis of late Puercan (Pu3) local faunas from across North America, with two cluster arrangement The first cluster (black convex hull) is comprised of the Croc Pot and Garbani Chanel deposits and Purgatory Hill local faunas; whereas, the second cluster (red convex hull) contains the Ferris Formation Pu3, Wagonroad, and De-na-zin Wash local faunas.

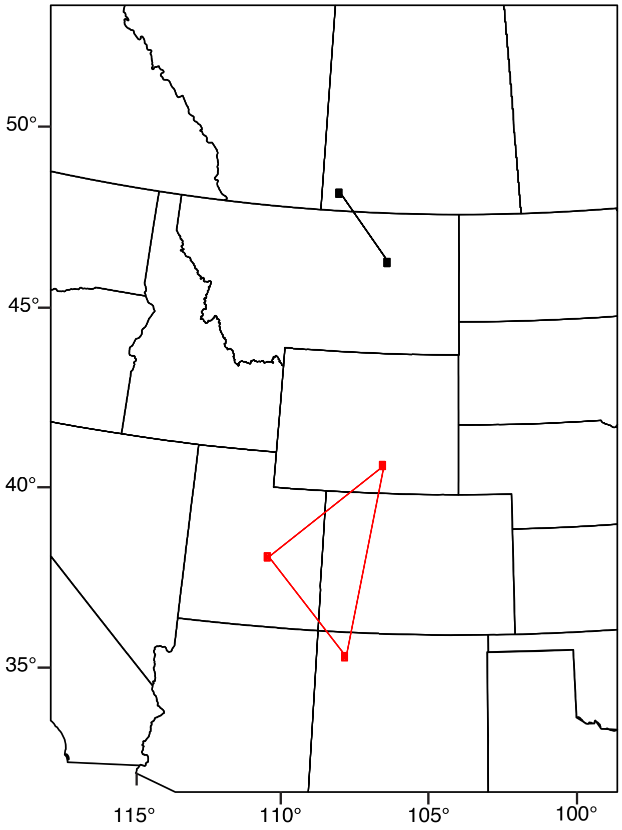


Figure 2.9.—Plot of the relative positions of the Lancian local faunas from across North America based on a non-metric multidimensional scaling, with a minimum spanning tree overlain. Note that two groupings are recovered, the first containing the Scollard, Gryde, Wounded Knee, Hell Creek of Montana, Claw Butte Anthills, and Black Butte Station local faunas, and the other grouping with Hell Creek of North Dakota, Hell Creek of South Dakota, Red Owl, Hewett's Foresight, Type Lance, and Pawnee local faunas. Aside from the placement of Claw Butte Anthills, these groupings are supported by the non-hierarchical clustering analysis, with red and black labels of the local faunas representing the two clusters.

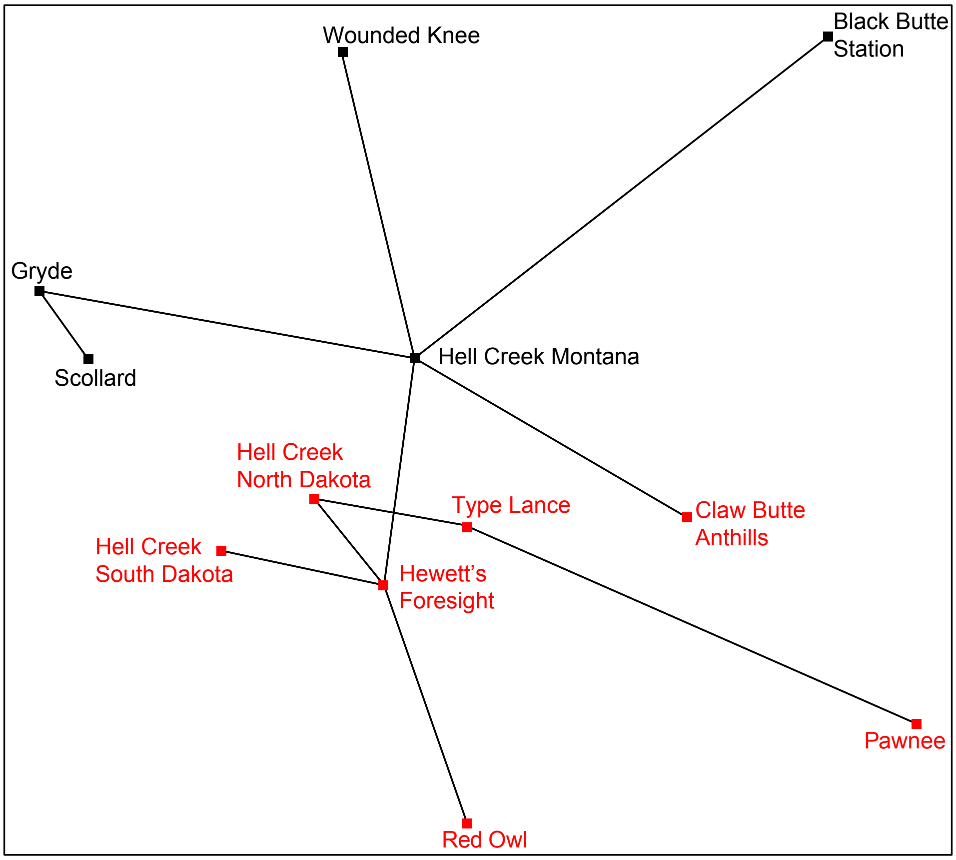


Figure 2.10.—Latitudinal ranges of Lancian mammalian genera across North America, based on their occurrences in local faunas and excluding taxa endemic to a single fauna. The faunal barrier proposed by Lehman (1987) at paleolatitude 50° N is indicated by the transparent red line. Red and black dots represent the occurrences of genera in the first and second clusters, respectively, recovered from the non-hierarchical cluster analysis.

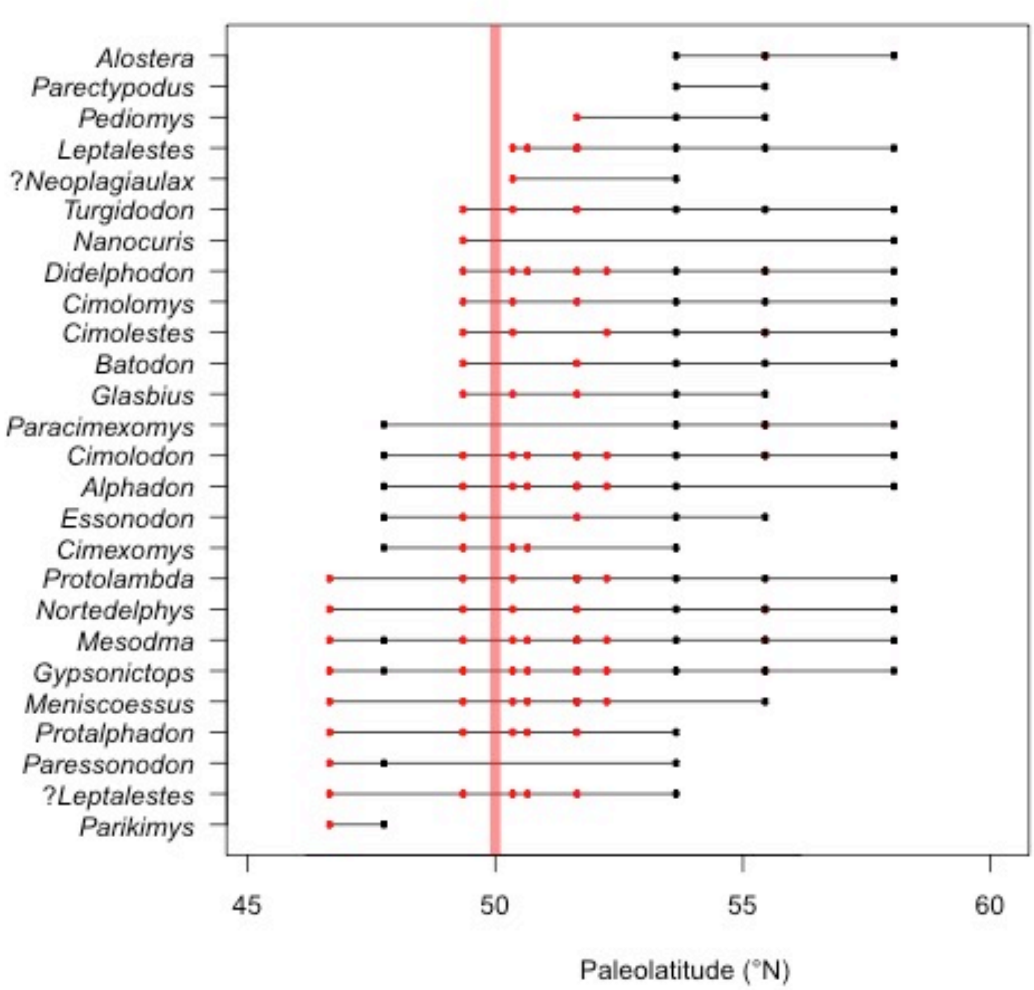


Figure 2.11.—Plot of the relative positions of the early Puercan (Pu1) local faunas from across North America based on a non-metric multidimensional scaling, with a minimum spanning tree overlain. No distinct groupings are obtained, although, similar to the non-hierarchical clustering analysis, the Spigot-Bottle and Lane's Little Jaw Site local faunas (red labeled local faunas) are closely positioned relatively to the other local faunas (black labeled local faunas).

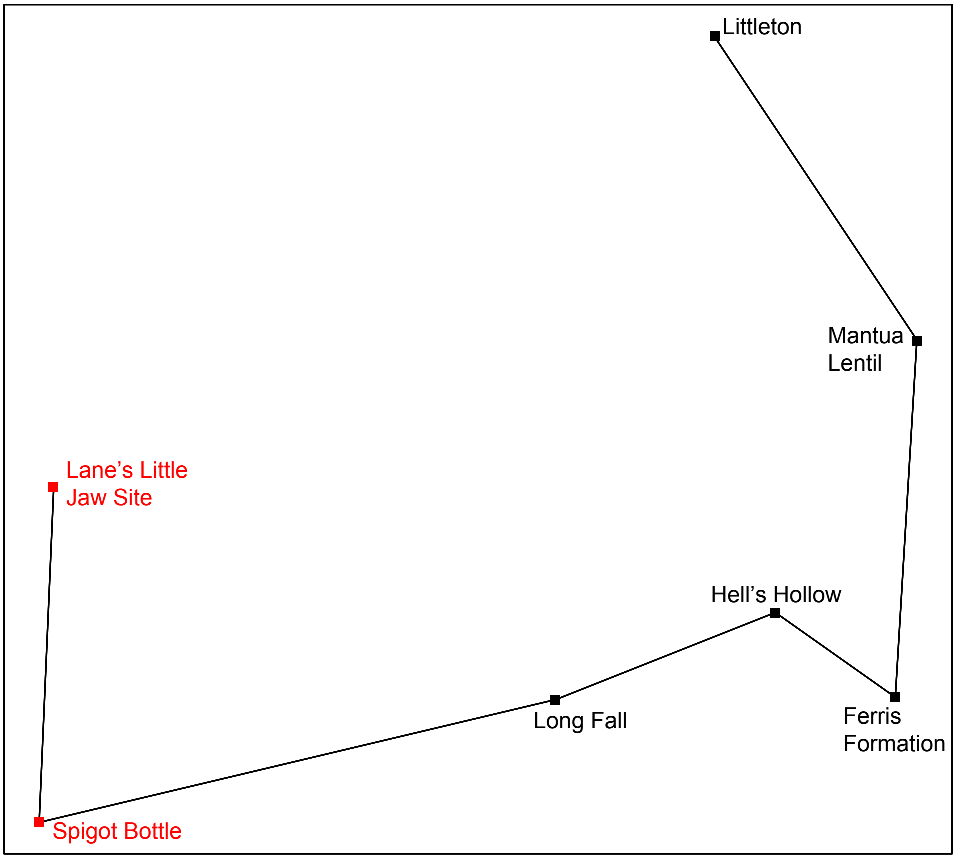


Figure 2.12.—Latitudinal ranges of early Puercan (Pu1) mammalian genera across North America, based on their occurrences in local faunas and excluding taxa endemic to a single fauna. Weil (1999) proposed the existence of faunal barrier between paleolatitudes 48 and 51°N, and this barrier is indicated by the partially transparent red line. Note that Weil (1999) suggested that the faunal barrier was between the Mantua Lentil of the Polecat Bench Formation of northern Wyoming and assemblages within the Ferris Formation of central Wyoming. Here, based on recalculate paleolatitude Mantua Lentil occurs at paleolatitude 50.5°N. Rather than altering the suggested barrier, this assemblage is presented within the barrier but analyzed with northerly assemblages. Red and black dots represent the occurrences of genera in the first and second clusters, respectively, recovered from the non-hierarchical cluster analysis.

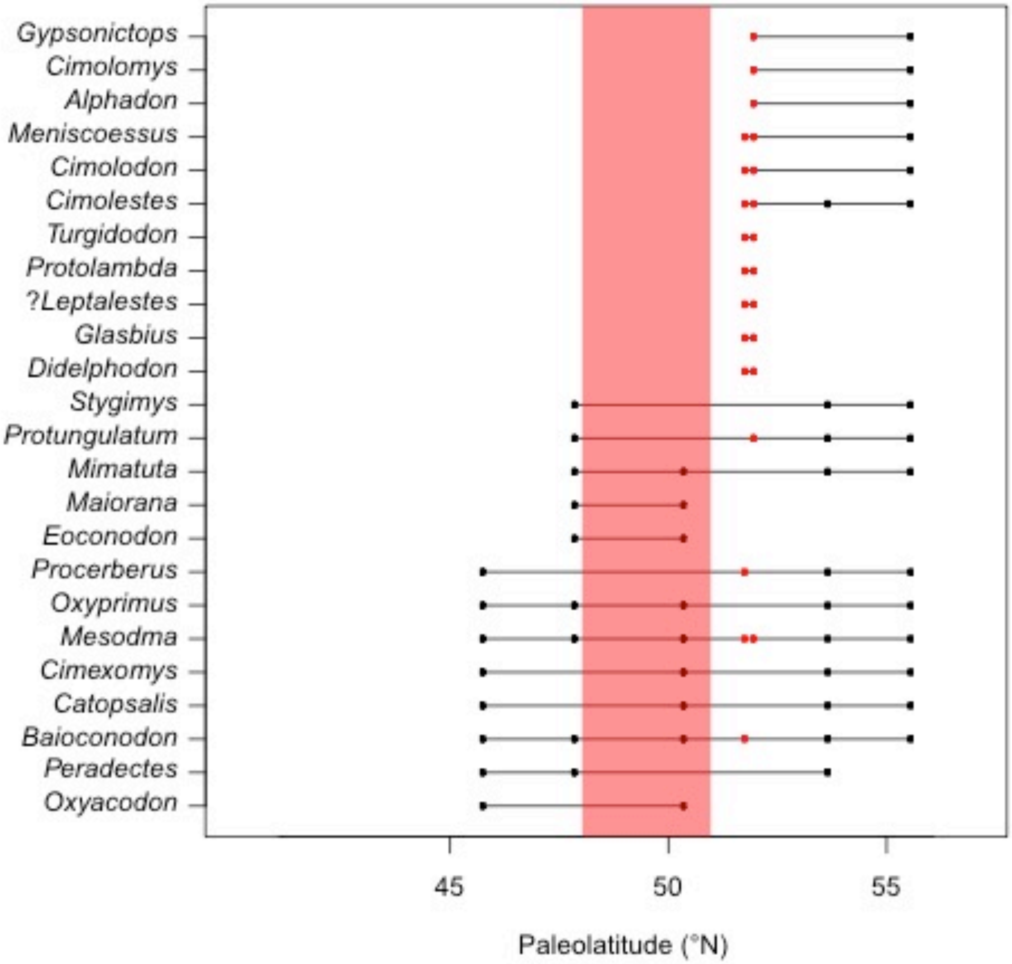

Gypsonictops
Cimolomys
Alphadon
Meniscoessus
Cimolodon
Cimolestes
Turgidodon
Protolambda
?Leptalestes
Glasbius
Didelphodon
Stygimys
Protungulatum
Mimatuta
Maiorana
Eoconodon
Procerberus
Oxyprimus
Mesodma
Cimexomys
Catopsalis
Baioconodon
Peradectes
Oxyacodon
45
50
55
Paleolatitude (°N)

Figure 2.13.—Plot of the relative positions of the middle Puercan (Pu2) local faunas from across North America based on a non-metric multidimensional scaling, with a minimum spanning tree overlain. Similar to the non-hierarchical clustering analysis, the three local faunas from New Mexico (i.e., West Flank of Kimbeto Wash, East Flank of Kimbeto Wash, and Betonnie-Tsosie Wash) form a grouping (black labeled local faunas), but the remaining local faunas (red labeled local faunas) do not group together.

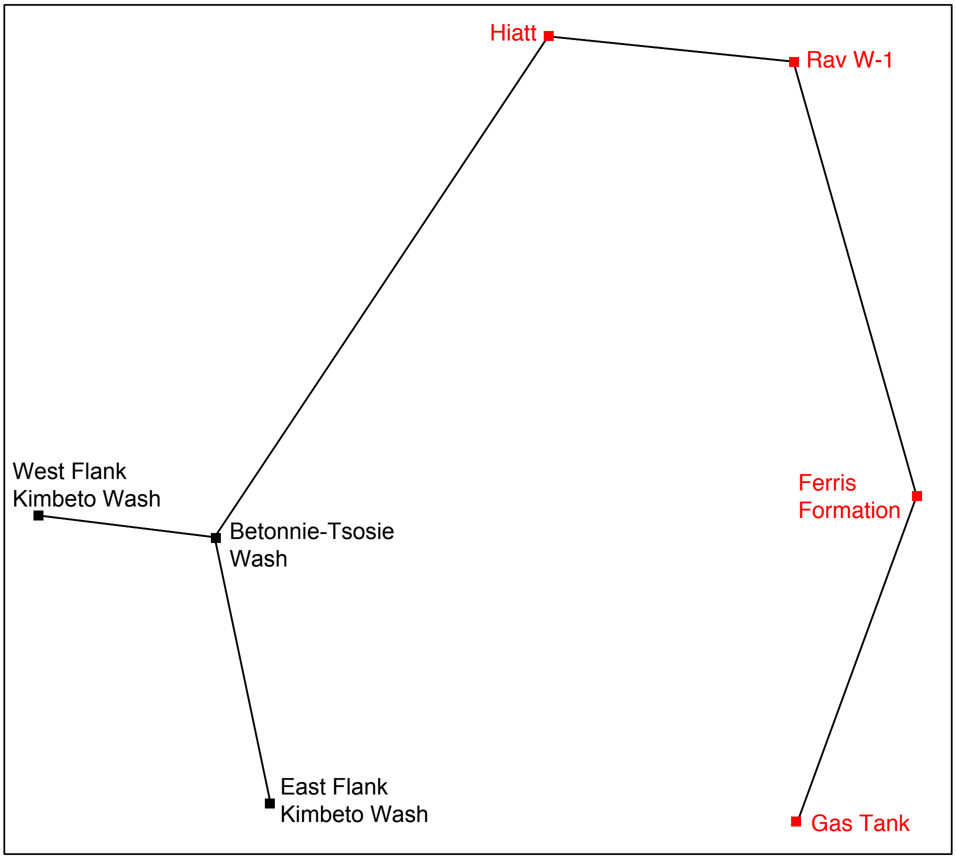


Figure 2.14.—Latitudinal ranges of middle Puercan (Pu2) mammalian genera across North America, based on their occurrences in local faunas and excluding taxa endemic to a single fauna. Weil (1999) proposed the existence of faunal barrier between paleolatitudes 48 and 51°N, and this barrier is indicated by the partially transparent red line. Red and black dots represent the occurrences of genera in the first and second clusters, respectively, recovered from the non-hierarchical cluster analysis.

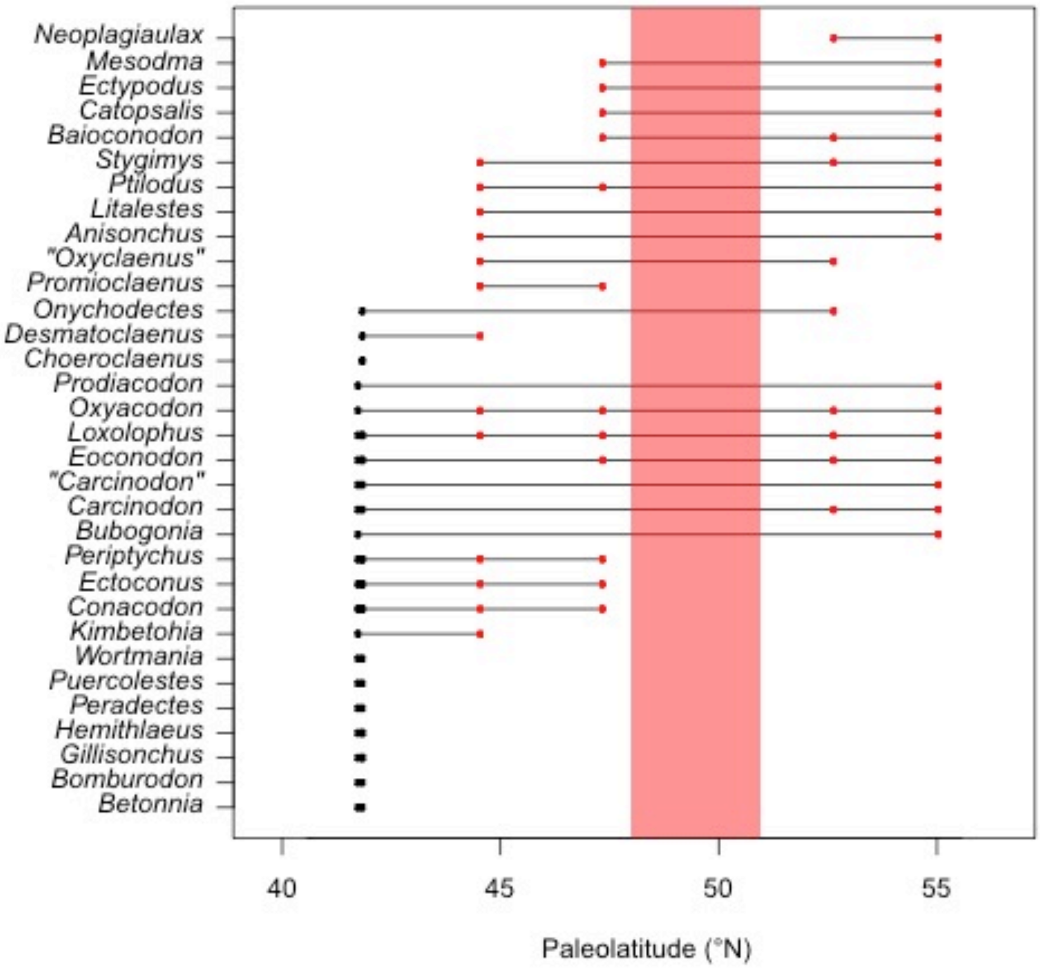


Figure 2.15.—Plot of the relative positions of the late Puercan (Pu3) local faunas from across North America based on a non-metric multidimensional scaling, with a minimum spanning tree overlain. No distinct groupings are obtained.

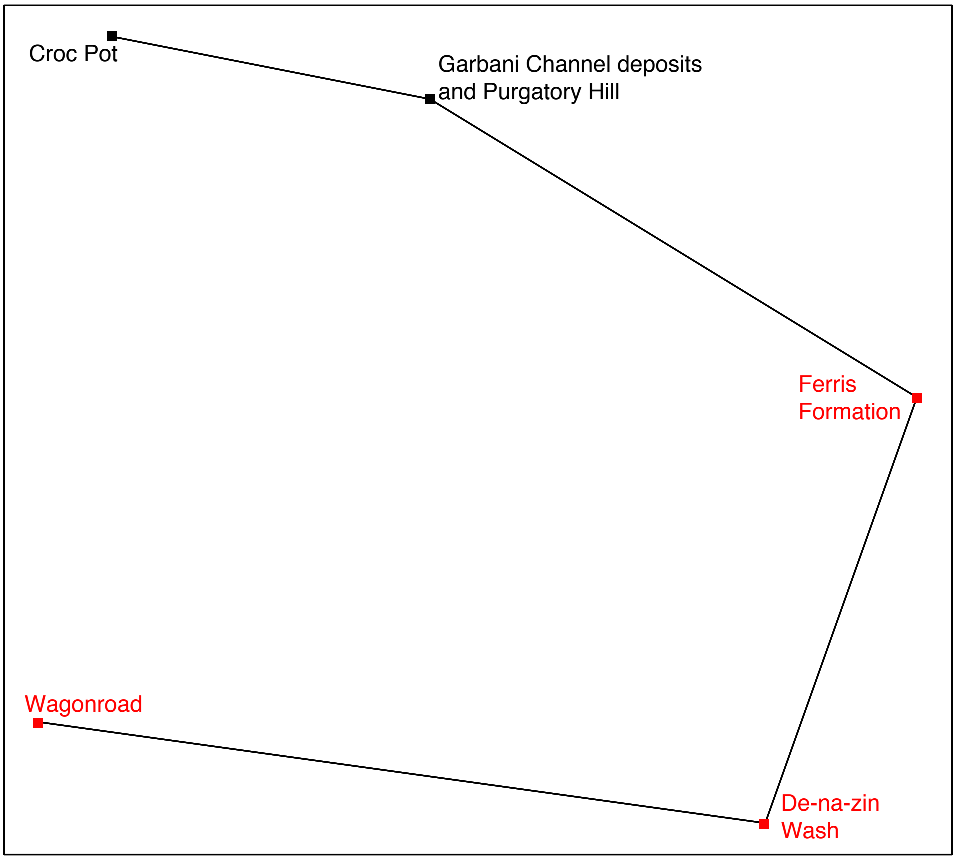
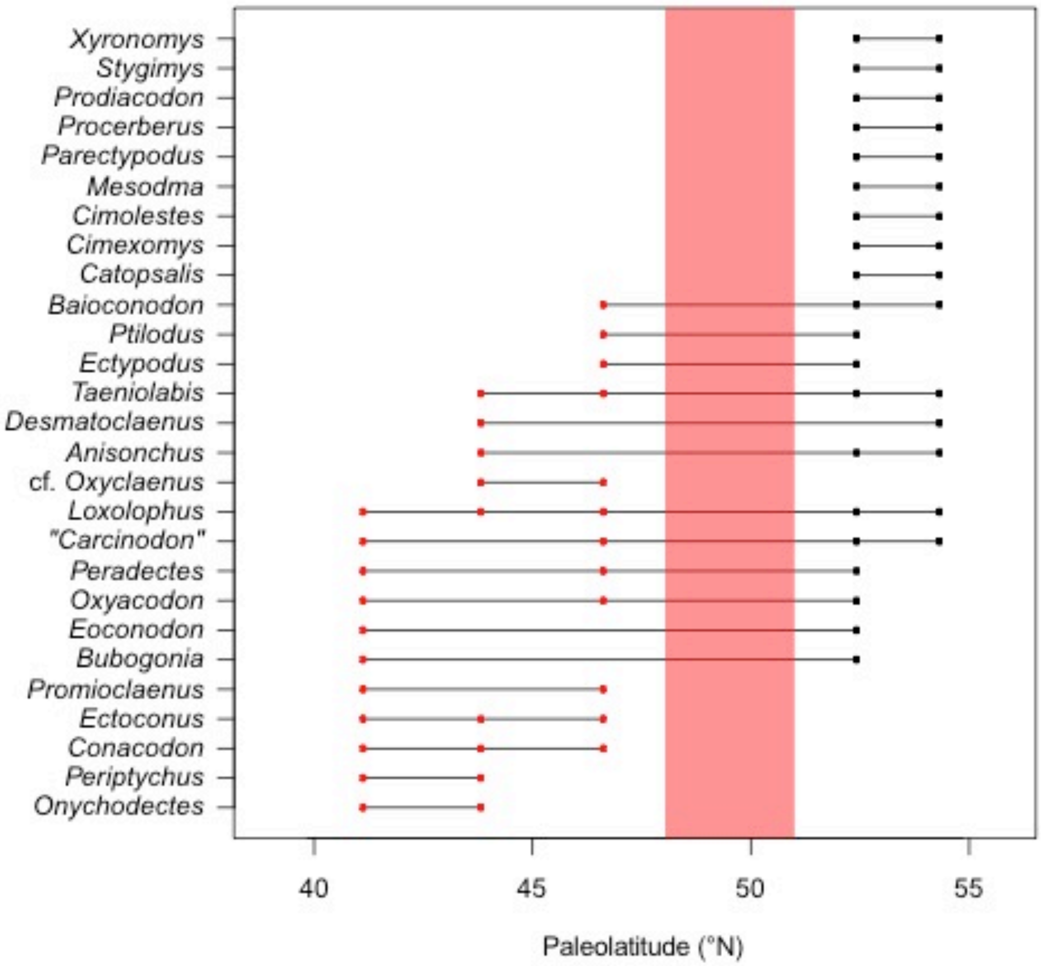


Figure 2.16.—Latitudinal ranges of late Puercan (Pu3) mammalian genera across North America, based on their occurrences in local faunas and excluding taxa endemic to a single fauna. Weil (1999) proposed the existence of faunal barrier between paleolatitudes 48 and 51°N, and this barrier is indicated by the partially transparent red line. Red and black dots represent the occurrences of genera in the first and second clusters, respectively, recovered from the non-hierarchical cluster analysis.



3 Compositional Differences and Similarities among Latest Cretaceous Mammalian Assemblages from the Western Interior of North America

3.1 Abstract

There is little question that many mammals, along with a great number and diversity of other animals and plants, became extinct at or near the Cretaceous/Paleogene boundary (approximately 65.6 million years ago) and that shortly after the dramatic events that marked the boundary, eutherian mammals underwent a remarkable taxonomic and morphological diversification. However, comprehensive studies directly relating the timing and patterns of the expansion of eutherians remain few, with recent findings suggesting faunal changes within the latest Cretaceous. To assess these changes, information on the relative abundances of mammals from eleven latest Cretaceous assemblages from the Western Interior of North America was compiled, and heterogeneity indices and a series of resampling analyses were used to generate assemblage-specific abundance estimates of each taxon based on the faunal composition of the Type Lance local fauna of Wyoming. Using these estimates, the faunal similarity among these assemblages was quantitatively assessed and genera that were unusually abundant or rare compared to the Type Lance were identified. The results suggest that the structure of latest Cretaceous mammalian assemblages across the Western Interior of North America was not homogeneous. A number of eutherians (e.g., *Cimolestes*, *Gypsonictops*) are more abundant in the northern assemblages relative to the faunal composition of the Type Lance and other more southerly sites, whereas some multituberculates (e.g., *Meniscoessus*) and marsupials (e.g., *Pediomys*)

are unusually rare in the northern assemblages. Although discriminating regional geographic patterns from temporal or local ecological effects remains difficult, the faunal composition of the more northerly assemblages suggests that eutherians were undergoing a radiation in the northern part of the Western Interior of North America during the latest Cretaceous and that the region may have been the source for mammalian immigrants into more southern localities during the earliest Paleocene.

3.2. Introduction

Although interest in episodes of elevated extinction and their associated causes has a long history (e.g., Cuvier, 1825), this attraction has been considerably heightened over the past 25 years with the widespread acceptance that at least five times in the Earth’s history, near synchronous, often rapid, global extinctions of many diverse organisms have occurred (Raup and Sepkoski, 1982). The effects of these extinction events on many organisms (and higher-level groups) have seemed relatively straightforward. For example, no trilobites have been recovered in sediments above the Permian/Triassic boundary (Erwin, 2006) and, perhaps most famously, not a single non-avian dinosaur has been discovered in rocks younger than the Cretaceous (e.g., Archibald, 1996; Fastovsky and Weishampel, 2005; but see Fassett et al., 2011 for a different opinion). For many other organisms, however, the effects of these events were not as devastating (or terminal) and, in many cases, provided ecological and evolutionary opportunities previously beyond their reach.

Of the previous studies that have closely examined mass extinctions, the vast majority have assumed that episodes of prolific diversification would ensue shortly afterwards as survivors radiate into newly vacated ecological niches (i.e., an adaptive radiation) (e.g., Simpson, 1944; Van Valen, 1978). Logistic models derived from ecological studies (e.g., Sepkoski, 1984), coupled with the dynamics of diversification into open ecological niches (e.g., Valentine, 1980), provided the appropriate theoretical support for these assumptions. But, while these general trends have been recognized in most extinction intervals, detailed empirical studies of individual events (e.g., Sahney and Benton, 2008; Wilson, 2014), and statistical modeling using trophic networks (e.g., Solé et al., 2002; Mitchell et al., 2012) demonstrate that the timing and patterns of these radiations are remarkably variable. These studies suggest that a better understanding of the dynamics of individual events and for individual clades is needed.

The evolutionary radiation of mammals near the Cretaceous/Paleogene boundary (K/Pg boundary) (approximately 65.6 million years ago) (Renne et al., 2013; Sprain et al., 2014) has long been seen as an example of an ecological release (i.e., the expansion of habitat or use of resources by populations into areas of lower species diversity with reduced interspecific competition [Gillespie, 2009]), with early Paleogene eutherians occupying numerous ecological roles after the extinction of the incumbent latest Cretaceous non-avian dinosaurs, and many primitive marsupials and rodent-like multituberculates (e.g., Van Valen and Sloan, 1977; Van Valen, 1978; Archibald, 1983). Yet, comprehensive studies directly relating the timing and patterns of the expansion of eutherians to this proposed ecological release remain few. In fact, Wilson and colleagues, in a series of recent papers focused on Lancian and Puercan local faunas from the Hell Creek Formation of southeastern Wyoming (the terms Lancian and Puercan refer to North American Land Mammal Ages [NALMAs] that are approximately equivalent to the uppermost Cretaceous and lowermost Paleogene; see discussion below) (Wilson, 2005; 2013; 2014; Wilson et al. 2012; Sprain et al. 2014), have reported that latest Cretaceous mammalian communities were somewhat unstable, with notable changes in mammalian species richness and evenness approximately 500 000 years prior to the K/Pg boundary.

In addition to these findings, Lillegraven (1969) previously noted the greater taxonomic richness and relative abundance of latest Cretaceous eutherian mammals within the Scollard local fauna of southcentral Alberta relative to their abundance in the Type Lance local fauna of southeastern Wyoming. Based on these observations, some researchers (e.g., Sloan, 1969, 1987; Lillegraven and McKenna, 1986; Anthony and Maas, 1990; Rowe et al. 1992; Weil, 1999; Donohue et al., 2013) have suggested that the northern part of the Western Interior of North America represented a distinct biogeographic province during parts of the Late Cretaceous and early Paleocene, separate from that in the south. Although Williamson (1996) and Hunter and Archibald (2002) contend that there is little differentiation between northern and southern faunas during the latest Cretaceous and maintain that the composition of these North American faunas was relatively homogeneous, the possibility that the northern part of the Western Interior of North America represents a distinct faunal province during parts of the Late Cretaceous and early Paleogene has broad implications for the patterns of mammalian evolution in North America.

Given these uncertainties, I quantitatively analyzed the relative abundances of latest Cretaceous mammals within assemblages across the Western Interior of North America, with particular focus on eutherian mammals. To accomplish this task, information on the occurrence and relative abundance of mammals from eleven localities from the latest Cretaceous, ranging from southcentral Alberta to southeastern Wyoming, were compiled. Heterogeneity indices were used to first assess mammalian generic richness and evenness among these assemblages, and resampling with replacement was employed to identify genera that are more or less abundant than expected based on their occurrence and abundance within the well-studied Type Lance local fauna from the Lance Formation of northeastern Wyoming (Clemens, 1964, 1966, 1973; Krause, 1992; Case et al., 2005; Wilson and Riedel, 2010). These findings provide new insights into the timing and patterns of the evolutionary radiation of mammals near the K/Pg boundary.

3.3 Materials and Methods

3.3.1 Biochronology and Latest Cretacecous "Transitional" Assemblages

Continental strata of the Late Cretaceous and early Paleogene of North America are temporally divided on the basis of fossil mammals into North American Land Mammal Ages (NALMAs) (Woodburne, 1987, 2004). NALMAs are not geochronological ages (see NACSN, 2005) but recent advances in magnetostratigraphy and isotope stratigraphy (e.g., Secord et al., 2006) have allowed a more precise correlation of continental strata to the geomagnetic polarity time scale. Mammalian-based biochronology continues to provide the finest chronologic resolution possible for non-marine sections of the Late Cretaceous and early Paleogene of North America.

Four Land Mammal Ages are recognized in the Late Cretaceous: from oldest to youngest, these are the Aquilan, Judithian, "Edmontonian", and Lancian (Cifelli et al., 2004). Within the Paleocene, four NALMAs are also recognized: the Puercan, Torrejonian, Tiffanian, and Clarkforkian, with each further divided into zones (e.g., the Puercan is further divided into three zones: Pu1, Pu2, and Pu3) (Lofgren et al., 2004). The Lancian/Puercan boundary has more conventionally been correlated with the Cretaceous/Paleogene boundary (e.g., Archibald et al. 1988), yet some authors (e.g., Archibald and Lofgren, 1990; Cifelli et al., 2004; Lofgren et al., 2004; Kelly, 2014) have suggested that the Puercan could be extended into the latest Cretaceous, based on the appearance of mammals thought to be restricted to the Puercan within latest Cretaceous assemblages. Although this study is centered on latest Cretaceous assemblages, regardless of their assignment to either the Lancian or Puercan, to clarify some confusion with "transitional" assemblages a discussion on latest Cretaceous mammalian assemblages is useful here.

Based on highly fossiliferous localities from the Tullock member of the Fort Union Formation and Hell Creek Formation in the Bug Creek valley and adjacent areas in northeastern Montana (Sloan and Van Valen, 1965; Van Valen and Sloan, 1965), and two localities from the Frenchmen and Ravenscrag formations of the Cypress Hills region of southwestern Saskatchewan (Johnston 1980; Johnston and Fox 1984; Fox, 1989, 1997), a Bugcreekian NALMA, intermediate between Lancian and Puercan, was formally proposed by Archibald (1987) and Sloan (1987). Assemblages from these sites contain fossil remains of dinosaurs and typical Lancian mammals, along with mammals thought to be restricted to the Paleocene. These discoveries led to the suggestion that the Bug Creek and Canadian assemblages were latest Cretaceous in age and presented direct evidence of the replacement of archaic Cretaceous mammals by more progressive Paleocene mammals, particularly eutherian mammals (e.g., Fox, 1997). For these reasons, these assemblages were cited as evidence that faunal turnover rates during the K/Pg boundary were gradual and not compatible with catastrophic events (e.g., Archibald and Clemens, 1982; Archibald, 1996).

However, purportedly "transitional" Bug Creek assemblages from northeastern Montana were later discovered to occur in Paleocene channel-fill deposits (Lofgren, 1995), with latest Cretaceous dinosaur and mammal remains reworked (i.e., deposited, exhumed, and subsequently reburied) from the underlying Hell Creek Formation and mixed with Paleocene fossils from the Tullock Member of the Fort Union Formation (Swisher et al., 1993). The amount of reworked specimens from samples of some of these Bug Creek assemblages has been conservatively estimated to range from 10% to 15% of the total collected number of specimens (Fiorillo, 1998). Following these discoveries, the concept of a Bugcreekian NALMA was abandoned and, for the purposes of studying the patterns of mammalian evolution in the Western Interior, Bug Creek assemblages can only be cautiously considered.

In contrast to the Bug Creek assemblages, a latest Cretaceous age for the Long Fall horizon, Medicine Hat Brick and Tile (MHBT) Quarry (Johnston and Fox, 1984; Fox, 1989) and Frenchman-1 (Fr-1) assemblage (Johnston 1980) from southern Saskatchewan appears to be supported by lithostratigraphic, biostratigraphic, and, at least for the Fr-1 assemblage, palynological evidence. Although quarrying operations have destroyed the locality since its initial discovery (but see Fox and Scott, 2011), the Long Fall horizon occurred at the base of the Ravenscrag Formation at the MHBT Quarry and originally laid 3 meters stratigraphically below beds containing the early Puercan (Pu1/ Pu2) Rav W-1 horizon (Johnston and Fox, 1984; and see Fox and Scott, 2011 for a discussion on the age assignment of the Rav W-1 horizon). Lerbekmo (1985) contended that both fossil-bearing horizons at the Quarry were parts of the same Paleocene point bar deposits and, according to this interpretation, that the "typical" Cretaceous fossils at Long Fall had been eroded out of underlying stratigraphic beds and redeposited into Paleocene sediments, similar to the Bug Creek localities. However, as shown by Johnston and Fox (1984) and Fox (1997), a disconformity was present between the two fossil beds at the quarry, and the upper and lower beds are unlikely to have been parts of the same depositional system.

The Fr-1 site is suggested to occur in the Frenchman Formation, although the Ferris Coal Seam, the regional marker for both the contact between the Frenchman Formation and overlying Ravenscrag Formation, and the K/Pg boundary, is absent in the vicinity (Johnston, 1980; Fox 1989, 1990, 1997). Post-depositional erosion (i.e., reworking) of the site is contested by the presence of articulated remains of non-avian dinosaurs from what is suggested to be the same horizon several hundreds of meters to the east of the site, and the relatively high abundance of typical Lancian mammals (Johnston, 1980; Fox 1989, 1990, 1997). More substantially, however, palynomorphs have been recovered from the site and, based on palynozones of the Western Interior of North America (Nichols and Sweet, 1993; Nichols, 2002, 2009), suggest an uppermost Cretaceous age (Fox et al., 1995; Fox, 1997). Despite support for a latest Cretaceous age for the Long Fall and Fr-1 assemblages, both local faunas are frequently and often explicitly excluded from studies on patterns of mammalian evolution across the K/Pg boundary (e.g., Hunter and Archibald, 2002).

In addition to these assemblages, Archibald et al. (2011; also see Hunter and Archibald, 2002 and Zhang, 2009) recently provided a preliminary list of the mammalian taxa from the Spigot-Bottle local fauna of the Hell Creek Formation of southeastern Montana and reported the presence of a previously unknown species of *Protungulatum*, *P. coombsi*, from the site. The first appearance of the genus *Protungulatum* is usually regarded as the beginning of the Puercan; however, because the assemblage occurs within sediments deposited during the latest Cretaceous magnetostratigraphic chron 30N (Hicks et al., 2002; Renne et al., 2013), Archibald et al. (2011) assigned the assemblage to the Lancian. These authors suggested that the Lancian/Puercan boundary could remain correlated with the Cretaceous/Paleogene boundary, with the onset of the Puercan restricted to the first appearance of *Protungulatum donnae* rather than the genus more generally.

Kelly (2014) also recently provided identifications and descriptions of mammals from Lane's Little Jaw Site from the Hell Creek Formation of southeastern Montana. Similar to these other "transitional" assemblages, Lane's Little Jaw Site contains both typical Lancian mammals and several eutherian mammals thought to be restricted to the Puercan, including the cimolestan *Procerberus* and "arctocyonid" condylarth *Baioconodon*. However, aside from these mammalian fossils, non-avian dinosaurs are also present in the assemblage, and the assemblage does not appear to represent a mixture of Paleocene and latest Cretaceous sediments (Kelly, 2014). Kelly (2014) suggests that the Lancian/Puercan boundary might be time transgressive and, despite being recovered in latest Cretaceous rocks, tentatively assigned Lane's Little Jaw Site Quarry to the Puercan.

Commenting on the "transitional" assemblages from western Canada, Cifelli et al. (2004) suggested that these assemblages might be latest Cretaceous in age and that the beginning of the Puercan could be diachronous across the Western Interior of North America. With the discovery of a number of mammals more typical of the Puercan in the latest Cretaceous Spigot-Bottle local fauna and Lane's Little Jaw Site, including *Protungulatum*, a number of other archaic "ungulates", and some cimolestans, an increasing amount of evidence supports this claim and it seems likely that the Puercan does extend into the latest Cretaceous, at least in some regions. A better understanding of latest Cretaceous and earliest Paleocene mammalian biochronology is clearly needed, and revisions to the current definitions seem likely but any amendments are beyond the scope of this research. For the purposes of this study, an assignment to either the Lancian or Puercan is not essential; instead, as stated previously, this research centered on local faunas recovered from latest Cretaceous sediments.

Aside from these nomenclatural issues with the Lancian/Puercan boundary, it is also important to note that the beginning of the Lancian is poorly constrained, principally owing to the sparseness of "Edmontonian" mammalian fossils and the lack of index taxa from this biozone. As a result, the duration of the Lancian is uncertain but is estimated to be approximately 3 million years (Cifelli et al., 2004; Wilson et al., 2010). Based on a newly updated and refined chronostratigraphic framework for the Hell Creek Formation of Montana (see Wilson, 2014), all local faunas assigned to the Lancian within the region are thought to have been recovered from rocks that range in age from roughly 67.5 to 65.6 million years old (also see Wilson, 2005; Wilson et al. 2010; Holroyd et al., 2014; Sprain et al. 2014).

3.3.2 Assemblages

The analyses focus on the occurrence and relative abundances of mammalian genera from eleven North American latest Cretaceous assemblages, ranging from southcentral Alberta to southeastern Wyoming (Figure 3.1). Local faunas that are conventionally assigned to the Lancian include the Scollard local fauna from the Scollard Formation of southcentral Alberta (Lillegraven, 1969; Lillegraven and

McKenna, 1986; Fox, 1989, 1994, 1997; Fox and Naylor, 2003), Wounded Knee (Fox, 1989, 1997) and Gryde (Storer, 1991) local faunas from the Frenchman Formation of southwestern Saskatchewan, Hell Creek local fauna (including Tuma, Just Past Celeste, Hauso 1, and Flat Creek) (Archibald, 1982; Lillegraven and McKenna, 1986; Johansen, 1996; Wilson, 2005, 2014) and Muddy Tork local fauna (Hunter et al. 1997; Hunter, 1999; Hunter and Archibald, 2002) from the Hell Creek Formation of eastern Montana, Hell Creek North Dakota local fauna (including Marmath, and Pretty, Sunset, and Mud buttes) from the Hell Creek Formation of southwestern North Dakota (Hunter and Pearson, 1996; Hunter and Archibald, 2002), the Type Lance local fauna from the Lance Formation of eastern Wyoming (Clemens, 1964, 1966, 1973; Krause, 1992; Case et al., 2005; Wilson and Riedel, 2010), and Hewett's Foresight local fauna from the Lance Formation of northwestern Wyoming (Webb, 2001) (Figure 3.1). Possible Puercan assemblages from the latest Cretaceous include the Long Fall horizon from the Ravenscrag Formation of southwestern Saskatchewan (Johnston and Fox 1984; Fox, 1989, Fox, 1997, 2005), and the Spigot Bottle local fauna (Hunter and Archibald, 2002; Zhang 2009; Archibald et al. 2011) and the recently described Lane's Little Jaw Site local fauna (Kelly, 2014), both discovered in sediments of the Hell Creek Formation in southeastern Montana.

Conspicuously excluded from this analysis are local faunas from which abundance data were not available and those with small sample sizes (i.e., fewer than 40 specimens), such as the faunas from the Fr-1 site of southwestern Saskatchewan (see discussion above) (Johnston, 1980; Fox, 1989, 1990, 1997) and the Prince Creek Formation of the North Slopes of Alaska (Clemens and Nelms, 1993; Clemens, 2003). I also removed assemblages in which only some of the taxonomic groups have been formally described, including the Red Owl locality from the Fox Hills Formation of South Dakota (Wilson, 1983), Alamo Wash local fauna from the Kirtland Formation of northwestern New Mexico (Flynn, 1986; Williamson and Weil, 2008), and Black Butte Station local fauna from the Lance Formation of southwestern Wyoming (Donohue et al. 2012).

3.3.3 Number of Identified Specimens

The number of identified specimens (NISPs) for higher-level mammalian groups are summarized in Table 3.1; NISPs are also separately provided for multituberculates, metatherians, and eutherian genera in Tables 3.2, 3.3, and 3.4, respectively. Although genus-level data are examined in this study, rather than species-level occurrence, the taxonomy and specimen counts are somewhat similar to those presented by Hunter and Archibald (2002) in their study of latest Cretaceous mammalian fauna from North America but with several notable differences. In particular, I included several recently identified taxa, such as the taeniodont eutherian *Schowalteria* from the Scollard local fauna (Fox and Naylor, 2003) and the cimolomyid multituberculate *Paressonodon* from the Hell Creek local faunas of Garfield County (see Wilson, 2014). Recent taxonomic revisions are also included in this analysis (e.g., Case et al. 2005; Davis, 2007), including the recognition of *Nortedelphys jasoni* (see Williamson et al., 2012). I used the list of the mammals from the Spigot-Bottle local fauna of southeastern Montana more recently provided by Archibald et al. (2011; also see Zhang 2009), and included information on Lane's Little Jaw Site (Kelly et al. 2014) and Hewett's Foresight local fauna as presented in the unpublished dissertation of Webb (2001); notably, Donohue et al. (2012) (mistakenly referring to the assemblage as "Hewitt's Foresight One local fauna") also included information on the mammalian fauna from this assemblage, yet omitted specimens unassigned to species (e.g., *Mesodma* sp.).

3.3.4.Recalibrated Number of Identified Specimens

As reported by Holroyd et al. (2013; in prep.), studies that use NISP counts commonly assume that the specimen being counted, whether the count is performed at the level of the family, genus, species, or any other taxonomic grouping, is identified with a high degree of probability once the specimen is collected and accessioned in the collections of an institution. However, knowledge of most extinct organisms is incomplete and not all taxa are as readily identifiable as others. Holroyd et al. (2013; in prep.) recognized this problem as taxonomic detection bias or, more plainly, the bias resulting from an inability to detect the presence of a fossil taxon at an appropriate taxonomic level. The effects of this bias are particularly apparent when specimens within a sample are only identifiable to taxonomic levels above that of the species.

To account for the influence of taxonomic detection bias, I generated taxon-specific detection probabilities for each of the mammalian genera present in the latest Cretaceous assemblages (Table 3.5). Using these probabilities in combination with the NISPs counts, I calculated recalibrated number of identifiable specimen counts (rNISPs) with the equation provided by Holroyd et al. (2013; in prep.):

$$\mathrm{rNISP_i} = \mathrm{NISP_i}\left(1 + \left(1 - \left(\frac{\mathrm{nIDE_i}}{\mathrm{nE_i}}\right)\right)\right)$$

where, for each taxon (i) the detection probability represents the number of identifiable elements ($nIDE_i$) divided by the total number of elements in the dentition (nE_i), and the complementary percentage subtracted from one (Table 3.5). These recalibrated counts estimate the number of specimens that exist in the sample but which are unidentified. The recalibrated number of identified specimens (rNISPs) for the eleven latest Cretaceous assemblages are summarized in Table 3.6 and rNISPs are provided for multituberculates, metatherians, and eutherians in Tables 3.7, 3.8, and 3.9, respectively. These numbers were employed for the statistical analyses described below.

3.3.5 Heterogeneity indices

Heterogeneity indices are simple, descriptive statistical summaries that reflect the manner in which abundance is distributed among the different taxa within a sample (Magurran, 2004). Heterogeneity indices often differ in whether taxonomic richness (i.e., the absolute number of taxa, at a specific taxonomic level, in a given sample) or evenness (i.e., the relative abundances of taxa within a given sample) is emphasized, and if rare or dominant taxa are more heavily underscored (Whittaker, 1972; Magurran, 2004). To compare the community structure among the eleven assemblages, I calculated two heterogeneity indices, the Simpson's and Equitability indices, and their 95% confidence intervals using *PAST* version 3.06 (Paleontological Statistics Software Package [Hammer et al. 2001]).

Simpson's index of diversity (Simpson, 1949) is calculated as $1 - D = \Sigma {p_i}^2$, where p_i is the relative abundance of genus i within the faunal assemblage, and values of this index ranges from 0 to 1, with 0 indicating that all taxa are equally abundant within a fauna and 1 designating a fauna that is dominated by a single taxon. Simpson's index focuses on the abundances of the most common taxon and is most effective at measuring heterogeneity among small samples. The Equitability index (Lloyd and Ghelardi, 1964) is derived from Shannon's index and calculated as $J = \frac{-\Sigma p_i \ln p_i}{\ln S}$ $(i = 1,2, \dots, p)$, with p_i as the proportion of genus i within the fauna and S as the total number of genera within the fauna. Similar to Simpson's index, the Equitability index ranges from 0 to 1, with 0 indicating a fauna that is comprised of a single taxon and 1specifying a fauna with numerous taxa. This index centers on the relationship among the relative abundances of the taxa included in the sample, emphasizing species richness over evenness and lessening the influence of the most and least abundant taxa. The Equitability index can provide biased results with small sample sizes due to its dependence on species richness (Whittaker, 1972; Magurran, 2004).

3.3.6 Resampling with replacement

Resampling with replacement is a widely used non-parametric statistical method that provides estimates on the precision of a sample parameter (e.g., mean, median, variance) based on the repeated subsampling of the available data (Efron, 1979; Efron and Tibshirani, 1993; Simon 1997; Lunneborg, 2000; Good, 2005). The approach involves few assumptions, other than random sampling, and is less abstract than many conventional statistical methods (e.g., Simon and Bruce 1991; Simon, 1997; Lunneborg, 2000). In addition, although missing data and low count sizes can limit the interpretations, resampling with replacement has previously been shown to provide results comparable to those of more rigorous statistics (e.g., Simon and Bruce 1991; Mooney and Duval, 1993; Simon, 1997; Verhagen, 2007).

Here, following the methods of Holroyd and Hutchison (2002) and Strömberg (2009), I utilized resampling with replacement to help identify genera within latest Cretaceous assemblages that are more or less abundant than anticipated based on their presence and diversity from the Type Lance local fauna. This assemblage of fossils was chosen as the reference sample because of the large number of specimens recovered from the geographically closely spaced localities that comprise the local fauna and the high diversity of mammals. To begin the resampling procedure, I generated subsamples based on the taxa within the reference sample that were equal in size to the number of specimens recovered from each of the remaining ten latest Cretaceous assemblages. This procedure was repeated 1000 times to construct assemblage-specific abundance estimates of each taxon and to create standard 95% confidence intervals of the mean abundance. A taxon was considered more or less abundant, relative to its presence and abundance within the Type Lance local fauna, if the number of specimens recovered from the assemblage was either higher or lower than the upper or lower bounds of the confidence interval, respectively.

The analysis was performed using the statistical program R version 3.0.2 (R Development Core Team, 2015) (see Appendix 1).

3.4 Results

3.4.1 Conventional and Recalibrated Number of Identified Specimens

Owing to the differential detection probabilities of the mammals from the latest Cretaceous local faunas, disparities between the conventional number of identifiable specimen counts (Tables 3.1-3.4) and recalibrated counts (Table 3.6-3.9) are evident. In fact, as no genus within the study possesses a dentition in which each isolated element can be identified, all rNISP counts are larger than their corresponding NISP counts. Some of these differences are comparatively negligible (e.g., the abundance of the taeniodont *Schowalteria* within the Scollard local fauna, NISP = 1 and rNISP = 1.1) but many others are quite substantial (e.g., the abundance of *Alphadon* within the Hewett's Foresight local fauna, NISP = 481 versus rNISP = 808.1).

Aside from these differences, it is also notable that the detection probabilities are not randomly distributed. The detection probabilities among multituberculate and eutherian genera, in particular, are generally higher than those possessed by metatherian genera (Table 3.5). As a result, for any counts that do not incorporate this heterogeneity (i.e., NISPs), the relative abundance of metatherian genera will be depressed in comparison to these other mammalian genera (also see Holroyd et al. 2013).

3.4.2 Heterogeneity indices

Although slight differences exist between the two heterogeneity indices, a similar pattern is evident among the eleven latest Cretaceous mammalian faunas (Figures 3.2 and 3.3). Both indices indicate that the Long Fall horizon of southwestern

Saskatchewan and Lane's Little Jaw Site Quarry of southeastern Montana are among the most taxonomically rich and heterogeneous faunas from the latest Cretaceous of North America, with the Hell Creek local fauna of eastern Montana equally rich based on the Simpson's index (Figure 3.2) and only somewhat less even based on the Equitability index (Figure 3.3). According to both heterogeneity indices, the Type Lance local fauna of eastern Wyoming is slightly less diverse than these three local faunas. The Scollard local fauna of southcentral Alberta is slightly more diverse than the Type Lance local fauna based on the Simpson's index, but considerably less diverse than the Type Lance local fauna based on the Equitability index.

The Spigot-Bottle local fauna of southeastern Montana is similar in taxonomic evenness to the Scollard local fauna according to the Equitability index (Figure 3.3) but less taxonomically rich based on Simpson's index (Figure 3.2). Both heterogeneity indices indicate that diversity in Hewett's Foresight local fauna of northwestern Wyoming and the Gryde local fauna of southeastern Saskatchewan was comparatively low and, in fact, the Gryde local fauna ranks as the lowest among the eleven local faunas based on Equitability index. The 95% confidence intervals for the Muddy Tork local fauna of southeastern Montana and Hell Creek North Dakota local fauna from southeastern North Dakota are comparatively large, as a result of the small size of the samples, but both faunas are among the least diverse faunas.

3.4.3 Resampling with replacement

The resampling analyses reveal a number of differences between the Type Lance local fauna of northeastern Wyoming and the other latest Cretaceous assemblages from North America. Perhaps most notably, eutherian mammals are generally more abundant in northern assemblages from western Canada than expected based on their relative abundance within the Type Lance (Tables 3.10 and 3.13). In particular, *Cimolestes* is considerably more abundant within the Scollard local fauna from southcentral Alberta, and within the Wounded Knee and Gryde local faunas of southwestern Saskatchewan. *Gypsonictops* is also somewhat more abundant than expected within the Scollard local fauna, and *Batodon* is slightly more plentiful in the Scollard and Gryde than at the Type Lance. The occurrence and abundance of several eutherians unknown (e.g., *Mimatuta, Oxyprimus, Schowalteria*) or comparatively uncommon elsewhere (e.g., *Alostera*) in some of these northerly assemblages, including the Scollard, Wounded Knee, and Long Fall local faunas, provides further support for these results.

In addition to these findings, a number of marsupials are unusually rare in these northern assemblages (Table 3.12). In comparison to the Type Lance local fauna, *Pediomys*, *Protolambda*, ?*Leptalestes*, and *Didelphodon* are much less common in the Scollard local fauna and, as well as these taxa, *Alphadon*, *Protalphadon*, and *Leptalestes* are also rarer within the Gryde local fauna. Moreover, while the distributions beyond the confidence intervals are slight, a similar pattern is seen within the Wounded Knee local fauna and Long Fall horizon. In contrast to these rare marsupials, *Nortedelphys* is considerably more abundant within the Wounded Knee local fauna and, especially, the Gryde local fauna; *Alphadon* and *Leptalestes* are also notably more abundant in the Scollard local fauna. Although *Mesodma* is much more abundant in the Scollard and Gryde local faunas, most multituberculate genera are less common in western Canada, with *Meniscoessus*, *Cimolodon*, and *Cimolomys* particularly rare within these assemblages (Table 3.7).

The latest Cretaceous local faunas from Montana and North Dakota are also notably different from the Type Lance (Table 3.6). The well-studied Hell Creek local fauna from Garfield County of Montana contains several metatherians that are either considerably more abundant or much more rare than anticipated based on their abundance at the Type Lance local fauna (Table 3.8). Specifically, *Alphadon*, *Protalphadon*, *Turgidodon*, *Leptalestes*, and *Glasbius* are more common, whereas *Pediomys*, *Protolambda*, ?*Leptalestes*, and *Didelphodon* are substantially more rare. A similar pattern is also revealed by the multituberculates from the Hell Creek local fauna, with *Essonodon*, *Meniscoessus*, and, especially, *Mesodma* abundant, and *Cimolomys* and *Cimolodon* scarce (Table 3.7). *Batodon* and *Alostera* are the only eutherian mammals that are more abundant than expected based on their abundance within the Type Lance, and *Cimolestes* and, especially, *Gypsonictops* are more rare.

Within the Spigot-Bottle local fauna of southeastern Montana, *Batodon* is somewhat more abundant than anticipated, and the presence of *Paranyctoides* and *Protungulatum* are also notable differences; *Gypsonictops* is the only eutherian that is more rare (Table 3.9). Among the metatherians, *Albertatherium*, *Nortedelphys*, *Leptalestes*, *Alphadon*, and, especially, *Pediomys* are more common; *Hatchertherium*, *Nanocuris*, *Protalphodon*, and *Glasbius* are slightly less common and ?*Leptalestes*, *Protolambda*, and *Didelphodon* are considerably rarer. Many of the multituberculates within the assemblage are less common than expected, particularly *Meniscoessus*, *Cimolomys*, and *Cimolodon*, but *Mesodma* is substantially and *Essonodon* somewhat more abundant.

Although the samples from the Muddy Tork and North Dakota local fauna are relatively small, based on the resampling analyses, most mammals are less common than expected. In fact, the only mammal identified from these local faunas that is considerably more abundant than anticipated based on its abundance from the Type Lance is the multituberculate *Meniscoessus*, although *Protolambda* and *Didelphodon* within the Muddy Tork local fauna and *Batodon* and *Essonodon* from the North Dakota local fauna are slightly more abundant. The recently described fauna from Lane's Little Jaw Site is also comparatively small and many of the identified mammals are rarer than expected, including *Gypsonictops*, *Pediomys*, *Protolambda*, and *Cimolomys*. However, the presence and increased abundance of several eutherians (e.g., *Baioconodon*, *Palaeoungulatum*, and *Procerberus*) and *Meniscoessus* are also documented from Lane's Little Jaw Site (Kelly, 2014) (Table 3.9).

The composition of mammals within the Hewett's Foresight local fauna from the Lance Formation of Wyoming is markedly different from that within the Type Lance local fauna (Table 3.6). For instance, all three of the eutherians identified from the assemblage are less common than expected, with *Gypsonictops* and *Cimolestes* notably rare (Table 3.9). Most of the metatherians are also scarce, particularly *Pediomys*, *Protolambda*, ?*Leptalestes*, and *Didelphodon*; however, *Alphadon* and, to a much lesser extent, *Leptalestes* are more abundant (Table 3.8). Similarly, many of the multituberculates (e.g., *Cimolomys*, *Meniscoessus*, and *Cimolodon*) are less common, but *Mesodma* is considerably more abundant (Table 3.7)

3.5 Discussion

3.5.1 Faunal composition of latest Cretaceous mammalian assemblages

The present analyses reveal several interesting features of the composition of latest Cretaceous mammalian assemblages across North America. First, the findings indicate that the faunal structure of the eleven latest Cretaceous assemblages is not uniform. Rather, based on the results of both heterogeneity indices, the Long Fall horizon, Hell Creek of Montana, and Lane's Little Jaw Site local faunas are more diverse than the other local faunas (Figures 3.2 and 3.3). Values for the Scollard, Type Lance, and several other local faunas, including those from the Spigot-Bottle and Wounded Knee assemblages, are slightly lower than those of the Long Fall horizon, Hell Creek of Montana, and Lane's Little Jaw Site. In contrast to these faunas, the Gryde and Muddy Tork local faunas, as well as the Hell Creek local fauna of North Dakota are generally less diverse.

In addition to detecting differences among these latest Cretaceous faunal assemblages, mammalian genera that contributed to the compositional heterogeneity among these faunas were identified, using resampling methods and the well-studied Type Lance local fauna as a reference sample. The results of these analyses principally suggest that some of the more northerly assemblages, including the Scollard and Long Fall horizon local faunas, contain a higher abundance of eutherians than expected based on their occurrence and relative abundance within the Type Lance local fauna (Table 3.9). In particular, several archaic "ungulates", including *Protungulatum, Mimatuta* and *Baioconodon*, and the leptictid *Procerberus* are more abundant within the Long Fall horizon. Within the Scollard local fauna, *Gypsonictops* and *Batodon* are somewhat more abundant and *Cimolestes* is considerably more abundant, and the presence of *Alostera* and *Schowalteria* are also notable within the assemblage (Table 3.13). *Cimolestes* is also slightly more abundant than expected in the Wounded Knee and Gryde local faunas. Moreover, both multituberculate and metatherian mammals are less common within these more northerly localities (Tables 3.10-3.12).

Aside from these more northern assemblages, eutherians are also comparatively more abundant within Lane's Little Jaw Site, particularly given the small number of identified specimens recovered from the site (Table 3.12). Similar to the Long Fall horizon local fauna, the presence and abundance of *Procerberus* and several archaic "ungulates" is especially notable, with *Baioconodon* and the newly recognized *Palaeoungulatum* reported from the local fauna (Table 3.11). As previously noted, along with Long Fall horizon and Spigot Bottle, Lane's Little Jaw Site has been suggested to represent an extension of the Puercan Land Mammal Age into the Cretaceous. Although eutherians are not noticeably more abundant within Spigot-Bottle, these "transitional" assemblages are markedly different from the Type Lance.

Differences between the Type Lance and assemblages from northern Wyoming and Montana are also present. A number of multituberculates and metatherians are substantially less abundant (e.g., *Pediomys*, *Didelphodon*, *Cimolomys*) or more abundant (e.g., *Alphadon*, *Mesodma*) within the Hell Creek local fauna (Tables 3.11 and 3.12). Similarly, within the Hewett's Foresight local fauna, many multituberculates and metatherians are considerably less common than anticipated (e.g., *Pediomys*, *Cimolomys*, *Meniscoessus*) but some are more abundant, particularly *Alphadon* and

Mesodma. At both of these sites, however, few eutherian mammals are more abundant relative to their abundance within the Type Lance local fauna (Table 3.13).

In contrast to these findings, Archibald and Hunter (2002, p. 211), using correspondence analyses and a series of Mantel tests to examine community structure among latest Cretaceous mammalian faunas, reported that these faunas were "extremely similar in composition and do not vary greatly with distance". Yet, aside from the obvious differences between statistical approaches, these authors evaluated species occurrences and Number of Identified Specimens (NISPs), rather than information on genera and recalibrated NISP counts. Moreover, because of the uncertainty with the age of the assemblage, Hunter and Archibald (2002) excluded the Long Fall horizon, one of the only "transitional" latest Cretaceous assemblages recognized at the time. With the identification of taxonomic detection biases (see discussion above) and the recovery of additional latest Cretaceous assemblages with mammals more typical of the Puercan (e.g., Spigot-Bottle, Lane's Little Jaw Site), it seems reasonable to include these data here in comparisons among latest Cretaceous faunas.

3.5.2 Mammalian faunal dynamics during the latest Cretaceous

Taken together, these analyses demonstrate that the taxonomic richness and evenness among latest Cretaceous North American mammalian faunas were not homogeneous and that important changes in the composition of these faunal assemblages were well underway during this time. Lillegraven (1969), Johnston and Fox (1984), Fox (1989; 1997), Clemens (2002, 2010), and Wilson (2005; 2013; 2014;

Wilson et al. 2012) previously noted similar differences among latest Cretaceous assemblages. Wilson (2014; also see Sprain et al. 2014) recently suggested that changes in the taxonomic richness and evenness of latest Cretaceous mammalian faunas from northeastern Montana could have been the outcome of environmental disturbances and, more broadly, part of the press-pulse extinction scenario presented by Arens and West (2008; and see Bender et al. 1984 and Arens et al. 2014). The press-pulse scenario suggests that environmental stresses (i.e., the press disturbances) burden organisms that are struggling to adapt and, in close succession with instantaneous events (i.e., the pulse disturbances), can cause immediate mass extinctions. Within the Western Interior of North America, the Late Maastrichtian Event (i.e., a brief warming event thought to be closely associated with the Deccan flood basalt eruptions [see, e.g., Li and Keller 1998a, 1998b; Keller, 2001; Wilf et al., 2003, Nordt et al., 2003; Tobin et al., 2012]) and the regression of the Western Interior epicontinental seaway would have contributed to faunal instability in latest Cretaceous faunal assemblages from Montana (Wilson, 2014; Sprain et al., 2014). These changes, in combination with the bolide impact at the Cretaceous/Paleogene boundary, (representing the pulse disturbance) ultimately resulted in the heightened levels of extinction. Following these destructive aspects of the extinction event, episodes of rapid taxonomic and morphological diversification of some surviving mammalian lineages and new immigrants to northeastern Montana occurred.

The press disturbances identified by Wilson (2014) to be acting on mammals from northeastern Montana also likely influenced mammals elsewhere in North America during the latest Cretaceous and facilitated changes among other local mammalian faunas. However, as revealed here, the effects of these events on assemblages outside of northeastern Montana appear to have been somewhat different. As noted by Arens et al. (2014), press disturbances that might be harmful or even deleterious for some organisms can be beneficial for others. Within the Scollard, Long Fall, Spigot-Bottle, and Lane's Little Jaw Site local faunas, faunal instability caused by the climate change and the regression of the epicontinental seaway appears to have provided the opportunity for the expansion of eutherian mammals (Table 3.13). The possibility of temporal differences among these latest Cretaceous assemblages obviously complicates this scenario (e.g., latest Cretaceous Puercan assemblages could be stratigraphically younger than more conventionally labeled Lancian assemblages [see discussion above]); however, regardless of the biochronologic age assignments, changes within these faunas occurred during the latest Cretaceous, prior to the bolide impact and the demise of dinosaurs. These conclusions not only underscore the complexity among latest Cretaceous local mammalian faunas but also support suggestions of a more gradual, stepwise reduction in the number of groups during the latest Cretaceous mass extinction (e.g., Clemens et al., 1981; Archibald and Clemens, 1982; Archibald et al., 2010; Wilson, 2005, 2014), rather than a single catastrophic event (e.g., Alvarez et al., 1980; Schulte et al., 2010).

3.5.3 Biogeographic differences among faunal assemblages

As noted earlier, Lillegraven (1969) previously reported the greater relative abundance and diversity of Paleocene-like eutherians in latest Cretaceous faunas at higher latitudes, in relation to approximately contemporaneous faunas further south.

This idea was further supported by several recent studies, including the description of a new taeniodont from the Scollard local fauna of southcentral Alberta that extended the stratigraphic range of this eutherian lineage from the middle Puercan of the San Juan Basin, New Mexico to the Lancian (Fox and Naylor 2003). The presence of eutherians in these northern assemblages led Sloan (1969) and Russell (1975) to contend that during the Late Cretaceous there was an invasion of North America by eutherian immigrants from Asia (see Beard, 1998 for a more thorough review).

The role of immigration in latest Cretaceous and early Paleocene assemblages in northeastern Montana was examined in detail by Weil and Clemens (1998; also see Weil 1999, and Clemens 2002, 2010). In their analyses, the authors recognized three categories of mammals residing in the geographic study area: residents, aliens and unknowns (Weil and Clemens 1998; Clemens 2002). Clemens' (2002) summary of these studies revealed that the Lancian mammalian faunas in northeastern Montana were composed of a great majority of resident taxa, species, or closely related sister species, which were present in one or more local faunas of the preceding North American interval. In comparison, the earliest Puercan local faunas were dominated by alien species, those whose ancestors did not precede them in the study area. Wilson (2014) similarly noted the influence of immigration during the earliest Paleocene in northeastern Montana.

The three "transitional" assemblages included in this analysis, including the Long Fall horizon, Lane's Small Jaw Site, and Spigot-Bottle, indicate that some mammals, especially eutherians, were already present and comparatively diverse in North America during the latest Cretaceous. The sudden appearance of these groups in the earliest Paleocene of Montana suggests that these local mammalian faunas might have been the product of dispersal from these other regions after the K/Pg boundary. These findings provide some support to the ideas of Fox (1968, 2005), Weil (1999), Weil and Krause (2008), and Clemens (2010) that early Paleocene immigrants in North America were not derived from Late Cretaceous Asian mammals but were likely descendants from mammals that lived in currently unsampled environments in the Western Interior of North America prior to the K/Pg boundary.

3.5.4 Ordinal Origins

A number of recent studies on the evolution of mammals during the Late Cretaceous and Paleocene have focused on the timing of differentiation of the major inter- and intraordinal clades of eutherians (e.g., Alroy, 1999; Kumar and Hedges, 1998; Springer et al., 2003; Meredith et al., 2011; dos Reis et al., 2012, 2014; O'Leary et al., 2013). From these studies, three competing models, mainly distinguished by the proposed timing of these radiation events in regards to the K/Pg boundary, have emerged: (1) explosive, (2) long fuse, and (3) short fuse models (see Archibald and Deutschman, 2001 for a review). The explosive model suggests that all interordinal origination and intraordinal divergence occurred within the earliest Paleogene (e.g., Alroy, 1999; Foote et al., 1999; Wible et al., 2007; O'Leary et al., 2013). The long fuse model postulates interordinal divergence early in the Late Cretaceous followed by intraordinal diversification in the earliest Paleogene (e.g., Springer et al., 2003; Meredith et al., 2011). The short fuse model contends that all interordinal and some intraordinal differentiation occurred in the early Cretaceous (Kumar and Hedges, 1998).

Although some studies show limited support for the short fuse model (e.g., Bininda-Emonds et al., 2007), several compelling studies (e.g., Foote et al., 1999) have shown that such an early origination and diversification is unlikely, and the short fuse model is not discussed further here.

The fossil record, providing the only direct evidence of the occurrence of mammalian lineages in the past, has conventionally supported the explosive model (e.g., Alroy, 1999). The recent broad-scale phylogenetic analyses by Wible et al. (2007) and O'Leary et al. (2013) that incorporated morphological characters demonstrate that all fossil mammals recovered from Cretaceous sediments (some previously recognized as member of extant groups) fall outside of the living eutherian orders and further seem to corroborate this view. With the emergence of comprehensive molecular-based studies (e.g., Springer et al., 2003; Bininda-Emonds et al., 2007; Meredith et al. 2011), it has been argued that consensus currently favors the long fuse model. The recent recognition of several crown-group eutherians in the earliest Paleocene, including the oldest known members of Carnivora (Fox et al., 2010) and Primates (Fox and Scott, 2011) in the western Canadian fossil record, also seems to suggests that some interordinal origination occurred in the Cretaceous.

Although the relationships between many latest Cretaceous and early Paleogene eutherians and those living today are still controversial (e.g., Wible et al., 2007; Boyer et al., 2010), support for the presence and diversity of eutherian groups in the latest Cretaceous has implications for the evolutionary history of the group. It is increasingly clear, based on my present findings, that some eutherians, particularly "archaic" ungulates, were undergoing a radiation prior to the K/Pg boundary. In addition, the diversity of eutherians before and after the boundary may have been more similar than the fossil record currently indicates.

3.6 Conclusions

The timing and patterns of latest Cretaceous and early Paleogene mammalian evolution have become an important focus of study as a consequence of recent interest in extinctions at the end of the Mesozoic (Archibald, 1996; Hunter and Archibald, 2002; Wilson 2005, 2014). In the Western Interior of North America, the richest and most extensively studied succession of latest Cretaceous mammals in the world is preserved from Texas to northern Alaska (Cifelli et al., 2004). Yet, as documented here, a considerable number of differences are present among latest Cretaceous assemblages. Most notably, eutherian mammals are more diverse in some of the more northerly latest Cretaceous assemblages, including several “transitional” localities that are often recognized as containing evidence of the replacement of archaic mammals by more progressive (i.e., eutherian) mammals (e.g., Fox, 1989).

These findings suggest that some eutherians, especially primitive ungulates, originated and underwent some diversification and expansion during the latest Cretaceous, prior to the demise of the non-avian dinosaurs and more primitive multituberculates and metatherians. Environmental changes (i.e., the Late Maasstrichtian Event and the regression of the Western Interior epicontinental seaway) could have facilitated these changes and provided the opportunity for the expansion of eutherian mammals within these assemblages. In addition, as revealed here, taxa from some of these latest Cretaceous “transitional” assemblages may have been the source for mammalian immigrants into localities within the Hell Creek Formation of northeastern Montana during the earliest Paleocene (Clemens, 2002, 2010).

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Table 3.1.—The number of identifiable specimens for higher-level mammalian groups among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Multitubeculata	253	22	40	511	885	27	662	22	45	1049	74
Metatheria	111	52	4	366	688	15	372	11	2	738	597
Eutheria	289	26	28	149	154	0	140	19	3	480	480
TOTAL	653	100	72	1026	1727	42	1174	52	50	2267	1151

Table 3.2.—The number of identifiable specimens for multitubericulate genera among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Cimexomys	0	0	4	0	0	0	0	0	0	7	7
Catopsalis	0	0	11	0	0	0	0	0	0	0	0
Paracimexomys	9	2	0	1	27	0	0	0	0	0	0
Essonodon	0	1	0	0	24	0	6	0	11	1	0
Cimolomys	10	0	2	18	36	0	13	0	0	89	24
Meniscoessus	0	2	1	2	175	24	87	8	29	186	11
Paressondon	0	0	0	0	1	0	0	0	0	0	0
Stygimys	0	0	11	0	0	0	0	0	0	0	0
Clemensodon	0	0	0	0	0	0	0	0	0	3	0

Mesodma	168	14	8	482	477	3	529	6	2	313	407
?Neoplagiaulax	0	0	0	0	15	0	0	0	0	0	2
Parectypodus	0	0	0	4	2	0	0	0	0	0	0
Cimolodon	66	3	3	4	128	0	27	8	3	450	29

Table 3.3. —The number of identifiable specimens for metatherian genera among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Nortedelphys	1	0	0	0	0	0	10	0	0	3	0
Hatcheritherium	0	0	0	0	0	0	0	0	0	1	0
Nanocuris	1	0	0	1	0	0	0	0	0	1	0
Albertatherium	0	0	0	0	0	0	4	0	0	0	0
Alphadon	53	47	2	309	203	0	34	0	0	28	481
Protalphadon	0	0	0	0	39	0	6	0	0	19	14
Turgidodon	8	0	0	17	44	1	17	1	0	14	5
Pediomys	9	3	2	30	57	2	161	1	0	152	45
Protolambda	2	0	0	6	90	5	47	2	2	152	6

Leptalestes	0	0	0	0	51	0	40	2	0	130	16
?Leptalestes	26	0	0	0	49	1	27	0	0	26	25
Didelphodon	11	1	0	3	73	6	21	4	0	196	4
Glasbius	0	1	0	0	82	0	5	1	0	16	1

Table 3.4.—The number of identifiable specimens for eutherian genera among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Alostera	1	3	0	1	1	0	0	0	0	0	0
Baioconodon	0	0	3	0	0	0	0	8	0	0	0
Protungulatum	0	0	11	0	0	0	1	0	0	0	0
Mimatuta	0	0	4	0	0	0	0	0	0	0	0
Paleoungulatum	0	0	0	0	0	0	0	8	0	0	0
Oxyprimus	0	0	1	0	0	0	0	0	0	0	0
Gypsonictops	110	15	5	102	106	0	102	0	1	314	63
Batodon	9	0	0	7	10	0	4	0	1	1	0
Cimolestes	168	8	2	39	37	0	31	1	1	52	11

Procerberus	0	0	2	0	0	0	0	2	0	0	0
Paranyctoides	0	0	0	0	0	0	2	0	0	0	0
Schowalteria	1	0	0	0	0	0	0	0	0	0	0

Table 3.5.—Detection probabilities for mammalian genera from select latest Cretaceous local faunas across the Western Interior of North America.

Higher-level taxonomic group	Family	Genus	Identifiable tooth positions	Identifiable teeth/Total number of teeth	Detection probability	"Recalibration factor"
Multituberculata	Incertae sedis	*Cimexomys*	I1.P4.M1-2/p4.m1-2	12/26	0.46153846	1.53846154
		Catopsalis	I1.P4.M1-2/i1.p4.m1-2	16/26	0.61538462	1.38461538
		Paracimexomys	I1.P4.M1-2/p4.m1-2	12/26	0.46153846	1.53846154
	Cimolomyidae	*Essonodon*	P4.M1-	10/26	0.38461538	1.61538462

		2/m1-2			
	Cimolomys	I1.P4.M1-2/i1.p4.m1-2	16/26	0.61538462	1.38461538
	Meniscoessus	I1.P4.M1-2/i1.p4.m1-2	16/26	0.61538462	1.38461538
	Paressonodon	M1-2	2/26	0.07692308	1.92307692
Eucosmodontidae	*Stygimys*	I1.P4.M1-2/i1.p4.m1-2	16/24	0.66666667	1.33333333
?Eucosmodontidae	*Clemensodon*	p4	2/24	0.08333333	1.91666667
Neoplagiaulacidae	*Mesodma*	P4.M1-2/p4.m1-2	12/26	0.46153846	1.53846154
	?Neoplagiaulax	P4.M1-	12/26	0.46153846	1.53846154

			2/p4.m1-2			
		Parectypodus	P4.M1-2/p4.m1-2	12/26	0.46153846	1.53846154
	Cimolodontiae	*Cimolodon*	I1.P4.M1-2/i1.p4.m1-2	16/26	0.61538462	1.38461538
Metatheria	Incertae sedis	*Nortedelphys*	M1-4/m1-4	16/50	0.32	1.68
		Hatcheritherium	M1	2/50	0.04	1.96
	Deltatherididae	*Nanocuris*	M2/m1-4	10/50	0.20	1.80
	“Alphadontidae”	*Albertatherium*	M1-4/m1-4	16/50	0.32	1.68
		Alphadon	M1-4/m1-4	16/50	0.32	1.68
		Protalphadon	M1-4/m1-4	16/50	0.32	1.68
		Turgidodon	P3.M1-4/p3.m1-4	20/50	0.40	1.60
	Pediomyidae	*Pediomys*	M1-4/m1-4	16/50	0.32	1.68

		Protolambda	P3.M1-4/p3.m1-4	20/50	0.40	1.60
		Leptalestes	M1-4/m1-4	16/50	0.32	1.68
		?Leptalestes	M1-4/m1-4	16/50	0.32	1.68
	Stagodontidae	*Didelphodon*	C.P1-3.M1-4/c.p1-3.m1-4	32/50	0.64	1.36
	Glasbiidae	*Glasbius*	M1-4/m1-4	16/50	0.32	1.68
Eutheria	Incertae sedis	*Alostera*	M1-2/m1	6/44	0.13636364	1.86363636
	“Arctocyonidae”	*Baioconodon*	P3-4.M1-3/p3-4.m1-3	20/44	0.45454545	1.54545454
		Protungulatum	P3-4.M1-3/p3-4.m1-	20/44	0.45454545	1.54545454

		3			
Periptychidae	*Mimatuta*	P3-4.M1-3/p3-4.m1-3	20/44	0.45454545	1.54545454
	Paleoungulatum	M2/p3-4.m1-3	12/44	0.27272727	1.72727273
?Hyopsodontidae	*Oxyprimus*	P3-4.M1-3/p3-4.m1-3	20/44	0.45454545	1.54545454
Gypsonictopsidae	*Gypsonictops*	P3-4.M1-3/p3-4.m1-3	20/44	0.45454545	1.54545454
Cimolestidae	*Batodon*	P4.M1-3/p3-4.m1-3	18/44	0.40909091	1.59090909

	Cimolestes	P3-4.M1-3/p3-4.m1-3	20/44	0.45454545	1.54545454
	Procerberus	P3-4.M1-3/p3-4.m1-3	20/44	0.45454545	1.54545454
?Nyctitheriidae	*Paranyctoides*	P4.M1-3/p4.m1-3	16/44	0.36363636	1.63636364
Stylinodontidae	*Schowalteria*	I2-3.C.P1-4.M1-3/i2-3.c.p1-4.m1-3	40/44	0.90909091	1.09090909

Table 3.6.—The recalibrated number of identifiable specimens for higher-level mammalian groups among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Multitubeculata	377.5	33.7	57.0	783.1	1363.3	44.9	1025.1	29.6	73.7	1558.6	731.9
Metatheria	181.8	87.0	6.7	611.3	1119.4	22.7	613.2	16.7	3.2	1163.5	1000.5
Eutheria	445.7	41.1	43.3	230.6	238.5	0	216.5	33.7	4.7	566.9	114.3
TOTAL	1005.0	161.8	107.0	1625.0	2721.2	67.6	1854.8	80.0	81.6	3289.0	1846.7

Table 3.7.—The recalibrated number of identifiable specimens for multituberculate genera among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Cimexomys	0	0	6.2	0	0	0	0	0	0	10.8	10.8
Catopsalis	0	0	15.2	0	0	0	0	0	0	0	0
Paracimexomys	13.8	3.1	0	1.5	41.5	0	0	0	0	0	0
Essonodon	0	1.6	0	0	38.8	0	9.7	0	17.8	1.6	0
Cimolomys	13.8	0	2.8	24.9	49.8	0	18.0	0	0	123.2	33.2
Meniscoessus	0	3.4	1.7	3.4	294.0	40.3	146.2	13.4	48.7	312.5	18.5
Paressondon	0	0	0	0	1.9	0	0	0	0	0	0
Stygimys	0	0	14.7	0	0	0	0	0	0	0	0
Clemensodon	0	0	0	0	0	0	0	0	0	5.8	0

Mesodma	258.5	21.5	12.3	741.5	733.8	4.6	813.8	9.2	3.1	481.5	626.2
?Neoplagiaulax	0	0	0	0	23.1	0	0	0	0	0	3.1
Parectypodus	0	0	0	6.2	3.1	0	0	0	0	0	0
Cimolodon	91.3	4.2	4.2	5.5	177.2	0	37.4	11.1	4.2	623.1	40.2

Table 3.8.—The recalibrated number of identifiable specimens for metatherian genera among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Nortedelphys	1.68	0	0	0	0	0	16.8	0	0	5.0	0
Hatcheritherium	0	0	0	0	0	0	0	0	0	2.0	0
Nanocuris	1.8	0	0	1.8	0	0	0	0	0	1.8	0
Albertatherium	0	0	0	0	0	0	7.7	0	0	0	0
Alphadon	89.0	79.0	3.4	519.1	341.0	0	57.1	0	0	47.0	808.1
Protalphadon	0	0	0	0	65.5	0	10.1	0	0	31.9	23.5
Turgidodon	12.4	0	0	26.3	68.0	1.5	26.3	1.5	0	21.6	7.7
Pediomys	15.1	5.0	3.4	50.4	95.8	3.4	270.5	1.5	0	255.4	75.6
Protolambda	3.2	0	0	9.6	144.0	8.0	75.2	3.1	3.2	243.2	9.6

Leptalestes	0	0	0	0	85.7	0	67.2	3.4	0	218.4	26.9
?Leptalestes	43.7	0	0	0	82.3	1.7	45.4	0	0	43.7	42.0
Didelphodon	15.0	1.4	0	4.1	99.3	8.2	28.6	5.4	0	266.6	5.4
Glasbius	0	1.7	0	0	137.8	0	8.4	1.7	0	26.9	1.7

Table 3.9.—The recalibrated number of identifiable specimens for eutherian genera among select latest Cretaceous local faunas from the Western Interior of North America. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight; TPL = Type Lance.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	TPL	HWF
Alostera	1.9	5.6	0	1.9	1.9	0	0	0	0	0	0
Baioconodon	0	0	4.6	0	0	0	0	12.4	0	0	0
Protungulatum	0	0	17.0	0	0	0	1.5	0	0	0	0
Mimatuta	0	0	6.2	0	0	0	0	0	0	0	0
Paleoungulatum	0	0	0	0	0	0	0	12.3	0	0	0
Oxyprimus	0	0	1.5	0	0	0	0	0	0	0	0
Gypsonictops	170.0	23.2	7.7	157.6	163.8	0	157.6	0	1.5	485.3	97.4
Batodon	14.3	0	0	11.1	15.9	0	6.4	0	1.6	1.6	0
Cimolestes	258.5	12.3	3.1	60.0	56.9	0	47.7	1.5	1.5	80	16.9

Procerberus	0	0	3.2	0	0	0	0	3.4	0	0	0
Paranyctoides	0	0	0	0	0	0	3.3	0	0	0	0
Schowalteria	1.1	0	0	0	0	0	0	0	0	0	0

Table 3.10.—Differences in the relative abundance of higher-level groupings among select latest Cretaceous fauna local faunas from the Western Interior of North America, using resampling with replacement, and the presence and relative abundance of mammals from the Type Lance local fauna of Wyoming as the reference sample. Groups that are significantly more abundant than expected, represented by the number of specimens beyond the upper threshold of the confidence interval, are shown with positive values; whereas, groups that are significantly less abundant than expected, represented by the number of specimens beyond the lower threshold of the confidence interval, are shown with negative values. Recalibrated numbers of identified specimens were employed. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	HWF
Multitubeculata	-82.0	-29.1	17.2	30.0	73.8	18.6	163.7	2.3	40.5	-126.9
Metatheria	-149.4	47.2	-16.9	77.2	173.1	-1.0	-31.3	-3.1	-11.2	374.3
Eutheria	258.2	11.1	26.3	-45.0	-222.4	-7.1	-97.3	18.8	-6.4	-190.3

Table 3.11.—Differences in the relative abundance of multituberculate genera among select latest Cretaceous fauna local faunas from the Western Interior of North America, using resampling with replacement, and the presence and relative abundance of multituberculates from the Type Lance local fauna of Wyoming as the reference sample. Genera that are significantly more abundant than expected, represented by the number of specimens beyond the upper threshold of the confidence interval, are shown with positive values; whereas, genera that are significantly less abundant than expected, represented by the number of specimens beyond the lower threshold of the confidence interval, are shown with negative values. Recalibrated numbers of identified specimens were employed. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	HWF
Cimexomys	-1.6	0	5.1	-3.3	-7.0	0	-4.0	0	0	2.7
Catopsalis	0	0	15	0	0	0	0	0	0	0
Paracimexomys	13.0	3.0	0	1.0	41.0	0	0	0	0	0
Essonodon	0	0.7	0	-0.006	36.8	0	7.9	0	16.8	-0.1

Cimolomys	-19.3	-3.6	0	-31.0	-48.6	-0.9	-46.1	-1.1	-1.2	-30.9
Meniscoessus	-87.6	-8.4	-5.7	-142.7	29.9	31.5	-21.3	3.3	37.9	-148.5
Paressondon	0	0	0	0	1	0	0	0	0	0
Stygimys	0	0	14	0	0	0	0	0	0	0
Clemensodon	-0.5	0	0	-1.4	-3.3	0	-1.7	0	0	-1.7
Mesodma	102.7	0	0	493.7	328.1	-2.7	532.3	0	-5.1	345.8
?Neoplagiaulax	0	0	0	0	23.0	0	0	0	0	3.0
Parectypodus	0	0	0	6.0	3.0	0	0	0	0	0
Cimolodon	-89.0	-21.0	-11.3	-291.3	-330.0	-9.2	-302.4	0	-7.5	-298.4

Table 3.12.—Differences in the relative abundance of metatherian genera among select latest Cretaceous fauna local faunas from the Western Interior of North America, using resampling with replacement, and the presence and relative abundance of metatherians from the Type Lance local fauna of Wyoming as the reference sample. Genera that are significantly more abundant than expected, represented by the number of specimens beyond the upper threshold of the confidence interval, are shown with positive values; whereas, genera that are significantly less abundant than expected, represented by the number of specimens beyond the lower threshold of the confidence interval, are shown with negative values. Recalibrated numbers of identified specimens were employed. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	HWF
Nortedelphys	0	77.3	0	515.5	-3.3	0	12.1	0	0	-1.7
Hatcheritherium	0	0	0	0	-0.5	0	-0.1	0	0	-0.1
Nanocuris	0.2	0	0	0.002	-0.5	0	-0.04	0	0	-0.05
Albertatherium	0	0	0	0	0	0	7	0	0	0

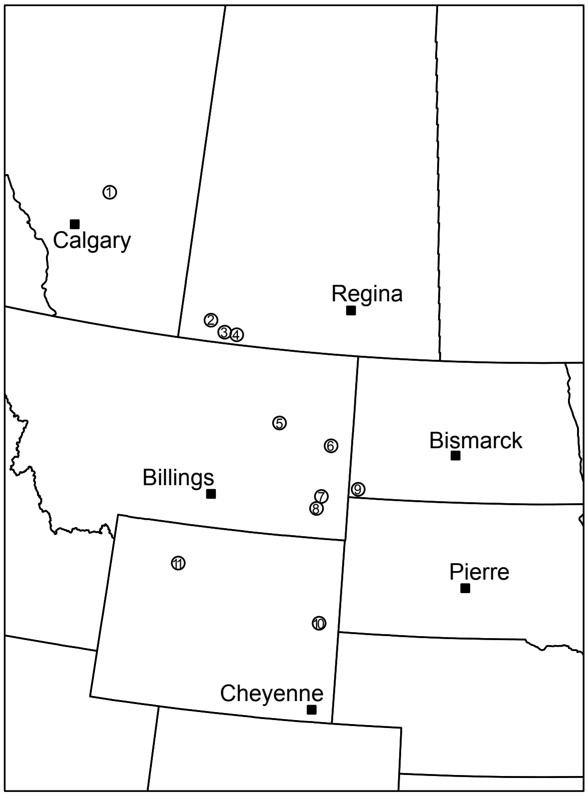
Alphadon	71.4	-0.8	0.5	-19.9	299.6	0	27.0	0	-0.1	778.2
Protalphadon	-6.8	-0.2	-0.002	-12.5	37.3	0	-4.8	0	0	2.8
Turgidodon	3.7	-0.01	0	13.5	48.9	0	11.8	0	0	-2.7
Pediomys	-55.7	-3.9	-2.2	-67.6	-110.0	0	119.0	-2.5	-3.8	-60.2
Protolambda	-64.3	-8.4	-4.8	-103.8	-51.4	1.1	-55.1	-0.4	-0.5	-120.1
Leptalestes	-59.7	-7.5	-4.3	-100.9	-90.0	-2.4	-48.5	0	-3.0	-89.3
?Leptalestes	27.0	-0.7	-0.2	-18.0	44.2	0	17.6	0	-0.1	14.9
Didelphodon	-59.4	-8.5	-5.3	-119.4	-115.3	0.4	-113.9	0	-4.0	-136.3
Glasbius	-5.5	0	0	-10.2	113.6	0	-4.0	0	0	-11.1

Table 3.13.—Differences in the relative abundance of eutherian genera among select latest Cretaceous fauna local faunas from the Western Interior of North America, using resampling with replacement, and the presence and relative abundance of eutherian from the Type Lance local fauna of Wyoming as the reference sample. Genera that are significantly more abundant than expected, represented by the number of specimens beyond the upper threshold of the confidence interval, are shown with positive values; whereas, genera that are significantly less abundant than expected, represented by the number of specimens beyond the lower threshold of the confidence interval, are shown with negative values. Recalibrated numbers of identified specimens were employed. Localities abbreviations are as follows: SCL = Scollard; LFL = Long Fall; WKN = Wounded Knee; GRD = Gryde; HCM= Hell Creek Montana; MDT = Muddy Tork; HCND = Hell Creek North Dakota; SBT = Spigot Bottle; LLJS = Lane's Little Jaw Site; HWF = Hewett's Foresight.

	SCL	WKN	LFL	GRD	HCM	MDT	SBT	LLJS	HCND	HWF
Alostera	1.0	5.0	0	1.0	1.0	0	0	0	0	0
Baioconodon	0	0	4.0	0	0	0	0	12.0	0	0
Protungulatum	0	0	17.0	0	0	0	1.5	0	0	0
Mimatuta	0	0	6.0	0	0	0	0	0	0	0

Paleoungulatum	0	0	0	0	0	0	0	12.0	0	0
Oxyprimus	0	0	1.0	0	0	0	0	0	0	0
Gypsonictops	13.5	0	-4.5	-72.7	-230.1	-6.8	-106.5	-8.0	-7.5	-164.6
Batodon	13.2	0	0	10.0	13.8	0	4.9	0	0.8	-0.04
Cimolestes	229.5	6.6	0	16.0	-6.9	-0.4	0	0	0	-24.7
Procerberus	0	0	3.0	0	0	0	0	3.0	0	0
Paranyctoides	0	0	0	0	0	0	3.0	0	0	0
Schowalteria	1.0	0	0	0	0	0	0	0	0	0

Figure 3.1.—Outline map of the Western Interior of North America with location of fossil assemblages yielding latest Cretaceous mammals. Comparative local faunas, with respective sources of faunal data are: (1) Scollard (Lillegraven, 1969; Lillegraven and McKenna, 1986; Fox, 1989, 1994, 1997; Fox and Naylor, 2003), (2) Gryde (Storer, 1991), (3) Wounded Knee (Fox, 1989, 1997), (4) Long Fall horizon (Johnston and Fox 1984; Fox, 1989; Fox, 1997), (5) Hell Creek of Montana (Archibald, 1982; Lillegraven and McKenna, 1986; Johansen, 1996; Wilson, 2005, 2014), (6) Lane's Little Jaw Site (Kelly, 2014), (7) Muddy Tork (Hunter et al. 1997; Hunter, 1999; Hunter and Archibald, 2002), (8) Spigot Bottle (Hunter and Archibald, 2002; Zhang 2009; Archibald et al., 2011), (9) Hell Creek of North Dakota (Hunter and Pearson, 1996; Hunter and Archibald, 2002), (10) Type Lance (Clemens, 1964, 1966, 1973; Krause, 1992; Case et al., 2005; Wilson and Riedel, 2010), and (11) Hewett's Foresight (Webb, 2001).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Bismarck
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Pierre
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Cheyenne

Figure 3.2.—Simpson’s Index and 95% confidence intervals for latest Cretaceous local mammalian faunas from the Western Interior of North America. Locality abbreviations are as follows: SC = Scollard; LF = Long Fall; WK = Wounded Knee; GR = Gryde; HC = Hell Creek Montana; MT = Muddy Tork; ND = Hell Creek North Dakota; SB = Spigot Bottle; LLJ = Lane’s Little Jaw Site; HF = Hewett’s Foresight; TL = Type Lance.

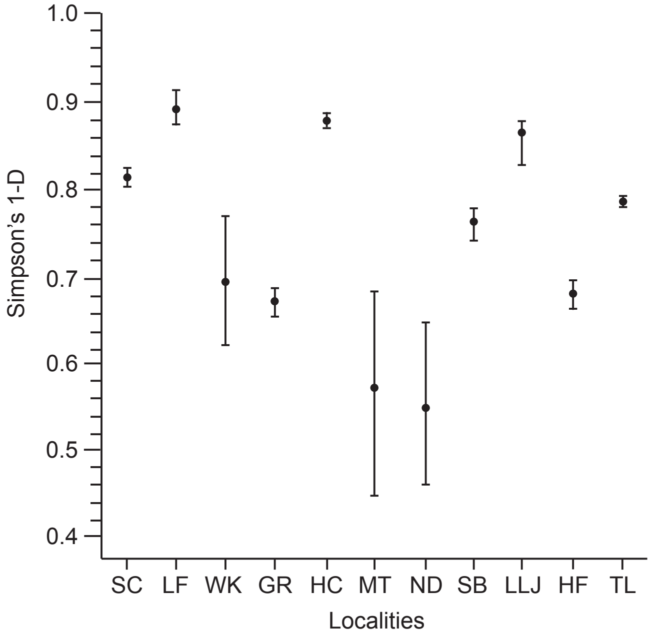
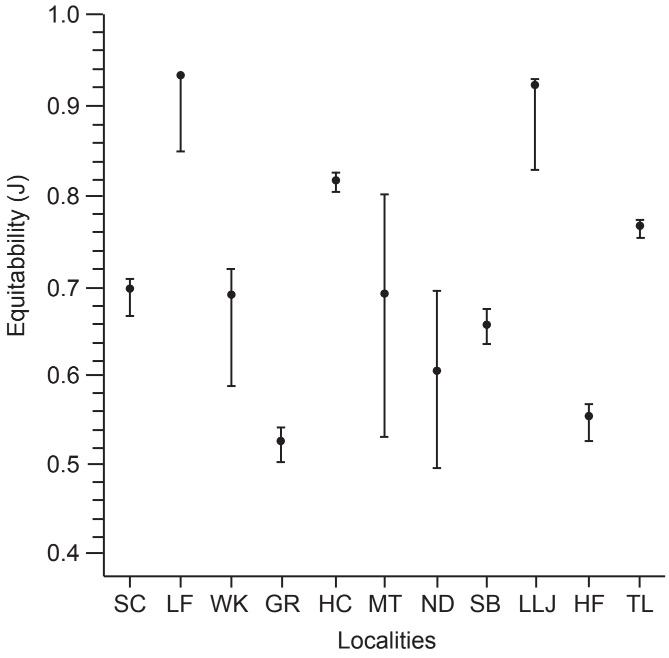


Figure 3.3. —Equitability Index and 95% confidence intervals for latest Cretaceous local mammalian faunas from the Western Interior of North America. Locality abbreviations are as follows: SC = Scollard; LF = Long Fall; WK = Wounded Knee; GR = Gryde; HC = Hell Creek Montana; MT = Muddy Tork; ND = Hell Creek North Dakota; SB = Spigot Bottle; LLJ = Lane's Little Jaw Site; HF = Hewett's Foresight; TL = Type Lance.



4 The Latitudinal Diversity Gradient within Latest Cretaceous and Paleocene Mammalian Assemblages from the Western Interior of North America

4.1 Abstract

The latitudinal diversity gradient (i.e., the increase in taxonomic richness from the poles to the equator) is one of the most widely recognized patterns in modern ecology. Although the establishment and maintenance of this phenomenon is poorly understood, the gradient is commonly suggested to have been in place through most of the last 544 million years. Several recent studies, however, have demonstrated that certain taxonomic groups did not conform to this pattern during parts of the Mesozoic and early Cenozoic. Here, using least-squares regression analyses on a large dataset of latest Cretaceous and Paleocene mammalian assemblages from North America (from approximately 69 to 57 million years ago), I report that a latitudinal diversity gradient was not established during this interval, with no statistical differences in mammalian taxonomic richness across latitude during the latest Cretaceous and Paleocene. A linear modeling approach based on the number of assemblages within each geological formation and the site-occupancy of genera within these formations reveals a strong association between taxonomic richness and sampling intensity; yet, even after mediating for the variance in sampling intensity among formations, a latitudinal diversity gradient comparable to the present is still not recovered. Instability among North American mammalian communities near the Cretaceous/Paleogene boundary could have contributed to these patterns, but I suggest that a shallow temperature

gradient and more equable climates during this interval are more likely mechanisms that the absence of a latitudinal diversity gradient.

4.2 Introduction

The geographic distribution of extant mammals across the globe is distinctively patterned. Mammalian body mass and geographic range size, for instance, has generally been demonstrated to increase from the equator towards the poles (e.g., Bergmann, 1847; Rensch, 1938; Mayr, 1956; Rapoport, 1982; Stevens, 1989; Ribas and Schoereder, 2006). Perhaps the most striking of these patterns, however, is the latitudinal diversity gradient or, more plainly, the increase in taxonomic richness from the poles to the equator. This pattern has been recognized for over 200 years (von Humboldt, 1808; and see Hawkins, 2001), and across most mammalian lineages and most continents (e.g., Simpson, 1964; McCoy and Connor, 1980; Currie, 1991; Kaufman, 1995; Badgley and Fox, 2000; Lyons and Willig, 2002; Weir and Schluter, 2007; and see Willig et al., 2003 for a more comprehensive review). Within North America, for instance, where a steep latitudinal diversity has been reported among mammals, species richness ranges from approximately 80 species across latitude 35°N to just 40 near latitude 60°N (Simpson, 1964; Badgley and Fox, 2000).

While the presence of the latitudinal diversity gradient is well studied, the mechanisms that might have established and helped maintain this gradient are still somewhat unclear (Willig et al., 2003; Hillebrand, 2004; Mittelbach et al., 2007), and hypotheses and speculations about the causal factors of the latitudinal diversity gradient continue to increase (e.g., Platt, 1964; Willig et al., 2003; Mannion et al., 2014). Brown and Lomolino (1998) and Gaston (2000), for instance, have identified and distinguished over 25 suggested causes for the gradient. Prominent among the many hypotheses is the focus on climate (e.g., Willig et al., 2003; Erwin, 2009; Archibald et al., 2010), geographic area (e.g., Terborgh, 1973; Rosenzweig, 1995; Blackburn and Gaston, 1997; Mannion et al., 2012), and regional history (i.e., tropical communities are often less perturbed by broad-scale abiotic changes) (e.g., Willig al., 2003; Wiens and Donoghue, 2004; Mittelbach et al., 2007; Field et al., 2009).

Although climate, geography, and regional histories are known to have changed considerably through the history of the Earth, the latitudinal diversity gradient is generally suggested to have persisted throughout much of the Phanerozoic (from approximately 544 million years ago to the present) (see e.g., Ricklefs, 1987; Crane and Lidgard, 1989; Crame, 2001; Hillebrand, 2004; Leighton, 2005; Jablonski et al., 2006; Mannion et al. 2014). Several recent studies, however, have challenged these ideas (e.g., Archibald et al., 2010; Mannion et al., 2012). Mannion et al. (2012) revealed that non-avian dinosaurian richness throughout much of the Mesozoic peaked within more temperate paleolatitudes. Moreover, Rose et al. (2011), in one of the few papers to quantitatively analyze the latitudinal diversity gradient in extinct mammals (but also see Fraser et al., 2014), reported that a latitudinal diversity gradient in middle Paleocene mammals from the Western Interior of North America (from approximately 61.5 to 58 million years ago) was not present and that there were no differences in taxonomic richness across latitude. These findings not only suggest that the latitudinal diversity gradient in for certain groups was not established during the Mesozoic and parts of the early Cenozoic, but also help to identify the possible mechanisms that led to the modern gradient.

In light of these recent articles, I assess the presence of the latitudinal diversity gradient in latest Cretaceous and Paleocene mammalian assemblages across the

Western Interior of North America (from approximately 69 to 57.5 million years ago). I use least-squares linear regressions to evaluate patterns of mammalian taxonomic richness among latest Cretaceous and Paleocene assemblages from North America. In addition, using a modeling approach based on counts of the number of assemblages among geological formations and site-occupancy of genera within these formations (see discussion below), I examine the influence of differential sampling on these patterns. The results of this study provide new insights on observed differences of richness among formations and the establishment of one of the most widely recognized patterns in biodiversity.

4.3 Material and Methods

4.3.1 Data

To reconstruct latitudinal diversity gradients within the latest Cretaceous and early Paleogene from the Western Interior of North America, mammalian faunal composition and richness for assemblages within the latest Cretaceous Lancian North American Land Mammal Age and the three oldest Land Mammal Ages of the Paleocene (i.e., the Puercan, Torrejonian, and Tiffanian) were assembled (see Cifelli et al., 2004; Lofgren et al., 2004). The resulting dataset is comprised of 188 latest Cretaceous and Paleocene fossil assemblages, with information on nearly 500 genera, and roughly spanning from paleolatitudes 35 to 60°N (Figures 4.1-4.4; see Appendix 2). Published literature was the principal resource for retrieving these data, with some data obtained from unpublished literature (e.g., dissertations) and the Paleobiology Database using the Fossilworks Gateway [http://www.fossilworks.org]. Paleolatitudes were calculated using modern latitudes, the Apparent Polar Wander Path presented by Torsvik et al. (2012, table 3), and a customized R function (M. Vavrek, unpublished software). Within the dataset, tentative taxonomic assignments (e.g., “cf.”, “?”) were discarded and the taxon was assigned to the designated genus. Also, as taxonomic richness is the focus of this study, higher taxonomic assignments listed within a local fauna that does not contain a representative of the group at a lower taxonomic level are retained; for instance, the identification of Microcosmodontidae genus and species indeterminate from the early Puercan Long Fall horizon of southeastern Saskatchewan (see Fox, 1989, 1997) is maintained in the dataset as there is no other reference to a genus within the family from the local fauna. Conversely, higher taxonomic assignments are removed if a representative of the group is identified at a lower taxonomic level. Mammals that are not formally named but are suggested to represent a previously undescribed taxon (e.g., ?Purgatoriidae genus and species indeterminate A and ?Purgatoriidae genus and species indeterminate B from the earliest Torrejonian Farrand Channel and Horsethief Canyon local faunas of northeastern Montana [Clemens and Wilson, 2009]) are also retained in the dataset.

The taxonomic history of many of the mammals included within this study is remarkably muddled. Several groups have been the focus of recent, comprehensive taxonomic studies (e.g., latest Cretaceous metatherians [e.g., Davis, 2007]) and I included many of the suggested revisions from these studies here. However, although not intended to reflect any decisive opinions on the validity of certain taxa, a number of taxonomic decisions were made within this study. For example, *Mckennatherium* Simpson, 1935 is considered a valid taxon but *Diacocherus* Gingerich, 1983 is recognized as a synonym of *Adunator* Russell, 1964 (see Secord, 2008); "*Leptacodon*" *packi* Jepsen, 1930 and "*L.*" *munusculum* Simpson, 1935 are considered distinct from other members of the genus (e.g., *L. rosei* Gingerich, 1987, *L. tener* Matthew and Granger, 1921) and are assigned to ?*Leptacodon* (see Scott, 2008; Manz and Bloch, in press); and *Didymictis dellensis* is recognized as a valid taxon (see Rankin, 2009).

4.3.2 Statistical Methods

Latitudinal richness gradients were first constructed as the slope of a linear regression of the taxonomic richness for each assemblage from a faunal zone on the paleolatitude of the assemblage. Following this, taxonomic richness values were calculated for each formation within each faunal interval. Once grouped, latitudinal richness gradients were evaluated as the slope of a linear regression of the taxonomic richness for each formation on the mean paleolatitude of the fossil assemblages within the formation. Notably, Rose et al. (2011) grouped assemblages into nine geographic regions (e.g., Northern Alberta [north of paleolatitude 59.5°N], Southern Alberta [south of paleolatitude 59.5°N]), based on quadrats that Simpson (1964) and Badgley and Fox (2000) assembled with data on extant mammals. However, given the major shifts in climate and paleogeography across the last 66 million years, it is unlikely that these regions maintain much resemblance to those in the past and are actually sampling different environments. Grouping assemblages within formations, although presenting its own issues (see Benton et al. [2011] for a discussion), is a more suitable approach as geological formations are generally defined on similar facies or sets of facies, and likely comprise a smaller number of habitats.

To determine whether the observed patterns are simply artifacts of differential sampling intensities, I used a similar modeling method to that outlined by Smith and McGowan (2007), Lloyd (2012) and Mannion et al. (2012). In this approach, both the number of assemblages within each formation and the site occupancy (i.e., the total number of observed and unique genus-assemblage pairs) within each formation were calculated and used as proxies for sampling. The natural logarithm of the taxonomic richness and the number of assemblages from each formation were assessed with linear regressions. The slopes of the linear regressions of the natural logarithm of the generic richness within each geological formation and natural logarithm of site-occupancy within each formation were also subsequently examined. Finally, the residuals of this latter regression were used to examine the correlation between variance in the number of assemblages and the number of genera within each formation on the mean paleolatitude of the assemblages within each formation.

All analyses were performed in R version 3.0.2 (R Development Core Team, 2015).

4.4 Results

For all four faunal interval zones examined, spanning the latest Cretaceous and early Paleogene, the slopes of the regressions of mammalian taxonomic richness on the paleolatitude of each assemblage do not differ significantly from zero (Figures 4.5-4.8). Moreover, these regressions indicate that there is little correlation between richness and latitude, with the r^2 values ranging from just 0.0002 to 0.087. Similarly, the slopes of the regression of taxonomic richness for each formation on the mean paleolatitude of the fossil assemblages within the formation are not statistically different from zero for the four intervals (Figures 4.9-4.12). These regressions also provide little explanation for differences in richness. In fact, for the highest correlation, based on the Lancian assemblages, variation in paleolatitude explains only 35.5% of the variation in generic richness.

In contrast to these findings, most of the linear regressions of taxonomic richness and the number of assemblages within each formation show slightly higher correlations, with r^2 values for the four faunal intervals ranging from 0.158 to 0.696 (Figures 4.13-4.16). The correlations based on assemblages from the Lancian, Puercan and Tiffanian are also statistically significant. Generic richness is also significantly correlated with the site-occupancy of genera within each formation (Figures 4.17-4.20). More precisely, the r^2 values for the four intervals are higher than 0.80 and all of the correlations are highly significant. In addition, the regressions of the residuals of the richness versus the site-occupancy within each formation analysis on paleolatitude show little correlation. This suggests that differences in the taxonomic richness among formations, even without the influence of differential sampling, are still not strongly linked with paleolatitude (Figures 4.21-4.24).

4.5 Discussion

The latitudinal diversity gradient is one of the most widely recognized ecological patterns (Platt, 1964; Brown and Lomolino, 1998; Gaston, 2000; Hawkins, 2001; Willig et al., 2003; Hillebrand, 2004; Mittelbach et al., 2007). Although the establishment and maintenance of this phenomenon is poorly understood, the gradient is commonly suggested to have been in place through most of the last 544 million years (see e.g., Ricklefs, 1987; Crane and Lidgard, 1989; Crame, 2001; Hillebrand, 2004; Leighton, 2005; Jablonski et al., 2006; Mannion et al. 2014). Several recent studies, however, have demonstrated that certain taxonomic groups did not conform to this pattern during parts of the Mesozoic and early Cenozoic. Mannion et al. (2012), for instance, showed that non-avian dinosaurian richness throughout the Mesozoic was higher in temperate latitudes than tropical latitudes. Studying diversity trends in Eocene insects from North America, Archibald et al. (2010) discovered that the richness among assemblages within more temperate latitudes during this interval was comparable to that from modern tropical latitudes.

More importantly, for the purposes of this study, Rose et al. (2011) reported that a latitudinal diversity gradient in middle Paleocene mammals from the Western Interior of North America (from approximately 61.5 to 58 million years ago) was absent (i.e., no differences in taxonomic richness across latitude). Rose et al. (2011) assessed a number of possible reasons for this pattern, including sampling biases, homogeneity among faunas, topographic relief, and a reduced latitudinal temperature gradient during this interval. However, none of these causes were thought by these authors to sufficiently explain the lack of a latitudinal diversity gradient. Given these findings, Rose et al. (2011) suggested that climate and mammalian communities during the Paleocene were unstable, with some of the poorly understood archaic mammals from this interval (e.g., multituberculates, condylarths) potentially responding differently than extant mammals. Mannion et al. (2014) further suggested that, despite the latitudinal variation in temperature reported by Rose et al. (2011), low seasonality might have led to the absence of a diversity gradient.

Similar to the results of Rose et al. (2011), my findings indicate that the modern latitudinal diversity gradient, at least among mammals, was not established within North America during the latest Cretaceous and early Paleogene; rather, a diversity gradient during this interval was not present, with no differences in mammalian taxonomic richness with latitude (Figures 4.5-4.12). Moreover, although a linear modeling approach was employed here rather than sample-standardizations, as with the study of Rose et al. (2011), correlation between the generic richness within each geological formation and the occurrence of taxa within each formation suggests that differences in diversity may reflect variability in sampling. In particular, a robust relationship was revealed between the taxonomic richness of mammals within each geological formation and site-occupancy (i.e., the number of observed and unique genus-assemblage pairs) within each formation (Figures 4.17-4.20). The residuals of the regression between generic richness within a formation and the site-occupancy of taxa within each formation reflect variance in richness that is not explained by sampling (Mannion et al., 2012, 2014). The linear correlations between these residuals and paleolatitude for the four intervals are not significant and the low values of the r^2 further indicate that few of the residual differences in richness, after accounting for differential sampling intensity among latest Cretaceous and earliest Paleogene assemblages, are strongly associated with paleolatitude (Figures 4.21-4.24); these findings provide added support to those of Rose et al. (2011).

Despite these results corroborating some of the findings of Rose et al. (2011), a close examination of the methods and conclusions of these authors provokes some concerns. Perhaps most importantly, Rose et al. (2011) examined oxygen isotope values among phenacodontid condylarths from Torrejonian and Tiffanian assemblages across North America and inferred, based on these data, that the temperature gradient during this interval was relatively steep and similar to the modern gradient. A close examination of the time intervals and geographic areas from which the sampled specimens used to construct the temperature gradient were recovered reveals several apprehensions. Specifically, the gradient presented by these authors is based on sampled specimens from the middle Torrejonian (To2) to the early middle Tiffanian (Ti3) (from approximately 62.5 to 59.5 million years ago). Oxygen isotope records from benthic foraminifera indicate that global temperatures varied across this interval of time, with cooling occurring during the middle Paleocene after a long-term warming trend (e.g., Zachos et al, 2001); fossil floral composition and leaf margin data (e.g., Wolfe and Upchurch, 1987; Wolfe, 1994), as well as non-mammalian faunal data (Markwick, 1998) further support these trends. These changes in the mean annual temperature through the Torrejonian and Tiffanian could influence differences among the oxygen isotope values obtained by Rose et al. (2011), with differences in the isotopic values encompassing variance in both time and geography (see Fricke and Wing, 2004 for similar concerns).

In fact, by separately assessing the Torrejonian and early Tiffanian (Ti1) oxygen isotope oxygen values recorded by Rose et al. ([2011], supplementary material, table DR2), differences within the temperature gradient are apparent. The temperature gradient from the Torrejonian samples recovers a relatively steep slope, similar to the gradient presented by these authors (Rose et al., 2011, fig. 3), although this is entirely contingent on a single value from the Crazy Mountains Basin of southern Montana (Figure 4.25). In contrast, the gradient recovered from the earliest Tiffanian values, based solely on specimens from Alberta and southern Montana, displays a nearly flat temperature slope (Figure 4.26); a simple two-sample unpaired t-test also shows that the mean isotope values between these two regions are not statistically different (t-value = 1.174; p-value = 0.250). Based on these findings, it seems clear that without restricting comparisons of isotopic values to smaller time intervals and broader geographic ranges, it is not possible to reliably reconstruct a continental climate curve for the middle Paleocene from the existing distribution of data.

In addition to these findings, Rose et al. (2011) noted that the recovery of a steep latitudinal temperature gradient differs from studies that examined the temperature gradient among Late Cretaceous and early Paleogene palynomorphs and floras (Wolfe and Upchurch, 1987; Johnson and Ellis, 2002; Sluijs et al., 2006), but were comparable to some studies that analyzed isotopes from this time interval (e.g., Fricke and Wing, 2004; Ufnar et al., 2004). Their interpretations of several of these studies, however, are somewhat peculiar. Fricke and Wing (2004), for instance, noted a "two-slope" temperature gradient over North America during the early Eocene, with the gradient between 30 and 50°N steeper than at present and the gradient from 50 to 80°N much shallower. The samples examined by Rose et al. (2011) span the two suggested temperature gradients of Fricke and Wing (2004), ranging from paleolatitudes 33.5 to 61.5°N. Ufnar et al. (2004) examined oxygen isotope values of sphaerosiderites (minute

$FeCO_3$ nodules that formed in ancient wetland soils) and siderite-bearing paleosols to reconstruct the paleohydrology of Late Cretaceous environments across North America. Temperature is incorporated as a parameter in their analyses but a steep temperature gradient is not mentioned and certainly never assessed. Hence, based on the literature, including the studies cited here and others (e.g., Greenwood and Wing, 1995; Amiot et al., 2004; Sluijs et al., 2009), the steep temperature gradient proposed by Rose et al. (2011) can only be considered with some caution or, at the very least, as an unusual and unique discovery.

Given these concerns of the study by Rose et al. (2011), I consider the temperature gradient during the Late Cretaceous and early Paleogene to have been shallow and I suggest that a shallow temperature gradient was one of the principal mechanisms leading to the lack of a latitudinal diversity gradient among mammals from this interval. Mammalian faunal instability during the latest Cretaceous and early Paleogene has been demonstrated (e.g., Mitchell et al., 2012; Wilson, 2014; Chapter One of this dissertation) and, as proposed by Rose et al. (2011), also could have contributed to this pattern. Additionally, although assessments of seasonality within North America during the latest Cretaceous and early Paleogene are few (e.g., Wolfe and Upchurch, 1987; Valdes et al., 1996; Falcon-Lang, 2003), more equable climates during these intervals also could have resulted in the absence of a diversity gradient; notably, an increase in seasonality is reported during the Eocene (e.g., Eldrett et al., 2009, 2014), and Archibald et al. (2010) and Mannion et al. (2012) have suggested that the modern latitudinal diversity gradient may have developed shortly after this time.

4.6 Conclusions

The world's richest discovered succession of mammals from the latest Cretaceous and early Paleocene is preserved in continental strata of the Western Interior of North America (Cifelli et al., 2004; Lofgren et al., 2004). The present study suggests that the modern latitudinal diversity gradient, one of the widely recognized patterns in ecology, was not established among these mammalian assemblages. Instead, the latitudinal diversity gradient during this time did not significantly differ from a flat gradient. Although a strong correlation between mammalian taxonomic richness and sampling intensity is present, differential sampling between formations does not significantly alter this recorded pattern.

Notably, Rose et al. (2011) also reported the absence of a latitudinal diversity gradient within mammalian assemblages from the middle Paleocene; however, based on their examined oxygen isotope values, concluded that the temperature gradient during this middle Paleocene was steep. A close assessment of the specimen samples used to support these claims reveals some concerns. As a result, I do not accept the conclusions of Rose et al. (2010); instead, I propose that a weak latitudinal temperature gradient contributed to the absence of a diversity gradient. Faunal instability (e.g., Mitchell et al., 2012; Chapter one of this dissertation) and more equable climates (Wolfe and Upchurch, 1987; Falcon-Lang, 2003) could also have led to a flattened diversity gradient.

4.7 Literature Cited

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Figure 4.1.—Outline map of the Western Interior of North America with the location of the Lancian mammalian assemblages.

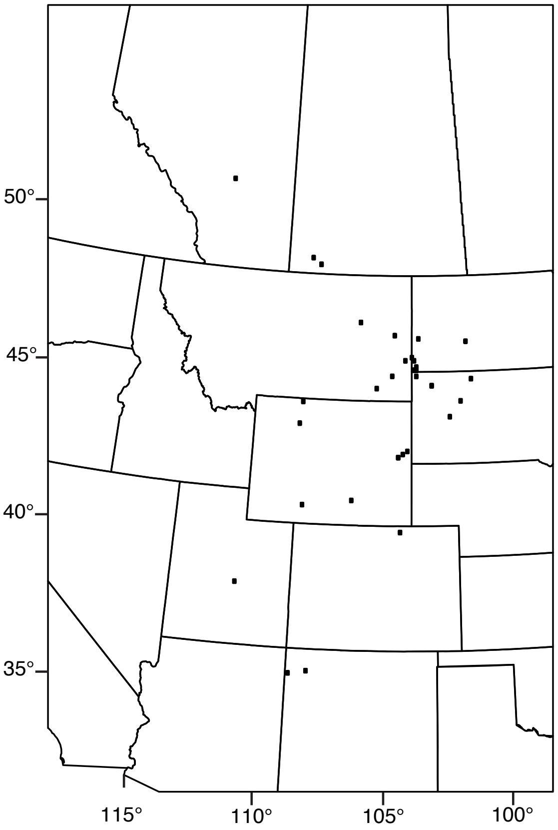


Figure 4.2.—Outline map of the Western Interior of North America with the location of the Puercan mammalian assemblages

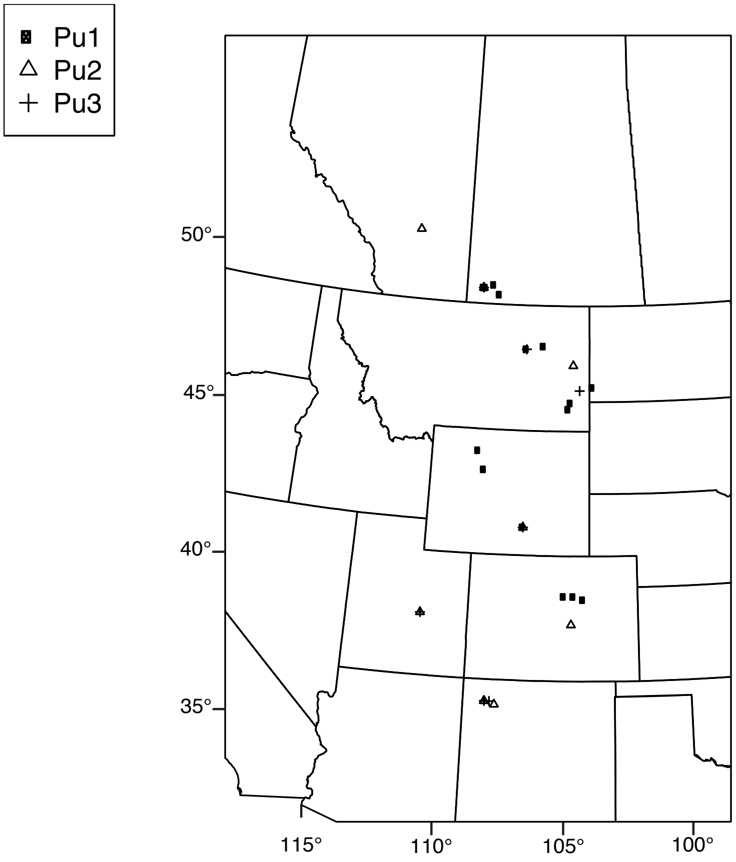


Figure 4.3.—Outline map of the Western Interior of North America with the location of the Torrejonian mammalian assemblages.

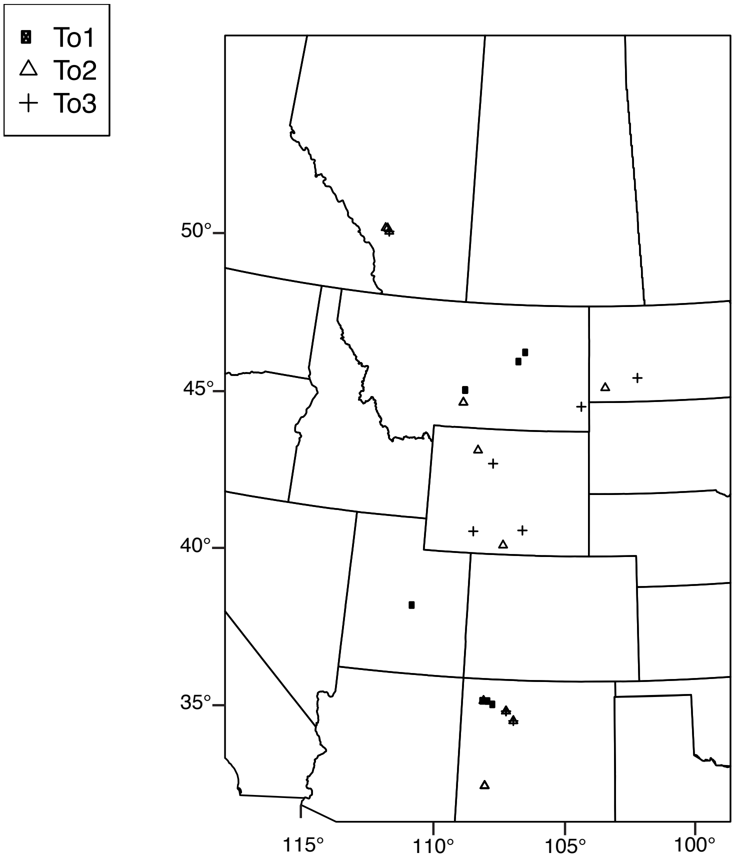


Figure 4.4.—Outline map of the Western Interior of North America with the location of the Tiffanian mammalian assemblages

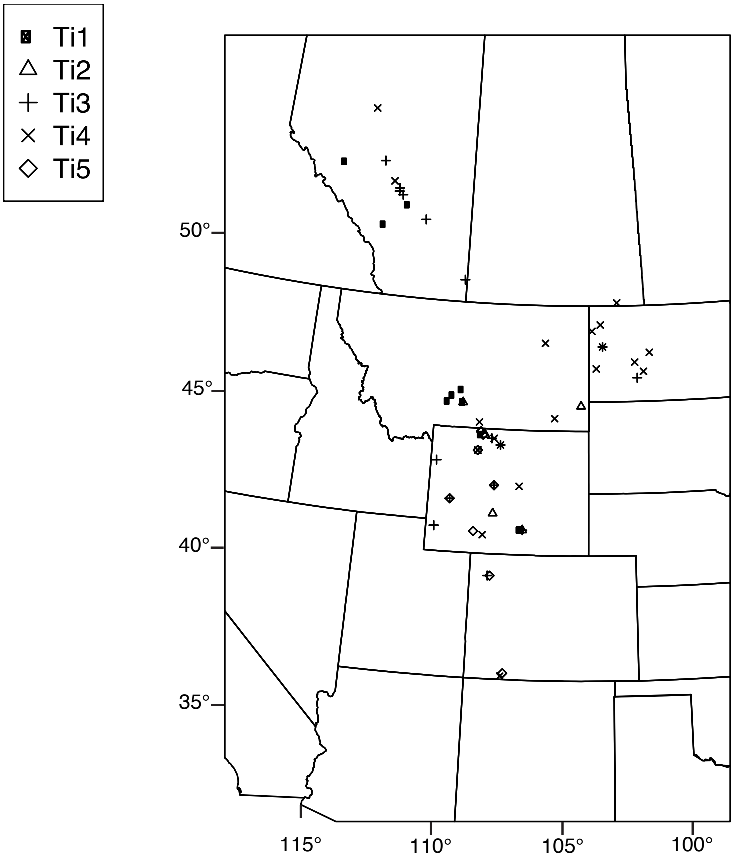


Figure 4.5.—Least squares linear regression for generic richness among Lancian assemblages from the Western Interior of North American and paleolatitude of assemblages. The slope of the regression is not statistically significant (t-value = 1.803, p-value = 0.080).

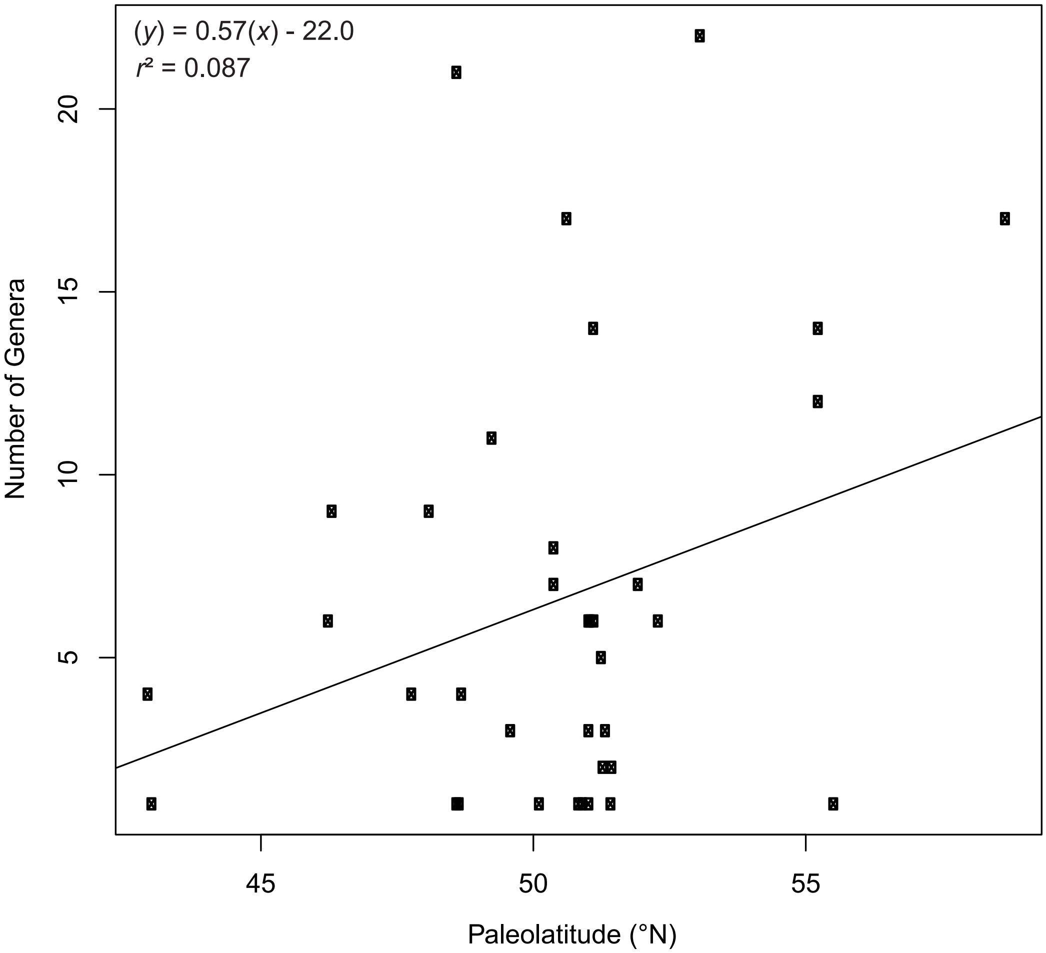


Figure 4.6.—Least squares linear regression for generic richness among Puercan assemblages from the Western Interior of North American and paleolatitude of assemblages. The slope of the regression is not statistically significant (t-value = -0.093, p-value = 0.926).

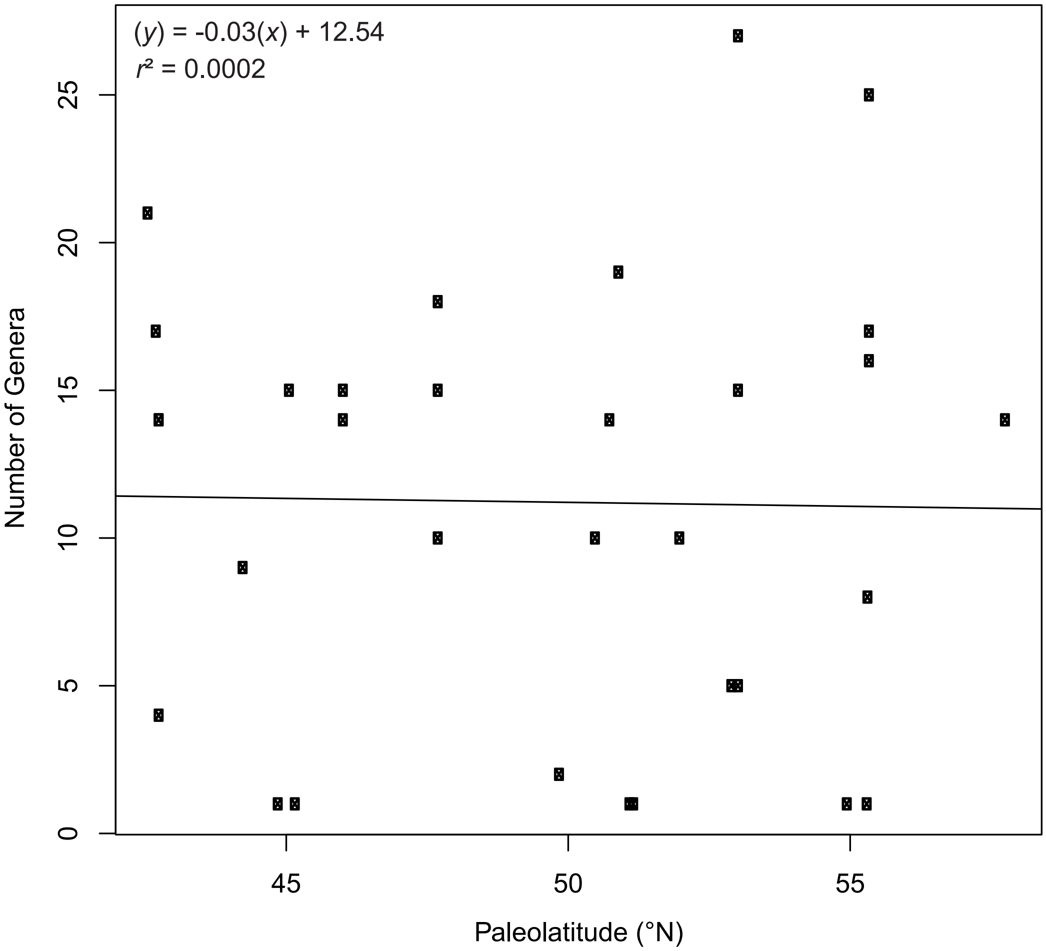


Figure 4.7.—Least squares linear regression for generic richness among Torrejonian assemblages from the Western Interior of North American and paleolatitude of assemblages. The slope of the regression is not statistically significant (t-value = 0.893, p-value = 0.377).

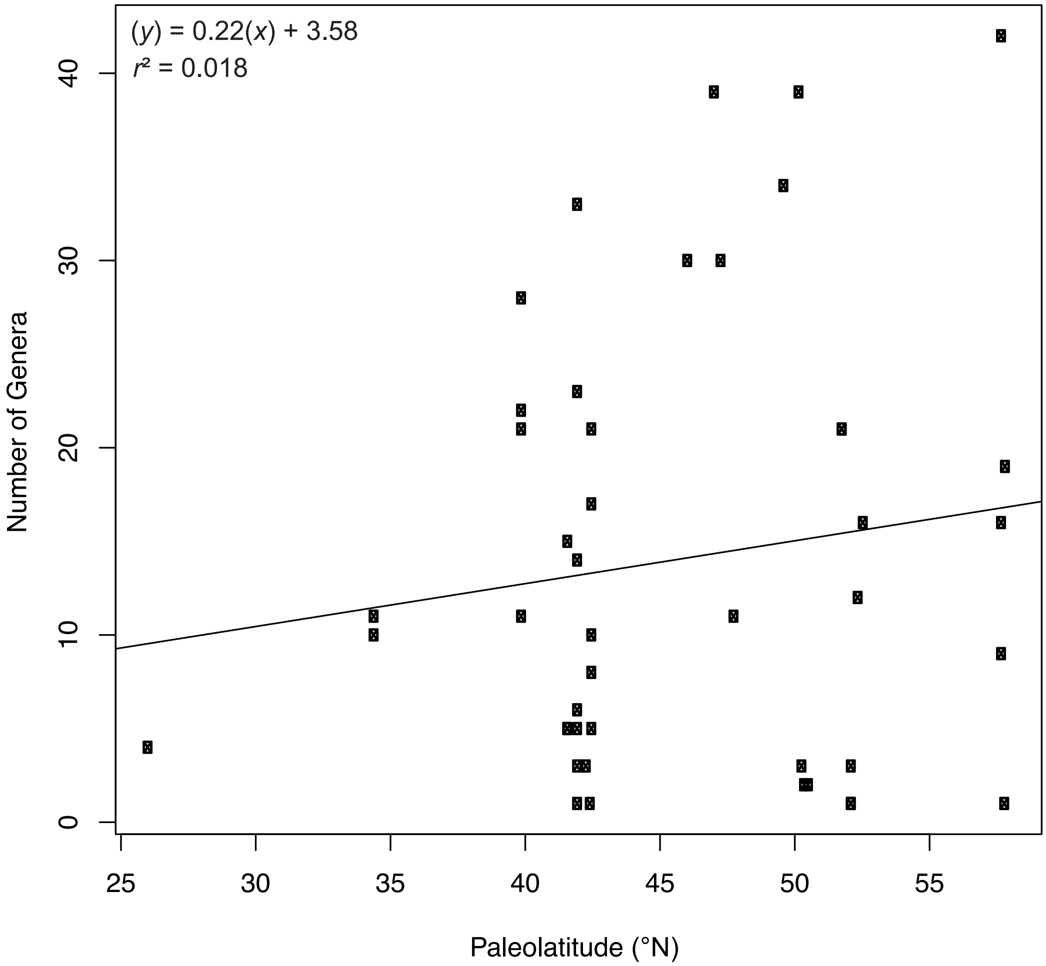


Figure 4.8.—Least squares linear regression for generic richness among Tiffanian assemblages from the Western Interior of North American and paleolatitude of assemblages. The slope of the regression is not statistically significant (t-value = 1.904, p-value = 0.061).

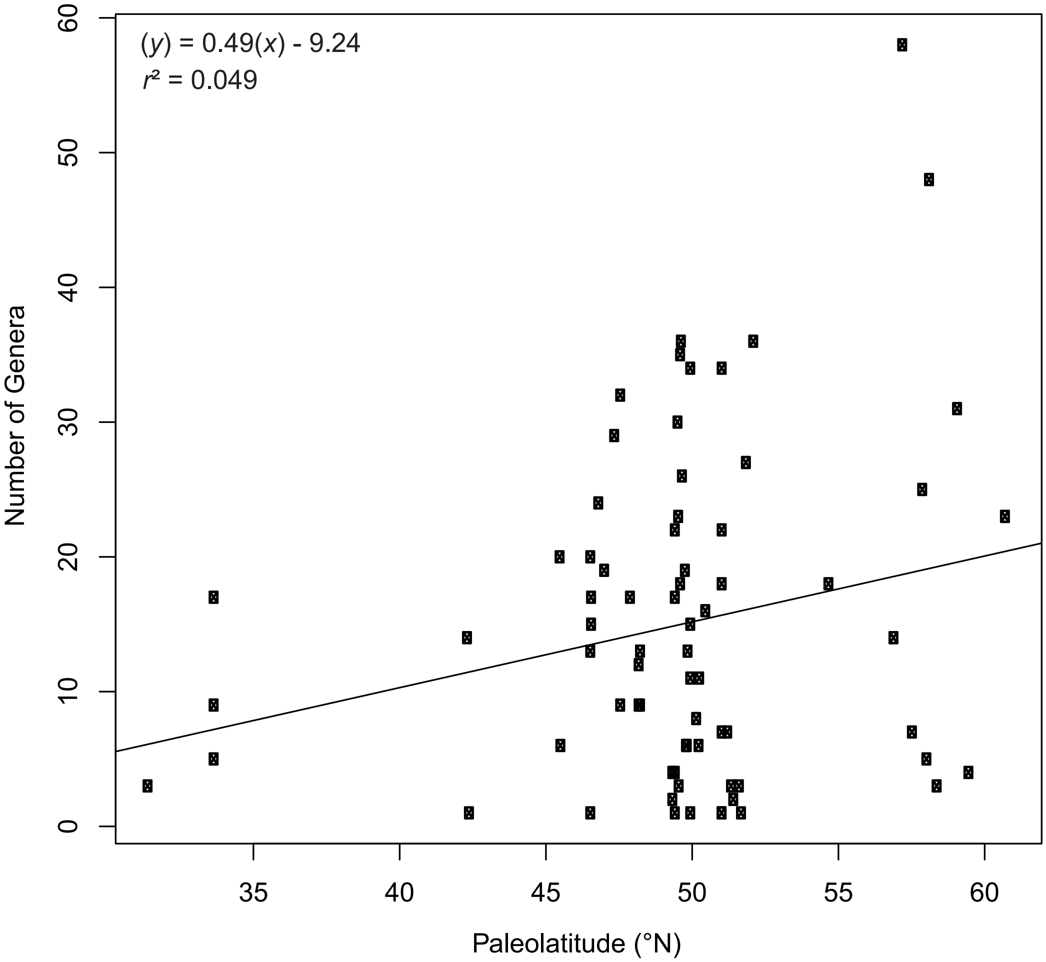


Figure 4.9.—Least squares linear regression for generic richness within each geological formation from the Lancian of the Western Interior of North American and mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = 1.965, p-value = 0.090).

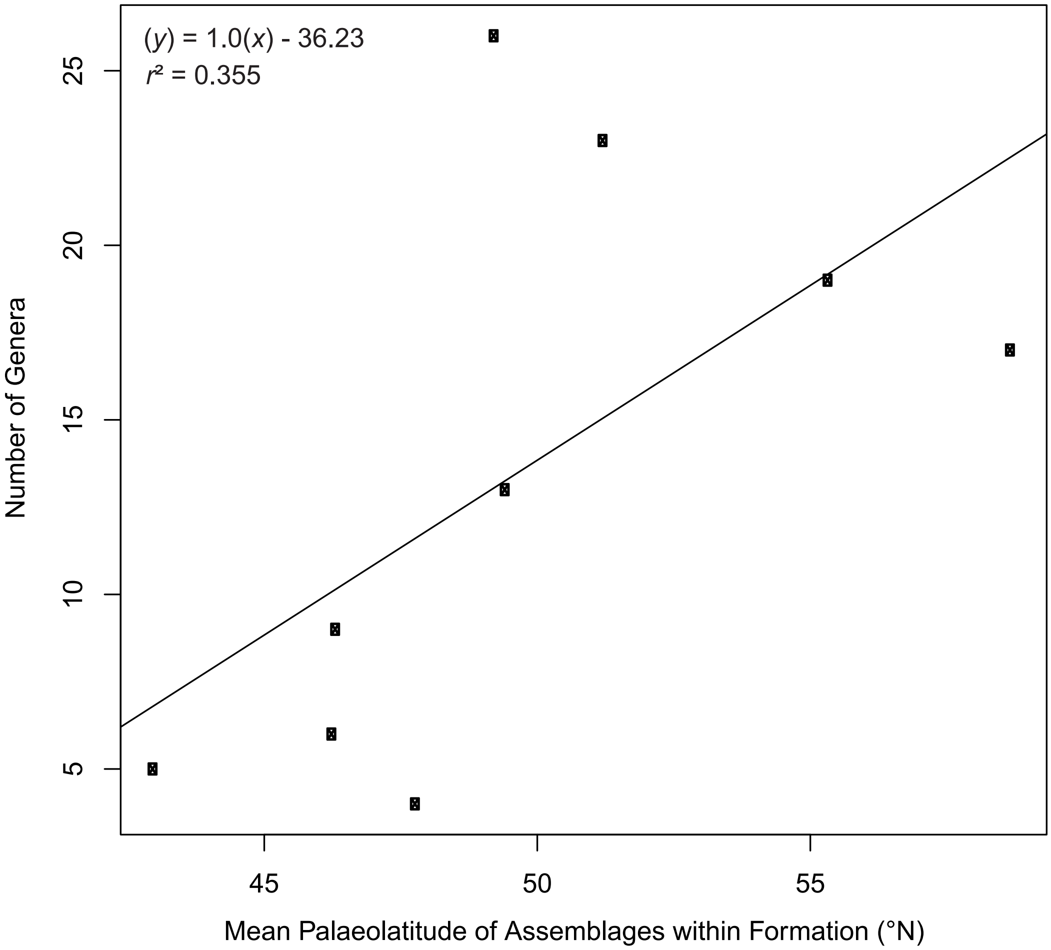


Figure 4.10.—Least squares linear regression for generic richness within each geological formation from the Puercan of the Western Interior of North American and mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = -0.124, p-value = 0.904).

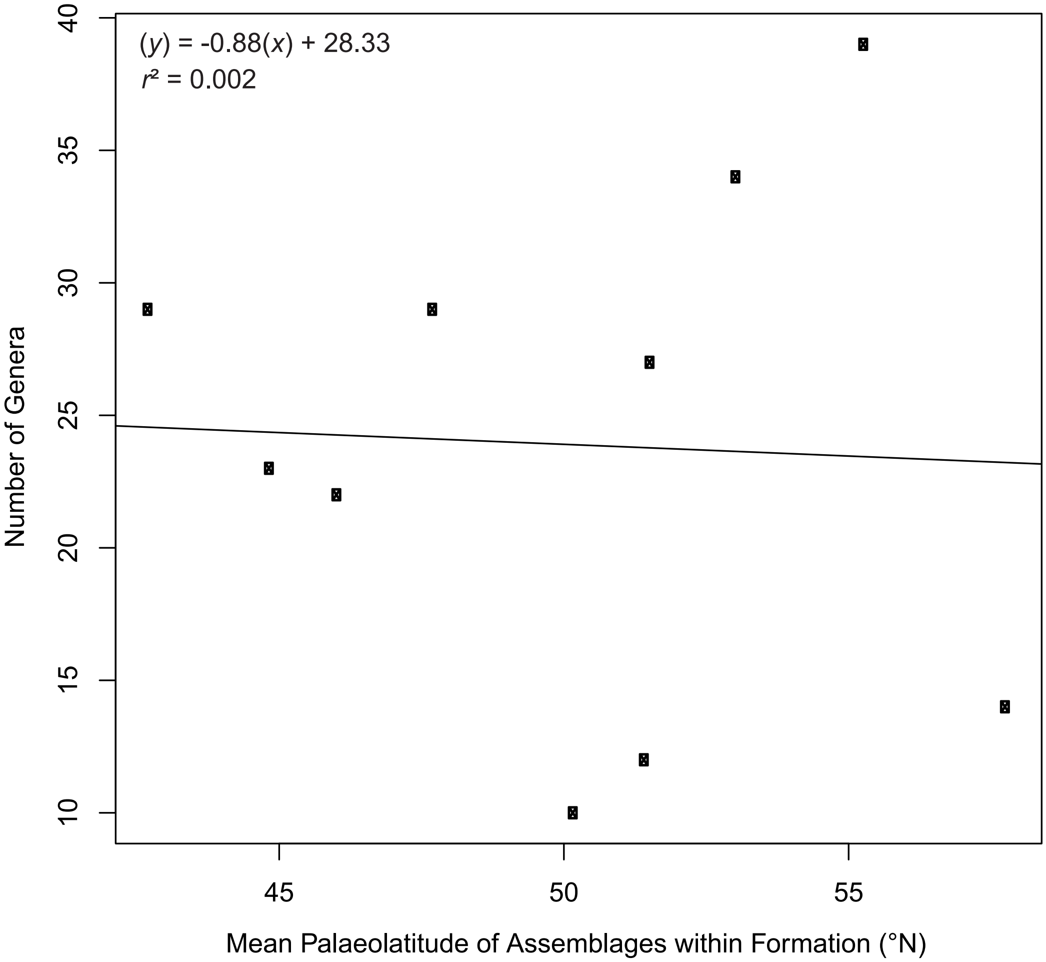


Figure 4.11.—Least squares linear regression for generic richness within each geological formation from the Torrejonian of the Western Interior of North American and mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = -0.020, p-value = 0.984).

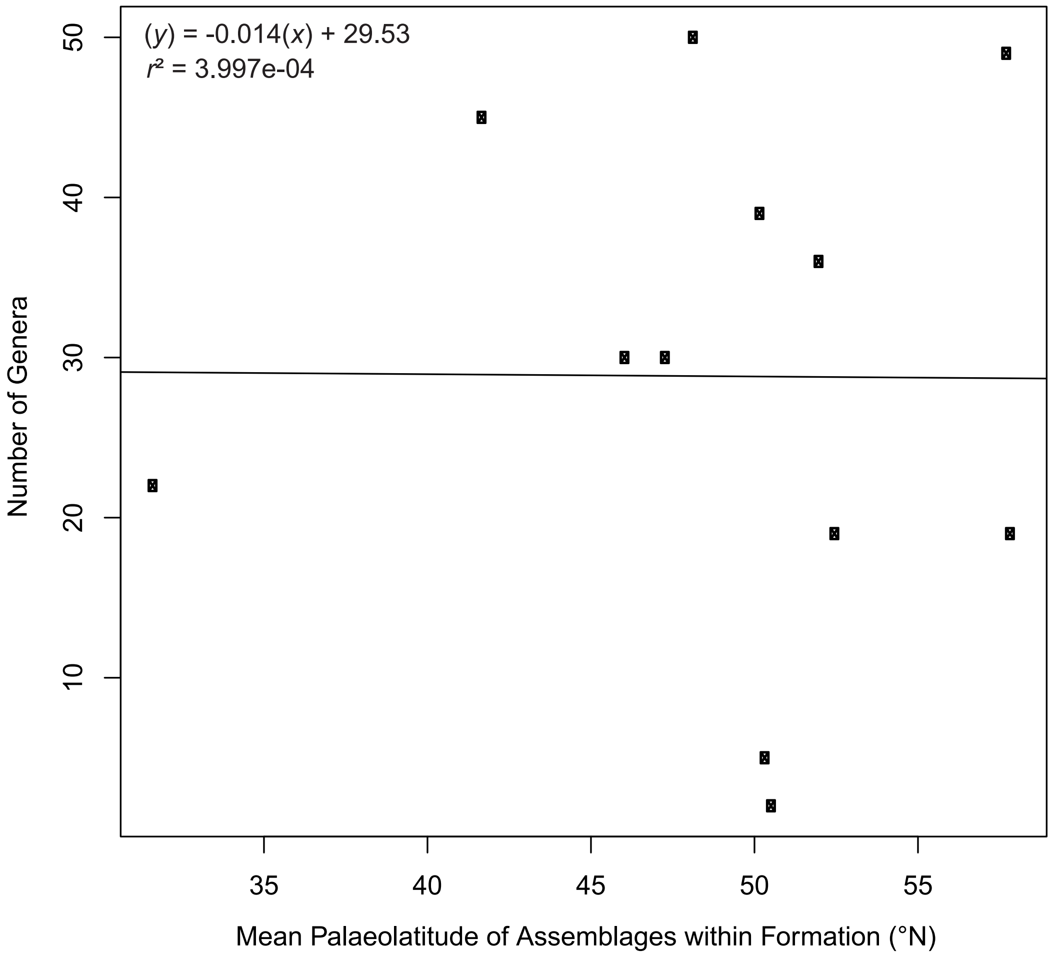


Figure 4.12.—Least squares linear regression for generic richness within each geological formation from the Tiffanian of the Western Interior of North American and mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = 1.549, p-value = 0.145).

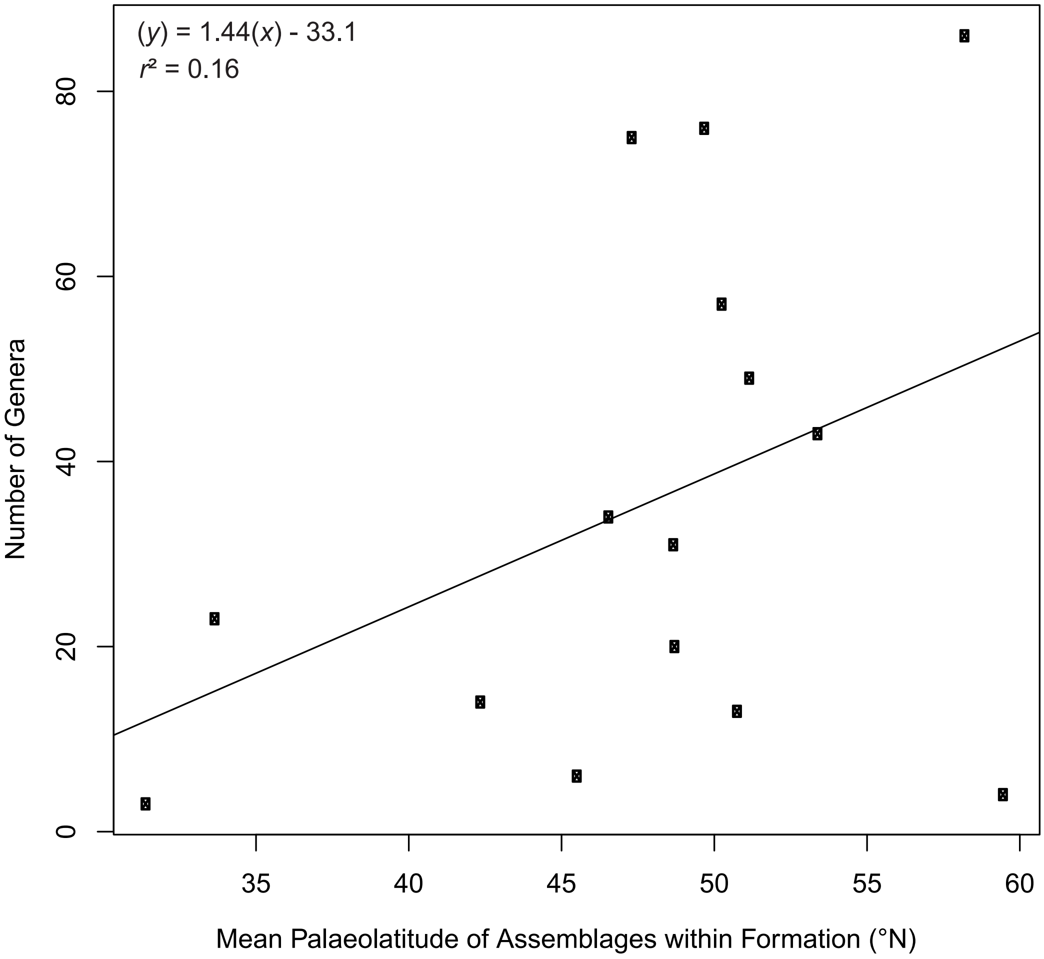


Figure 4.13.—Least squares linear regression for the natural logarithm of the generic richness within each geological formation from the Lancian of the Western Interior of North American and natural logarithm of the number of assemblages within each formation. The slope of the regression is statistically significant (t-value = 2.460, p-value = 0.043).

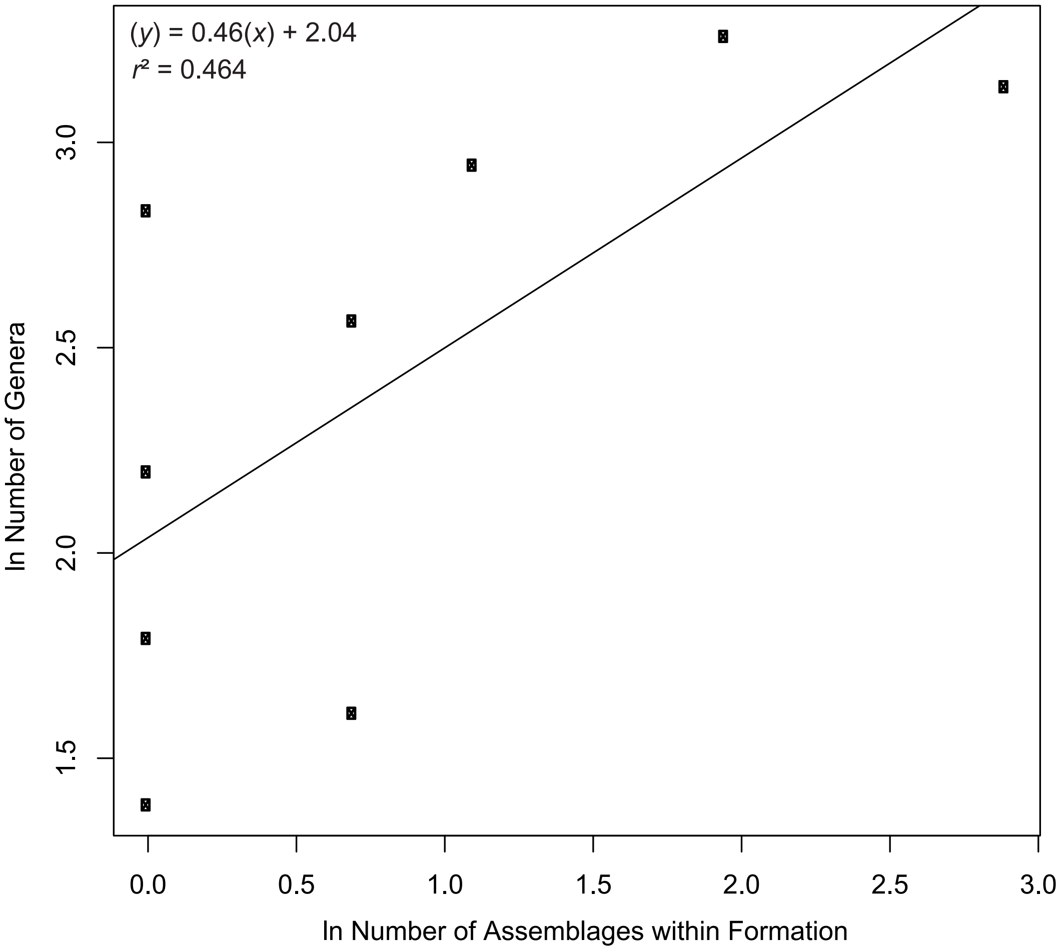


Figure 4.14.—Least squares linear regression for the natural logarithm of the generic richness within each geological formation from the Puercan of the Western Interior of North American and natural logarithm of the number of assemblages within each formation. The slope of the regression is statistically significant (t-value = 2.394, p-value = 0.044).

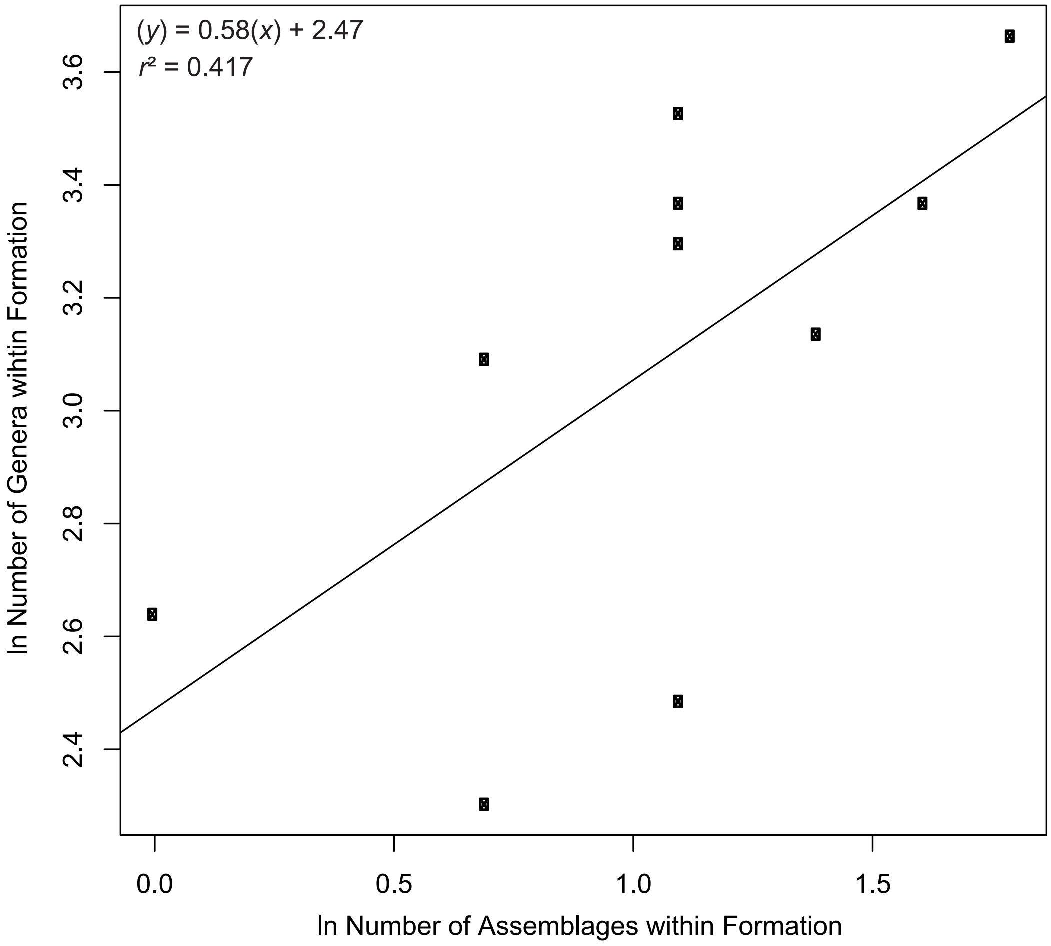


Figure 4.15.—Least squares linear regression for the natural logarithm of the generic richness within each geological formation from the Torrejonian of the Western Interior of North American and natural logarithm of the number of assemblages within each formation. The slope of the regression is not statistically significant (t-value = 1.371, p-value = 0.20).

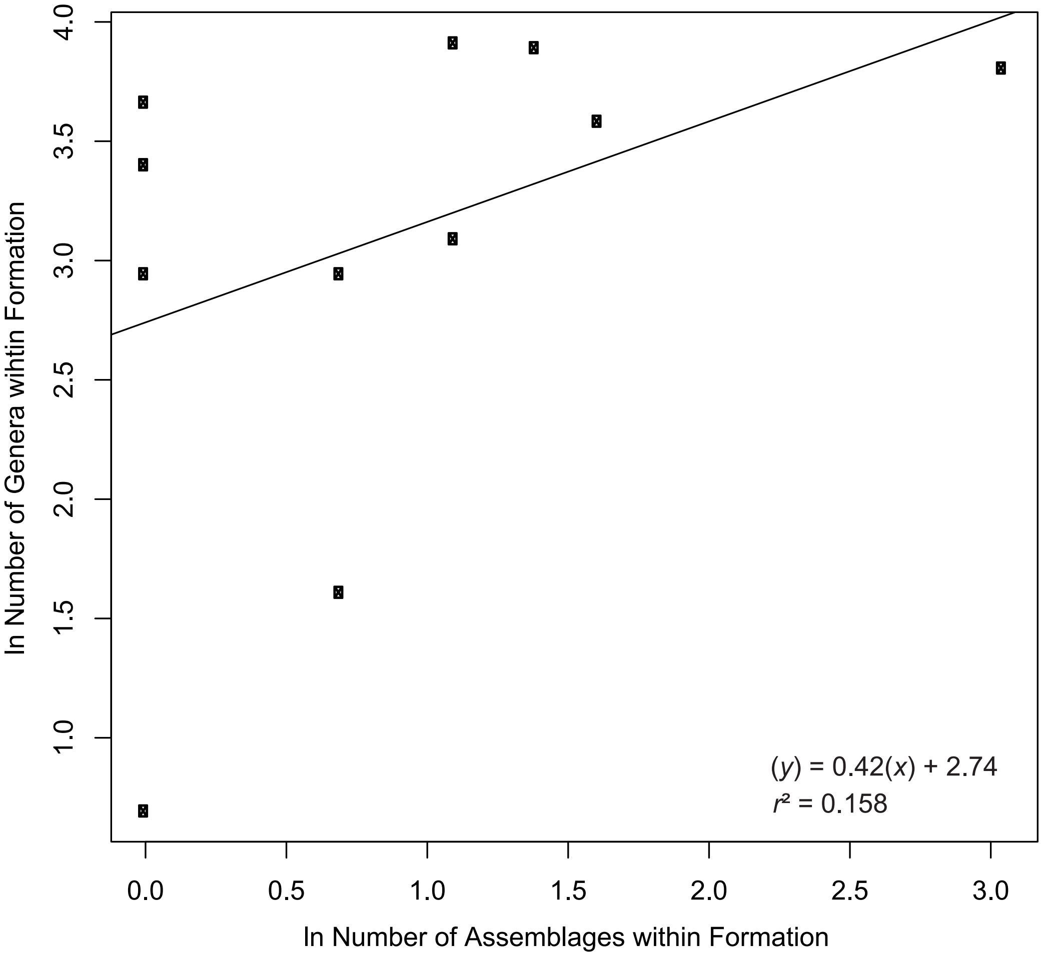


Figure 4.16.—Least squares linear regression for the natural logarithm of the generic richness within each geological formation from the Tiffanian of the Western Interior of North American and natural logarithm of the number of assemblages within each formation. The slope of the regression is statistically significant (t-value = 5.455, p-value < 0.001).

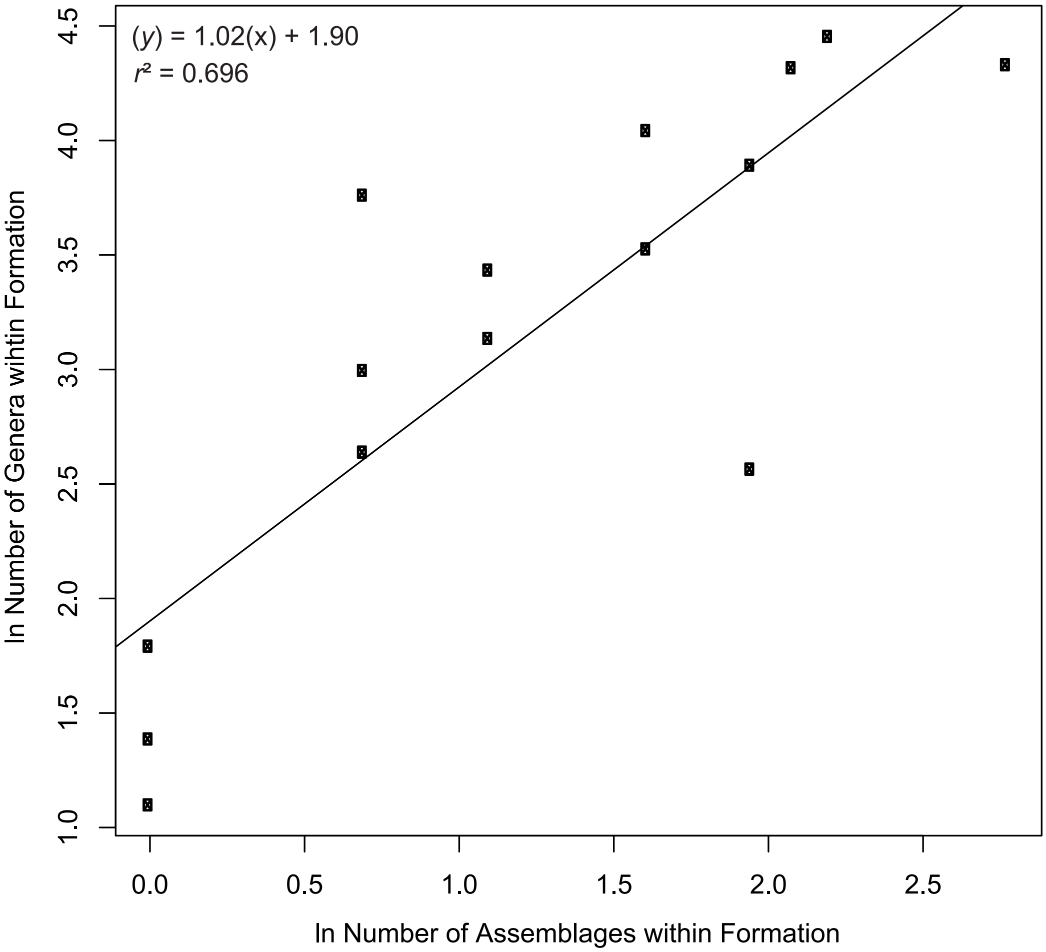


Figure 4.17.—Least squares linear regression of the natural logarithm of the generic richness within each geological formation from the Lancian of the Western Interior of North American and natural logarithm of the site-occupancy of genera within each formation. The slope of the regression is statistically significant (t-value = 7.406, p-value < 0.001).

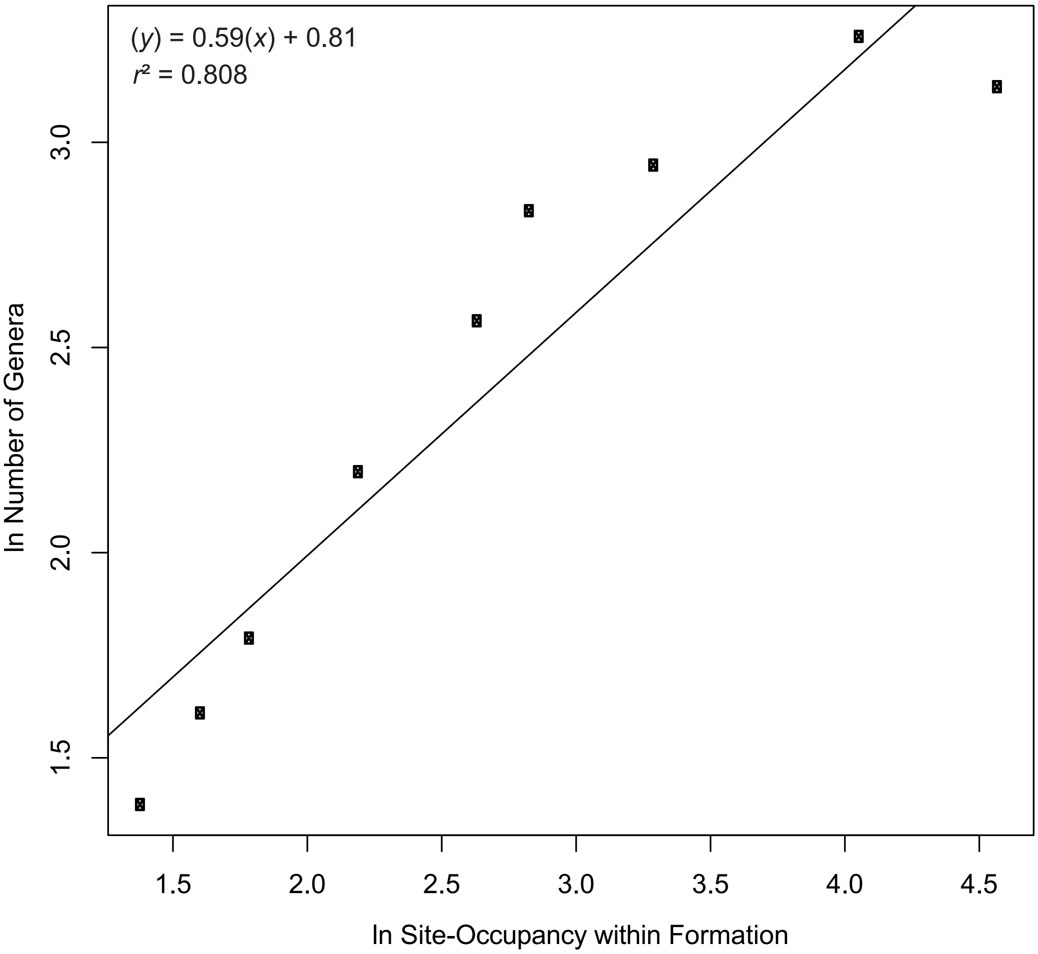


Figure 4.18.—Least squares linear regression of the natural logarithm of the generic richness within each geological formation from the Puercan of the Western Interior of North American and natural logarithm of the site-occupancy of genera within each formation. The slope of the regression is statistically significant (t-value = 9.333, p-value < 0.001).

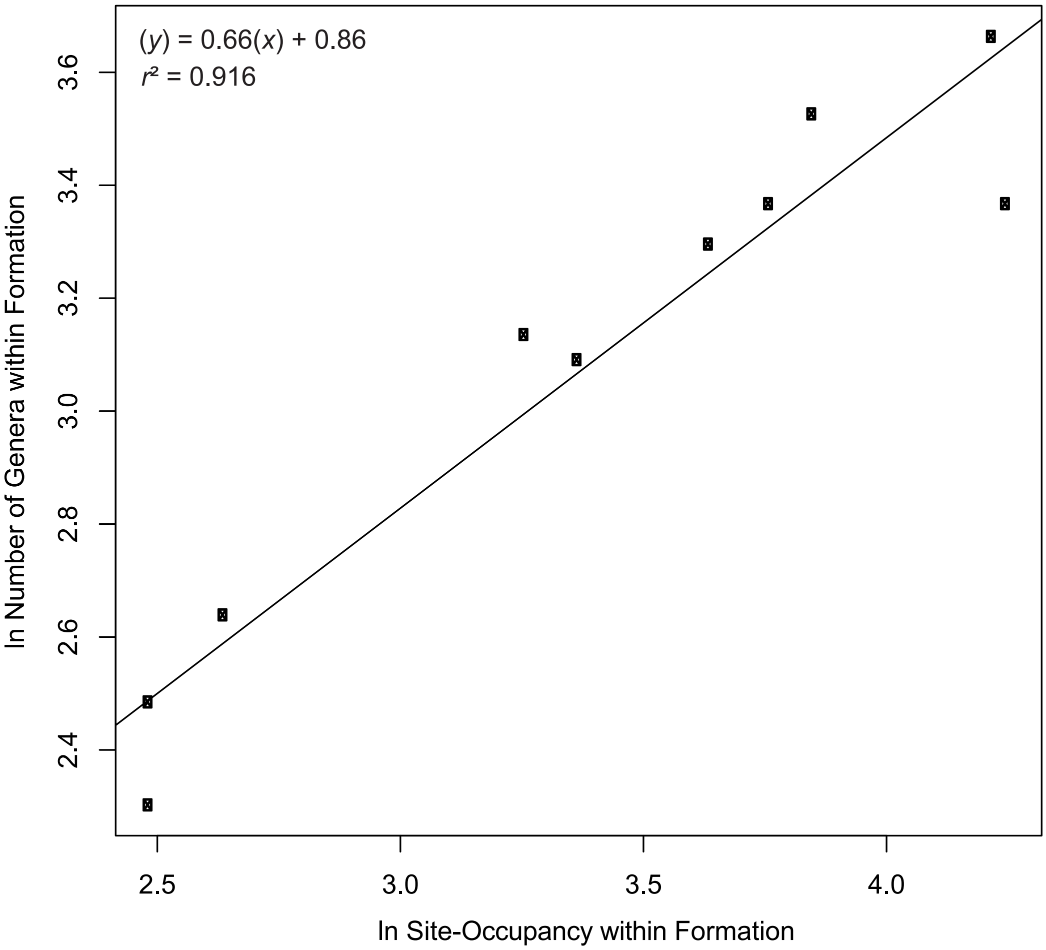


Figure 4.19.—Least squares linear regression of the natural logarithm of the generic richness within each geological formation from the Torrejonian of the Western Interior of North American and natural logarithm of the site-occupancy of genera within each formation. The slope of the regression is statistically significant (t-value = 8.088, p-value < 0.001).

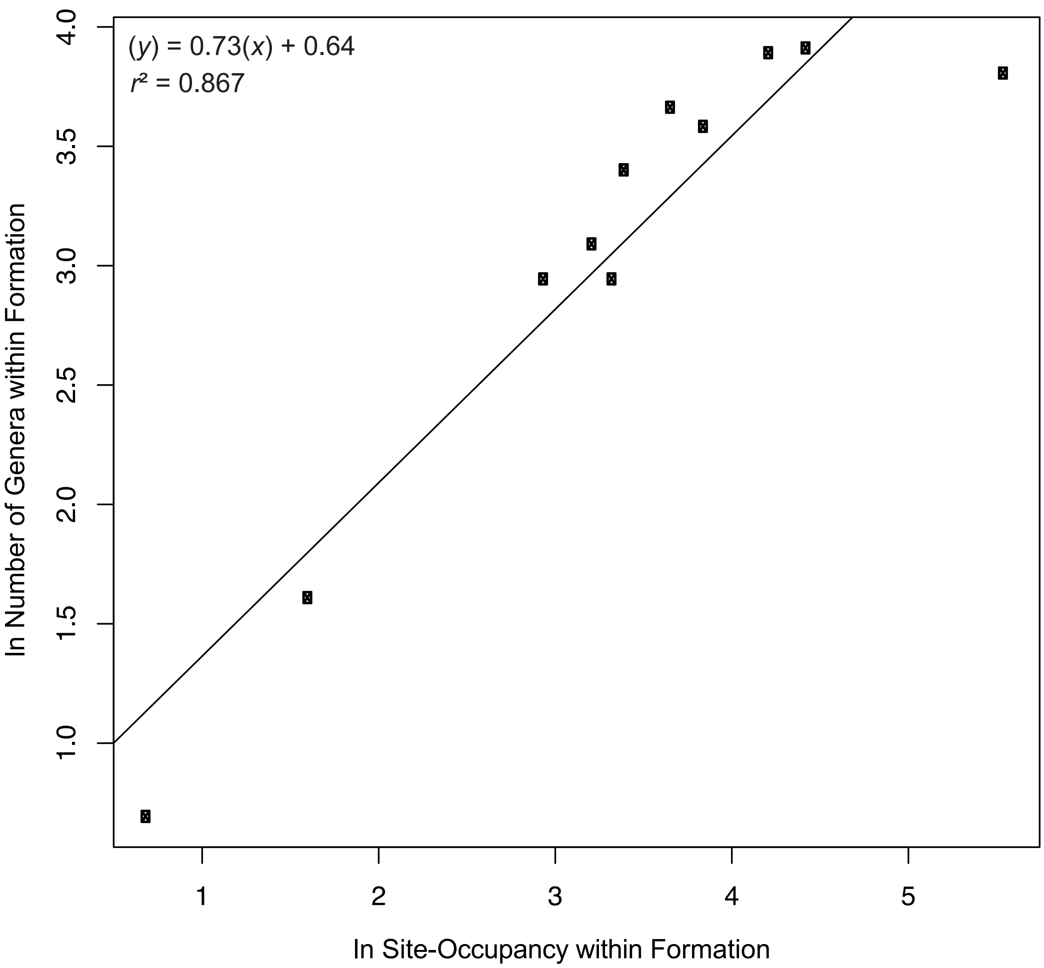


Figure 4.20.—Least squares linear regression of the natural logarithm of the generic richness within each geological formation from the Tiffanian of the Western Interior of North American and natural logarithm of the site-occupancy of genera within each formation. The slope of the regression is statistically significant (t-value = 24.851, p-value < 0.001).

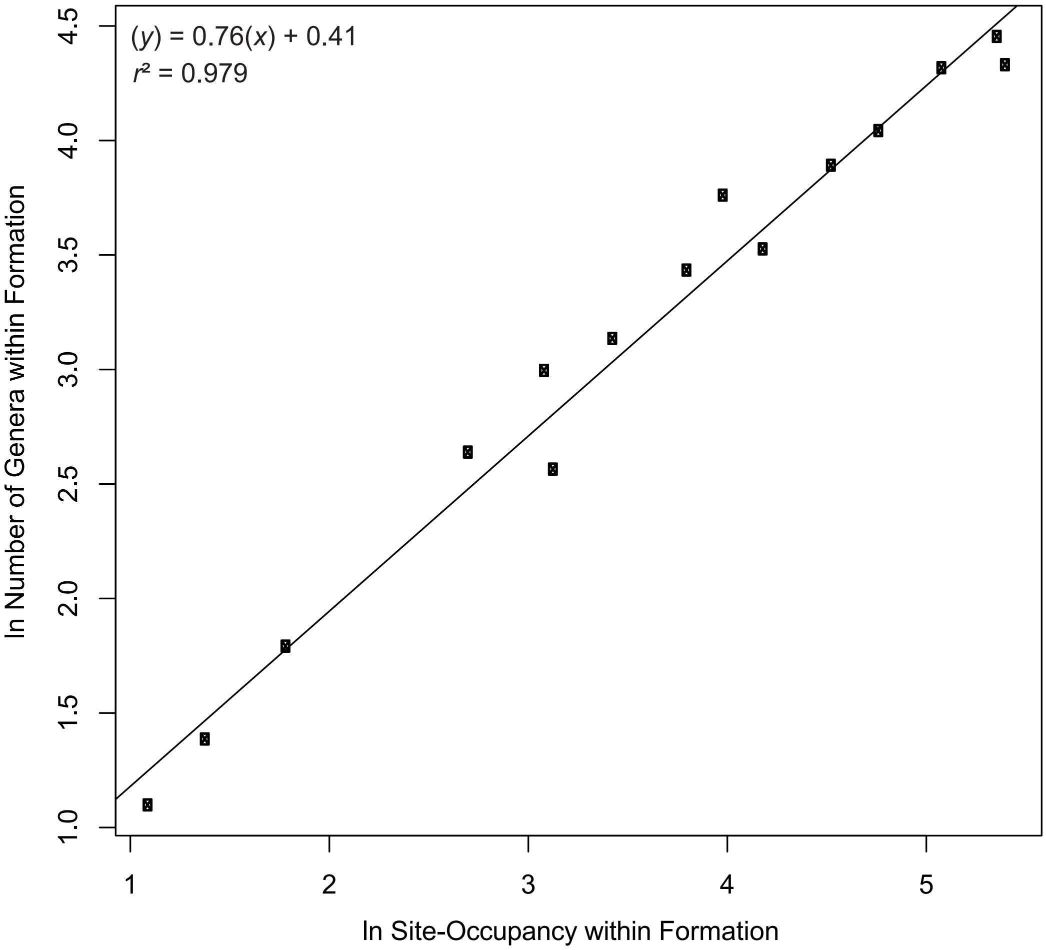


Figure 4.21.—Linear regression of residuals of regression of the natural logarithm of the generic richness within each geological formation from the Lancian of the Western Interior of North American versus natural logarithm of the site-occupancy of genera within each formation and the mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = 1.738, p-value = 0.126).

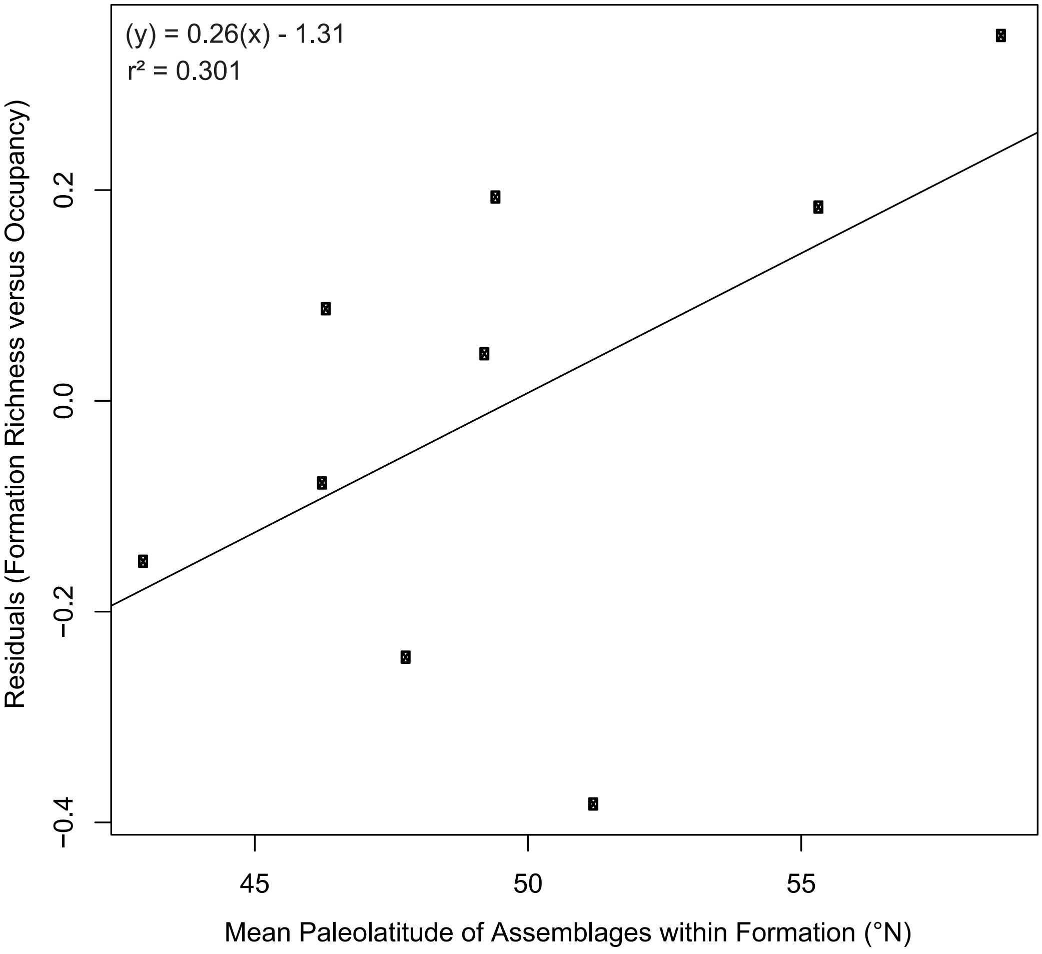


Figure 4.22.—Linear regression of residuals of regression of the natural logarithm of the generic richness within each geological formation from the Puercan of the Western Interior of North American versus natural logarithm of the site-occupancy of genera within each formation and the mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = 1.164, p-value = 0.278).

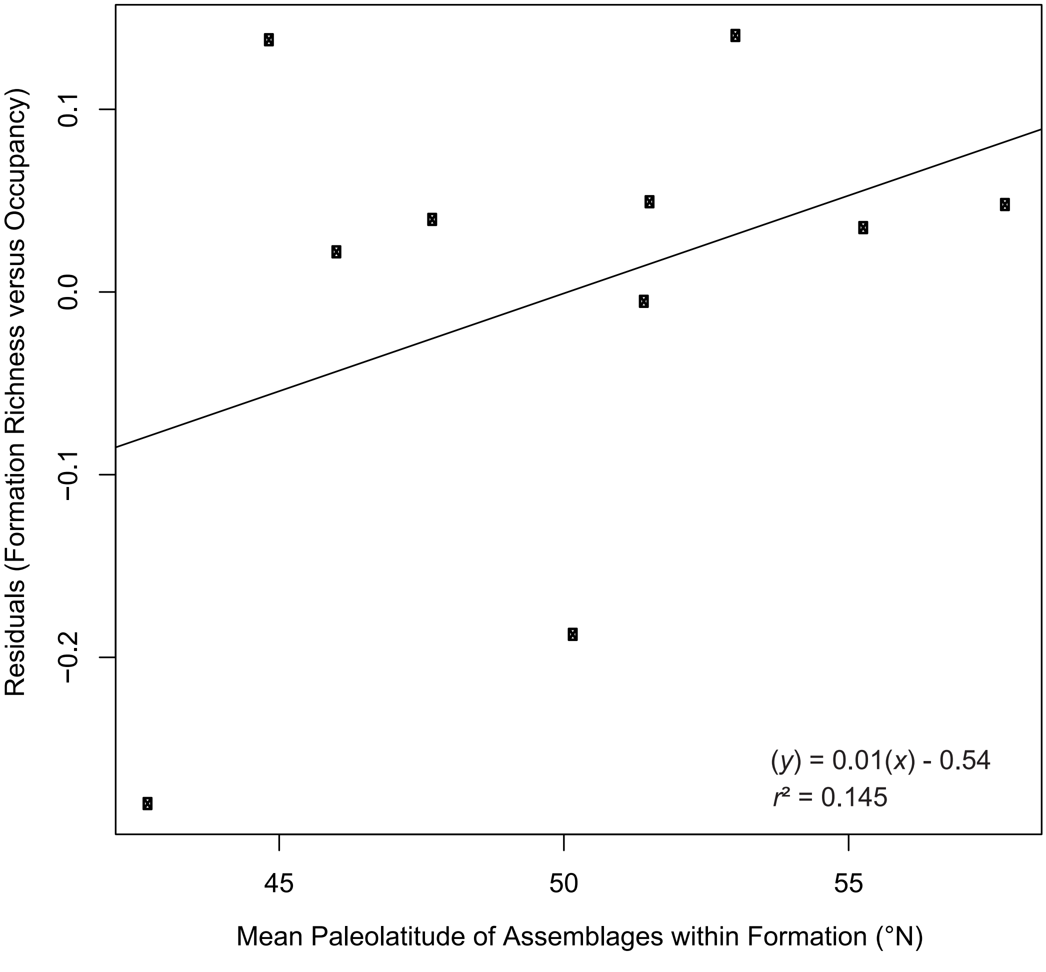


Figure 4.23.—Linear regression of residuals of regression of the natural logarithm of the generic richness within each geological formation from the Torrejonian of the Western Interior of North American versus natural logarithm of the site-occupancy of genera within each formation and the mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = 0.647, p-value = 0.532).

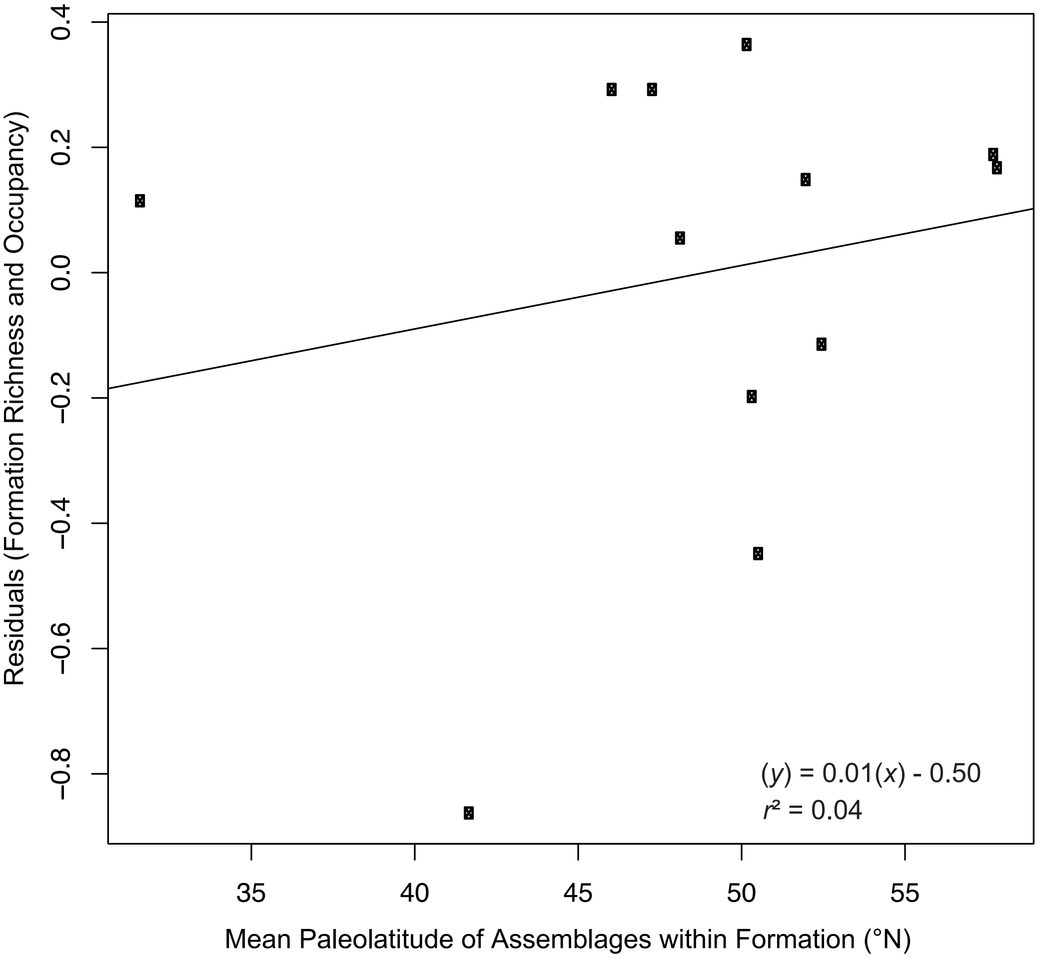


Figure 4.24.—Linear regression of residuals of regression of the natural logarithm of the generic richness within each geological formation from the Tiffanian of the Western Interior of North American versus natural logarithm of the site-occupancy of genera within each formation and the mean paleolatitude of the assemblages within the formation. The slope of the regression is not statistically significant (t-value = -0.096, p-value = 0.925).

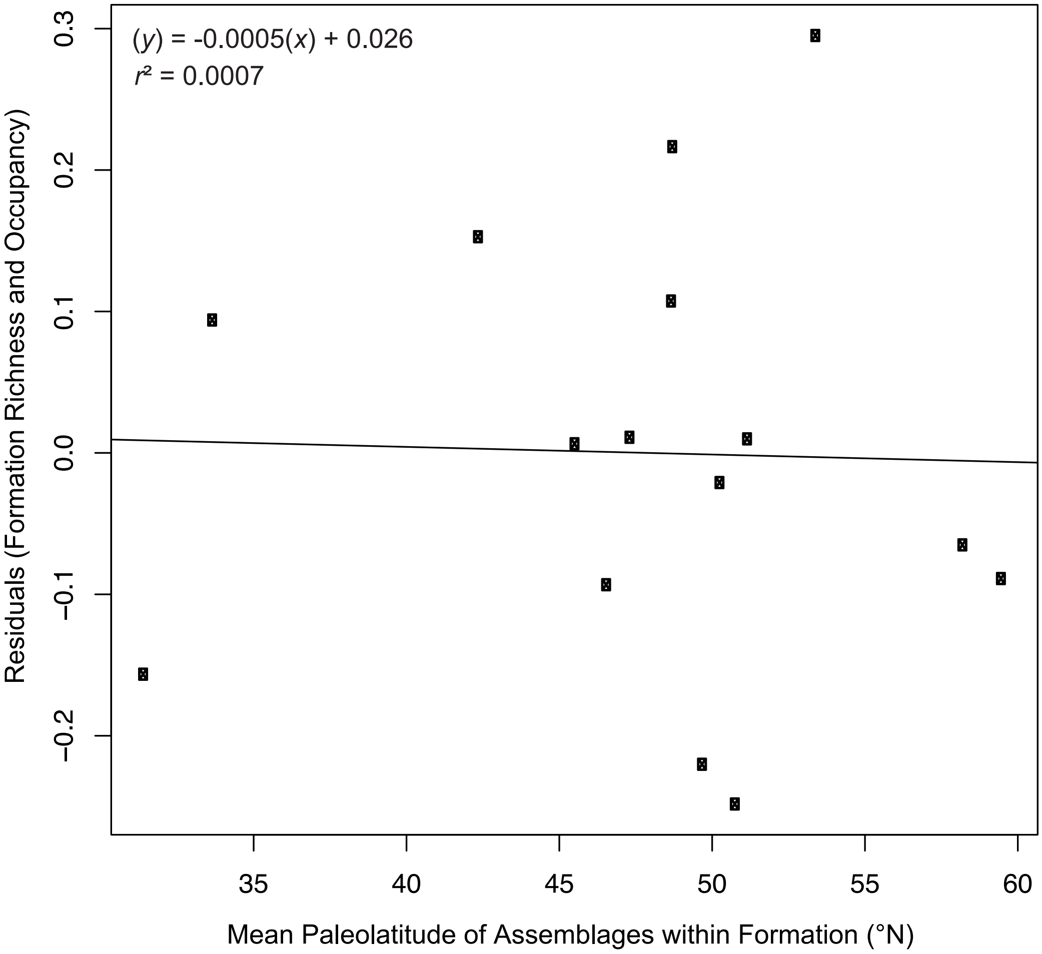


Figure 4.25.—Least squares linear regression of oxygen isotope gradient from biogenic $\delta^{18}O$ (Vienna Standard Mean Ocean Water) in middle Torrejonian (To2) mammals from the San Juan Basin of New Mexico and Crazy Mountain Basin of southern Montana. The slope of the regression is statistically significant (t-value = -3.552, p-value = 0.001). Data obtained from Rose et al. (2011, supplementary material, table DR2).

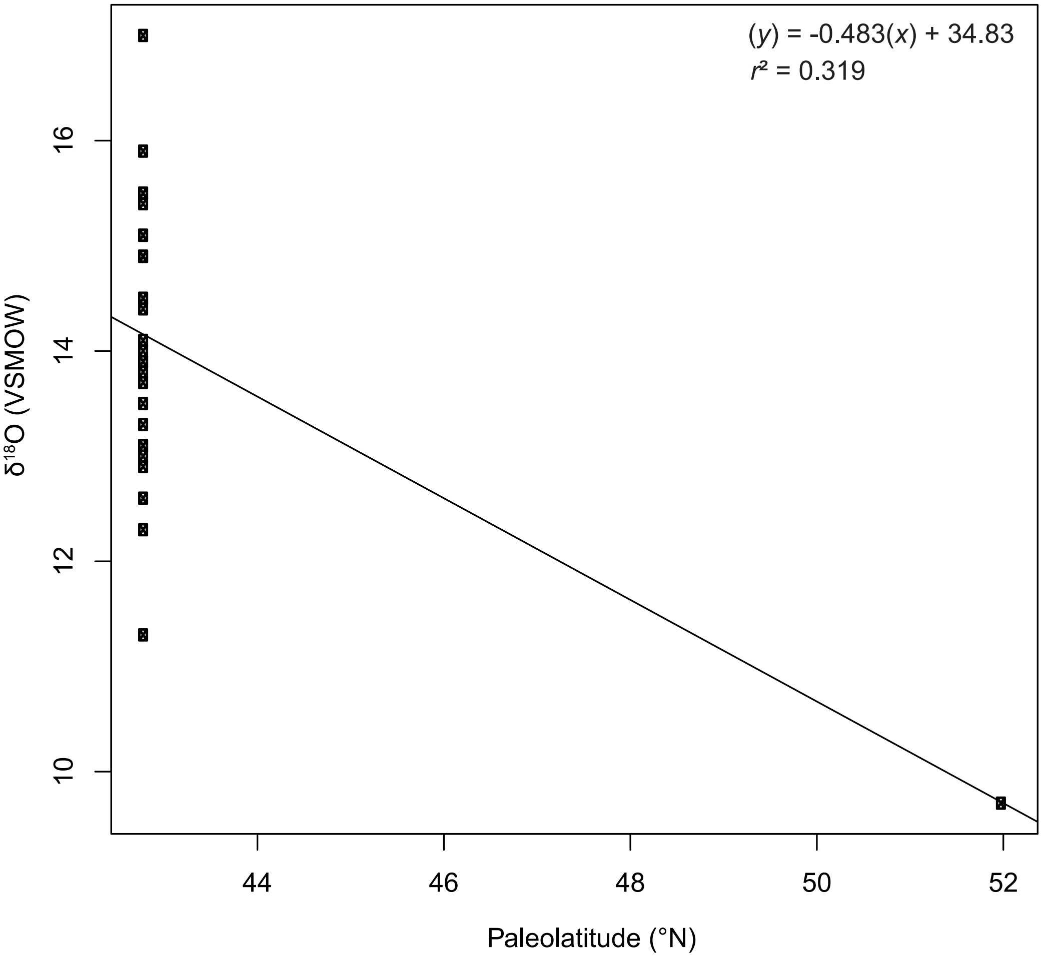
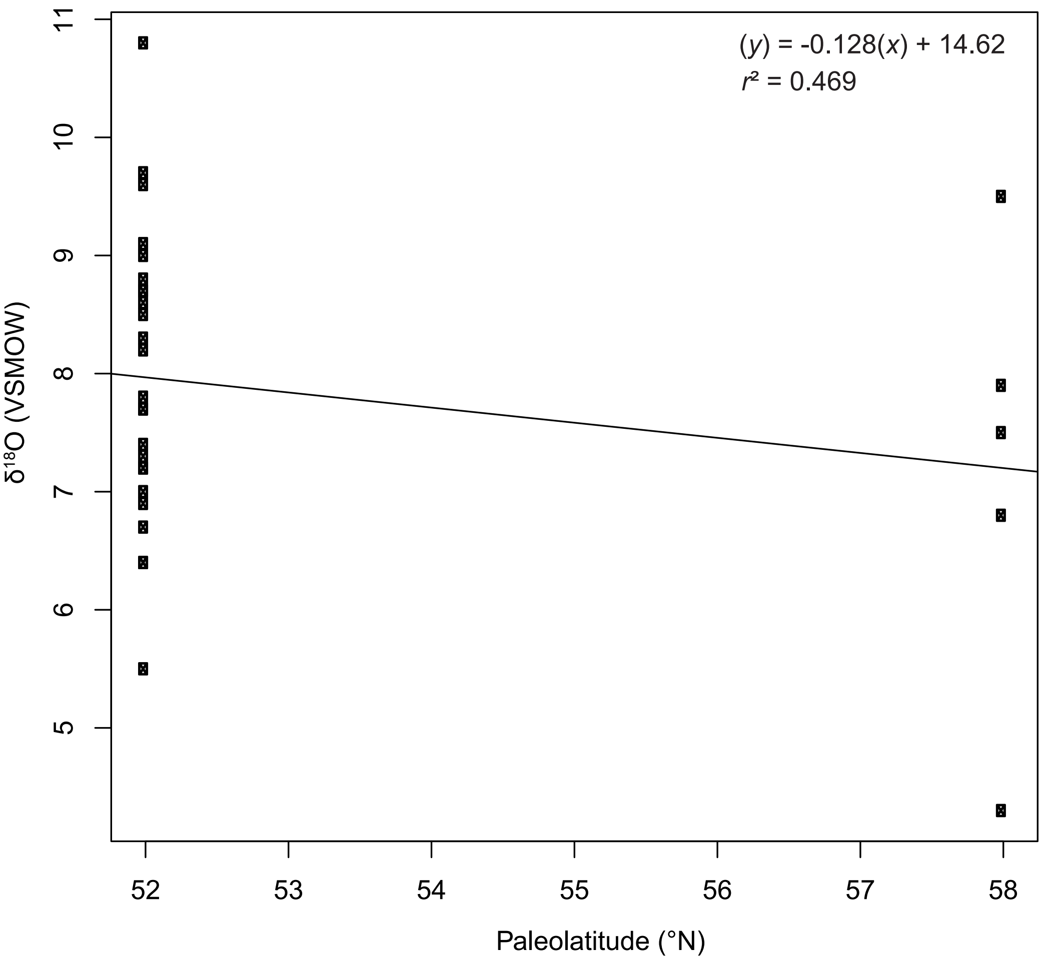


Figure 4.26.—Least squares linear regression of oxygen isotope gradient from biogenic $\delta^{18}O$ (Vienna Standard Mean Ocean Water) in earliest Tiffanian (Ti1) mammals from the Crazy Mountain Basin of southern Montana and Alberta Basin of central Alberta. The slope of the regression is not statistically significant (t-value = -1.174, p-value = 0.250). Data obtained from Rose et al. (2011, supplementary material, table DR2).



5 Summary and Conclusions

5.1 Dissertation Summary

The patterns of latest Cretaceous and early Paleogene mammalian evolution have become an important focus of study as a consequence of interest in the dramatic adaptive radiation that mammals underwent after the catastrophic events near the Cretaceous/Paleogene boundary (K/Pg boundary) (approximately 65.6 million years ago) (see e.g., Matthew, 1915; Van Valen, 1978; Archibald, 1982; Alroy, 1999; Springer et al., 2003; Wible et al., 2009; Fox and Scott, 2011). The world's richest discovered succession of mammals from this time interval, offering direct evidence of these patterns, is preserved in continental strata of North America (Cifelli et al., 2004; Lofgren et al., 2004). Throughout much of the late Mesozoic and early Cenozoic, this region was tectonically active, with the emergence of the Cordilleran orogenic fold-thrust belt and Western Interior foreland basin. Several major marine transgressions also occurred during this interval and resulted in the development of the Western Interior epicontinental seaway that bisected the continent during the Late Cretaceous (DeCelles, 2004; Miall et al 2008).

The latest Cretaceous and Paleogene are further marked by episodes of rapid climatic warming and cooling (e.g., Zachos et al., 2001) and intensive volcanism (e.g., Courtillot et al., 1988; Keller et al., 2008). Mammals were undoubtedly affected by these disturbances (e.g., Archibald, 1982, 1996, in Archibald and Fastovsky, 2004; Clemens, 2002; Wilson, 2014), however, much remains uncertain about some basic issues, including patterns of mammalian richness and evenness across North America. To better comprehend the evolutionary dynamics of mammals across the Late

Cretaceous and early Paleogene, I focused on the paleobiogeography of mammals from the Western Interior of North America.

Chapter Two tested the hypothesis that the northern and southern parts of the Western Interior of North America represented distinct biogeographic provinces during parts of the Late Cretaceous and early Paleogene (e.g., Sloan, 1969; Lillegraven, 1969; Anthony and Maas, 1990; Rowe et al., 1992; Weil, 1999; Williamson and Weil, 2008; Donohue et al., 2013) and the implications of discrete evolutionary processes possibly operating in these different regions. To accomplish this task, information on latest Cretaceous and early Paleocene mammalian fossil occurrences were compiled in a newly constructed dataset. The presence of biogeographic provinces were assessed with non-hierarchical cluster analyses, non-metric multidimensional scaling, minimum spanning trees, and simple chi-squared analyses. The results of these analyses provided little quantitative support for the presence of mammalian faunal provinciality during this interval.

The relative abundances of mammalian genera from the latest Cretaceous of North America were examined in Chapter Three. A standardized resampling approach was employed to generate assemblage-specific abundance estimates of each mammalian genus based on the faunal composition from the well-studied Type Lance local fauna from the Lance Formation of northeastern Wyoming (Clemens, 1964, 1966, 1973; Krause, 1992). Using these estimates, the faunal similarity between these assemblages was quantitatively assessed and genera that were unusually abundant or rare compared to the Type Lance were identified. The results generally reveal that eutherians were more abundant in the northern assemblages relative to the faunal composition of the Type Lance and other more southerly sites, whereas some multituberculates and marsupials are unusually rare in the northern assemblages. These findings reveal that some eutherians, especially primitive ungulates, originated and underwent some diversification and expansion during the latest Cretaceous, prior to the demise of the dinosaurs and more primitive multituberculates and metatherians. Environmental changes associated with the Late Maastrichtian Event and regression of the Western Interior epicontinental seaway (see Wilson, 2014) are suggested to have led to these changes and provided the opportunity for the expansion of eutherian mammals within these latest Cretaceous assemblages.

Finally, in Chapter Four, the latitudinal diversity gradient within latest Cretaceous and early Paleogene mammals from North America was assessed. The modern latitudinal diversity gradient (i.e., the increase in taxonomic richness from the poles to the equator) is often suggested to have been in place through most of the Phanerozoic (see e.g., Ricklefs, 1987; Crane and Lidgard, 1989; Crame, 2001; Hillebrand, 2004; Leighton, 2005; Jablonski et al., 2006). Several recent studies, however, have shown that this pattern might not be as general as previously thought (e.g., Archibald et al., 2010; Rose et al., 2011; Mannion et al. 2012). Using least-squares regression analyses, a latitudinal diversity gradient within latest Cretaceous and early Paleogene mammals is shown here to have been absent, with no statistical differences in taxonomic richness across latitude during this interval. A strong association between taxonomic richness and sampling intensity is revealed but, after mediating for the variance in sampling intensity among formations, a latitudinal diversity gradient comparable to the present is still not recovered. Unlike previous studies (e.g., Rose et al., 2011), a shallow temperature gradient during the Late Cretaceous and early Paleogene, along with more equable climates throughout much of this interval, are suggested to have led to this pattern; instability within North American mammalian communities near the K/Pg boundary could also have resulted in the lack of a latitudinal gradient.

Collectively, these studies suggest that the paleogeography and climatic changes that characterized the latest Cretaceous and early Paleogene of the Western Interior of North America resulted in complex biogeographic patterns among mammals from this interval, unlike those from earlier parts of the Late Cretaceous and those seen within modern times. These studies also underscore the value of critically assessing hypotheses concerning biogeographic patterns to better understand the interactions between mammals and their environments. The different approaches employed within these studies, including both conventional techniques (e.g., similarity indices) and more advanced ordination and clustering methods, further demonstrated the importance of quantitative analyses in these examinations. Although future attempts should be made to integrate information from outside the Western Interior of North America (see discussion below), the compilation of information on latest Cretaceous and early Paleogene mammalian fossil occurrences from the Western Interior of North America, including taxonomic, geographic, and stratigraphic data, forms a critical resource for other evolutionary analyses.

5.2 Localities outside of the Western Interior of North America

Because the available record of Late Cretaceous and early Paleogene mammalian faunas is geographically concentrated in deposits in the Western Interior of North America, the discussions in this dissertation have centered on the patterns of mammalian biogeography and evolution evinced from this region. Several discoveries of faunas outside of the Western Interior, however, offer new opportunities to reevaluate patterns of evolution among approximately contemporaneous mammalian faunas. Some of these faunas have been recovered in Virginia (Rose, 1999, 2010), Louisiana (Simpson, 1932), and South Carolina (Schoch 1998).

Perhaps the best known of these exceptions is the early Eocene Red Hot local fauna from the Gulf Coastal Plain of Mississippi (Beard, 2008; Beard and Dawson, 2009). The Red Hot local fauna samples a remarkably different ecosystem than those present in the mid-latitude Western Interior Basin during this time interval. For example, the paleolatitude of the Bighorn Basin of northern Wyoming, a basin that has yielded the most diverse and abundant early Eocene mammalian fossils, was roughly near paleolatitude 47°N, whereas that of the Red Hot local fauna of Mississippi was approximately 32°N (Harrington, 2003). The climate of the Bighorn Basin during the early Eocene was characterized as warm, with the mean annual temperatures near 20°C and mean annual precipitation near 670-683 millimeters (Kraus and Riggins, 2007). The climate of the Gulf Coastal Plain, in comparison, was tropical, with the mean annual temperature estimated to be 26-27°C and mean annual precipitation exceeding 500 centimeters (Wolfe and Dilcher, 2000).

In the most recent report, Beard and Dawson (2009) recognize the fossil remains of 33 mammalian taxa from the Red Hot local fauna, including 20 previously unknown species, and one species previously only known from early Eocene deposits in northern Europe and another previously only reported from Mongolia and China. These findings, like those previously presented by Gingerich (2003) and Bowen et al. (2002), underscore the intercontinental dispersal patterns of mammals near the Paleocene/Eocene boundary. Additionally, if the nine taxa that are considered indeterminate at the species level are disregarded, 20 of the 24 species (or roughly 83 percent) are endemics; based on these findings, Beard and Dawson (2009) suggest that substantial biogeographic provincialism was established in North America during the early Eocene. Similar to discoveries in the Bighorn Basin (Gingerich, 1989; Chester et al., 2010), Beard and Dawson (2009) also comment on the presence of several small-bodied mammals, relative to their older, late Paleocene relatives.

Middle Paleocene assemblages from the Goler Formation of the northern part of the Mojave Desert in southcentral California represent other important exceptions (e.g., McKenna, 1955, 1960; McKenna et al., 1987; Lofgren et al., 2002, 2008, 2014; Albright et al., 2009; Williamson and Lofgren, 2014). Although much remains to be studied, the assemblages from the Goler Formation were likely deposited in a near-coastal setting, with high seasonal precipitation (Torres and Gaines, 2011, 2013). Evidence based on detrital zircons recovered from fluvial deposits indicate that southern California was separated from the Western Interior during the early Paleogene (Ingersoll et al., 2013) and only four of the 20 species (just 20 percent) identified from the Goler assemblages can be confidently assigned to species known from basins in the Western Interior (Lofgren et al., 2014). Similar to the comments of Beard and Dawson (2009), Lofgren et al. (2014) and Williamson and Lofgren (2014) suggest that southern California likely represented a distinct biogeographic province during this time.

These few exceptions, documenting mammalian evolution in sometimes dramatically different ecosystems, permit detailed and thorough comparisons to contemporaneous localities in the Western Interior. These types of comparisons are fundamental to our understanding of the influence of paleogeography and climate in the evolutionary history of mammals. As noted by Lofgren et al. (2004), faunal data are needed throughout all latitudes of North America to more fully assess the shifting patterns.

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Appendix 1.—R script employed to assess compositional similarities and differences among latest Cretaceous mammalian assemblages, using resampling with replacement and the Type Lance local fauna as the reference sample.

```
##########################################
#Read in the relative abundance matrix
data<-read.csv(file.choose(),header=T,stringsAsFactors=T)

#Organize data from assemblage and occurrence matrix, including rounding
#recalibrated number of identified specimens (i.e., rNISP) to lower integer
data2<-data[,c(2:ncol(data))]
rownames(data2)<-data[,1]
data<-floor(data2)
total.occs<-sum(colSums(data))
tax.prop<-total.occs/nrow(data)
tax.site<-floor(tax.prop/ncol(data)) # rounded, too!!

stream<-stack(data)[,1]
stream<-stream+1
hist(log(stream))

#Create a list of the mammalian genera from the Type Lance local fauna that will be
#subsampled
```

```
a<-8 # column with information mammalian occurrence and abundances from the Type
#Lance local fauna
genlist<-c()
for(i in 1:nrow(data)){
 temp<-data[,a]
 genlist<-c(genlist,rep(i,temp[i]))
}

#Subsample mammalian genera from the Type Lance based on the number of taxa
#within the comparative local faunas
#Note that using site.sampled[[5]], for instance, will retrieve all iterations for the local
#fauna in the fifth column
#Set to sample 1000 times
no.samples<-1000
site.sampled<-list()
for(i in 1:ncol(data)){
 temp<-matrix(0,nrow=nrow(data),ncol=no.samples)
 for(j in 1:no.samples){
   temp2<-table(sample(genlist,sum(data[,i])))
#use replace=T if you want to compare a small site to larger things
   for(k in 1:length(temp2)){
     taxa.temp<-names(temp2[k])
     temp[as.numeric(taxa.temp),j]<-temp2[k]
```

```
   }
 }
 site.sampled[[i]]<-temp
}

#Calculate means and standard deviations for taxa and for each of the comparative
#local faunas
site.sd<-site.means<-matrix(ncol=ncol(data),nrow=nrow(data))
for(i in 1:length(site.sampled)){
 site.means[,i]<-rowMeans(site.sampled[[i]])
 site.sd[,i]<-apply(site.sampled[[i]],1,sd)
}

#Calculate the number of specimens that extend beyond the range of the null (2*SD)
#from the rNISP data
outside.con.ints<-matrix(0,nrow=nrow(data),ncol=ncol(data))
for(i in 1:nrow(data)){
 for(j in 1:ncol(data)){
   mean.temp<-site.means[i,j]
   sd.temp<-site.sd[i,j]
   data.temp<-data[i,j]
   range.temp<-c(mean.temp-sd.temp,mean.temp+sd.temp)
   if(data.temp<=range.temp[1]){
```

```
    outside.con.ints[i,j]<-data.temp-range.temp[1]
  }else if(data.temp>=range.temp[2]){
    outside.con.ints[i,j]<-data.temp-range.temp[2]
  }
 }
}

rownames(outside.con.ints)<-rownames(site.means)<-rownames(site.sd)<-
rownames(data)
colnames(outside.con.ints)<-colnames(site.means)<-colnames(site.sd)<-colnames(data)

#Write the csv files
write.csv(outside.con.ints,file="outside.con.ints.csv")
write.csv(site.means,file="site.means.csv")
write.csv(site.sd,file="site.sd.csv")
```

APPENDIX 2.—Taxonomic, Stratigraphic, and Geographic Information of Latest Cretaceous and Early Paleogene Mammalian Assemblages from the Western Interior of North America.

Table S4.1.—Occurrences of mammalian genera within Lancian local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: PP = *Pediomys* Point (Clemens and Nelms, 1993; Clemens, 1995, 2003), SC = Scollard (Lillegraven, 1969; Lillegraven and McKenna, 1986; Fox, 1989, 1994, 1997; Fox and Naylor, 2003; Case et al., 2005; Wilson and Riedel, 2010; Williamson et al., 2012), WK = Wounded Knee (Fox, 1989, 1997), GR = Gryde (Storer, 1991; Johanson, 1996a; Case et al., 2005; Williamson et al., 2012), CC = Chambery Coulee (Fox et al., 2007), LM = Little Missouri Badlands (PTRM V92067) (Hunter and Pearson, 1996; Hartman, 1999; Hunter and Archibald, 2002), PB = Pretty Butte (Hunter and Archibald, 2002), MM = Marmath (Hunter and Archibald, 2002), SB = Sunset Butte (Hunter and Pearson, 1996; Hunter and Archibald, 2002), MB = Mud Butte (Hunter and Archibald, 2002), PT3 = PTRM V89003 (Hunter and Archibald, 2002), PT4 = PTRM V89004 (Hunter and Archibald, 2002), SF = Stumpf (Hoganson et al., 1994; Murphy et al., 1995; Kielan-Jaworowska et al., 2004), MR = Miller Ranch (Hunter and Archibald, 2002), IR = Iron Lightning (Waage, 1968; Clemens et al., 1979; Kielan-Jaworowska et al., 2004), RO = Red Owl (Wilson, 1987), JP = Joe Painter (Wilson, 1983), EU = Eureka (Wilson, 1983), BH = Black Horse (Wilson, 1965; Clemens, 1966; Archibald, 1982; Fox and Naylor, 1986; Kielan-Jaworowska et al., 2004), HD = Harding County (Wilson, 1965; Sloan and Russell, 1974; Archibald, 1982; Lillegraven, 1987; Kielan-Jaworowska et al., 2004; Case et al., 2005), HCM = Hell Creek Montana (Simpson, 1927a; Clemens, 1968; Archibald, 1982; Johanson, 1996a; Wood and Clemens, 2001; Kielan-Jaworowska et al., 2004; Wilson, 2005, 2014), MT = Muddy Tork (Hunter et al., 1997), PWD = Powderville (Bryson, 1952; Clemens et al., 1979), CB = Claw Butte (Hunter and Archibald, 2002), FL = Fallon County (Clemens et al., 1979; Archibald, 1982), TL = Type Lance (Clemens, 1964, 1966, 1973; Novacek and Clemens, 1977; Krause, 1992; Case et al., 2005; Wilson and Riedel, 2010), GL = General Lance (Wilson and Riedel, 2010), GW = Greasewood Creek (Whitmore and Martin, 1986), MC = Mule Creek Junction (Whitmore, 1985), BBS = Black Butte Station (Clemens et al., 1979; Breithaupt, 1982; Donohue et al., 2013), DBH = Dumbbell Hill (Dyer, 1948; Clemens et al., 1979), HF = Hewett's Foresight (Webb, 2001), FFL = Ferris Formation Lancian (Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), PA = Pawnee (Carpenter, 1979; Diem, 1999; Wilson et al., 2010), DC = Dragon Canyon (Clemens, 1961; Cifelli and Muizon, 1998; Cifelli et al., 1999), AW = Alamo Wash (Lehman, 1981; Flynn 1986), and NM5 = New Mexico Museum of Natural History L-4005 (Williamson and Weil, 2008).

Genera	PP	SC	WK	GR	CC	LM	PB	MM	SB	MB	PT3	PT4	SF	MR	IL	RO	JP	EU	BH
Alostera	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alphadon	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0
Batodon	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bubodens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cimexomys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Cimolestes	0	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Cimolodon	1	1	1	1	0	1	0	1	1	0	1	1	0	1	0	1	0	1	0
Cimolomys	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Clemensodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Didelphodon	0	1	1	1	0	1	1	0	1	1	1	1	0	1	0	1	0	1	1
Essonodon	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glasbius	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gypsonictops	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	1	0
Hatchertherium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Leptalestes*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Leptalestes	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Meniscoessus	0	0	1	0	0	1	1	1	1	0	1	1	1	1	1	1	1	1	0
Mesodma	0	1	1	1	0	1	0	0	1	0	0	1	0	1	0	1	1	1	0
Nanocuris	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
?*Neoplagiaulax*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nortedelphys	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Paracimexomys	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parectypodus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paressonodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parikimys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pediomys	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Protalphadon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Protolambda	0	1	0	1	0	1	0	0	1	0	0	1	0	1	0	0	1	1	0
Schowalteria	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Telacodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turgidodon	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table S4.1 (continued).—Occurrences of mammalian genera within Lancian local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: PP = *Pediomys* Point (Clemens and Nelms, 1993; Clemens, 1995, 2003), SC = Scollard (Lillegraven, 1969; Lillegraven and McKenna, 1986; Fox, 1989, 1994, 1997; Fox and Naylor, 2003; Case et al., 2005; Wilson and Riedel, 2010; Williamson et al., 2012), WK = Wounded Knee (Fox, 1989, 1997), GR = Gryde (Storer, 1991; Case et al., 2005; Williamson et al., 2012), CC = Chambery Coulee (Fox et al., 2007), LM = Little Missouri Badlands (PTRM V92067) (Hunter and Pearson, 1996; Hartman, 1999; Hunter and Archibald, 2002), PB = Pretty Butte (Hunter and Archibald, 2002), MM = Marmath (Hunter and Archibald, 2002), SB = Sunset Butte (Hunter and Pearson, 1996; Hunter and Archibald, 2002), MB = Mud Butte (Hunter and Archibald, 2002), PT3 = PTRM V89003 (Hunter and Archibald, 2002), PT4 = PTRM V89004 (Hunter and Archibald, 2002), SF = Stumpf (Hoganson et al., 1994; Murphy et al., 1995; Kielan-Jaworowska et al., 2004), MR = Miller Ranch (Hunter and Archibald, 2002), IR = Iron Lightning (Waage, 1968; Clemens et al., 1979; Kielan-Jaworowska et al., 2004), RO = Red Owl (Wilson, 1987), JP = Joe Painter (Wilson, 1983), EU = Eureka (Wilson, 1983), BH = Black Horse (Wilson, 1965; Clemens, 1966; Archibald, 1982; Fox and Naylor, 1986; Kielan-Jaworowska et al., 2004), HC = Harding County (Wilson, 1965; Sloan and Russell, 1974; Archibald, 1982; Lillegraven, 1987; Kielan-Jaworowska et al., 2004; Case et al., 2005), HCM = Hell Creek Montana (Simpson, 1927a; Clemens, 1968; Archibald, 1982; Johanson, 1996a; Wood and Clemens, 2001; Kielan-Jaworowska et al., 2004; Wilson, 2005, 2014), MT = Muddy Tork (Hunter et al., 1997), PWD = Powderville (Bryson, 1952; Clemens et al., 1979), CB = Claw Butte (Hunter and Archibald, 2002), FL = Fallon County (Clemens et al., 1979; Archibald, 1982), TL = Type Lance (Clemens, 1964, 1966, 1973; Krause, 1992; Case et al., 2005; Wilson and Riedel, 2010), GL = General Lance (Wilson and Riedel, 2010), GW = Greasewood Creek (Whitmore and Martin, 1986), MC = Mule Creek Junction (Whitmore, 1985), BBS = Black Butte Station (Clemens et al., 1979; Breithaupt, 1982; Donohue et al., 2013), DBH = Dumbbell Hill (Dyer, 1948; Clemens et al., 1979), HF = Hewett's Foresight (Webb, 2001), FFL = Ferris Formation Lancian (Eberle and Lillegraven, 1998a, 1998b; Lillegraven and Eberle, 1999), PA = Pawnee (Carpenter, 1979; Diem, 1999; Wilson et al., 2010), DC = Dragon Canyon (Clemens, 1961; Cifelli and Muizon, 1998; Cifelli et al., 1999), AW = Alamo Wash (Lehman, 1981; Flynn 1986), and NM5 = New Mexico Museum of Natural History L-4005 (Williamson and Weil, 2008).

Genera	HD	HCM	MT	PWD	CB	FL	TL	GL	GW	MC	BBS	DBH	HF	FFL	PA	DC	AW	NM5
Alostera	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alphadon	0	1	0	0	1	0	1	0	0	0	1	1	1	0	0	1	1	0
Batodon	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Bubodens	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cimexomys	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0
Cimolestes	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
Cimolodon	0	1	0	0	1	0	1	0	0	1	1	1	1	1	0	0	0	0
Cimolomys	0	1	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0
Clemensodon	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Didelphodon	0	1	1	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0
Essonodon	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0
Glasbius	0	1	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	1
Gypsonictops	0	1	0	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0
Hatchertherium	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
?*Leptalestes*	0	1	0	0	1	0	1	0	0	0	0	0	1	0	1	0	0	0
Leptalestes	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0
Meniscoessus	1	0	1	1	1	1	1	0	0	1	0	0	1	1	1	0	1	0
Mesodma	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	1	1	0
Nanocuris	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
?*Neoplagiaulax*	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nortedelphys	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
Paracimexomys	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
Parectypodus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Paressonodon	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Parikimys	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
Pediomys	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Protalphadon	0	1	0	0	1	0	1	0	0	0	0	0	1	1	1	0	0	0
Protolambda	0	1	1	0	1	0	1	0	0	1	0	0	1	0	1	1	0	0
Schowalteria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Telacodon	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Turgidodon	0	1	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0

Table S4.2.—Occurrences of mammalian genera within early Puercan (Pu1) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: FR = Frenchman-1 (Johnston 1980; Fox, 1988, 1990a, 1995, 1997), LF = Long Fall (Johnston and Fox, 1984; Fox, 1988, 1990a, 1997; Fox and Youzwyshyn, 1994), PC = Pine Cree (Russell, 1974; Van Valen, 1978; Johnston and Fox, 1984), FF = French Fry (Fox, 2002), HH = Hell's Hollow (Archibald, 1981, 1982; Archibald et al., 1983a, 1983b), MCK = McKeever (Archibald, 1982; Archibald et al., 1983a, 1983b), MCG = McGuire (Lofgren, 1995), FF1 = Ferris Fromation Pu1 (Eberle and Lillegraven, 1998a, 1998b; Eberle, 1999; Lillegraven and Eberle, 1999), ML = Mantua Lentil (Jepsen, 1930, 1940; Van Valen, 1978), LDY = Leidy (Van Valen, 1978), LTT = Littleton (Middleton, 1982, 1983; Williamson, 1996; Middleton and Dewar, 2004), NCL = Nicole's Mammal Jaw locality (DMNH locality 2557) (Eberle, 2003), DOX = Denver Oxyclaenodon (DMNH locality 299) (Eberle, 2003), SB = Spigot Bottle (Hunter and Archibald, 2002; Zhang, 2009; Archibald et al., 2011), LLJS = Lane's Little Jaw Site (Kelly, 2014), and MM = Merle's Mecca (Hunter and Hartman, 2003).

Genera	FR	LF	PC	FF	HH	MCK	MCG	FF1	ML	LDY	LTT	NCL	DOX	SB	LLJS	MM
Acheronodon	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Albertatherium	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Alphadon	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Alticonus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Ampliconus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Auraia	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Baioconodon	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0
Batodon	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Catopsalis	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0
Carcinodon	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cimexomys	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0
Cimolestes	1	1	0	0	1	1	0	0	0	0	0	0	0	1	1	0
Cimolodon	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Cimolomys	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Conacodon	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Didelphodon	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Earendil	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Eoconodon	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Glasbius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Gypsonictops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
?*Kimbetohia*	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Leptalestes	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
?*Leptalestes*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Maiorana	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Meniscoessus	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Mesodma	1	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Microcosmodon	1	1	0	1	1	0	0	1	1	0	1	0	0	1	1	0
Microcosmodontidae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Mimatuta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nortedelphys	0	0	0	0	1	1	0	1	1	1	0	0	0	0	0	0
Oxyacodon	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
"*Oxyclaenus*"	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0

Oxyprimus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Palaeoungulatum	0	1	0	0	1	0	0	1	1	0	1	0	0	0	0	0
Paracimexomys	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Paranyctoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pediomys	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Peradectes	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Palaeoryctidae	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0
Periptychidae	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Procerberus	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Prodiacodon	0	1	0	0	1	0	0	0	0	0	1	0	0	0	1	0
Protalphadon	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Protolambda	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Protungulatum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
Ragnarok	1	1	0	0	0	1	0	1	0	0	0	1	0	1	0	0
Stygimys	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	0
Turgidodon	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Xyronomys	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0

Table S4.3.—Occurrences of mammalian genera within middle Puercan (Pu2) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: RAV = Rav-W1 horizon (Johnston and Fox, 1984; Fox, 1988, 2005; Fox et al., 2010a; Fox and Scott, 2011), WNT = Wintering Hills (Rankin and Fox, 2007; Fox et al., 2014), PITA = PITA Flats (Hunter, 1999; Hunter and Hartman, 2003), GT = Gas Tank (Spieker, 1960; Van Valen, 1978; Robison, 1986; Eberle, 1996; Lofgren et al., 2005, 2012), CB = Corral Bluffs, Jimmy Camp Creek, and West Bijou Creek (Middleton ,1982, 1983; Williamson, 1996, Eberle, 1999), FF2 = Ferris Formation Pu2 (Eberle and Lillegraven, 1998a, 1998b; Eberle, 1999; Lillegraven and Eberle, 1999), WFK = West Flank Kimbeto Wash (Williamson, 1996; Williamson and Brusatte, 2013), EFK = East Flank Kimbeto Wash (Lucas and Williamson, 1993; Williamson, 1996; Lucas, 2011; Williamson and Carr, 2012; Williamson and Brusatte, 2013), BTW = Betonnie Tsosie Wash (Reynolds, 1936; Williamson, 1996; Clemens and Williamson, 2005; Williamson and Carr, 2012; Williamson and Brusatte, 2013).

Genera	RAV	WNT	PITA	GT	CB	FF2	WFK	EFK	BTW
Alticonus	0	0	0	0	0	1	0	0	0
Alveugna	0	0	0	0	0	1	0	0	0
Ampliconus	0	0	0	0	0	1	0	0	0
Anisonchus	1	1	0	1	1	0	0	0	0
Baioconodon	1	0	1	0	0	1	0	0	0
Betonnia	0	0	0	0	0	0	1	0	1
Bomburodon	0	0	0	0	0	0	0	1	1
Bubogonia	1	0	0	0	0	0	0	0	1
Carcinodon	1	1	1	0	0	0	0	1	1
"*Carcinodon*"	1	0	0	0	0	0	0	1	1
Catopsalis	1	0	0	0	0	1	0	0	0
Chacopterygus	0	0	0	0	0	0	1	0	0
Cimexomys	1	0	0	0	0	0	0	0	0
Cimolestes	1	0	0	0	0	0	0	0	0
Choeroclaenus	0	0	0	0	0	0	1	1	0
Conacodon	0	0	0	1	1	1	1	1	1
Desmatoclaenus	0	1	0	1	1	0	0	1	0
Dissacus	0	0	0	0	0	0	0	1	0
Ectoconus	0	0	0	1	1	1	1	1	1
Ectypodus	1	1	0	0	0	1	0	0	0
Eoconodon	1	0	1	0	0	1	1	1	1
Escatepos	0	0	0	0	0	0	0	0	1
Gillisonchus	0	0	0	0	0	0	1	1	1
Haploconus	0	0	0	1	0	0	0	0	0
Hemithlaeus	0	0	0	0	0	0	1	1	1
Kimbetohia	0	0	0	1	0	0	0	0	1
Litalestes	1	0	0	1	0	0	0	0	0
Litomylus	1	0	0	0	0	0	0	0	0
Loxolophus	1	1	1	1	1	1	1	1	1
Mesodma	1	1	0	0	0	1	0	0	0
Microcosmodon	1	0	0	0	0	0	0	0	0
Mioclaenidae	0	0	0	0	1	0	0	0	0

Mimatuta	0	0	0	0	0	1	0	0	0
Mithrandir	0	0	0	0	0	1	0	0	0
Neoplagiaulax	1	0	1	0	0	0	0	0	0
Neoplagiaulacidae	0	0	0	0	1	0	0	0	0
Onychodectes	0	0	1	0	0	0	1	0	0
Oxyacodon	1	0	1	1	0	1	0	0	1
"*Oxyclaenus*"	0	1	1	1	1	0	0	0	0
Palaeoryctidae	0	1	0	0	0	0	0	0	0
Pandemonium	0	1	0	0	0	0	0	0	0
Pantolestidae	0	1	0	0	0	0	0	0	0
Parectypodus	1	1	0	0	0	0	0	0	0
Peradectes	0	0	0	0	0	0	1	0	1
Periptychus	0	0	0	1	1	1	1	1	1
Platymastus	0	0	0	0	0	0	0	0	1
Procerberus	1	0	0	0	0	0	0	0	0
Prodiacodon	1	1	0	0	0	0	0	0	1
Promioclaenus	0	0	0	1	0	1	0	0	0
Protungulatum	0	0	0	0	0	1	0	0	0
Ptilodus	1	0	0	1	0	1	0	0	0
Ptilodontidae	0	1	0	0	0	0	0	0	0
Puercolestes	0	0	0	0	0	0	1	0	1
Purgatorius	1	1	0	0	0	0	0	0	0
Ravenictis	1	0	0	0	0	0	0	0	0
Robertschochia	0	0	0	0	0	0	0	1	0
Stygimys	1	0	1	1	0	0	0	0	0
Taeniolabis	0	0	0	1	0	0	0	0	0
Tinuviel	0	0	1	0	0	0	0	0	0
Tiznatzinia	0	0	0	0	0	0	0	0	1
Wortmania	0	0	0	0	0	0	1	0	1
Xyronomys	1	0	0	0	0	0	0	0	0

Table S4.4.—Occurrences of mammalian genera within late Puercan (Pu3) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: CP = Croc Pot (Fox, 1990a, 2005), GRB = Garbani Channel and Purgatory Hill (Van Valen and Sloan, 1965; Clemens, 1974, 2002, 2004, 2006, 2010, 2013, 2015; Novacek, 1977; Simmons, 1987; Van Valen, 1994; Weil, 1998), BT = Bechtold (Simmons, 1987), FF3 = Ferris Formation Pu3 (Eberle and Lillegraven, 1998a, 1998b; Eberle, 1999; Lillegraven and Eberle, 1999), WGN = Wagonroad (Gazin, 1941; Tomida and Butler, 1980; Robison, 1986; Cifelli et al., 1995; Williamson, 1996; Eberle, 1999), DNZ = De-na-zin Wash (AMNH locality 2, upper fossil level) (Williamson, 1996; Williamson and Carr, 2012; Williamson and Brusatte, 2013), and WW = Willow Wash (Williamson and Weil, 2011; Williamson et al., 2011).

Genera	CP	GRB	BCHT	FF3	WGN	DNZ	WW
Anisonchus	1	1	0	0	1	0	0
Baioconodon	1	1	0	1	0	0	0
Besseocetor	0	0	0	0	1	0	0
Betonnia	0	0	0	0	0	0	1
Bomburodon	0	0	0	0	0	1	0
Bubogonia	0	1	0	0	0	1	0
"*Carcinodon*"	1	1	0	1	0	1	0
Catopsalis	1	1	0	0	0	0	0
Chacomylus	0	0	0	0	0	0	1
Choeroclaenus	0	0	0	0	0	1	0
Cimexomys	1	1	0	0	0	0	0
Cimolestes	1	1	0	0	0	0	0
Conacodon	0	0	0	1	1	1	0
Desmatoclaenus	1	0	0	0	1	0	0
Ectoconus	0	0	0	1	1	1	0
Ectypodus	0	1	0	1	0	0	0
Ellipsodon	0	0	0	0	1	0	0
Eoconodon	0	1	0	0	0	1	0
Eucosmodon	0	1	0	0	0	0	0
Gillisonchus	0	0	0	0	0	1	0
Haploconus	0	0	0	0	1	0	0
Litomylus	0	1	0	0	0	0	0
Loxolophus	1	1	0	1	1	1	0
Mesodma	1	1	0	0	0	0	0
Microcosmodon	0	1	0	0	0	0	0
Mithrandir	0	0	0	1	0	0	0
Mixodectidae	0	0	0	0	1	0	0
Neoplagiaulax	0	1	0	0	0	0	0
Onychodectes	0	0	0	0	1	1	0
Oxyacodon	0	1	0	1	0	1	0
Oxyclaenus	0	0	0	1	1	0	0
Oxyprimus	1	0	0	0	0	0	0

Pandemonium	0	1	0	0	0	0	0
Parectypodus	1	1	0	0	0	0	0
Peradectes	0	1	0	1	0	1	1
Periptychus	0	0	0	0	1	1	0
Procerberus	1	1	0	0	0	0	0
Prochetodon	1	0	0	0	0	0	0
Prodiacodon	1	1	0	0	0	0	0
Promioclaenus	0	0	0	1	0	1	0
Protoselene	0	0	0	1	0	0	0
Protungulatum	0	0	0	1	0	0	0
Ptilodus	0	1	0	1	0	0	0
Ptilodontidae	0	0	0	0	1	0	0
Puercolestes	0	0	0	0	0	1	1
Purgatorius	0	1	0	0	0	0	0
Stygimys	1	1	0	0	0	0	0
Taeniolabis	1	1	1	1	1	0	0
Tiznatzinia	0	0	0	0	0	1	0
Wortmania	0	1	0	0	0	1	0
Xyronomys	1	1	0	0	0	0	0

Table S4.5.—Occurrences of mammalian genera within late Torrejonian (To1) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: FC = Farrand Channel (Archibald 1982; Clemens and Wilson 2009), HF = Horsethief Canyon (Archibald 1982; Clemens and Wilson 2009), S65 = Simpson locality 65 (Simpson 1937b; Sloan 1987), S09 = Simpson locality 9 (Simpson 1937b; Sloan 1987), S78 = Simpson locality 78 (Simpson 1937b; Sloan 1987), DRG = Dragon localities (Gazin 1938, 1939, 1941; MacIntyre, 1966; Tomida and Butler 1980; Tomida, 1981; Williamson 1996; Lucas et al., 1997), KTZ = Kutz Canyon (NMMNH L-2659 and 2660) (Williamson 1996), DNT = De-na-zin Wash (AMNH locality 3) (Williamson 1996), N692 = NMMNH L-692 (Williamson 1996), BTT = Betonnie Tsosie Wash ('lowest Torrejonian') (Williamson 1996), DG = Dogie locality (LSUMG VL-108) (Standhardt 1986; Williamson 1996) , and TT = Tom's Top (LSUMG VL-111) (Standhardt 1986; Williamson 1996).

Genera	FC	HF	S65	S09	S78	DRG	KTZ	DNT	N692	BTT	DG	TT
Acmeodon	0	0	0	0	0	1	0	0	0	0	0	0
Anisonchus	1	1	0	0	0	1	0	0	1	0	0	0
Aphronorus	0	0	0	0	0	1	0	0	0	0	0	0
Baioconodon	0	0	0	0	0	0	0	0	0	0	1	0
Bessoecetor	0	0	0	0	0	1	0	0	0	0	0	0
Bomburodon	0	0	0	0	0	0	0	0	0	0	1	0
Bryanictis	0	0	0	0	0	1	0	0	0	0	0	0
Catopsalis	0	0	0	0	0	1	0	0	0	0	0	0
Chriacus	1	1	0	0	1	1	0	0	0	0	0	0
Cimolestidae	1	0	0	0	0	0	0	0	0	0	0	0
Cimolodon	0	0	0	0	0	0	0	0	0	0	1	0
Claenodon	0	0	0	1	0	0	0	0	0	0	0	0
Conoryctella	0	0	0	0	0	1	0	0	0	0	0	0
Desmatoclaenus	0	0	0	0	0	1	0	0	0	0	0	0
Didelphidae	0	0	0	0	0	1	0	0	0	0	0	0
Draconodus	0	0	0	0	0	1	0	0	0	0	0	0
Dracontolestes	0	0	0	0	0	0	0	0	0	0	0	0
Deuterogonodon	0	0	0	0	0	0	0	0	0	1	0	0
Ellipsodon	0	0	0	0	0	1	0	0	0	0	0	0
Eoconodon	1	1	0	0	0	0	0	0	0	0	1	0
Eucosmodontidae	1	0	0	0	0	0	0	0	0	0	0	0
Gelastops	0	0	0	0	0	0	0	0	0	0	1	0
Goniacodon	0	0	0	0	0	1	0	0	0	0	0	0
Haploconus	0	0	0	0	0	1	0	0	0	0	1	0
Litaletes	1	0	0	0	0	1	0	0	0	0	0	0
Loxolophus	0	0	0	0	0	1	0	0	0	0	0	0
Mesodma	1	1	0	0	0	0	0	0	0	0	0	0
Microcosmodon	0	1	0	0	0	0	0	0	0	0	0	0
Mimotricentes	1	1	0	1	0	1	0	0	1	0	0	0
Mioclaenus	0	0	0	0	0	0	1	0	1	1	0	0
Mixodectes	0	0	0	0	0	0	0	0	0	0	0	1
Mixodectidae	0	0	0	0	0	1	0	0	1	0	0	0

Myrmecoboides	0	0	0	0	0	0	0	0	0	0	0	0
Neoplagiaulax	1	1	0	0	0	0	0	0	0	0	0	0
Oxyclaenus	1	1	0	0	0	1	0	0	0	0	0	0
Oxytomodon	0	1	0	0	0	1	0	0	0	0	0	0
Palaechthon	0	0	0	0	0	1	0	0	1	0	0	1
Pantolestidae	0	0	0	0	0	1	0	0	0	0	0	0
Parectypodus	0	0	0	0	0	1	0	0	0	0	0	0
Paromomys	1	1	0	0	0	1	0	0	1	0	0	0
Peradectes	0	0	0	0	0	0	0	0	0	0	1	0
Periptychus	0	0	0	0	0	1	1	1	1	1	1	0
Prodiacodon	1	0	0	0	0	0	0	0	1	0	0	0
Promioclaenus	1	0	0	0	0	1	0	0	1	0	0	0
Prothryptacodon	1	0	0	0	0	0	0	0	0	0	0	0
Protictis	0	0	0	0	0	1	1	0	0	0	1	1
Protoselene	0	0	0	0	0	1	0	0	1	0	0	0
Ptilodus	0	0	1	0	0	1	0	0	0	0	1	0
?Purgatoriidae A	0	1	0	0	0	0	0	0	0	0	0	0
?Purgatoriidae B	1	1	0	0	0	0	0	0	0	0	0	0
Stygimys	0	0	0	0	0	0	0	0	0	0	0	1
Stylinodontidae	0	0	0	0	0	1	0	0	0	0	0	0
Tetraclaenodon	0	0	0	1	0	0	1	0	0	0	0	0
Triisodon	0	0	0	0	0	0	1	0	0	0	0	0
Triisodontidae	1	0	0	0	0	0	0	0	0	0	0	0
Viridomys	0	0	0	0	0	0	0	0	0	0	1	0

Table S4.6.—Occurrences of mammalian genera within middle Torrejonian (To2) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: WHO = Who Nose? (Scott, 2003, 2010; Scott and Fox, 2005), EDW = Edworthy Park (Fox et al., 2010b), BSP = Bearspaw localities (Scott et al., 2013), BRW = Brown Ranch (Hunter 1999; Clemens and Wilson 2009), GDL = Gidley (Simpson 1937b; Rose 1981; Krause, 1987), SBL = Siberling (Simpson 1937b; Rose 1981), SW = Swain Quarry (Rigby, 1980; Johanson, 1996b), RB = Rock Bench Quarry (Jepsen 1930, 1940; Rose 1981), KTZ = Kutz Canyon (AMNH Locality 'Sec. 3, T27N, R11W', KU locality 4) (Taylor, 1981; Williamson 1996; Lucas et al., 1997; Silcox and Williamson, 2012), BGP = ‘Big Pocket’ (KU locality 13) (Williamson 1996), AMA = AMNH localities ‘1 or 2 miles west of Angel Peak’ (Williamson 1996), NM1482 = NMMNH L-1482 (Williamson 1996), GLL = Gallegos Canyon, AMNH Locality 1 (Lucas, 1984; Williamson 1996; Lucas et al., 1997; Williamson and Lucas, 1997), KMB8 = Head of Kimbeto Wash (AMNH locality 8 [in part], KU locality 9 ['Little Pocket']) (Williamson 1996), S44 = 44 Store localities low and high (AMNH locality 9 [in part?]) (Williamson 1996), ESC = Escavada Wash (AMNH locality 14 [in part, lower horizon]) (Williamson 1996), T93 = Torrejon Wash (NMMNH L-2693 and 2714) (Williamson 1996), T09 = Torrejon Wash (NMMNH L-2709) (Williamson 1996), T24 = East Branch of Torrejon Wash (NMMNH L-2724, AMNH locality 11 [in part?]) (Williamson 1996), T11 = East Branch of Torrejon Wash (AMNH locality 11 lower horizon) (Williamson 1996), MDC = Mesa de Cuba and Mesa Portales (AMNH localities

222, 226, 229, and 230) (Williamson 1996; Silcox and Williamson, 2012), and MDD = Middle Peak and Alligator Alley (TMM V40147) (Standhardt 1986; Williamson 1996).

Genera	WHO	EDW	BSP	BRW	GDL	SBL	SW	RB	KTZ	BGP	AMA	NM1482
Acheronodon	1	0	0	0	0	0	0	0	0	0	0	0
Acmeodon	0	0	0	0	0	0	1	0	0	1	1	0
Alopocosmodon	0	0	1	0	0	0	0	0	0	0	0	0
Anconodon	1	0	1	0	1	0	0	1	0	0	0	0
Ankalagon	0	0	0	0	0	0	0	0	0	0	0	0
Anisonchus	0	0	0	0	1	0	1	1	1	1	1	0
Anisazia	0	0	0	0	0	0	0	0	0	0	0	0
Aphronorus	1	0	1	0	0	1	0	1	0	0	0	0
Arctocyon	1	0	1	0	0	0	1	0	0	0	1	1
Baiotomeus	1	0	0	0	0	0	0	0	0	0	0	0
Bessoecetor	1	0	1	0	0	1	1	0	0	0	0	0
Boreocyon	1	0	0	0	0	0	0	0	0	0	0	0
Bryanictis	0	0	1	0	1	1	0	1	0	1	0	0
Catopsalis	0	0	0	0	0	0	0	1	0	0	0	0
Chriacus	1	0	1	0	0	0	1	1	1	1	1	1
Claenodon	0	0	0	0	1	0	0	1	0	0	0	0
Conoryctella	0	0	0	1	0	0	0	0	1	1	0	0
Conoryctes	0	0	0	0	0	1	0	1	0	0	1	0
Coriphagus	0	0	0	0	0	1	0	1	1	1	0	0
Deltatherium	0	0	0	0	0	0	0	0	1	1	1	1
Deuterogonodon	0	0	0	0	0	0	0	0	1	1	1	0
Didymictus	0	0	0	0	0	0	0	0	0	0	0	0
Dissacus	0	0	0	1	0	1	1	1	0	0	0	0
Ectypodus	1	0	0	0	0	1	1	0	0	0	0	0
Edworthia	0	1	0	0	0	0	0	0	0	0	0	0
Ellipsodon	0	0	0	0	0	1	0	0	0	1	0	0
Elpidophorus	1	0	1	0	0	1	0	0	0	0	0	0
Elphidotarsius	0	0	0	0	1	0	0	0	0	0	0	0
Eucosmodon	0	0	0	0	0	1	0	1	0	0	0	0
Eudaemonema	0	0	1	0	1	1	0	1	0	0	0	0
Gelastops	1	0	0	0	1	1	1	1	0	0	0	0
Goniacodon	0	0	1	0	0	0	1	1	1	1	1	1

Haplaletes	0	0	0	0	1	0	1	1	0	1	0	0
Haploconus	0	0	0	0	0	0	1	0	1	1	1	0
Huerfanodon	0	0	0	0	0	0	0	0	0	0	0	0
Ignacius	1	0	1	0	0	0	0	1	0	0	0	0
Intyrictis	0	0	0	0	0	0	1	0	0	0	0	1
Jepsenella	0	0	0	0	1	0	1	1	0	0	0	0
Krauseia	1	0	0	0	0	0	0	0	0	0	0	0
Leptacodon	0	0	0	0	0	0	1	0	0	0	0	0
?Leptacodon	1	0	0	0	0	0	0	1	0	0	0	0
Limaconyssus	1	0	0	0	0	0	0	0	0	0	0	0
Litaletes	0	0	0	0	1	0	1	1	0	0	0	0
Litomylus	1	0	0	0	1	0	1	1	0	0	1	0
Mckennatherium	1	0	0	0	1	0	1	1	0	0	0	0
Metachriacus	0	0	0	0	0	1	0	0	0	0	0	0
Mesodma	1	0	0	0	0	0	0	0	0	0	0	0
Microclaenodon	0	0	0	0	0	0	0	1	1	1	0	0
Mimetodon	1	0	0	0	1	0	0	1	0	0	0	0
Mimotricentes	0	0	0	0	0	1	1	1	1	1	1	0
Mioclaenus	0	0	0	0	0	0	0	0	1	1	1	0
Mixodectes	0	0	0	0	0	0	1	0	1	1	1	1
Myrmecoboides	0	0	0	0	0	0	1	1	0	0	0	0
Navajovius	1	0	0	0	0	0	0	0	0	0	0	0
Neoplagiaulax	1	0	0	0	0	0	1	0	0	0	0	0
Palaechthon	0	0	0	0	0	1	1	0	1	1	0	0
Palaeictops	0	0	0	0	0	0	0	1	0	0	0	0
Palaeoryctes	0	0	0	0	0	0	1	0	0	1	0	0
Palaeoryctidae	1	0	0	0	0	0	0	0	0	0	0	0
Palenochtha	1	0	0	0	1	0	1	1	0	0	0	0
Paleotomus	1	0	0	0	0	0	1	0	0	0	0	0
Pantolambda	0	0	0	0	0	0	0	1	1	0	0	1
Pararyctes	1	0	0	0	0	0	0	0	0	0	0	0
Parectypodus	1	0	1	0	0	0	0	0	0	0	0	0
Paromomys	0	0	0	0	1	1	1	1	0	0	0	0

Pentacodon	0	0	0	0	0	0	0	0	1	1	1	0
Peradectes	0	0	0	0	0	0	0	0	0	1	0	1
Periptychus	0	0	0	0	0	0	1	0	1	1	1	0
Phenacodus	0	0	0	0	0	0	0	0	0	0	0	0
Picrodus	1	0	0	0	1	1	1	1	0	0	0	0
Plesiolestes	1	0	1	0	0	0	0	1	0	0	0	0
Ptilodus	1	0	1	0	0	1	1	1	0	0	0	0
Presbyteria	1	0	0	0	0	0	0	0	0	0	0	0
Procerberus	1	0	0	0	0	0	0	0	0	0	0	0
Prodiacodon	1	0	0	0	0	0	1	0	0	1	1	0
Promioclaenus	1	0	1	0	1	0	1	1	1	1	1	0
Pronothodectes	1	0	1	0	0	0	0	1	0	0	0	0
Prothryptacodon	1	0	1	0	0	0	1	0	0	0	0	0
Protogonodon	0	0	0	0	0	0	1	0	0	0	0	0
Protoselene	0	0	0	0	0	0	0	0	1	1	1	1
Protictis	1	0	0	0	1	1	1	1	1	1	1	0
Psittacotherium	0	0	0	0	0	1	0	0	1	1	1	1
Psydronyctia	1	0	0	0	0	0	0	0	0	0	0	0
Simpsonictis	1	0	0	0	1	0	1	1	0	0	0	0
Stygimys	1	0	1	0	0	0	0	1	0	0	0	0
Swaindelphys	0	0	0	0	0	0	1	0	0	0	0	0
Taeniodonta	0	0	0	0	0	0	0	0	0	0	0	0
Tetraclaenodon	0	0	1	0	1	1	1	1	1	1	1	1
Torrejonia	1	0	0	0	0	0	0	0	0	0	0	0
Tricentes	0	0	0	0	1	0	0	1	0	0	0	0
Triisodon	0	0	0	0	0	0	0	0	1	1	0	0
Unuchinia	1	0	0	0	0	0	0	0	0	0	0	0
Xanclomys	0	0	0	0	0	0	1	0	0	0	0	0
Xyronomys	1	0	0	0	0	0	1	0	0	0	0	0

Table S4.6 (continued).—Occurrences of mammalian genera within middle Torrejonian (To2) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: WHO = Who Nose? (Scott, 2003, 2010; Scott and Fox, 2005), EDW = Edworthy Park (Fox et al., 2010b), BSP = Bearspaw localities (Scott et al., 2013), BRW = Brown Ranch (Hunter 1999; Clemens and Wilson 2009), GDL = Gidley (Simpson 1937b; Rose 1981; Krause, 1987), SBL = Siberling (Simpson 1937b; Rose 1981), SW = Swain Quarry (Rigby, 1980; Johanson, 1996b), RB = Rock Bench Quarry (Jepsen 1930, 1940; Rose 1981), KTZ = Kutz Canyon (AMNH locality 'Sec. 3, T27N, R11W', KU locality 4) (Taylor, 1981; Williamson 1996; Lucas et al., 1997), BGP = 'Big Pocket' (KU locality 13) (Williamson 1996), AMA = AMNH localities '1 or 2 miles west of Angel Peak' (Williamson 1996; Meehan and Wilson, 2002), NM1482 = NMMNH L-1482 (Williamson 1996), GLL = Gallegos Canyon (AMNH locality 1) (Lucas, 1993; Williamson 1996; Lucas et al., 1997; Williamson and Lucas, 1997), KMB8 = Head of Kimbeto Wash (AMNH locality 8 [in part], KU locality 9 ['Little Pocket']) (Williamson 1996), S44 = 44 Store localities low and high (AMNH locality 9 [in part?]) (Williamson 1996), ESC = Escavada Wash (AMNH Locality 14 [in part, lower horizon]) (Williamson 1996), T93 = Torrejon Wash (NMMNH L-2693 and 2714) (Williamson 1996), T09 = Torrejon Wash (NMMNH L-2709) (Williamson 1996), T24 = East Branch of Torrejon Wash (NMMNH L-2724, AMNH locality 11 [in part?]) (Williamson 1996), T11 = East Branch of Torrejon Wash (AMNH locality 11 lower horizon) (Williamson 1996), MDC = Mesa de Cuba and Mesa Portales

(AMNH localities 222, 226, 229, and 230) (Williamson 1996), and MDD = Middle Peak and Alligator Alley (TMM V40147) (Standhardt 1986; Williamson 1996).

Genera	GLL	KMB8	S44	ESC	T93	T09	T24	T11	MDC	MDD
Acheronodon	0	0	0	0	0	0	0	0	0	0
Acmeodon	0	0	0	0	0	0	0	0	0	0
Alopocosmodon	0	0	0	0	0	0	0	0	0	0
Anconodon	0	0	0	0	0	0	0	0	0	0
Ankalagon	0	1	0	0	0	0	0	0	0	0
Anisonchus	1	1	1	0	0	1	0	1	1	0
Anisazia	0	1	0	0	0	0	0	0	0	0
Aphronorus	0	0	0	0	0	0	0	0	0	0
Arctocyon	0	0	1	0	0	1	0	0	0	0
Baiotomeus	0	0	0	0	0	0	0	0	0	0
Bessoecetor	0	0	0	0	0	0	0	0	0	0
Boreocyon	0	0	0	0	0	0	0	0	0	0
Bryanictis	0	0	0	0	0	0	0	0	0	0
Catopsalis	0	0	0	0	0	0	0	0	0	0
Chriacus	1	1	0	0	0	0	0	0	1	0
Claenodon	0	0	0	0	0	0	0	0	0	0
Conoryctella	0	0	0	0	0	0	0	0	0	0
Conoryctes	0	0	0	0	0	0	0	0	0	0
Coriphagus	0	1	1	0	1	0	0	0	0	0
Deltatherium	1	1	0	0	0	1	0	0	1	0
Deuterogonodon	1	0	0	0	0	0	0	0	0	0
Didymictus	0	0	0	0	0	0	0	0	0	0
Dissacus	0	0	0	0	0	0	0	0	0	0
Ectypodus	0	0	0	0	0	0	0	0	0	0
Edworthia	0	0	0	0	0	0	0	0	0	0
Ellipsodon	1	1	1	1	0	0	0	0	1	0
Elpidophorus	0	0	0	0	0	0	0	0	0	0
Elphidotarsius	0	0	0	0	0	0	0	0	0	0
Eucosmodon	0	0	0	0	0	0	0	0	0	0
Eudaemonema	0	0	0	0	0	0	0	0	0	0
Gelastops	0	0	0	0	0	0	0	0	0	0
Goniacodon	1	0	0	0	0	1	1	0	1	0

Haplaletes	0	0	0	0	0	0	0	0	1	0
Haploconus	1	1	0	0	0	0	0	0	0	1
Huerfanodon	0	1	0	0	0	0	0	0	0	0
Ignacius	0	0	0	0	0	0	0	0	0	0
Intyrictis	0	0	0	0	0	0	0	0	0	0
Jepsenella	0	0	0	0	0	0	0	0	0	0
Krauseia	0	0	0	0	0	0	0	0	0	0
Leptacodon	0	0	0	0	0	0	0	0	0	0
?Leptacodon	0	0	0	0	0	0	0	0	0	0
Limaconyssus	0	0	0	0	0	0	0	0	0	0
Litaletes	0	0	0	0	0	0	0	0	0	0
Litomylus	0	0	0	0	0	0	0	0	0	0
Mckennatherium	0	0	0	0	0	0	0	0	0	0
Metachriacus	0	0	0	0	0	0	0	0	0	0
Mesodma	0	0	0	0	0	0	0	0	0	0
Microclaenodon	0	0	0	0	0	0	0	0	0	0
Mimetodon	0	0	0	0	0	0	0	0	0	0
Mimotricentes	1	1	0	0	0	0	0	0	1	1
Mioclaenus	1	1	1	0	0	0	0	0	1	0
Mixodectes	0	1	0	0	0	0	0	0	0	0
Myrmecoboides	0	0	0	0	0	0	0	0	0	0
Navajovius	0	0	0	0	0	0	0	0	0	0
Neoplagiaulax	0	0	0	0	0	0	0	0	0	0
Palaechthon	0	0	0	0	0	0	0	0	0	0
Palaeictops	0	0	0	0	0	0	0	0	0	0
Palaeoryctes	0	0	0	0	0	0	0	0	0	0
Palaeoryctidae	0	0	0	0	0	0	0	0	0	0
Palenochtha	0	0	0	0	0	0	0	0	0	0
Paleotomus	0	0	0	0	0	0	0	0	0	0
Pantolambda	1	1	1	1	0	0	0	0	0	0
Pararyctes	0	0	0	0	0	0	0	0	0	0
Parectypodus	0	0	0	0	0	0	0	0	0	0
Paromomys	0	0	0	0	0	0	0	0	0	0

Pentacodon	0	0	0	0	0	0	0	0	1	0
Peradectes	0	0	0	0	0	0	0	0	0	0
Periptychus	1	1	1	1	1	0	1	0	1	1
Phenacodus	0	0	0	0	0	0	0	0	0	0
Picrodus	0	0	0	0	0	0	0	0	0	0
Plesiolestes	0	1	0	0	0	0	0	0	0	0
Ptilodus	0	0	0	0	0	0	0	0	0	0
Presbyteria	0	0	0	0	0	0	0	0	0	0
Procerberus	0	0	0	0	0	0	0	0	0	0
Prodiacodon	0	0	0	0	0	0	0	0	0	0
Promioclaenus	1	1	0	0	0	0	1	0	1	0
Pronothodectes	0	0	0	0	0	0	0	0	0	0
Prothryptacodon	0	0	0	0	0	0	0	0	0	0
Protogonodon	0	0	0	0	0	0	0	0	0	0
Protoselene	1	1	0	0	0	0	0	0	1	0
Protictis	1	1	0	0	0	0	0	0	1	0
Psittacotherium	1	1	0	1	0	0	0	0	0	1
Psydronyctia	0	0	0	0	0	0	0	0	0	0
Simpsonictis	0	0	0	0	0	0	0	0	0	0
Stygimys	0	0	0	0	0	0	0	0	0	0
Swaindelphys	0	0	0	0	0	0	0	0	0	0
Taeniodonta	0	0	0	0	0	0	0	0	0	0
Tetraclaenodon	1	1	1	0	0	1	1	0	1	1
Torrejonia	0	0	0	0	0	0	0	0	0	0
Tricentes	0	0	0	0	0	0	0	0	0	0
Triisodon	1	1	0	1	1	1	1	0	0	0
Unuchinia	0	0	0	0	0	0	0	0	0	0
Xanclomys	0	0	0	0	0	0	0	0	0	0
Xyronomys	0	0	0	0	0	0	0	0	0	0

Table S4.7.—Occurrences of mammalian genera within late Torrejonian (To3) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: CLG = Calgary 2E (Russell 1926, 1929, 1932, 1958; Russell 1967; Krause 1978; Fox 1990a), NRD = Nordic Ski (Krause 1978; Fox 1990a), LLHR = Lloyd and Hare (Hartman and Kihm, 1999), CDR = Cedar Mountain sites (Hartman, 1986), BRKT = The Breaks (To3 level) (Higgins, 2003), RSP = Rock Springs (To3) (UW localities V77009, V77010, V77012, V77014, V78055) (Winterfeld, 1982), ESCV = Escavada Wash (AMNH locality 14 [head of Escavada Wash]) (Williamson, 1996; Rose and Lucas, 2000), WT10 = West Branch of Torrejon Wash, (AMNH Locality 10 upper horizon) (Williamson, 1996; Williamson and Taylor, 2011), and ET10 = East Branch of Torrejon Wash, (AMMH Locality 10 upper horizon) (Williamson, 1996; Williamson and Taylor, 2011).

Genera	CLG	NRD	MDC	LLHR	CDR	BRKT	RSP	ESCV	WT10	ET10
Acmeodon	0	0	0	0	1	0	1	0	1	1
Adunator	0	0	0	0	0	0	0	0	0	0
Anconodon	1	1	0	0	1	1	0	0	0	0
Anisonchus	0	0	0	0	1	1	1	1	1	1
Ankalagon	0	0	0	0	0	0	0	0	0	1
Aphronorus	0	1	0	0	1	1	1	0	0	0
Arctocyon	0	0	0	0	0	0	0	1	1	1
Avunculus	0	0	0	0	1	0	0	0	0	0
Baiotomeus	1	0	1	0	0	1	0	0	0	0
Bessoecetor	0	0	0	0	1	0	0	0	0	0
Bryanictis	0	0	0	0	1	0	0	0	0	0
Bubogonia	0	1	0	0	0	0	0	0	0	0
Captosalis	1	1	0	0	0	1	0	0	0	0
Coriphagus	0	0	0	0	1	0	0	0	0	1
Chriacus	0	0	0	0	1	1	1	0	1	1
Claenodon	1	0	0	0	1	1	0	0	0	0
Colpoclaenus	0	0	0	0	0	0	0	1	1	1
Conoryctes	0	0	0	0	0	0	0	1	1	1
Dissacus	0	0	0	0	0	0	0	1	1	1
Ectocion	0	0	0	0	0	1	0	0	0	0
Ectypodus	0	0	0	0	1	0	0	0	0	0
Eucosmodon	1	0	0	0	0	0	0	0	0	0
Eudaemonema	0	1	0	0	1	1	0	0	0	0
Escavadodon	0	0	0	0	0	0	0	1	0	0
Gelastops	0	1	0	0	1	1	1	0	0	0
Goniacodon	0	0	0	0	0	0	0	0	0	1
Haplaletes	0	0	0	0	1	0	0	0	0	1
Ignacius	0	1	0	0	0	0	0	0	0	0
Intyrictis	0	0	0	0	0	0	0	0	1	1
Jepsenella	0	0	0	0	1	0	0	0	0	0
Krauseia	0	0	0	0	0	1	0	0	0	0
Litaletes	0	0	0	0	1	1	0	0	0	0

Litocherus	0	0	0	0	1	1	0	0	0	0
Litomylus	0	1	0	0	1	1	1	1	1	1
Mckennatherium	0	0	0	0	1	0	1	0	0	1
Mesodma	0	1	0	0	1	1	0	0	0	0
Microclaenodon	0	0	0	0	0	0	0	0	0	1
Mimetodon	0	1	0	0	1	0	0	0	0	0
Mimotricentes	0	0	0	0	1	1	0	1	1	1
Mioclaenus	0	0	0	0	0	0	0	1	1	1
Mixodectes	0	0	0	0	0	0	0	1	1	1
Navajovius	0	0	0	0	0	1	0	0	0	0
Neoplagiaulax	1	1	0	0	1	1	0	0	0	0
Palaechthon	0	0	0	0	1	1	0	0	0	1
Palaeoryctes	0	0	0	0	0	0	1	0	0	1
Paleotomus	0	0	0	0	0	1	0	0	0	0
Palenochtha	0	0	0	0	1	1	0	0	0	0
Pantolambda	0	0	0	1	0	0	0	1	1	1
Parectypodus	0	1	0	0	0	1	0	0	0	0
Paromomys	0	0	0	0	1	1	0	0	0	0
Periptychus	0	0	0	0	0	1	0	1	1	1
Peradectes	0	0	0	0	0	0	0	0	0	1
Pentacodon	0	0	0	0	0	0	0	0	1	1
Phenacodus	0	0	0	0	0	1	0	0	0	0
Picrodus	0	0	1	0	1	0	0	0	0	0
Plesiolestes	0	0	0	0	0	1	0	0	1	1
Prodiacodon	0	1	0	0	1	1	0	0	1	1
Promioclaenus	0	0	0	0	1	1	0	1	1	1
Pronothodectes	1	0	1	0	1	0	1	0	0	0
Prothryptacodon	0	0	0	0	1	0	0	0	0	1
Protoselene	0	0	0	0	0	0	0	1	1	1
Protictis	0	1	0	0	1	0	0	1	1	1
Psittacotherium	0	0	0	0	0	0	0	0	1	1
Ptilodus	1	1	0	0	1	1	1	0	0	0
Swaindelphys	0	0	0	0	0	0	0	0	1	1

Tetraclaenodon	1	1	0	1	1	1	1	1	1	1

Table S4.8.—Occurrences of mammalian genera within earliest Tiffanian (Ti1) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: DSS = Diss (Fox 1983, 1990a; Scott, 2008), CCH = Cochrane 1 and 2 (Simpson, 1927b; Russell, in Rutherford, 1927; Russell 1958; Russell 1967; Krause, 1978; Gingerich, 1982; Youzwyshyn, 1988; Fox 1990a, 2011; Fox et al., 1992; Fox and Youzwyshyn, 1994; Scott et al., 2002, 2006; Scott and Fox, 2005; Scott, 2008), AAR = Aaron's locality (Fox, 1990a; Scott and Fox, 2005; Scott, 2008, 2010b), BGT = Bangtail (Gingerich et al. 1983), DGL = Douglass (Krause and Gingerich 1983; Krause and Maas 1990; Scott and Krause, 2006), DND = Donald (McCullough et al., 2004; Bloch et al., 2006), GLN = Glennie (Hartman and Krause 1993), BNG = Bingo (Hartman and Krause, 1993; Silcox et al., 2001; Zack et al., 2005; Bloch et al., 2006), PLB = Plan B (St. Clair et al., 2008, 2010), GRY = Grayson Ridge (Secord 1998; Higgins 2003), HLF = Halfway Hill (Secord 1998; Higgins 2003), CCN = C-Con (Schiebout 1974; Rapp et al. 1983; Schiebout et al. 1987), and BRK1 = The Breaks (Ti1 level) (Higgins, 2003).

Genera	DSS	CCH	AAR	BNG	DGL	DND	GLN	BNG	PLB	GRY	HLF	CCN	BRK1
Acheronodon	0	1	0	0	0	0	0	0	0	0	0	0	0
Acmeodon	0	0	0	0	1	1	0	1	0	1	0	0	1
Allocosmodon	0	0	0	0	1	0	0	0	0	0	0	0	0
Anconodon	0	1	0	0	1	1	0	0	0	0	1	0	0
Anisonchinae	0	1	0	0	0	0	0	0	0	0	0	0	0
Aphronorus	0	1	0	1	0	1	0	1	1	0	0	0	1
Arctocyon	0	1	0	0	1	0	0	0	0	1	1	0	0
Baiotomeus	0	1	0	0	0	0	0	0	0	1	1	0	1
Bessoecetor	0	1	0	0	1	1	0	0	0	0	0	0	0
Bisonalveus	0	1	0	0	1	0	0	0	0	0	0	0	0
Boreocyon	1	1	1	0	0	0	0	0	0	0	0	0	0
Caenolambda	0	0	0	0	0	0	0	0	0	0	0	1	0
Carpodaptes	0	1	0	0	0	0	0	0	0	0	0	0	0
"Cervictis"	0	1	0	0	0	0	0	0	0	0	0	0	0
Chriacus	0	1	0	0	1	1	0	0	0	0	0	0	1
Colpoclaenus	0	0	0	0	1	0	0	0	0	0	0	0	0
Coriphagus	0	0	0	0	0	0	0	0	0	0	0	0	1
Creodonta	0	1	0	0	0	0	0	0	0	0	0	0	0
Dissacus	0	1	0	0	1	0	0	0	0	1	0	0	0
Ectocion	0	1	1	0	1	1	0	1	1	1	0	0	0
Ectypodus	0	0	0	1	0	0	0	0	0	0	0	0	0
Elphidotarsius	0	1	0	0	1	1	1	1	0	0	0	0	0
Elpidophorus	0	1	0	0	1	0	0	0	0	0	0	0	0
Eucosmodontidae	0	1	0	0	1	0	0	0	0	0	0	0	0
Eudaemonema	0	1	0	0	0	0	0	0	0	0	0	0	0
Fractinus	0	0	0	0	0	0	0	0	0	0	0	0	1
Gelastops	0	0	0	0	0	0	0	0	0	0	1	0	1
Gingerichia	0	1	0	0	1	0	1	1	0	0	0	0	0
Goniacodon	0	0	0	0	0	0	0	1	1	0	0	0	0
Haplaletes	0	0	0	0	0	0	0	0	0	0	1	0	0
Horolodectes	0	1	0	0	0	0	0	0	0	0	0	0	0
Ignacius	0	1	0	0	1	1	0	0	0	0	0	0	0

"Insidioclaenus"	0	1	1	0	0	0	0	0	0	0	0	0	0
Intyrictis	0	0	0	0	0	0	0	0	0	0	1	0	0
Joffrelambda	0	1	0	0	0	0	0	0	0	0	0	0	0
Krauseia	0	1	0	0	0	0	0	0	0	0	0	0	0
?Leptacodon	0	1	0	1	1	0	0	0	0	0	0	0	0
Limaconyssus	0	1	0	0	0	0	0	0	0	0	0	0	0
Litocherus	0	1	1	0	0	0	0	0	0	0	0	0	0
Litomylus	0	1	1	0	1	0	0	0	0	1	0	0	1
Mesodma	0	1	0	0	1	0	0	0	0	0	0	0	0
Microsyopidae	0	1	0	0	0	0	0	0	0	0	0	0	0
Mimetodon	0	1	0	0	1	0	0	0	0	0	1	0	0
Mimotonidae	0	1	0	0	0	0	0	0	0	0	0	0	0
Mimotricentes	0	0	0	0	0	0	0	0	0	1	1	0	0
Mioclaenus	0	0	0	0	0	0	0	0	0	1	0	0	0
Myrmecoboides	0	1	0	1	1	0	0	0	0	0	0	0	0
Nannodectes	0	1	0	1	1	1	0	0	0	0	0	0	1
Neoplagiaulax	1	1	0	0	1	1	0	0	0	0	1	0	1
Oxyprimus	0	1	0	0	0	0	0	0	0	0	0	0	0
Palaechthon	0	0	0	1	0	0	0	0	0	0	1	0	1
Palaeoryctes	0	1	0	0	0	0	0	0	0	0	0	0	0
Palaeoryctidae	0	0	0	0	1	0	0	0	0	0	0	0	0
Palenochtha	0	0	0	0	0	1	0	0	0	0	0	0	0
Paleotomus	0	1	0	0	1	1	0	0	0	1	1	0	1
Pantolambda	0	0	0	0	0	0	0	0	0	1	0	0	1
Pararyctes	1	1	0	0	0	0	0	0	0	0	0	0	0
Parectypodus	1	1	0	0	0	0	0	0	0	0	1	0	0
Paromomys	0	0	0	0	0	0	0	0	0	1	0	0	0
Paromomyidae	0	0	0	0	0	0	0	1	0	0	0	0	0
Pentacosmodon	0	1	0	0	0	0	0	0	0	0	0	0	0
Peradectes	0	1	0	0	1	1	0	0	0	0	0	0	0
Periptychus	0	0	0	0	0	0	0	0	0	1	0	1	1
Phenacodus	0	0	0	0	1	1	0	0	0	0	0	1	0
Picrodus	0	1	0	1	1	1	0	0	0	0	0	0	0

Plesiadapis	0	1	0	0	1	0	0	0	0	0	0	0	1
Plesiolestes	0	1	0	0	0	0	0	0	0	0	1	0	1
Pristinictis	0	1	0	0	0	0	0	0	0	0	0	0	0
Prochetodon	0	1	1	0	0	0	0	0	0	0	0	0	0
Prodiacodon	0	1	0	0	1	0	0	0	0	0	0	0	0
Promioclaenus	0	0	0	0	0	1	0	0	0	1	1	1	1
Pronothodectes	0	1	0	0	0	0	0	0	0	0	0	0	0
Protictis	0	1	0	0	1	0	0	0	0	0	0	0	0
Protoselene	0	0	0	0	0	0	0	0	0	0	1	0	1
Psydronyctia	0	1	0	0	0	0	0	0	0	0	0	0	0
Ptilodus	0	1	0	0	1	1	0	0	0	1	1	1	1
Raphictis	0	1	0	0	0	0	0	0	0	0	0	0	0
Simpsonictis	0	0	0	0	1	0	0	0	0	0	0	0	0
Tetraclaenodon	0	0	0	0	0	0	0	0	0	1	0	0	1
Thryptacodon	0	1	1	0	1	1	0	0	0	0	1	0	0
Titanoides	0	0	0	0	1	0	0	0	0	0	0	0	0
Torrejonia	0	1	0	0	0	0	0	0	0	0	0	0	0
Unuchinia	0	1	0	0	0	0	0	0	0	0	0	0	0
"Xynolestes"	0	1	0	0	0	0	0	0	0	0	0	0	0

Table S4.9.—Occurrences of mammalian genera within late early Tiffanian (Ti2) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: WHT = White site, 7-up Butte, Highway Blowout (Lofgren et al., 2004), SCA = Scarritt (Simpson 1936, 1937a, 1937b; Kristalka 1973; Rose 1981; Krause and Mass 1990), UM263 = University of Michigan locality 263 (Gingerich, 1976; Secord et al. 2006; Secord, 2008), SDD = Saddle (Gazin 1956), and BRK2 = The Breaks (Ti2 level) (Higgins, 2003).

Genera	WHT	SCA	UM263	SDD	BRK2
Anconodon	0	0	0	1	0
Arctocyon	0	0	1	1	0
Bessoecetor	0	1	0	0	0
Bisonalveus	0	0	0	1	0
Caenolambda	0	0	0	1	0
Carpodaptes	0	1	0	0	0
Chriacus	0	1	0	1	0
Claenodon	0	1	0	0	0
Colpoclaenus	0	0	0	1	0
Desmatoclaenus	0	0	0	1	0
Dissacus	0	1	0	0	0
Ectocion	1	0	1	0	0
Ectypodus	0	1	0	1	0
Elpidophorus	0	1	0	0	0
Haplaletes	0	0	0	1	0
Ignacius	0	1	0	0	0
Labidolemur	0	0	0	1	0
Leptacodon	0	1	0	0	0
Litocherus	0	1	0	1	0
Litomylus	0	0	0	1	0
Mentoclaenodon	0	0	0	1	0
Mesodma	0	1	0	1	0
Mimotricentes	0	0	0	1	0
Mioclaenus	0	0	0	1	0
Nannodectes	0	1	0	1	0
Neoplagiaulax	0	1	0	0	0
Pararyctes	0	1	0	1	0
Paromomys	0	0	0	0	0
Palaeosinopa	0	1	0	0	0
Paleotomus	0	1	0	0	0
Peradectes	0	0	0	1	0
Phenacodus	1	0	1	1	0

Picrodus	0	0	0	1	0
Plesiadapis	1	1	1	1	0
Prodiacodon	0	0	0	1	0
Promioclaenus	0	0	0	1	1
Protictis	0	1	0	0	0
Protoselene	0	0	0	1	0
Ptilodus	0	1	1	1	0
Simpsonictis	0	0	0	1	0
Thyptacodon	0	1	0	1	0
Titanoides	0	1	1	0	0
Torrejonia	0	0	0	1	0
Unuchinia	0	1	0	0	0

Table S4.10.—Occurrences of mammalian genera within early middle Tiffanian (Ti3) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: HND = Hand Hills West upper level (Fox 1990a; MacDonald 1996; Scott, 2005; Scott and Fox, 2005), Blindman River localities (including DW-1, DW-2, DW-3, and Mel's Place) (Fox 1984a, 1984b, 1984c, 1984d, 1990a, 1990b, 1990c, 1991, 2005; Scott, 2005, 2008, 2010a, 2010b; Scott and Fox, 2005; Scott et al., 2006; Boyer, Scott, and Fox, 2012), BRB = Burbank (Fox, 1990a; Scott, 2008), JFR = Joffre Bridge localities (including Erickson's Landing, Joffre Bridge Roadcuts, and Joffre Bridge Mammal Site No. 1) (Fox, 1990a, 2005; Scott and Fox, 2005; Scott, 2008), BRH = Birchwood (Webb, 1996; Fox, 2005; Scott and Fox, 2005; Scott, 2006, 2010a, 2010b; Scott et al., 2006), PLP = Police Point (Krishtalka 1973; Krause 1978; Fox 1990a; Scott, 2005), BRS = Brisbane (Holtzman, 1978; Hartman and Kihm 1991, 1995; Kihm and Hartman 2004), WHT = White's River Basin Survey Site (Hartman and Kihm 1991), CDR = Cedar Point (Simons, 1960; West, 1971, 1973, 1976; Rose, 1975; Krishtalka 1976a, 1976b; Gingerich, 1976, 1980b, 1983; Van Valen 1978; Rose 1981; Gingerich and Winkler 1985; Gunnell 1988; Thewissen 1990; Secord, 2008), Jepsen Quarry (Secord, 2008), CHP = Chappo Type locality (Dorr and Gingerich, 1980; Gunnell, 1994), LDG = Ledge Quarry (Gazin, 1956; Beard, 2000), BTT = Battle Mountain (Dorr, 1978), RYB = Ray’s Bonebed (Schiebout 1974; Standhardt 1986; Schiebout et al. 1987), OHC = Ohio Creek sites (Burger, 2007), and BRK3 = The Breaks (Ti3 level) (Higgins, 2003).

Genera	HND	BLD	BRB	JFR	BRH	PLP	BRS	WHT	CDR	JPQ	CHP	LDG	BTT	RYB	OHC	BRK3
"Adapisorella"	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
"Adeloxenus"	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adunator	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Aletodon	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0
Allocosmodon	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0
Anconodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Aphanocyon	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Arctocyon	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0
Barylambda	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Bessoecetor	0	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0
Bisonalveus	1	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0
Boreocyon	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caenolambda	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
Carpocristes	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Carpodaptes	0	1	1	1	1	1	1	0	1	0	1	0	0	0	0	0
Cedrocherus	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
"Cervictis"	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chiromyoides	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1
Chriacus	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1
Claenodon	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
Colpocleanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cyriacotherium	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Didymictis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dissacus	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0
Dorraletes	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Ectocion	0	1	0	1	1	1	1	0	1	1	1	1	1	0	0	0
Ectypodus	1	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0
Elphidotarsius	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Elpidophorus	0	1	0	1	1	1	0	0	1	0	0	0	0	0	0	0
Eudaemonema	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Gelastops	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Haplaletes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0

Horolodectes	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Ignacius	0	1	0	1	1	1	1	0	1	0	1	0	0	0	0	0
"Insidioclaenus"	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
"Joffrelambda"	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Labidolemur	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Lambertocyon	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
?Leptacodon	0	1	0	1	1	1	0	0	1	0	1	0	0	0	0	0
Leptacodon	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0
Leptonysson	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Limaconyssus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Litocherus	1	1	0	1	1	0	1	0	1	0	1	0	1	0	0	0
Litolestes	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Litomylus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Melaniella	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mesodma	0	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0
Microcosmodon	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Micromomys	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mimetodon	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
Mimotricentes	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
Myrmecoboides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Nannodectes	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1
Navajovius	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
"Nayloria"	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Neoplagiaulax	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0	1
Niphredil	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nyctitherium	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pachyaena	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Palaechthon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pantodonta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Pararyctes	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0
Parectypodus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1
Paromomys	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Palaeoryctes	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0

Paleotomus	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Peradectes	1	1	0	1	0	1	1	0	1	0	1	0	0	0	0	0
Periptychus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Phenacodus	0	0	0	0	0	0	0	0	1	0	1	1	1	1	0	1
Picrodus	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0
Picrodontidae	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Plesiadapis	0	0	0	0	1	1	1	0	1	0	1	1	1	0	0	1
Plesiolestes	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Presbyteria	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prochetodon	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Prodiacodon	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Promioclaenus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Pronothodectes	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0
Protictis	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0
Protoselene	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
"Psydronyctia"	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ptilodus	0	1	0	1	1	1	1	0	1	0	1	0	1	0	0	1
Raphictis	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	0
Saxonella	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Taeniodonta	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Thryptacodon	0	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0
Titanoides	0	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0
Titanoideidae	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tricentes	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
"Typhlodelphys"	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tytthaena	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Unuchinia	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0
"Xynolestes"	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0

Table S4.11.—Occurrences of mammalian genera within late middle Tiffanian (Ti4) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: CR= Crestomere School (Fox, 1990a; Scott, 2006, 2008), SW = Swan Hills (Russell 1967; Krishtalka 1973; Krause 1978; Gingerich 1986; Stonley, 1988; Fox, 2005; Scott, 2006), RC = Roche Percée (Krause, 1977, 1978; Rose and Krause, 1982; Fox, 1990a, 2005; Scott, 2006; Rankin, 2009, 2014), WN = Wannagan Creek Quarry (Holtzman 1978; Erickson 1991, 1999), JD = Judson (Holtzman 1978; Kihm and Hartman 2004), RV = Riverdale (Holtzman 1978), CS = Cross locality (Kihm, Krause, and Hartman, 2004), RD = Red Spring (Kihm, Hartman, and Krause, 1993; Kihm, Krause, and Hartman, 2004), WT = Witter (Kihm, Krause, and Hartman, 2004), OLV = Olive (Wolberg, 1979), CRC = Circle (Wolberg, 1979), SB = Seaboard (Secord, 2008), FSH = Fossil Hollow (Secord, 2008), LGD = Long Draw (Secord, 2008), CRT = Croc Tooth (Secord, 2008), DV = Divide (Bloch et al., 2001, 2004; Secord, 2008), SND = Sand Draw (Secord, 2008), UW = UWV77005 (Winterfeld, 1982), MS = Mason Pocket (Simpson, 1935a, 1935b, 1935c).

Genera	CR	SW	RC	WN	JD	RV	CS	RD	WT	OLV	CRC	SB	FSH	LG	CRT	DV	SND	UW	MS
Aaptoryctes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0
Aatotomus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Adunator	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0
Acmeodon	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Anacodon	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Apatemys	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Arctocyon	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	0	1	0
Bessoecetor	0	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	1	0
Bisonalveus	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Bryanictis	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Caenolambda	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Carpodaptes	0	0	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	1
Carpolestes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Carpomegodon	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Chiromyoides	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1
Chriacus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colpoclaenus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Cyriacotherium	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0
Didymictis	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0
Dipsalodon	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Dissacus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Dorraletes	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ectocion	0	0	1	1	1	1	0	1	0	0	1	0	1	1	1	1	0	1	0
Ectoganus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ectypodus	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1
Elpidophorus	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
Entomolestes	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eucosmodontidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	0
Gelastops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Haplaletes	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Haplolambda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Hyopsodontidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Ignacius	0	0	1	1	1	0	0	0	0	1	1	0	0	1	1	1	0	1	1
Labidolemur	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Lambertocyon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Leptacodon	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	1	0	1	1
Leptolambda	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Leptonysson	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Limaconyssus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Litocherus	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Litolestes	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0
Litomylus	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Mesodma	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Microcosmodon	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Micromomys	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microsyops	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Mimetodon	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
Nannodectes	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1
Navajovius	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1
Neoplagiaulax	0	0	1	1	1	0	0	1	0	1	1	0	0	1	1	1	0	1	0
Nyctitherium	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Onchocherus	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pagonomous	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Palaeoryctes	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0
Palaeosinopa	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	1	0
Paleotomus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Pantodonta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Pararyctes	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Parectypodus	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Peradectes	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Phenacodaptes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phenacodus	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	1	0	1	0
Phenacolemur	0	0	0	1	0	0	0	0	0	1	1	0	1	0	1	0	1	0	0
Picrodus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Plagiomenidae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0

Plesiadapis	0	0	1	1	1	1	0	0	0	1	1	1	1	1	1	1	1	1	0
Prochetodon	0	0	1	0	1	0	0	1	0	0	0	0	1	1	0	1	0	0	0
Prodiacodon	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0
Protentomodon	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Protictis	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Ptilodus	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	1	0	1	1
Raphictis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
Scenopagus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Talpavus	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Thryptacodon	0	0	1	1	1	0	0	0	0	1	1	0	1	1	1	1	0	1	1
Titanoides	0	0	1	0	1	1	1	0	1	1	0	0	0	0	1	1	0	0	0
Tricentes	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Unuchinia	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Utemylus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Viverravus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
Xenacodon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
"Xynolestes"	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zanycteris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Table S4.12.—Occurrences of mammalian genera within late middle Tiffanian (Ti5) local faunas from the Western Interior of North America. Presence (1) and Absence (0). Locality abbreviations, with respective sources of faunal data, are: ZLM = Zalmout Quarry (Secord, 2008), Y2K = Y2K Quarry (Secord, 2002, 2008; Secord et al., 2002; Bloch et al., 2004), PRN = Princeton Quarry (Rose 1981; Bloch et al., 2004; Secord 2008), SCH = Schaff (Bloch et al., 2004; Secord, 2008), FRT = Fritz Quarry (Secord, 2008), JPV = Jepsen Valley (Secord, 2008), TTN = *Titanoides* locality (Gazin, 1956), RCK = Rock Springs (Ti5) (University of Wyoming localities V76008, V77059, V77060, V78052, V78053, and V78054) (Winterfeld 1982), DLL = Dell Creek Quarry (Dorr, 1952, 1958, 1977; Gingerich, 1980a; Gingerich and Winkler, 1985), UCM = University of Colorado Museum locality 92177 (Burger and Honey, 2008; Burger, 2013), JBB = Joe's Bonebed (Schiebout, 1974; Standhardt, 1986; Schiebout et al., 1987), and BYF = Bayfield (Simpson, 1935a, 1935b, 1935c).

Genera	ZLM	Y2K	PRN	SCH	FRT	JPV	TTN	RCK	DLL	UCM	JBB
Aaptoryctes	0	0	0	0	0	0	0	0	1	0	0
Adunator	0	1	1	1	0	0	0	1	1	0	0
Aletodon	0	0	0	0	0	0	0	1	0	0	0
Apternodus	0	0	1	0	0	0	0	0	0	0	0
Arctocyon	0	1	1	0	0	0	0	0	0	0	1
Arctocyonides	0	0	0	0	0	0	0	0	0	1	0
Arctodontomys	0	1	0	0	0	0	0	0	0	0	0
Bessoecetor	0	0	0	0	0	0	0	1	0	0	0
Carpodaptes	0	0	0	0	0	0	0	0	0	1	0
Carpolestes	1	1	1	1	1	0	0	1	0	0	0
Carpocristes	0	0	0	0	0	0	0	0	1	0	0
Chiromyoides	0	0	0	0	0	0	0	1	1	1	1
Claenodon	0	0	0	0	0	0	0	1	0	0	0
Didelphidae	0	0	1	0	0	0	0	0	0	0	0
Didymictis	0	0	1	0	0	0	0	0	1	0	0
Dissacus	0	0	1	0	0	0	0	1	0	0	0
Dorraletes	0	0	0	0	0	0	0	0	1	0	0
Ectocion	1	1	1	0	0	0	1	1	0	1	0
Ectoganus	0	0	0	0	0	0	0	0	0	0	0
Ectypodus	0	1	1	0	0	0	0	0	1	1	1
Haplaletes	0	0	0	0	0	0	0	0	0	1	1
Haplomylus	0	0	0	0	0	0	0	0	0	1	0
Ignacius	1	0	0	0	0	0	0	0	1	1	0
Jepsenella	0	0	0	0	0	0	0	0	0	0	1
Labidolemur	0	1	0	0	0	0	0	0	0	0	0
Lambertocyon	0	0	0	0	0	0	0	1	0	0	1
?Leptacodon	0	1	1	0	0	1	0	0	0	0	0
Leptacodon	0	0	0	1	0	0	0	1	0	1	0
Litocherus	0	0	0	0	0	0	1	0	0	0	0
Litolestes	0	1	1	1	0	0	0	1	0	0	0
Litomylus	0	0	0	0	0	0	0	1	0	1	0
Microcosmodon	0	1	1	1	0	0	0	0	0	0	0

Micromomys	0	1	1	1	0	0	0	0	0	0	0
Mimetodon	0	0	1	0	0	0	0	0	0	0	1
Mingotherium	0	0	0	0	0	0	0	0	0	0	0
Mioclaenus	0	0	0	0	0	0	1	0	0	0	0
Mylanodon	0	1	0	0	0	0	0	0	0	0	0
Nannodectes	0	0	0	0	0	0	0	1	0	1	1
Navajovius	0	0	0	0	0	0	0	0	0	0	1
Neoliotomus	0	0	1	0	0	0	0	0	0	0	0
Neoplagiaulax	0	0	1	0	0	0	0	0	0	0	0
Nyctitheriidae	0	0	1	0	0	0	0	0	0	0	0
Paleictops	0	1	1	0	0	0	0	0	0	0	1
Palaeoryctes	0	1	1	1	0	0	0	0	0	0	0
Palaeosinopa	0	0	0	0	0	0	0	0	1	0	0
Paleotomus	0	0	0	0	0	0	0	0	1	0	0
Parectypodus	0	1	1	0	0	0	0	0	0	0	1
Pentacosmodon	0	0	1	0	0	1	0	0	0	0	0
Peradectes	0	0	1	0	0	0	0	1	0	0	0
Phenacodaptes	0	0	1	1	0	0	0	1	0	1	0
Phenacodus	1	0	1	0	0	0	1	0	0	1	1
Phenacolemur	1	1	1	1	0	0	0	0	0	0	1
Picrodus	0	0	0	0	0	0	0	1	0	0	0
Plagioctenodon	0	1	0	0	0	0	0	0	0	0	0
Plesiadapis	1	1	1	1	0	0	1	1	1	1	0
Princetonia	0	1	1	1	0	0	0	0	0	0	0
Prochetodon	0	1	1	1	0	0	0	0	0	0	0
Prodiacodon	0	1	1	0	0	0	0	0	0	0	0
Propalaeanodon	0	0	1	0	0	1	0	0	0	1	0
Protictis	0	0	0	0	0	0	0	1	0	1	0
Ptilodus	0	0	0	0	0	0	0	0	1	1	1
Scenopagus	0	0	0	0	0	0	1	0	0	0	0
Taeniodonta	0	0	0	0	0	0	0	0	0	0	1
Thryptacodon	0	0	1	0	0	0	1	1	1	1	0
Titanoides	0	0	0	0	0	0	1	0	0	0	0

Tricentes	0	0	0	0	0	0	0	0	0	0	1
Unuchinia	0	0	1	1	0	0	0	0	0	0	0
Utemylus	0	0	0	0	0	0	1	0	0	0	0
Viverravus	0	1	1	1	0	0	0	0	0	0	0
Wyonycteris	0	0	1	1	0	0	0	0	0	0	0
Zanycteris	0	0	0	0	0	0	0	0	0	1	1

Table S4.13.—Stratigraphic and geographic information for Lancian mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Pediomys Point	Alaska	Prince Creek	70	-151.6	83.3	-119.1
Scollard	Alberta	Scollard	51.8	-113	58.7	-93.8
Wounded Knee	Saskatchewan	Frenchman	49.3	-108.4	55.3	-90.7
Gryde	Saskatchewan	Frenchman	49.3	-108.4	55.3	-90.7
Chambery Coulee	Saskatchewan	Frenchman	49.5	-108.8	55.5	-91.0
Little Missouri Badlands	Montana/North Dakota	Hell Creek	47	-103.7	52.0	-87.2
Pretty Butte	North Dakota	Hell Creek	46.4	-104	51.5	-87.9
Marmath	North Dakota	Hell Creek	46.3	-103.9	51.4	-87.8
Sunset Butte	North Dakota	Hell Creek	46.1	-103.8	51.1	-87.8
Mud Buttes	North Dakota	Hell Creek	46	-103.8	51.1	-87.9
PTRM V89003	North Dakota	Hell Creek	46	-103.8	51.1	-87.9
PTRM V89004	North Dakota	Hell Creek	46	-103.8	51.1	-87.9
Stumpf	North Dakota	Hell Creek	46.9	-101.5	51.3	-85.0
Miller Ranch	North Dakota	Hell Creek	46	-103.9	51.1	-88.0
Iron Lightning	South Dakota	Fox Hills	45	-101.8	49.6	-86.4
Red Owl	South Dakota	Fox Hills	44.5	-102.3	49.3	-87.2
Joe Painter	South Dakota	Hell Creek	45.5	-103.1	50.4	-87.5
Eureka	South Dakota	Hell Creek	45.5	-103.1	50.4	-87.5
Black Horse	South Dakota	Hell Creek	45.7	-101.3	50.1	-85.5
Harding County	South Dakota	Hell Creek	45.8	-103.8	50.9	-88.0
Hell Creek Montana	Montana	Hell Creek	47.5	-106.4	53.1	-89.7
Muddy Tork	Montana	Hell Creek	47.1	-104.8	52.3	-88.3
Powderville	Montana	Hell Creek	45.4	-105.6	50.9	-90.1
Claw Butte	Montana	Hell Creek	45.8	-104.9	51.1	-89.1
Fallon County	Montana	Hell Creek	46.3	-104.3	51.5	-88.2
Type Lance	Wyoming	Lance	43.2	-104.6	48.6	-90.2
General Lance	Wyoming	Lance	43.2	-104.6	48.6	-90.2
Greasewood Creek	Wyoming	Lance	43.3	-104.4	48.7	-90.0
Mule Creek Junction	Wyoming	Lance	43.4	-104.2	48.7	-89.7
Black Butte Station	Wyoming	Lance	41.6	-108.7	48.1	-95.3
Dumbbell Hill	Wyoming	Lance	44.9	-108.9	51.3	-93.9
Hewett's	Wyoming	Lance	44.2	-109	50.7	-94.3

Foresight Ferris Formation (Lancian)	Wyoming	Ferris	41.8	-106.6	47.8	-93.0
Pawnee	Colorado	?Laramie	40.8	-104.5	46.3	-91.3
Dragon Canyon	Utah	North Horn	39	-111.3	46.3	-99.3
Alamo Wash	New Mexico	Ojo Alamo	36.3	-108.2	43.0	-97.2
NMMNH L-4005	New Mexico	Ojo Alamo	36.2	-108.9	43.0	-97.9

Table S4.14.—Stratigraphic and geographic for early Puercan (Pu1) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Fr-1	Saskatchewan	Ravenscrag	49.5	-109.1	55.3	-90.1
Long Fall	Saskatchewan	Ravenscrag	49.5	-109.2	55.4	-90.2
Pine Cree Park	Saskatchewan	Ravenscrag	49.6	-108.7	55.3	-89.6
French Fry	Saskatchewan	Ravenscrag	49.3	-108.4	55.0	-89.5
Hell's Hollow	Montana	Tullock Member of Fort Union	47.6	-107	53.1	-89.2
McKeever Ranch	Montana	Tullock Member of Fort Union	47.6	-107	53.1	-89.2
McGuire Creek	Montana	Hell Creek	47.7	-106.2	52.9	-88.3
Ferris Formation (Pu1)	Wyoming	Ferris	41.9	-106.9	47.7	-92.4
Mantua Lentil	Wyoming	Polecat Bench/Fort Union	44.3	-109	50.5	-93.3
Leidy Quarry	Wyoming	Polecat Bench/Fort Union	43.7	-108.7	49.9	-93.3
Littleton	Colorado	Denver	39.7	-104.7	45.1	-91.2
Nicole's Mammal Jaw locality	Colorado	Denver	39.6	-104.3	44.9	-90.9
Denver Oxyclaenodon	Colorado	Denver	39.7	-105.1	45.2	-91.7
Spigot Bottle	Montana	Hell Creek	45.9	-104.9	50.9	-88.1
Lane’s Little Jaw Site	Montana	Hell Creek	45.7	-105	50.8	-88.3
Merle's Mecca	North Dakota	Fort Union	46.4	-103.9	51.1	-86.8

Table S4.15.—Stratigraphic and geographic information for middle Puercan (Pu2) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Rav.W1	Saskatchewan	Ravenscrag	49.5	-109.2	55.4	-90.2
Wintering Hills	Alberta	Scollard	51.2	-112.5	57.8	-92.4
PITA Flats	North Dakota	Fort Union	47.1	-104.8	52.0	-87.3
Gas Tank	Utah	North Horn	39	-111	46.0	-98.1
Corral Bluffs, Jimmy Camp Creek, West Bijou Creek	Colorado	Denver	38.8	-104.8	44.3	-91.8
Ferris Formation (Pu2)	Wyoming	Ferris	41.9	-106.9	47.7	-92.4
West Flank Kimbeto Wash	New Mexico	Nacimiento	36.3	-108.2	42.8	-96.4
East Flank Kimbeto Wash	New Mexico	Nacimiento	36.3	-108.2	42.8	-96.4
Betonnie Tsosie Wash	New Mexico	Nacimiento	36.2	-107.8	42.6	-96.0

Table S4.16.—Stratigraphic and geographic information for late Puercan (Pu3) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Croc Pot	Saskatchewan	Ravenscrag	49.5	-109.2	55.4	-90.2
Garbani Channel and Purgatory Hill	Montana	Tullock Member of Fort Union	47.6	-107	53.1	-89.2
Bechtold	Montana	Ludlow Member	46.3	-104.5	51.2	-87.5
Ferris Formation (Pu3)	Colorado	Ferris	41.9	-106.9	47.7	-92.4
Wagonroad	Utah	North Horn	39	-111	46.0	-98.1
De-na-zin Wash	New Mexico	Nacimiento	36.3	-108	42.7	-96.2
Willow Wash	New Mexico	Nacimiento	36.3	-108.2	42.8	-96.4

Table S4.17.—Stratigraphic and geographic information for early Torrejonian (To1) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Farrand Channel	Montana	Tullock Member of Fort Union	47.5	-107	52.6	-88.3
Horsethief Canyon	Montana	Tullock Member of Fort Union	47.2	-107.3	52.4	-88.8
Simpson 65	Montana	Lebo	46.2	-109.7	52.2	-91.9
Simpson 9	Montana	Lebo	46.2	-109.7	52.2	-91.9
Simpson 78	Montana	Lebo	46.2	-109.7	52.2	-91.9
Dragon	Utah	North Horn	39.2	-111.3	46.1	-97.5
Kutz Canyon (NMMNH L-2659 and 2660)	New Mexico	Nacimiento	36.3	-108.2	42.5	-95.7
De-na-zin Wash (AMNH locality 3)	New Mexico	Nacimiento	36.3	-108	42.5	-95.5
Lowest Torrejonian of Kimbeto Wash (NMMNH L-692)	New Mexico	Nacimiento	36.3	-108.2	42.5	-95.7
Betonnie Tsosie Wash ('lowest Torrejonian')	New Mexico	Nacimiento	36.2	-107.8	42.3	-95.3
Dogie	Texas	Tornillo	29.2	-103.2	34.5	-93.5
Tom's Top	Texas	Tornillo	20.3	-103.6	26.1	-97.0

Table S4.18.—Stratigraphic and geographic information for middle Torrejonian (To2) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Who Nose?	Alberta	Paskapoo	51	-114.1	57.7	-93.0
Edworthy Park	Alberta	Paskapoo	51.1	-114.2	57.9	-93.1
Bearspaw	Alberta	Porcupine Hills	51.1	-114.3	57.9	-93.2
Brown Ranch	North Dakota	Fort Union	46.4	-103.3	50.6	-85.3
Gidley	Montana	Lebo	45.8	-109.8	51.8	-92.3
Silberling	Montana	Lebo	45.8	-109.8	51.8	-92.3
Swain	Wyoming	Fort Union	41.3	-107.7	47.1	-92.7
Rock Bench	Wyoming	Polecat Bench/Fort Union	44.3	-109	50.2	-92.4
Kutz Canyon (AMNH locality 'Sec. 3, T27N, R11W', KU locality 4)	New Mexico	Nacimiento	33.6	-108	39.9	-96.7
'Big Pocket' (KU locality 13)	New Mexico	Nacimiento	33.6	-108	39.9	-96.7
AMNH localities "1 or 2 miles west of Angel Peak'	New Mexico	Nacimiento	33.6	-108	39.9	-96.7
NMMNH L-1482 and 2658	New Mexico	Nacimiento	33.6	-108	39.9	-96.7
Gallegos Canyon (AMNH locality 1)	New Mexico	Nacimiento	36.3	-108.2	42.5	-95.7
Head of Kimbeto Wash (AMNH locality 8 [in part], KU locality 9 ['Little Pocket'])	New Mexico	Nacimiento	36.3	-108.2	42.5	-95.7
44 Store localities low and high (AMNH locality 9?)	New Mexico	Nacimiento	36.3	-108.2	42.5	-95.7
Escavada	New Mexico	Nacimiento	35.7	-107	41.6	-94.7

Wash (AMNH locality 14 [in part])						
Torrejon Wash (NMMNH L-2693 and 2714)	New Mexico	Nacimiento	36	-107.3	42.0	-94.9
Torrejon Wash (NMMNH L-2723)	New Mexico	Nacimiento	36	-107.3	42.0	-94.9
Torrejon Wash (NMMNH L-2709)	New Mexico	Nacimiento	36	-107.3	42.0	-94.9
East Branch of Torrejon Wash (NMMNH L-2724, AMNH locality 11 [in part])	New Mexico	Nacimiento	36	-107.3	42.0	-94.9
East Branch of Torrejon Wash (AMNH locality 11)	New Mexico	Nacimiento	36	-107.3	42.0	-94.9
Mesa de Cuba and Mesa Portales	New Mexico	Nacimiento	35.7	-107	41.6	-94.7
Middle Peak and Alligator Alley	Texas	Tornillo	29.2	-103.2	34.5	-93.5

Table S4.19.—Stratigraphic and geographic information for late Torrejonian (To3) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Calgary 2E	Alberta	Paskapoo	51.0	-114.1	57.7	-93.0
Nordic Ski	Alberta	Paskapoo	51.0	-114.1	57.7	-93.0
Lloyd and Hare	North Dakota	Tongue River Member of Fort Union	46.7	-101.8	50.3	-86.8
Cedar Mountain Sites	Montana/Wyoming	Fort Union	43.9	-108.3	50.4	-83.6
The Breaks (To3)	Wyoming	Hanna	41.8	-106.9	49.7	-91.9
Rock Springs (To3)	Wyoming	Fort Union	41.7	-109	47.3	-91.6
Escavada Wash (AMNH locality 14)	New Mexico	Nacimiento	35.7	-107	47.8	-93.8
West Branch of Torrejon Wash (AMNH locality 10)	New Mexico	Nacimiento	36.0	-107.3	41.6	-94.7
East Branch of Torrejon Wash (AMMH locality 10)	New Mexico	Nacimiento	36.0	-107.3	42.0	-94.9

Table S4.20.—Stratigraphic and geographic information for earliest Tiffanian (Ti1) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Diss	Alberta	Coalspur	53	-116.8	59.5	-94.6
Cochrane 1 and 2	Alberta	Paskapoo	51.2	-114.4	57.3	-93.6
Aaron's locality	Alberta	Paskapoo	51.9	-113.3	57.6	-91.9
Bangtail	Montana	Melville	45.8	-110.5	51.3	-93.3
Douglass	Montana	Melville	45.8	-109.8	51.1	-92.6
Donald	Montana	Melville	45.8	-109.8	51.1	-92.6
Glennie	Montana	Melville	46.2	-109.9	51.5	-92.5
Bingo	Montana	Melville	45.8	-109.8	51.1	-92.6
Plan B	Montana	Melville	46	-110.3	51.4	-93.0
Grayson Ridge	Wyoming	Hanna	41.8	-107	49.9	-92.3
Halfway Hill	Wyoming	Hanna	41.8	-107	46.6	-92.0
C-Con	Texas	Tornillo	29.2	-103.2	46.6	-92.0
The Breaks (Ti1)	Wyoming	Hanna	41.8	-106.9	33.7	-93.8

Table S4.21.—Stratigraphic and geographic information for late early Tiffanian (Ti2) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
White Site, 7-Up Butte, and Highway Blowout	Montana	Sentinel Butte	45.8	-104.4	49.6	-87.2
Scarritt	Montana	Melville	45.8	-109.8	51.1	-92.6
UM locality 263	Wyoming	Polecat Bench/Fort Union	44.8	-108.7	49.9	-92.1
Saddle	Wyoming	Fort Union	42.3	-108.2	47.4	-93.0
The Breaks (Ti2)	Wyoming	Hanna	41.8	-106.9	46.6	-91.9

Table S4.22.—Stratigraphic and geographic information for early middle Tiffanian (Ti3) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Hand Hills West, upper level	Alberta	Paskapoo	51.5	-112.3	57.0	-91.2
Blindman River	Alberta	Paskapoo	52.4	-113.8	58.2	-92.0
Burbank	Alberta	Paskapoo	52.3	-113.8	58.1	-92.1
Joffre Bridge	Alberta	Paskapoo	52.2	-113.6	57.9	-91.9
Birchwood	Alberta	Paskapoo	53.2	-114.7	59.1	-92.2
Police Point	Saskatchewan	Ravenscrag	49.7	-110.1	54.7	-90.3
Brisbane	North Dakota	Tongue River Member of Fort Union	46.7	-101.8	49.7	-84.1
White's River Basin Survey Site	North Dakota	Sentinel Butte	47.7	-103.4	51.1	-85.0
Cedar Point	Wyoming	Polecat Bench/Fort Union	44.7	-108.4	49.7	-91.8
Jepsen Quarry	Wyoming	Polecat Bench/Fort Union	44.5	-108	49.4	-91.6
Twin Creek	Wyoming	Evanston	41.8	-110.7	47.6	-95.8
Chappo Type	Wyoming	Fort Union	41.8	-110.7	47.6	-95.8
Ledge	Wyoming	Fort Union	43.2	-108.2	48.3	-92.5
Battle Mountain	Wyoming	Hoback	42.7	-110.1	48.3	-94.7
Love	Wyoming	Hoback	43.9	-110.8	49.6	-94.8
Ray's Bonebed	Texas	Tornillo	29.2	-103.2	33.7	-93.8
Ohio Creek	Colorado	Ohio Creek	40.3	-108.3	45.6	-94.1
The Break (Ti3)	Wyoming	Hanna	41.8	-106.9	46.6	-91.9

Table S4.23.—Stratigraphic and geographic information for late middle Tiffanian (Ti4) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Crestomere School	Alberta	Paskapoo	52.6	-114.1	58.4	-92.1
Swan Hills	Alberta	Paskapoo	54.8	-115.5	60.8	-91.6
Roche Percée	Saskatchewan	Ravenscrag	49.1	-102.7	52.2	-83.4
Wannagan Creek	North Dakota	Tongue River Member of Fort Union	47	-103.7	50.5	-85.7
Judson	North Dakota	Tongue River Member of Fort Union	46.9	-101.5	49.8	-83.7
Riverdale	North Dakota	Sentinel Butte	47.5	-101.2	50.3	-83.0
Cross locality	North Dakota	Sentinel Butte	47.7	-103.4	51.1	-85.0
Red Spring	North Dakota	Sentinel Butte	47.2	-101.9	50.2	-83.9
Witter Locality	North Dakota	Sentinel Butte	48.4	-103.5	51.7	-85.2
Olive	Montana	Tongue River Member of Fort Union	45.4	-105.6	51.8	-84.6
Circle	Montana	Tongue River Member of Fort Union	47.8	-106.1	49.6	-88.6
Seaboard Well	Wyoming	Polecat Bench/Fort Union	44.3	-109	51.9	-87.6
Fossil Hollow	Wyoming	Polecat Bench/Fort Union	44.3	-109	49.5	-92.7
Long Draw Quarry	Wyoming	Polecat Bench/Fort Union	45.2	-109	49.5	-92.7
Lower Sand Draw	Wyoming	Polecat Bench/Fort Union	44.5	-108	50.3	-92.2
Croc Tooth	Wyoming	Polecat Bench/Fort Union	44.7	-108.3	49.7	-91.7
Divide	Wyoming	Polecat Bench/Fort Union	44.7	-108.3	49.7	-91.7
Sand Draw Anthill	Wyoming	Polecat Bench/Fort	44.5	-108	49.4	-91.6

Mason Pocket	Colorado	Union Animas	37.1	-107.6	46.9	-93.8

Table S4.24.—Stratigraphic and geographic information for early late Tiffanian (Ti5) mammalian assemblages from the Western Interior of North America.

Locality	Province/State	Formation	Lat.	Long.	Paleolat.	Paleolong.
Zalmout	Wyoming	Polecat Bench/Fort Union	44.8	-108.8	49.9	-92.2
Y2K	Wyoming	Polecat Bench/Fort Union	44.3	-109	49.5	-92.7
Princeton	Wyoming	Polecat Bench/Fort Union	44.9	-108.9	50.0	-92.2
Schaff	Wyoming	Polecat Bench/Fort Union	44.9	-108.9	50.0	-92.2
Brice Canyon	Wyoming	Polecat Bench/Fort Union	44.3	-109	49.5	-92.7
Fritz	Wyoming	Polecat Bench/Fort Union	44.9	-108.9	50.0	-92.2
Jepsen Valley	Wyoming	Polecat Bench/Fort Union	44.9	-108.9	50.0	-92.2
Middle Sand Draw	Wyoming	Polecat Bench/Fort Union	44.5	-108	48.3	-92.5
Titanoides locality	Wyoming	Fort Union	43.2	-108.2	47.1	-94.1
Rock Springs Uplift (Ti5)	Wyoming	Fort Union	41.7	-109	48.3	-94.7
Dell Creek	Wyoming	Hoback	42.7	-110.1	45.5	-94.0
University of Colorado Museum locality 92177	Colorado	Fort Union	40.3	-108.2	33.7	-93.8
Joe's Bonebed	Texas	Tornillo	29.2	-103.2	49.9	-92.2

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