MAMMALIAN BODY SIZE CHANGE DURING THE PALEOCENE–EOCENE THERMAL MAXIMUM IN THE POWDER RIVER BASIN, WYOMING

by

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Mammalian Body Size Change during the Paleocene–Eocene Thermal Maximum in the Powder River Basin, Wyoming

Thesis directed by Associate Professor Jaelyn J. Eberle

The Paleocene–Eocene Thermal Maximum (PETM) represents a rapid global warming at the Paleocene–Eocene (PE) boundary. Research by others in Wyoming’s Bighorn Basin has demonstrated that certain mammalian taxa (e.g., the ‘condylarths’ *Ectocion* and *Copecion*, and the perissodactyl *Sifrhippus [=Hyracotherium]*) experienced a decrease in body size during the height of the PETM. To date, this phenomenon has not yet been documented in North American PE boundary-spanning mammalian faunas outside of the Bighorn Basin.

East of the Bighorn Basin in Johnson County, Wyoming, strata of the “Wasatch” formation in the Powder River Basin contain terrestrial records of the PETM, with mammalian faunas (in direct superposition) spanning latest Paleocene (late Clarkforkian) through earliest Eocene (early Wasatchian, including Wa0 and Wa1). Research from localities spanning the PETM allows us to test whether the dwarfing of mammalian taxa observed by researchers in the Bighorn Basin occurs in the Powder River Basin (and is therefore a more regional pattern).

Using tooth crown area as a proxy for body size, I looked for patterns of body size change during the PETM. The inclusion of the order Rodentia in our study adds an additional facet to the analysis of body size changes during the PETM. Results from the plesiadapiform *Arctodontomys*, the true primate *Cantius*, “condylarths” *Apheliscus* and *Hyopsodus*, and the rodent *Paramys* suggest that dwarfing occurred in the Powder River Basin during the Wa0 interval, similar to what others noted in the Bighorn Basin. However, the rodent *Acritoparamys*...
seems to show an increase in body size from late Clarkforkian to earliest Wasatchian (Wa0) time. I also document the first occurrence of the rare cylindrodontid rodent *Tuscalomys cf. T. majori* and describe four distinct rodent lower incisor morphologies. The recovery of additional teeth and further analysis of fossils from the Powder River Basin is critical to testing whether body size changes in mammalian taxa during the PETM extend beyond the boundaries of the Bighorn Basin. From a larger perspective, studies such as this should provide insight into the impacts of current and future global warming on today’s mammalian fauna.
DEDICATION

For Dad, the smartest man I’ll ever know.
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1. INTRODUCTION

1.1 Research Goals

The Paleocene–Eocene Thermal Maximum (PETM; ~55.8 Ma, Secord et al., 2006), at the Paleocene–Eocene (PE) boundary, represents a rapid and intense global warming with several hypothesized biotic implications. One of these implications is the geologically sudden appearance in North America of the modern orders Artiodactyla, Perissodactyla, and true Primates (Euprimates). In addition, within the Bighorn Basin of northern Wyoming, several taxa, such as *Copecion* and *Sifrhippus [=Hyracotherium in N. A., (Froehlich, 2002)]*, appear to undergo an “evolutionary dwarfing” at the onset of the Eocene (Gingerich, 2003). It has been proposed that this dwarfing is a result, in part, of Bergmann’s rule, where smaller-bodied species are generally found at lower latitudes, and therefore warmer temperatures, than their larger-bodied counterparts (Mayr, 1963).

Further research is needed in order to gain a better understanding of the faunal implications of the PETM. Because the majority of terrestrial research has been focused within a single basin, Wyoming’s Bighorn Basin, it is unknown whether the evolutionary dwarfing that occurred there during the PETM is endemic to that basin, or if it occurred on a regional (or even global) scale. By conducting similar research in more localities and basins whose strata span the PETM and the PE boundary, we can gain a better understanding of terrestrial events during the PETM.

I investigated mammalian body size changes in several taxa recovered from localities spanning the PETM in the Powder River Basin of northeast Wyoming. Following the research of Gingerich and others (Clyde and Gingerich, 1998; Gingerich, 2003; Rose et al., 2012; Secord et
I used tooth crown area as a proxy for body size. The following chapters discuss the methods and results of my testing the hypothesis: Is there evidence of evolutionary dwarfing (a manifestation of Bergmann’s rule) in mammalian lineages spanning the PETM in the Powder River Basin? In other words, can the body size changes that have been documented in the Bighorn Basin during the PETM be extended beyond the boundaries of that basin to a more regional scale?

1.1 History of Collection at the University of Colorado Museum (UCM)

In 1981, under the leadership of Peter Robinson, UCM began an extensive collecting project in the Powder River Basin, concentrating on the area between Pine Ridge, near Sussex, Johnson County, Wyoming and Pumpkin Buttes, to the northeast in Campbell County (Robinson and Ivy, 1994). Previous research by Delson (1971) had reported the area to be fossiliferous. Prior to UCM’s collecting efforts, it was thought that only Wa2 and younger fauna were represented in the “Wasatch” Formation. Beginning in 2000, concentrated collection by Robinson in the Chalk Butte area has resulted in 30 new UCM localities spanning latest Clarkforkian (Cf3) to early Wasatchian: 14 represent Cf3, 13 are Wa0, and 3 are Wa1 or ?Wa1/2 localities. This is the field area on which my research is based.

1.2 The Paleocene–Eocene Thermal Maximum (PETM)

The Cenozoic Era (the last ca. 66 Ma of Earth’s history) exhibits a broad-spectrum of dramatic climatic events. In addition to long-term shifts in the Earth’s climate, the early Cenozoic contained a series of short events known as hyperthermals, brief intervals of extreme global warming and massive carbon addition (Zachos et al., 2008). The most prominent of these
events, the PETM, occurred at the PE boundary. Coinciding with a global negative carbon isotope excursion (CIE), global temperatures rapidly increased an estimated 5–10°C within the initial phase of the PETM (~10–20 ka), followed by a slow recovery phase (Wing et al., 2005). The entire PETM is estimated to have spanned ~170 ka (Röhl et al., 2007). Biotic events occurring during the PETM include: a mass extinction of benthic foraminifera (Thomas and Shackleton, 1996); changes in planktonic biota (Kelly, 2002); the dispersal of land mammals between the continents of the Northern Hemisphere, specifically the geologically abrupt appearance of perissodactyls, artiodactyls, and true primates in North America (Bowen et al., 2002); and significant northerly plant range shifts (Harrington, 2003; Wing et al., 2005).

The underlying cause of the PETM remains uncertain. Hypotheses include the release of thermogenic methane through volcanism (Svensen et al., 2004) and the oxidization of organic matter in terrestrial environments (Higgins and Schrag, 2006). The most widely accepted hypothesis is the dissociation of deep-sea methane hydrates, releasing large amounts of greenhouse gases into the atmosphere (Dickens, 2008).

By far the most studied North American terrestrial locality spanning the PETM is the Bighorn Basin of northern Wyoming. In the Bighorn, the PETM has been identified in four separate locations: Polecat Bench (Magioncalda et al., 2004), Cabin Fork (Wing et al., 2005), Castle Gardens (Yans et al., 2006), and Sand Creek Divide (Rose et al., 2012). To the south, the Piceance Creek Basin of western Colorado preserves a negative CIE within a ~70 m section of strata (Burger, 2012). Paleocene and Eocene mammalian fauna are known from the Piceance Creek Basin, however the latest Paleocene and earliest Eocene are not represented (Burger, 2009). In the San Juan Basin of New Mexico, there is a basin-wide disconformity at contact between the Paleocene age Nacimiento Formation and Eocene San Jose Formation resulting in
the lack of PETM deposits (Milner et al., 2005). To the north, an “orange zone” interpreted as an intense terrestrial weathering profile occurs across PE boundary in the Williston Basin of North Dakota. While this “orange zone” lacks definitive evidence of a CIE, the palynoflora preserved within the upper part of the “orange zone” is similar to that associated with later stages of the PETM at Bighorn Basin localities (Clechenko et al., 2007). Along the Gulf Coast, the Red Hot Truck Stop locality in the upper Tuscaloosa Formation of Mississippi preserves earliest Eocene mammals, but no evidence of a late Paleocene mammalian fauna is known (Beard and Dawson, 2009).

The Powder River Basin in northeastern Wyoming contains the first North American mammalian record of the PETM in direct superposition, outside of the Bighorn Basin (Wing et al., 2003). Therefore, this seems to be the best place, to date, to test the hypothesis of whether evolutionary dwarfing observed in the Bighorn Basin also occurs during the PETM in the Powder River Basin.

1.3 Background to North American Land Mammal Ages (NALMA)

1.3.1 Historical background

In 1941, the Wood committee proposed a time scale for the Cenozoic of North America based on land mammal biostratigraphy, resulting in 18 North American Land Mammal Ages (NALMA). The goal was to define units of time characterized by faunal content rather than chronostratigraphic units, thus eliminating confusion for vertebrate paleontologists in correlating North American paleontological events to the European marine fossil-based sequence of epochs. NALMA are defined by four characteristics: index taxa, which are known only within a specific age; first and last appearances; and characteristic fossils that may appear in older or younger
deposits, but are most common within a specific age (Wood and Clark, 1941). The various co-authored chapters in Woodburne (2004) updated the definitions of these NALMA, based upon a high-resolution chronologic framework incorporating all available temporally significant data and applications (e.g. lithostratigraphy, biostratigraphy, magnetostratigraphy, and carbon isotope stratigraphy). In addition, Woodburne (2004 and authors within) eliminated the Dragonian NALMA, and added the Irvingtonian and Rancholabrean for a total of 19 Cenozoic NALMA currently.

The NALMA relevant to my research in the Powder River Basin are the Clarkforkian and Wasatchian, which straddle the PE boundary. The Clarkforkian–Wasatchian boundary correlates with a global-scale rapid environmental change, known as the Paleocene–Eocene Thermal Maximum (PETM), previously discussed.

1.3.2 Clarkforkian

Granger (1914) used the term Clark Fork to refer to a stratigraphic interval at Polecat Bench in the Clark’s Fork Basin of northwestern Wyoming, which contained taxa which he initially suggested were possibly of Paleocene age. Wood et al. (1941) proposed the term Clarkforkian as a North American provincial age, naming Granger’s locality near Polecat Bench as the type locality. Rose (1981) defined the Clarkforkian mammal age as starting with the first appearance of Rodentia and ending with the first appearance of Artiodactyla. He subsequently divided the Clarkforkian into three faunal zones: the Plesiadapis gingerichi, the Plesiadapis cookei, and the Phenacodus–Ectocion zones. Most relevant to my study is the third and youngest zone, the Phenacodus–Ectocion zone, later termed Cf3 by Archibald et al. (2004). It begins immediately following the last appearance of Plesiadapis cookei (Rose, 1981). It is further
recognized by the first appearance of *Esthonyx granger*, *Hyopsodus*, and *Phenacolemur praecox* (Lofgren et al., 2004). Some characteristic fossils include *Apatemys, Apheliscus, Barylamba, Coryphodon, Ectocion, Haplomylus, Phenacodus*, and *Phenacolemur*. Paleomagnetic correlation indicates that Cf3 occurs entirely within the magnetic polarity chron C24r (Butler and Coney, 1981). It spans from ~55.8–56.2 Ma (Secord et al., 2006).

### 1.3.3 Wasatchian

The Wasatchian is the first North American land mammal age in the Eocene. The beginning of the Wasatchian is marked by a major widespread dispersal of the modern orders Artiodactyla, Perissodactyla, and true Primates (Euprimates) (Robinson et al., 2004). First appearances include euprimates *Cantius* and *Teilhardina*, the perissodactyl *Sifrhippus* [=*Hyracotherium* in N. A., (Froehlich, 2002)], and the artiodactyl *Diacodexis*. Index taxa, restricted to the Wasatchian, include ‘insectivore’ *Diacodon*, and the perissodactyls *Homogalax*, and *Lambdotherium* (Robinson et al. 2004).

The term Wasatch was first used by Hayden (1869) for a group of formations near Evanston, Wyoming, just east of the Wasatch Mountains, later extended by Cope (1877, 1882) to include the San Juan Basin in New Mexico and Bighorn Basin in northwestern Wyoming. Granger (1914) recognized four assemblages of the lower Eocene in the Bighorn Basin: Sand Coulee, Greybull, Lysite, and Lost Cabin. These assemblages were later grouped together as consecutive zones in a single NALMA termed Wasatchian (Wood and Clark, 1941). Research by Gingerich and colleagues has divided the Wasatchian into eight biochrons, which from oldest to youngest are Wa0 to Wa7 (Gingerich, 1989; Gingerich and Smith, 2006). The early Wasatchian
includes biochrons Wa0–Wa2 (Sandcouleean), middle Wasatchian covers Wa3–Wa5 (Graybullian), and the late Wasatchian includes Wa6 (Lysitean) and Wa7 (Lostcabinian).

The Wasatchian biochrons pertinent to my study are Wa0 and Wa1. The PETM is represented by a unique mammalian fauna restricted to Wa0, exhibiting a diminutive body size in respect to its immediate predecessors and descendents (Gingerich, 2003). Characteristic taxa of Wa0 include *Apheliscus, Cantius, Diacodexis, Ectocion, Phenacodus, Phenacolemur*, and *Teilhardina*. Taxa restricted to Wa0 are *Cantius torresi, Arfia junnei, Copecion davisi, Diacodexis ilicis*, and *Sifrhippus sandrae* (Gingerich, 2001). The Wa0 biochron takes place entirely within the PETM, falling within magnetochron C24r, and is approximately 100 ka in duration (Secord et al., 2006).

Wa1 is distinguished from Wa0 by the presence of *Cantius ralstoni, Haplomylus speirianus*, and *Diacodexis metsiacus*. In addition, *Sifrhippus grangeri* is common in this interval, while it appears to be a very rare component of Wa0 faunas (Gingerich, 2001). Secord et al. (2006), estimates the duration of Wa1 to be approximately 200 ka.
2. BERGMANN’S RULE

2.1 Introduction

Many biogeographic patterns, distributions of taxa and their attributes in space and time (Hausdorf et al., 2007), were first established during the nineteenth century (e.g., Gloger, 1833; Bergmann, 1848; Allen, 1877; Cope, 1896). Bergmann’s rule, one of the best known patterns, states that races of homeothermic species living in warmer climates are smaller than races from cooler climates (Feldhamer, 2007). Although originally formulated to describe body size variations among species within a genus, today Bergmann’s rule is usually applied to intraspecific (within species) variation (Mayr, 1963). According to Bergmann (1848), there is a selective advantage for larger animals to have a lower surface area-to-volume ratio than smaller animals; therefore they radiate less body heat per unit of mass, causing them to stay warmer in cold climates while expending less energy. On the other hand, in warmer climates, the higher surface area-to-volume ratio of smaller animals facilitates heat loss through the skin, helping to cool the body. In a simple isometric scaling, linear dimensions increase in constant proportion. Therefore, as the length of an individual increases, the surface area will increase by a power of two, while its volume and mass will increase by a power of three (Mayr, 1963). In other words, the larger the body size, the smaller the surface area is in relation to it.

Bergmann’s rule proposes that ambient temperatures have a direct ecological and physiological effect on organisms. Because temperature tends to decrease from the equator to the poles, Bergmann’s rule is typically applied to body size changes across a latitudinal gradient (Ashton, 2002; Freckleton et al., 2003). While it is often interpreted as a direct response to temperature (Brown and Lee, 1969), the thermoregulatory mechanism originally proposed by Bergmann has been questioned by several researchers. For example, McNab (1971) postulated
that a correlation between latitude and change in body size is associated with other factors, such as competition and distribution of food sources. Others hypothesize that body size varies in response to a combination of climatic factors. James (1970) hypothesized that environmental variables associated with temperature and moisture, such as wet-bulb temperature (the lowest temperature that can be reached by evaporating water into the air), vapor pressure, and absolute humidity, are negatively correlated with body size variation.

While the original Bergmann’s rule related only to homoeothermic animals, mammals and birds, research has broadened to include poikilothermic animals, reptiles and amphibians. Salamanders and turtles follow the rule, while lizards and snakes follow the inverse of Bergmann’s rule (Ashton, 2002; Ashton and Feldman, 2003).

2.1.1 Bergmann’s rule in Paleontology

Support for Bergmann’s rule in the fossil record is challenging to demonstrate due to incompleteness of the fossil record, taphonomic bias, lack of full understanding of the environmental conditions, and difficulties in estimating body size. While paleontologists consider the lowest taxonomic unit in the fossil record to be a species (short for morphospecies, which is a species defined by its morphological characters preserved on the fossil), whether a morphospecies equates with a biological species (a group of potentially interbreeding populations genetically isolated from other groups) cannot be proven. In many cases, a strict inter- and intraspecific interpretation of Bergmann’s rule is not possible for fossil species. Rather, comparisons must be made within a fossil organism’s lineage (i.e., inter- versus intralineage interpretation of Bergmann’s rule). In addition, migration, endemism, and disjunct distribution make the study of Bergmann’s rule across a latitudinal gradient challenging. Rather
than using latitude as a proxy for temperature, paleontologists look for environmental clues such as changes in floral composition to indicate temperature change (e.g., Wing et al., 2003). Rapid warming at the beginning of the Eocene (the Paleocene–Eocene Thermal Maximum, or PETM) has been associated with modest changes in floral composition, mostly shifts in the relative abundances of taxa rather than large numbers of first or last appearances. Although floral change across the PE boundary has been studied in many areas, few fossils demonstrably come from the approximately 200 ka long PETM. The rarity of fossils from the PETM permits two hypotheses: PETM floras were similar to, or intermediate in composition between, Paleocene and Eocene floras; or they were distinct from both Paleocene and Eocene assemblages in having a high proportion of taxa that were temporary, thermophilic immigrants. The latter hypothesis is consistent with expectations developed from the study of late Quaternary floras, which demonstrate rapid northward range displacements in the wake of retreating continental glaciers.

Here we report lithological, paleontological and isotopic evidence for a PE boundary section in the lower “Wasatch” Formation of the southwestern Powder River Basin, Wyoming. Pollen samples from within the PETM interval do not record immigrants from the south, making it unlikely that there were rapid, continental-scale range displacements during the PETM. Floral response consisted of shifts in the relative abundances of native taxa at the beginning of or even prior to the PETM, followed by immigration of taxa from outside of North America, probably Europe, near the end of or possibly after the PETM (Wing et al., 2003).

Despite these challenges, the fossil record is an important resource for evolutionary and ecological studies. The Cenozoic North American mammalian record is particularly useful, as it has the most complete record of terrestrial biotic succession (Webb and Opdyke, 1995). Several studies of body size change in the fossil record across particular temporal intervals (e.g. PE
boundary) have shown responses to climate change that appear to follow Bergmann’s rule (two of which are described below). While these studies show correlations between mammalian evolution and temperature, other studies argue that the influence of climate change on mammalian evolution is only slight (Prothero, 1999; Alroy et al., 2000). Instead, mammalian evolution is hypothesized to be driven by several biological factors, including competition, escape from predation, and biomechanical and physiological optimality (Alroy et al., 2000). In addition, one cannot rule out the effect of northern range extensions and invasive species on a local population (Burger, 2012).

2.2 Examples of Bergmann’s rule in the Fossil Record

2.2.1 Bergmann’s rule in Pleistocene Neotoma

The Pleistocene Epoch has been a focus of many of studies regarding Bergmann’s rule because of its repeated and rapid glaciations, resulting in major impacts on the fauna and flora. For example, a series of studies on woodrats (Neotoma) have shown that they adapted to temperature increase since the last glacial maximum (~20 ka) through decreases in body size (Smith et al., 1995; Smith and Betancourt, 1998, 2003). Through the study of paleomiddens, which contain plant and animal remains along with fecal pellets, paleontologists have reconstructed the ecology and morphology of woodrats over the past 25,000 years (Smith et al., 1995). The width of a woodrat fecal pellet is closely correlated to body size with a 21% prediction error (Smith et al., 1995). Comparison of estimated body size changes in woodrats with changes in temperature since the last glacial maximum demonstrate that woodrats were larger during the cooler climate in the late Pleistocene, and decreased in size to near modern
body size by early in the Holocene when temperatures were warmer (Smith et al., 1995; Smith and Betancourt, 1998, 2003, 2006).

2.2.2 Bergmann’s rule in the Bighorn Basin at the PETM

The PE boundary (~55.8 Ma, Secord et al., 2006) represents a period of dramatic global warming over a short period of time, known as the Paleocene–Eocene Thermal Maximum (PETM; ~170 ka, Röhl et al., 2007). Coinciding with a global negative carbon isotope excursion (CIE), temperatures are estimated to have rapidly increased ~5–10°C within the initial phase of the PETM (~10–20 ka), followed by a slow recovery phase (Wing et al., 2005).

One of the most common genera in the Clarkforkian (late Paleocene) and early Wasatchian (earliest Eocene) faunal assemblages is the ‘condylarth’ Ectocion. In the Bighorn Basin, it is represented by a long lineage of Ectocion osbornianus. The Wa0 fauna at Polecats Bench however, is unusual because of the abundance of Ectocion parvus, which differs from E. osbornianus only in size (Gingerich, 1989). By estimating body mass through the tooth crown area of molars, E. parvus is estimated to be ~50% smaller than E. osbornianus (Gingerich, 2003). While E. parvus appears to be a distinctly smaller species that replaced E. osbornianus during Wa0, Gingerich (2003) hypothesized that it is an “evolutionarily dwarfed” member of the species E. osbornianus. Several other examples of evolutionary dwarfing are exhibited at Polecats Bench (Gingerich, 1989); however, some species such as Hyopsodus loomisi, appear to have no significant change in body size during the PETM (Gingerich, 2003). Gingerich proposed that elevated temperature, as well as elevated CO₂ concentrations, during the PETM were possible factors driving the evolutionary dwarfing of some mammalian taxa, conforming to Bergmann’s rule in terms of the expected direction of size change.
More recent research in the Cabin Fork area of the southern Bighorn Basin has yielded similar findings for the early equid *Sifrhippus [=Hyracotherium in N. A., (Froehlich, 2002)]* (Secord et al., 2012). While results are consistent with the hypothesis of evolutionary dwarfing as a response to temperature change, Secord et al. (2012) argue that an increase in temperature during the PETM is an insufficient explanation. The authors refer to several inconsistencies of Bergmann’s rule, for example that 25–35% of living mammals do not follow the rule (Ashton et al., 2000; Rodríguez et al., 2008), as support for their argument. Tests of alternative explanations such as increased aridity and CO₂ concentrations, however, fail to yield strong correlations to the observed body size changes (Secord et al., 2012). To date, temperature change remains the strongest hypothesis to explain the evolutionary dwarfing during the PETM.

Further research is needed in order to gain a better understanding of the faunal implications of the PETM. Because the majority of terrestrial research has been focused within a single basin, Wyoming’s Bighorn Basin, it is unknown whether the evolutionary dwarfing that occurred there during the PETM is endemic to that basin, or if it occurred on a regional (or even global) scale. By conducting similar research in more localities and basins whose strata span the PETM and PE boundary, we can gain a better understanding of terrestrial events during the PETM.

The Powder River Basin in northeastern Wyoming contains the first terrestrial record of the PETM in North America outside of the Bighorn Basin (Wing et al., 2003). Located 100 km east of the Bighorn Basin, the Powder River Basin is unique in being locally rich in small mammals and reptiles (Robinson, 1994). The formation of the surrounding mountain ranges during the Paleocene resulted in a large distribution of sediment into the Powder River Basin, creating an abundance of carbonaceous shales and lignites, indicative of a low-lying swamp
(Wing et al., 2003). To date, the majority of mammalian faunal analysis conducted in the Powder River Basin has been from localities that post-date the PETM (in the Wasatchian). I investigated mammalian body size changes in several taxa recovered from localities spanning the PETM in the Powder River Basin.
3. GEOLOGIC SETTING

3.1 Introduction

The Powder River Basin is an intermontane basin of Laramide origin covering about 22,000 square miles of northeast Wyoming and southeast Montana. It is asymmetrical, with the axis trending northwest to southeast near the western margin (Osmonson et al., 2011). In Wyoming, its borders are the Bighorn Mountains to the west, Casper Arch to the southwest, the Laramie Range to the south, the Hartville Uplift to the southeast, and the Black Hills to the east (Figure 1). Between 1,200 and 1,800 m of Paleogene strata consisting of the Fort Union, “Wasatch,” and White River Formations lies over ~ 2,100 m of Cretaceous strata (Sharp et al., 1964). In Wyoming, the Fort Union Formation of Paleocene age is exposed along basin margins. Strata mapped as Eocene aged “Wasatch” Formation rest conformably over the Fort Union Formation in the center of the basin and unconformably along the margins (Osmonson et al., 2011).
Figure 1: Map of late Paleocene and early Eocene depositional basins in the Rocky Mountains. Star represents field area included in this study. Modified from Dickinson et al. (1988).

The U.S. Geological Survey mapped the strata in this area as part of the Wasatch Formation of Eocene age, yet the Powder River Basin is physically separated from the type locality of the Wasatch Formation in the Green River Basin by the Wind River Basin with its
Wasatchian Indian Meadows and Wasatchian/Bridgerian Wind River Formations (Figure 1) (Robinson et al., 2004). In addition, Soister (1968) reported crossbedding in the sandstones of the Pumpkin Buttes in the southern region of the Powder River Basin, indicating a north-northwest stream flow. He concluded that sediment deposited in this area came from a river flowing north from the Hartville Uplift, rather than the Wind River, and therefore could not be derived from the same source area as the type Wasatch locality. Therefore, within the Powder River Basin, the “Wasatch” Formation is typically placed in quotes.

Generally, red-banded mudstone and siltstone strata of early Eocene age are common in the basins of the Rocky Mountain region (such as the Bighorn, Piceance Creek, and Sand Wash Basins). This zone corresponds with a widespread faunal change throughout the Rocky Mountain region, and specifically the geologically sudden appearance of the modern orders Artiodactyla, Perissodactyla, and Primates (Clyde and Gingerich, 1998). In the Powder River Basin, however, this characteristic red-banded lithology is absent in most of the Eocene rocks, occurring only in a small area southwest of Pumpkin Buttes, near Pine Ridge (Sharp et al., 1964).

In this southwest region of the Powder River Basin that is between Pumpkin Buttes and Pine Ridge (Figure 2), Cretaceous and Paleocene strata form the east-west trending Pine Ridge, with beds dipping 20–40 degrees north into the basin (Wing et al., 2003). The sediments of the “Wasatch” Formation in this area are drab, containing many carbonaceous shales and lignites, and this formation sits on the Fort Union Formation with a minor angular unconformity (Wing et al., 2003). The presence of these drab mudstones, carbonaceous shales and lignites of the “Wasatch” suggests that deposition of these fluvial deposits occurred in a generally reducing environment (Delson, 1971). Strata quickly shallow towards the basin axis, and by Chalk Butte (Figure 2), “Wasatch” strata dip only 4–7 degrees (Wing et al., 2003). Beginning at Chalk Butte,
the sediment transitions to “pedogenically altered red and variegated mudstones” similar to the Paleocene–Eocene sequences found in the southeastern part of the Bighorn Basin (Wing et al., 2003). This alternating red and variegated mudstone pattern is hypothesized to represent a drying trend (Kraus and Riggins, 2007).
Figure 2: UCM Localities in the Chalk Butte area of the Powder River Basin. Orange squares represent Clarkforkian 3 localities, yellow circles represent Wasatchian 0 localities, and pink diamonds represent Wasatchian 1 localities. Blue lines represent lingites. Map based on U.S. Geological Survey Sussex and House Creek Quadrangles (1:24,000).

The roughly 483 m of “Wasatch” Formation reported by Sharp (1964) not only produce earliest Eocene (Wasatchian) fauna, but also contain a distinct latest Paleocene (Clarkforkian) vertebrate fauna such as *Champosaurus gigas* (Robinson and Ivy, 1994). Of the index fossils reported for the Clarkforkian NALMA, which include *Apheliscus nitidus, Barylambda,*
Haplomylus simpsoni, and Plesiadapis cookeri (Lofgren et al., 2004), the pantodont Barylambda (specifically a femur) was found below the red bed sequence at Chalk Butte. Further, B. fabori, an index species for Cf3, is found directly below the red bed sequence, which alongside absence of typical earliest Wasatchian (Wa0) taxa, confirms the age as Cf3. Typical Wa0 taxa occur above the redbed sequence base, including Diacodexis, Sifrhippus, Teilhardenia and Cantius (Robinson, personal comm.). Consequently, I am certain that the Cf3–Wa0 transition is preserved at Chalk Butte.

3.2 Biotratigraphy

Wing et al. (2003) identified the Paleocene–Eocene Thermal Maximum (PETM) in the Chalk Butte area of the Powder River Basin based on four lines of evidence: the presence of prominent, laterally extensive red paleosols above drab, lignitic strata; characteristic Wa0 mammalian fauna, such as the euprimate Cantius torresi, occurring above the lowest red beds; the first appearance of Eocene index palynofloras above the Wa0 mammalian fauna; and carbon isotope values which suggest a shift similar to the CIE in the Bighorn Basin. However, this fourth line of evidence — the carbon isotope pattern — is challenging to interpret, and requires further, more refined analyses. The beginning of the CIE has yet to be determined in the Chalk Butte area (Fricke, 2013, personal comm.).

It is difficult to make bed-to-bed correlations in this region of the Powder River Basin due to many of the outcrops being obscured by vegetation. Fortunately, the presence of traceable carbonaceous shales and lignites throughout the section make relatively accurate physical correlations possible at some stratigraphic levels (Robinson, 2012, personal comm.). Wing et al. (2003) measured three sections near Chalk Butte, which I use as the basis of my stratigraphic
framework (Figure 3). At the base of all three sections is a single carbonaceous shale with lignitic zones — referred to as the Chalk Butte Marker Lignite (CBML) — which is traceable along exposures in the drainages and gullies throughout the field area. Other characteristic lithologies include a distinct gray mudstone, referred to as the White Marker Bed (WMB) and a red bed sequence occurring above it (Wing et al., 2003). I use these lithologies to correlate “age zones” within the field area. The West Prong Level (WMB to 5 m above) contains Cf3 fossils. The Cole Draw Level starts at the base of the red bed sequence and is of definite Wa0 age because it has Cantius torresi and Copecion davisii, two taxa that others have noted as restricted to Wa0 (Gingerich, 2001). The Carpenter Draw Level (10 to 20 m above the Cole Draw Level) represents a later interval of Wa0 and has also produced C. torresi.
Despite exhibiting a similar red bed sequence as found in the Bighorn Basin (Wing et al., 2003), the Powder River Basin differs from most other Laramide basins in its abundance of coal and bias towards microvertebrate fossils (Seeland, 1993; Robinson, 1994). While climatic and tectonic conditions were similar to the Wind River and Bighorn Basins, over 80 percent of the coal resources in Wyoming come from the Powder River Basin (Glass, 1980). A likely factor for the higher presence of coal may be regional paleogeography (Seeland, 1993). As the Wind River of Eocene age drained into the Powder River Basin, the volume of water flowing through
the basin greatly increased, favoring the accumulation and preservation of peat and the formation of thicker and more widespread coal beds (Seeland, 1993).
4. MATERIALS AND METHODS

4.1 Dental Terminology and Measurements

I use the universally accepted dental terminology proposed by Osborn (1907) when discussing the non-rodent molars (Figure 4) and terminology proposed by Korth (1994) for rodent molars (Figure 5).

<table>
<thead>
<tr>
<th>Letter(s)</th>
<th>Description</th>
</tr>
</thead>
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<tr>
<td>Lowercase letters (e.g., m1)</td>
<td>Designate teeth from lower jaws</td>
</tr>
<tr>
<td>Uppercase letters (e.g., M1)</td>
<td>Designate teeth from upper jaws</td>
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<td>B-L width</td>
<td>Buccolinguai width</td>
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</tbody>
</table>
Figure 4: Non-rodent molar terminology, originally proposed by Osborn (1907). Image modified from Burger (2009).
Figure 5: Rodent molar terminology, proposed by Korth (1994). Image modified from Rose and Koenigswald (2007).
4.2 Paleontological Methods

The majority of specimens were collected from the anthills of the Western harvester ant *Pogonomyrmex occidentalis*. The nest is an elliptical cone averaging 14 inches high and 1 m in diameter and is centered within a circular clearing typically 3–4 m wide (Scott, 1951). The surface of the cone is covered with a pebble roofing about 2–4 cm thick of coarser material. Averaging 2–3 mm in diameter, this material can consist of gravel, modern rodent bones, twigs, and in some cases fossils (Matthias and Carpenter, 2004). When constructing their nest, harvester ants mine fossils from as low as 3 m below the surface (McCook, 1881). In addition, surface collection can reach as far as 15 m from the nest (Robinson and Williams, 1997). Due to this large foraging range, careful consideration is used when selecting anthills to sample in order to reduce uncertainty in the stratigraphic intervals (Robinson and Kron, 1998).

The collection process consists of partial removal of the pebble roofing from the anthills, which is bagged in gallon sized Ziploc bags and brought back to the University of Colorado Museum of Natural History (UCM). The sediment is screen washed using 1 mm diameter sized screens, dried, and picked. The 2011 field season resulted in surface collection of 20 anthills. For all but two of these anthills, additional matrix was brought back to UCM to be washed and sorted. Along with the assistance of volunteers from the Western Interior Paleontological Society, sorting of the anthill pebble roofing material from the 2011 field season resulted in the addition of 33 potential specimens for my study.

Only individual mammalian teeth and jaws of the orders Rodentia, Primates, and ‘Condylarthra’ are included in the study. Identification of mammalian teeth was made through comparison with specimens at UCM and with descriptions in the literature. Molar specimens were measured using a Ehrenreich Photo-Optical Industries Shopscope on loan from J. A.
Lillegraven. Rodent incisors were measured using digital calipers. All measurements were recorded to the nearest hundredth of a millimeter.

Tooth crown area (anteroposterior length multiplied by buccolingual width, or L x W) was used to measure tooth size. This method was chosen because differences in crown shape have less influence on crown area than they do on individual length and width measurements (Gingerich et al., 1982). Length and width measurements were taken parallel and perpendicular, respectively, to the long axis of the tooth for molars (Figure 6). On rodent incisors, the anteroposterior diameter and the maximum buccolingual distance was measured (Figure 7).

Figure 6: Measurements taken on lower molars in occlusal view. Image modified from Burger (2009).
4.3 Estimating Body Mass

Estimating body mass in the mammalian fossil record can be difficult in that teeth are usually the only element abundant enough to allow the study of variability within a species (Gingerich, 1974). In a study comparing size variability of teeth in living mammals and closely related fossil species, Gingerich (1974) concluded that the m1 typically has the least variability among tooth positions. In a perfect world full of unlimited specimens, I could follow this practice. However, limited sample size has led me to evaluate all molar positions. This limited
sample size has also driven the kinds of taxa that I studied. I looked at genera spanning the PE boundary, as well as some limited to just Wa0 and Wa1. Specifically, I analyzed the plesiadapiform *Arctodontomys*, the true-primate *Cantius*, the ‘condylaths’ *Apheliscus* and *Hyopsodus*, and the rodents *Paramys* and *Acritoparamys*. I also decided to look at rodent incisors because of their abundance, unique dentition, and because this group has not been analyzed for size change during the PETM.
5. **SYSTEMATIC PALEONTOLOGY**

In order to gain a better understanding of the biotic effects of the PETM on mammalian fauna, I analyzed species that spanned the PE boundary. Specimens available for study included those from the orders ‘Condylarthra,’ Rodentia, and Primates. Specifically, I measured teeth of the ‘condylarths’ *Hyopsodus* and *Apheliscus*; the rodents *Tuscahomys*, *Paramys*, and *Acritoparamys*; and the primates *Arctodontomys* and *Cantius*. Analysis was restricted to species with the following two requirements: there must be more than one specimen for a single tooth position; and the species must cover at least two successive time zones (i.e., Cf3 and Wa0; or Wa0 and Wa1). Below, I provide comments for the taxa included in my study.

The format of this chapter was chosen because of its simplicity and familiarity of a traditional systematic paleontology organization. While I do not provide detailed descriptions of individual specimens, I feel that the organization of the chapter along the lines of traditional systematic paleontology sections seems the most practical (and efficient) way to list and organize the specimens utilized in my study, and to provide their measurements. Many of the specimens were initially identified to genus level by Robinson (and their identifications are listed in the UCM database). However, I refined several to species level, and I also document the first Clarkforkian occurrence of the rare cylindrodontid rodent *Tuscahomys* cf. *T. major*, from the Powder River Basin. Rodent incisors were previously identified to the family Ischiromyidae and in some cases only to the order Rodentia. This is a common treatment of isolated rodent incisors as it is extremely difficult to identify them to species (and even genus) without associated molars. This can be frustrating since rodent incisors are often abundant in faunal assemblages. Because of my limited sample size, I decided to test whether a change in size occurs in rodent
incisors as well, grouping them based on common shared morphologies (explained below). At the end of this chapter, I provide a comprehensive faunal list for late Clarkforkian (Cf3), earliest Wasatchian (Wa0), and early Wasatchian (Wa1 and ?Wa1/2) localities at Chalk Butte, based largely on previous identifications in the UCM database.

Order PRIMATES Linnaeus, 1758
Suborder PLESIADAPIFORMES Simons and Tattersall, 1972
Family MICROSYOPIDAE Osborn and Wortman, 1892

**ARCTODONTOMYS** Gunnell, 1985

*Arctodontomys cf. A. wilsoni*

(Table 1)

**Referred specimens**— UCM 101485, right M2 from UCM locality 2003045 (Wa0); UCM 98060, left M2 from UCM locality 2003030 (?Wa1/2).

**Known occurrences of A. wilsoni**— Willwood Formation, Clark’s Fork and Bighorn Basins (Wa0-3); ‘Wasatch’ Formation, Powder River Basin (Wa2-4); Wasatch Formation, Sand Wash Basin (Wa1-3); DeBeque Formation, Piceance Creek Basin (Wa1-4).

**Description and Discussion**— *Arctodontomys* is known from isolated teeth in the Powder River Basin. I use only the M2s for my analysis because it was the only tooth position with sufficient number of specimens; therefore, I comment only on these teeth here. Specimen morphologies are typical of *Arctodontomys* as described in Gunnell (1985). The species *A. wilsoni* is differentiated
from *A. simplicidens* by its diminutive size and the presence of a small paraconid on the p4, and from *A. nuptus* in being significantly smaller (Gunnell, 1985). With only isolated teeth, identification to species is tentative and based primarily on size. UCM 101485 falls within the ranges of *A. wilsoni* listed in Szalay (1969) and Burger (2009), while the stratigraphically higher UCM 98060 is closer to size ranges listed by Gunnell (1985).

Table 1: Measurements (in mm) of *Arctodontomys* cf. *A. wilsoni* from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
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<td>3.19</td>
<td>4.08</td>
<td>?Wa1/2</td>
</tr>
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</table>

Suborder EUPRIMATES Hoffstetter, 1978

Family ADAPIDAE Trouessart, 1879

*CANTIUS* Simons, 1962

**Comments**— In order to accommodate a dentary specimen with multiple molars, the length of lower molars of *Cantius* was measured from the front of the paracristid to the back of the postcristid, as described by Gingerich (1976).

I consider all specimens from the PETM of the Powder River Basin as a single North American lineage, as proposed by Gingerich (1995). With the exception of the m3, it is difficult to identify isolated teeth of *Cantius* to species with certainty. The cristid obilqua of m3 of *C. torresi*, is a straight line, running anteriorly from the hypoconid to the protoconid, while in
younger species of *Cantius*, it begins anterolunually from the hypoconid and then turns anterobuccally to join the protoconid (Robinson, 2013, personal comm.).

*Cantius torresi* Gingerich, 1986

(Table 2)

**Referred specimens**—UCM 48596, right m3, and UCM 48597, right m3, from UCM locality 83117; UCM 58254, left dentary fragment with m1–3 from UCM locality 86101; UCM 98014, right m2, and UCM 101949, left m3, from UCM locality 2003041; UCM 100969, right M3 from UCM locality 2004056 (all from Wa0).

**Known occurrences**—Willwood Formation, Clark’s Fork and Bighorn Basins (Wa0); ‘Wasatch’ Formation, Powder River Basin (Wa0).

**Description and Discussion**—*C. torresi* is restricted to Wa0 (Gingerich, 1986). The holotype of *C. torresi* differs from the younger *C. ralstoni* in “being smaller, having relatively square upper molars, and relatively broader and lower premolars and molars” (Gingerich, 1986), as well as the distinction of the cristid oblique on the m3 previously discussed. I assign all Wa0 specimens to *C. torresi* because they are smaller and have lower cusps, while the younger (Wa1) specimens are referred here to *C. ralstoni* because they are larger and have taller (more acute or pointed) cusps, following Gingerich’s (1986) differentiation of these two closely-related species. UCM 98014 (Rm2) appears to be enamel-less, suggesting it was digested by a crocodilian. Teeth that have passed through a crocodilian gut often lack enamel, but otherwise appear to be complete
(Fisher, 1981). Due to small sample size, I have included both upper molars (M3s) and lower molars (m1–m3) in my measurements (see Table 2).

*Cantius ralstoni* Matthew, 1915

(Table 2)

**Referred specimens**—UCM 52735, left m3; UCM 52830, right M3; UCM 63445, left m3; UCM 63446, left m1; and UCM 63447, right m2, all from UCM locality 85278 (Wa1).

**Known occurrences**—Willwood Formation, Clark’s Fork and Bighorn Basins, Wyoming (Wa1–3); ‘Wasatch’ Formation, Powder River Basin (Wa2–4); DeBeque Formation, Piceance Creek Basin (Wa1–2).

**Description and Discussion**— I assign all Wa1 specimens to *C. ralstoni* (see discussion above).

Table 2: Measurements (in mm) of *Cantius* from the Powder River Basin. Specimens 48596, 48597, 58254, 98014, 100969, 101949 are *C. torresi*, and 52735, 52830, 63445, 63446, and 63447 are *C. ralstoni*.

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<th>Position</th>
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Order ‘CONDYLARTHRA’ Cope, 1881

Family HYPOSODONTIDAE Trouessart, 1879

*HYOPSODUS* Leidy, 1870

*Hyopsodus* sp.

(Table 3)

**Referred specimens**—UCM 99042, right M2, from UCM locality 2004058 (Cf3); UCM 79082, left M2, from UCM locality 83117; UCM 100447, left M2, and UCM 101497, left M2, from UCM locality 2003045 (all from Wa0); UCM 101944, right M2, from UCM locality 2005085 (Wa1); UCM 98062, right M2, from UCM locality 2003030 (?Wa1/2).

**Known occurrences**—Late Clarkforkian to Middle Chadronian (see Archibald (1998), for list of specific localities).

**Description and Discussion**—Gazin (1962) provided the best description for the genus *Hyopsodus*. Only the M2s are included in my analysis and therefore, I comment only on these teeth here. Upper molars of *Hyopsodus* are low bunodont teeth. The M2 is nearly quadrilateral.
with six well-defined cusps. The paracone and metacone are roughly the same height. Due to the conservative tooth morphology on the genus, specific taxonomy of *Hyopsodus* is based primarily on the size of the lower m1 and stratigraphic occurrence. Unfortunately, with only isolated upped molars, I cannot make a specific identification.

Table 3: Measurements (in mm) of *Hyopsodus* sp. from the Powder River Basin.

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Family APHELISCIDAE Matthew, 1918

*APHELISCUS* Cope, 1875

*Apheliscus* sp.

(Table 4)

**Referred specimens**— UCM 98021 left m2, UCM 98025 right m2, and UCM 99047 right m1 from UCM locality 2002018; UCM 97795 left m2 and UCM 98150 left M3, from UCM locality 2003029; UCM 98047 right m2 from UCM locality 2003055; and UCM 98363 right m3 from UCM locality 2003057 (all from Cf3); UCM 55962 right M3, UCM 96171 left M1, UCM 96255 right m2, UCM 96256 right m3, UCM 96261 left m1, and UCM 96296 left m3 from UCM
locality 86101 (Wa0); UCM 101742 left m3, UCM 101743 right M3, and UCM 101946 right m3 from UCM locality 2005085 (Wa1); UCM 97790 left M1 from UCM 2003030 (Wa1 or Wa2).

**Known occurrences**— Late Tiffanian–Late Wasatchian (see Archibald (1998), for list of specific localities)

**Description and Discussion**— Rose (1981) gave the best description of *Apheliscus*. The lower molars are bunodont with reduced paraconid on m1 and a small paracristid (and no paraconid) on m2-3. The lower molars of *Apheliscus* also have well developed anterior cingulids. Species of *Apheliscus* are differentiated by size, specifically the m1. I have just two m1s, and consequently I have simply left them as *Apheliscus* sp. (following Robinson’s initial identifications). Although, UCM 99047 falls within the size range of *A. nitidus* m1s measured by Rose (1981), while UCM 96261 falls between the size ranges of *A. wapatiensis* (the smallest documented species of *Apheliscus*) and *A. insidiosus*. Due to small sample size, I have included both upper molars (M1s and M3s) and lower molars (m1–m3) in my measurements (see Table 4).

Table 4: Measurements (in mm) of *Apheliscus* sp. from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
</tr>
</thead>
<tbody>
<tr>
<td>99047</td>
<td>2002018</td>
<td>Rm1</td>
<td>2.47</td>
<td>1.58</td>
<td>Cf3</td>
</tr>
<tr>
<td>96261</td>
<td>86101</td>
<td>Lm1</td>
<td>2.23</td>
<td>1.47</td>
<td>Wa0</td>
</tr>
<tr>
<td>98021</td>
<td>2002018</td>
<td>Lm2</td>
<td>3.20</td>
<td>2.12</td>
<td>Cf3</td>
</tr>
<tr>
<td>98025</td>
<td>2002018</td>
<td>Rm2</td>
<td>3.21</td>
<td>2.13</td>
<td>Cf3</td>
</tr>
<tr>
<td>97795</td>
<td>2003029</td>
<td>Lm2</td>
<td>3.08</td>
<td>2.13</td>
<td>Cf3</td>
</tr>
<tr>
<td>98047</td>
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<td>2.13</td>
<td>Cf3</td>
</tr>
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<td>86101</td>
<td>Rm2</td>
<td>2.49</td>
<td>1.56</td>
<td>Wa0</td>
</tr>
</tbody>
</table>
Order RODENTIA Bowdich, 1821

Family CYLINDRODONTIDAE Miller and Gidley, 1918

*TUSCAHOMYS* Dawson and Beard, 2007


(Table 5)

**Comments**— *Tuscahomys* is considered the earliest known representative of the rodent family Cylindrodontidae (Dawson and Beard, 2007). It differs from paramyids in having greater lingual hypsodonty of the upper cheek teeth, an anteroposteriorly elongated protocone–hypocone ridge forming a distinct mure, and the hypocone area forming a relatively larger part of the lingual wall of M1–2 (Dawson and Beard, 2007). The lower molars of *Tuscahomys* have a well-developed hypolophid extending to the posterior cingulid (m1) or the mesoconid/ectolophid (m2) as well as a hypoconulid swelling on the posterolophid (Dawson and Beard, 2007).
complexity of its lower molars and distinctive upper molar morphology makes *Tuscahomys* easily distinguishable from *Paramys.*

**Referred specimens** — UCM 97784, right m1, and UCM 101931, right m1, from UCM locality 2002018; UCM 98367, right m1, from UCM locality 2002019; and UCM 98046, right m1, from UCM locality 2003051 (all Cf3).

**Known occurrences** — Red Hot local fauna, uppermost Tuscahoma Formation (Wa0); Willwood Formation, Bighorn Basin (Wa0); Smiley Draw local fauna in the Great Divide Basin (Wa4)

**Description and Discussion** — Both Dawson and Beard (2007) and Rose et al. (2012) provide descriptions of *Tuscahomys major*. The genus is relatively rare, known in the Bighorn Basin from only the Sand Creek Divide and Polecat Bench. Elsewhere, *Tuscahomys* is known from earliest (Wa0) through middle Wasatchian (Wa4) localities, whereas in the Powder River Basin, it occurs at three late Clarkforkian localities.

The specimens from the Powder River Basin are identified as *Tuscahomys* cf. *T. major*, due primarily to morphology; they bear the characteristic hypolophid extending to mesoconid and swollen hypoconulid on the posterolophid on m1 (Dawson and Beard, 2007). Although *T. major* is the largest species described, the Powder River Basin specimens fall in the range of the larger specimens given by Rose et al. (2012) at the Sand Creek Divide locality in the Bighorn Basin.

I did not include *Tuscahomys* in my analysis of size change across the PE boundary because it is known only from Cf3 in the Powder River Basin. However, it is nevertheless
important to document its occurrence in the Powder River Basin as the only known Clarkforkian occurrence of the genus.

Table 5: Measurements (in mm) of Tuscahomys cf. T. major from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
</tr>
</thead>
<tbody>
<tr>
<td>97784</td>
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<tr>
<td>101931</td>
<td>2002018</td>
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<td>2.66</td>
<td>2.23</td>
<td>Cf3</td>
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<tr>
<td>98367</td>
<td>2002019</td>
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<td>2.39</td>
<td>2.28</td>
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</tr>
</tbody>
</table>

Family ISCHYROMYIDAE Alston, 1876

Comments—The classification of paramyid rodents in relation to other ischyromids has been the subject of considerable debate (e.g., Wood, 1962; Korth, 1984; Ivy, 1990). McKenna and Bell (1997) considered Paramyinae a subfamily of Ichyromyiidae, and I follow this classification here.

It can be difficult to distinguish between the two species discussed below, as they are so similar morphologically. Actitoparamys atwateri differs from Paramys tauros by its smaller size, having a larger hypoconulid, and the separation of the entoconid from the posteriorlophid by a narrow valley (Korth, 1984). These characters can vary among both species and are obscured by wear making size the primary means for identification in worn specimens (Ivy, 1990).
ACRITOPARAMYS Korth, 1984

*Acritoparamys atawteri* Loomis, 1907

(Table 6)

**Referred specimens**— UCM 98385, right m1, from UCM locality 2000060; UCM 103097, left m1, from UCM locality 2002018; UCM 101465, left m1, from UCM locality 2003029; UCM 98258, left m1, from UCM locality 2003057 (all Cf3); UCM 106893, right m1, from UCM locality 2004056 (Wa0).

**Known occurrences**— Fort Union Formation, Washakie Basin (Cf2); Fort Union and Willwood Formations, Clark’s Fork and Bighorn Basins, Wyoming (Cf2–Wa5); Wasatch Formation, Washakie Basin (Wa1–4); DeBeque Formation, Piceance Creek Basin (Wa2–3); Wind River Formation (Wa6).

**Description and Discussion**— The m1s possess the characteristic large hypoconulid and the isolated entoconid of *A. atwateri*. All molars from the Powder River Basin are similar in morphology and measurements listed for *A. atwateri* by Korth (1984) and Ivy (1990).

Table 6: Measurements (in mm) of *Acritoparamys atwateri* from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
</tr>
</thead>
<tbody>
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<td>98385</td>
<td>2000060</td>
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<td>2.11</td>
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<td>103097</td>
<td>2002018</td>
<td>Lm1</td>
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<td>Cf3</td>
</tr>
<tr>
<td>101465</td>
<td>2003029</td>
<td>Lm1</td>
<td>2.40</td>
<td>2.24</td>
<td>Cf3</td>
</tr>
<tr>
<td>98258</td>
<td>2003057</td>
<td>Lm1</td>
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<td>2.16</td>
<td>Cf3</td>
</tr>
<tr>
<td>106893</td>
<td>2004056</td>
<td>Rm1</td>
<td>2.46</td>
<td>2.30</td>
<td>Wa0</td>
</tr>
</tbody>
</table>
**PARAMYS** Leidy, 1871

*Paramys taurus* Korth, 1984

(Table 7)

**Referred specimens**—UCM 100428, Lm1, from UCM locality 2002018; UCM 106895, left m1, from UCM locality 2003029; UCM 99206, Rm1, from UCM locality 2004058 (all Cf3); UCM 99700, right m1, from UCM locality 2003045; UCM 100967, Lm1, from UCM locality 2004056 (all Wa0).

**Known occurrences**—Fort Union and Willwood Formations, Clark’s Fork and Bighorn Basins, Wyoming (Cf2–Wa6); Wasatch Formation, Sand Wash Basin (Wa1–3); DeBeque Formation, Piceance Creek Basin (Wa1–3).

**Description and Discussion**—All m1s from PRB are similar in morphology and measurements listed for *P. taurus* in Ivy (1990) and Burger (2009), but are larger than specimens of *P. taurus* described in Rose et al. (2012).

Table 7: Measurements (in mm) of *Paramys taurus* from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
</tr>
</thead>
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<tr>
<td>100428</td>
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<td>106895</td>
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<td>2004058</td>
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<td>2.69</td>
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</tr>
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<td>2003045</td>
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<td>2.50</td>
<td>Wa0</td>
</tr>
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<td>100967</td>
<td>2004056</td>
<td>Lm1</td>
<td>2.59</td>
<td>2.45</td>
<td>Wa0</td>
</tr>
</tbody>
</table>
Ischyromyidae indet.

**Comments**— Ischyromyid incisors are among the most abundant specimens recovered in the Powder River Basin. The following specimens cannot be precisely assigned to genus without associated molars. I grouped incisors based on common shared morphologies (e.g. presence/absence of enamel sulcus, shape of cross-section (outline), and general size). I compared only lower incisors and recognized four distinct morphotypes that are briefly discussed below.

‘Ischyromyidae incisor morphotype A’

*(Table 8)*

**Referred specimens**— UCM 99019, right i, from UCM locality 2003049 (Cf3); UCM 106888, left i, from UCM locality 2005079 (Wa0).

**Description and Discussion**— This morphotype is distinctly smaller than the other morphotypes and transversely narrow.

Table 8: Measurements (in mm) of ‘Ischyromyidae incisor morphotype A’ from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
</tr>
</thead>
<tbody>
<tr>
<td>99019</td>
<td>2003049</td>
<td>Ri</td>
<td>0.57</td>
<td>1.38</td>
<td>Cf3</td>
</tr>
<tr>
<td>106888</td>
<td>2005079</td>
<td>Li</td>
<td>0.69</td>
<td>1.45</td>
<td>Wa0</td>
</tr>
</tbody>
</table>
‘Ischyromyidae incisor morphotype B’

(Table 9)

**Referred specimens**— UCM 98365, left i, from UCM locality 2002018 and UCM 101933, right i, from UCM locality 2003029 (both Cf3); UCM 8664, left i, from UCM locality 83117, and UCM 98700, left i, from UCM locality 2003045 (both Wa0).

**Description and Discussion**— This morphotype comprises mid-sized incisors which are transversely narrower than ‘morphotype C.’

Table 9: Measurements (in mm) of ‘Ischyromyidae incisor morphotype B’ from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
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</thead>
<tbody>
<tr>
<td>98365</td>
<td>2002018</td>
<td>Li</td>
<td>1.05</td>
<td>1.99</td>
<td>Cf3</td>
</tr>
<tr>
<td>101933</td>
<td>2003029</td>
<td>Ri</td>
<td>1.35</td>
<td>2.61</td>
<td>Cf3</td>
</tr>
<tr>
<td>86644</td>
<td>83117</td>
<td>Li</td>
<td>1.11</td>
<td>2.21</td>
<td>Wa0</td>
</tr>
<tr>
<td>98700</td>
<td>2003045</td>
<td>Li</td>
<td>1.31</td>
<td>2.16</td>
<td>Wa0</td>
</tr>
</tbody>
</table>

‘Ischyromyidae incisor morphotype C’

(Table 10)
**Referred specimens**— UCM 99048, right i, from UCM locality 2002018 (Cf3); UCM 106886, right i, from UCM locality 2003045 (Wa0); UCM 86014, left i, from UCM locality 85278 (Wa1).

**Description and Discussion**— This morphotype comprises mid-sized incisors which are oval in cross-section.

Table 10: Measurements (in mm) of ‘Ischyromyidae incisor morphotype C’ from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
</tr>
</thead>
<tbody>
<tr>
<td>99048</td>
<td>2002018</td>
<td>Ri</td>
<td>1.38</td>
<td>2.57</td>
<td>Cf3</td>
</tr>
<tr>
<td>106886</td>
<td>2003045</td>
<td>Ri</td>
<td>1.50</td>
<td>3.00</td>
<td>Wa0</td>
</tr>
<tr>
<td>86014</td>
<td>85278</td>
<td>Li</td>
<td>1.85</td>
<td>3.44</td>
<td>Wa1</td>
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</tbody>
</table>

‘Ischyromyidae incisor morphotype D’

(Table 11)

**Referred specimens**— UCM 97782, left i, and UCM 97783, left i, from UCM locality 2003029; UCM 98101, right i, from UCM locality 200304; UCM 98045, left i, from UCM locality 2003051; UCM 98376, left i, from UCM locality 2004050 (all Cf3).

**Description and Discussion**— This morphotype comprises large incisors with a faint sulcus. Specimens are only reported from Cf3.
Table 11: Measurements (in mm) of ‘Ischyromyidae incisor morphotype D’ from the Powder River Basin.

<table>
<thead>
<tr>
<th>UCM</th>
<th>Locality</th>
<th>Position</th>
<th>A-P length</th>
<th>B-L width</th>
<th>Subage</th>
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<td>97782</td>
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<td>Li</td>
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<td>2.75</td>
<td>Cf3</td>
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<td>97783</td>
<td>2003029</td>
<td>Li</td>
<td>1.25</td>
<td>2.25</td>
<td>Cf3</td>
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<td>2003040</td>
<td>Ri</td>
<td>1.36</td>
<td>2.57</td>
<td>Cf3</td>
</tr>
<tr>
<td>98045</td>
<td>2003051</td>
<td>Li</td>
<td>1.45</td>
<td>2.50</td>
<td>Cf3</td>
</tr>
<tr>
<td>98376</td>
<td>2004050</td>
<td>Li</td>
<td>1.24</td>
<td>2.18</td>
<td>Cf3</td>
</tr>
</tbody>
</table>
Figure 8: Mammalian Faunal List for the Chalk Butte Area of the Powder River Basin, based largely on previous identifications in the UCM database.

<table>
<thead>
<tr>
<th>Latest Clarkforkian (Cf3):</th>
<th>Earliest Wasatchian (Wa0):</th>
<th>Early Wasatchian (Wa1/2):</th>
</tr>
</thead>
<tbody>
<tr>
<td>Order Multituberculata</td>
<td>Order Multituberculata</td>
<td>Order Rodentia</td>
</tr>
<tr>
<td>Order Didelphimorpha</td>
<td>Order Didelphimorpha</td>
<td></td>
</tr>
<tr>
<td><em>Peradectes</em></td>
<td><em>Mimoperadectes</em></td>
<td><em>Acritoparamys</em></td>
</tr>
<tr>
<td>Superorder Leptictida</td>
<td><em>Peradectes</em></td>
<td><em>Paramys</em></td>
</tr>
<tr>
<td>Order Rodentia</td>
<td>Order Rodentia</td>
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</tr>
<tr>
<td><em>Acritoparamys</em></td>
<td><em>Acritoparamys</em></td>
<td><em>Cuatroprimis</em></td>
</tr>
<tr>
<td><em>Paramys</em></td>
<td><em>Paramys</em></td>
<td><em>Arctodontomys</em></td>
</tr>
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<td>Order Cimolesta</td>
<td>Order Cimolesta</td>
<td><em>Phenacolemur</em></td>
</tr>
<tr>
<td><em>Apatemys</em></td>
<td><em>Acritoparamys</em></td>
<td><em>Cantius</em></td>
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<tr>
<td><em>Barylambda</em></td>
<td><em>Paramys</em></td>
<td><em>Arctodontomys</em></td>
</tr>
<tr>
<td>Order Carnivora</td>
<td>Order Carnivora</td>
<td><em>Phenacolemur</em></td>
</tr>
<tr>
<td><em>Viverravus</em></td>
<td><em>Didelphodus</em></td>
<td><em>Chriacus</em></td>
</tr>
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<td>Order ‘Insectivora’</td>
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</tr>
<tr>
<td><em>Leptacodon</em></td>
<td><em>Coryphodon</em></td>
<td><em>Tricentes</em></td>
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<tr>
<td>Order Primates</td>
<td>Order Primates</td>
<td><em>Diacodexis</em></td>
</tr>
<tr>
<td><em>Carpoletes</em></td>
<td><em>Didymictis</em></td>
<td><em>Eohippus</em></td>
</tr>
<tr>
<td><em>Phenacolemur</em></td>
<td><em>Viverravus</em></td>
<td><em>Sifrhippus</em></td>
</tr>
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<td>Order Procreodi</td>
<td></td>
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<tr>
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<td><em>Talpavus</em></td>
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<tr>
<td>Order ‘Condylarthra’</td>
<td>Order ‘Condylarthra’</td>
<td></td>
</tr>
<tr>
<td><em>Apheliscus</em></td>
<td><em>Niptomomys</em></td>
<td></td>
</tr>
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<td><em>Haplomylus</em></td>
<td><em>Arctodontomys</em></td>
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<td><em>Phenacolemur</em></td>
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<td>Order Procreodi</td>
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<tr>
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<td><em>Teilhardina</em></td>
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<td><em>Thryptacodon</em></td>
<td><em>Cantius</em></td>
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<td><em>Tricentes</em></td>
<td><em>Arctodontomys</em></td>
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<td>Order Artiodactyla</td>
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<tr>
<td><em>Apheliscus</em></td>
<td><em>Diacodexis</em></td>
<td></td>
</tr>
<tr>
<td><em>Hyopsodus</em></td>
<td><em>Eohippus</em></td>
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<td><em>Copecon</em></td>
<td><em>Sifrhippus</em></td>
<td></td>
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<tr>
<td><em>Ectocion</em></td>
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<tr>
<td><em>Phenacodus</em></td>
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</tr>
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<td>Order Perissodactyla</td>
<td>Order Perissodactyla</td>
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6. RESULTS AND DISCUSSION

In the Polecat Bench area of the Bighorn Basin, Gingerich (1989) noted the presence of several species of genera which are significantly smaller in Wa0 than members of these same genera in either Cf3 or Wa1. He recognized six “dwarfed” genera: the tillodont *Azygonyx*; the ‘condylarths’ *Thryptacodon* and *Chriacus* (both arctocyonids), *Ectocion* and *Copecion* (both phenacodontids); and the edentate *Palaeanodon*. Continued studies in the Bighorn Basin have produced similar size differences in the McCullough Peaks region (Clyde and Gingerich 1998), Cabin Fork area (Secord et al., 2012), and Sand Creek Divide (Rose et al., 2012). The Powder River Basin is the only area outside the Bighorn Basin where fossils representing Cf3–Wa1, in direct superposition, are documented (most areas lack Wa0 or Cf3), and consequently is a good place to test the hypothesis: is there evidence of evolutionary dwarfing (a manifestation of Bergmann’s rule) in mammalian lineages spanning the PETM in the Powder River Basin? In other words, can the body size changes that have been documented in the Bighorn Basin during the PETM be extended beyond the boundaries of that basin to a more regional scale?

Although sample size for most taxa in the Powder River Basin is quite small (relative to the Bighorn samples of the same taxa), the Powder River Basin sample nevertheless shows trends in size changes across the PE boundary that are comparable to the Bighorn in having a size reduction during the PETM. Of the localities in the Bighorn, the Sand Creek Divide mammalian fauna (Rose et al., 2012) contains the smallest sample size and is the best comparison for my finds in the Powder River Basin. Because of the limited sample, I utilized all molar tooth positions (M/m1–M/m3). However, it should be noted that M/m3s tend to be less consistent morphologically, there is more variability in size, and this must be considered when interpreting the data. I plotted the natural log of tooth crown area of molars against time,
following studies by Gingerich (1989) and others, and I discuss the results of each taxon that I analyzed—Arctodontomys, Cantius, Hyopsodus, Apheliscus, Paramys, and Acritoparamys—below.

6.1 Primates

6.1.1 Arctodontomys cf. A. wilsoni

Three M2s were compared, two Wa0 in age and one from Wa1 (Figure 8). Specimens from Wa0 are ~15% smaller than the Wa1 tooth, showing the pattern of decreased body size during the PETM that was indicated by Gunnell (1985, 1989) for Arctodontomys in the Clark’s Fork Basin and by Rose et al. (2012) in the southern Bighorn Basin.

Figure 9: Tooth area [ln(L*W)] of M2 for Arctodontomys cf. A. wilsoni from Wa0 to Wa1 in the Powder River Basin.
6.1.2 Cantius

Tooth positions m1–m3 and M3 were compared, ranging from Wa0 to Wa1. Among the lower molars (Figure 9), results are variable. There is almost no change (~0.5%) in size of the two m1s between Wa0 and Wa1; however, this may simply reflect the tiny sample size. Among the m2s, one shows a similar pattern; however, one Wa0 specimen is ~7% smaller than the Wa1 m2, but it’s possible that its smaller size could be due to UCM 98014 lacking its enamel (as discussed in the previous chapter), which suggests that it may have passed through a crocodilian gut (Fisher, 1981). There is a range of size differences among m3s; however, the Wa0 specimens are generally smaller than the two Wa1 specimens. The two M3s, again, show a slight size change with the Wa0 M3 being only ~8% smaller than the Wa1 M3 (Figure 10). Cantius first appears in North America at the start of the Wasatchian, therefore is not considered dwarfed; however, the lineage has been shown to increase in size through time in the Clark’s Fork and Bighorn Basin (Gingerich, 1989; Rose et al., 2012).
Figure 10: Tooth area $[\ln(L \times W)]$ of m1–m3 of *Cantius* from Wa0 to Wa1 in the Powder River Basin.
Figure 11: Tooth area [ln(L*W)] for M3 of *Cantius* from Wa0 and Wa1 in the Powder River Basin.

6.2 ‘Condylarthra’

6.2.1 *Hyopsodus*

The M2s of *Hyopsodus* are a nice example of size change through the Cf3–Wa1 sequence (Figure 11). The change from Cf3 to Wa0 is slight, ranging from ~3–10% decrease in Wa0. From Wa0 to Wa1, the change is more significant, with a ~9–16% increase in size. Results correspond to pattern reported from the Clark’s Fork and Bighorn Basins (Gingerich, 1985; Gingerich and Smith, 2006).
6.2.2 *Apheliscus*

Tooth positions m1–m3, M1, and M3 were compared. The lower molars of *Apheliscus* show the expected pattern of smaller size during the Wa0 interval (Figure 12). The difference between the two m1s from Cf3 to Wa0 is much less than that of m2 or m3 (a decrease of ~13% for m1 compared to ~30% for m2 and m3). The upper molars of *Apheliscus* have mixed results. The Wa0 specimen M1 is ~7% smaller than the Wa1 specimen, which is expected, but the M3s continue to decrease in size throughout the entire sequence (Figure 13). As previously noted, M3s are more variable in size and morphology than other upper molar positions. With only a single representative of M3 for each time interval, the possibility of simple molar variability cannot be ruled out.
Figure 13: Tooth area [ln(L*W)] for m1–m3 of *Apheliscus* from Cf3 to Wa1 in the Powder River Basin.
Figure 14: Tooth area [ln(L*W)] for M1 and M3 of *Apheliscus* from Cf3 to Wa1 in the Powder River Basin.

6.3 Rodentia

6.3.1 *Paramys taurus*

Only m1s of *Paramys taurus* from Cf3 and Wa0 were analyzed. There is a small change in size, with a decrease of ~5–11% from Cf3 to Wa0 (Figure 14).
6.3.2 *Acritoparamys atwateri*

*Acritoparamys atwateri* is the only taxon that does not conform to the hypothesis of decreased body size during Wa0. In fact, the pattern is the opposite, with the single Wa0 m1 being ~1–8% larger than Cf3 specimens (Figure 15). The most likely cause of the larger Wa0 specimen is variation within the species. However, it should be noted that not all mammals follow Bergmann’s rule (Meiri and Dayan, 2003).

Figure 15: Tooth area [ln(L*W)] m1 of *Paramys* from Cf3 to Wa0 in the Powder River Basin
Figure 16: Tooth area [ln(L*W)] for m1 of *Acritoparamys* atwateri lower molars from Wa0 to Wa1 in the Powder River Basin.
7. CONCLUSIONS

It is apparent that the rapid and dramatic environmental change during the PETM played a role in mammalian evolution. While the full effect of the PETM remains unknown, biotic changes are observed, such as the geologically sudden appearance in North America of the modern orders Artiodactyla, Perissodactyla, and true Primates. In addition, within the Bighorn Basin an “evolutionary dwarfing” is documented during the Wa0 interval (Gingerich, 2003).

Bergmann’s rule proposes that ambient temperatures have a direct ecological and physiological effect on organisms. Among closely related populations of mammals, larger body size is found in colder environments, and smaller body size is found in warmer regions. The diminutive size observed in the Bighorn Basin has been interpreted, in part, as a manifestation of Bergmann’s rule (Gingerich, 2003).

I tested whether there is evidence of evolutionary dwarfing in mammalian lineages spanning the PETM in the Powder River basin. The significance of the “Wasatch” Formation in the Powder River Basin lies in the fact that it contains mammalian fauna (in direct superposition) spanning the PE boundary. It differs from other PETM localities in the relative size of fossils collected, being locally rich in small mammals and reptiles. The Powder River Basin sample size is too small to say whether the taxa present conform to Bergmann’s rule; however, it does show comparable patterns to the Bighorn Basin (Gingerich, 2003; Rose et al., 2012; Secord et al., 2012), specifically *Arctodontomys, Cantius, Apheliscus*, and *Hyopsodus*. Body size changes through the PETM have not been evaluated in the Bighorn Basin for rodents, therefore there are no direct comparisons available in the literature.

The overall changes in body size in the PETM of the Powder River Basin are less significant than that reported from the Bighorn Basin. It is interesting to note the similar pattern
of decreased size during Wa0 for all three lower molar positions in *Cantius* and *Apheliscus*, as well as the m1s of *Paramys*. In addition, the M2s of *Arctodontomys* and *Hyopsodus* display a similar change in body size through time. The rodent *Acritoparamys*, on the other hand, displays the opposite pattern. With such a small sample size, I cannot rule out the possibility that observed body size changes could simply be morphological variation within a species.

The depositional environment of the Powder River Basin, with its abundance of carbonaceous shales and lignites, is different from the Bighorn Basin, and likely affected the fossil preservation in each of these basins. There is a size bias towards smaller mammals in the Powder River Basin, save for a *Barylambda* femur and other associated bone frags. Meiri and Dayan (2003) concluded that smaller mammals are less likely to conform to Bergmann’s rule, citing small geographic ranges and habitat as two possible causes.

In addition, one cannot dismiss the hypothesis that this diminutive size that occurred in some mammalian taxa during Wa0 was the result of extrinsic forces, such as the displacement of larger species by a smaller species through northern range extension. Recent work in the Piceance Creek Basin of Colorado has resulted in the discovery of *Ectocion parvus* during the Clarkforkian, a species that is restricted to Wa0 in the Bighorn Basin. It is hypothesized that this smaller species of *Ectocion* extended its range northward during the elevated temperatures of the PETM (Burger, 2012). Range extension is a possible explanation for the presence of *Tuscahomys*, cf. *T. major* during the Clarkforkian of the Powder River Basin.

The recovery of additional teeth and further analysis of fossils from the Powder River Basin is critical to testing whether body size changes in mammalian taxa during the PETM extend beyond the boundaries of the Bighorn Basin. From a larger perspective, studies such as
this should provide insight into the impacts of current and future global warming on today’s mammalian fauna.
8. REFERENCES


Bergmann, C. 1848. Über Die Verhältnisse Der Wärmeökonomie Der Thiere Zu Ihrer Grösse.


