BODY SIZE EVOLUTION IN *LEPTOMERYX* AND RHINOCEROTINAE (*SUBHYRACODON* AND *TRIGONIAS*) ACROSS THE EOCENE – OLIGOCENE (CHADRONIAN – ORELLAN) BOUNDARY

by

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The final copy of this thesis has been examined by the signatories, and we find that both the content and the form meet acceptable presentation standards of scholarly work in the above mentioned discipline

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Body size Evolution in *Leptomeryx* and Rhinocerotinae (*Subhyracodon* and *Trigonias*) Across the Eocene – Oligocene (Chadronian – Orellan) boundary

Thesis directed by Assistant Professor Jaelyn J. Eberle

Research has shown that there was dramatic climate change, specifically a significant drop in temperature, across the Eocene – Oligocene (Chadronian – Orellan) boundary. However, few studies have looked at the effects of this climatic cooling on the terrestrial vertebrate fauna. My study focused on changes in mammalian body size across the Chadronian – Orellan transition, in particular within the small artiodactyl *Leptomeryx* and the large rhinocerotine perissodactyls, based upon fossils from the White River Group in the Northern Plains (Colorado, Wyoming, Nebraska, and South Dakota). Specifically, I tested whether Bergmann's Rule (which suggests that in a given taxon, those individuals inhabiting colder climates will be larger-bodied than those living in a warmer climate) occurred with climatic cooling across the Chadronian-Orellan boundary. With regard to the rhinocerotines, I used *Trigonias, Subhyracodon*, and specimens identified as Rhinocerotinae gen. indet. Rhinocerotineae gen.indet. specimens are missing their anterior dentition (which is what differentiates teeth of *Trigonias* from *Subhyracodon*), and consequently were simply identified only as Rhinocerotinae genus indet. Length and width measurements of upper and lower molars were used as a proxy for body size of both Chadronian and Orellan representatives of two lineages of *Leptomeryx*, (*L. speciosus* – *L. evansi* lineage and *L. yoderi* – *L. mammifer* – *L. exilis* lineage). The two lineages of

Leptomeryx showed a statistically significant decrease in tooth size in the Orellan. The Rhinocerotinae show a significant decrease in tooth size across the Chadronian – Orellan transition. Although other researchers have noted that only one *Leptomeryx* lineage survived the Eocene-Oligocene transition, this research suggests that both lineages survived this boundary. The decrease in body size with decrease in temperature in *Leptomeryx* and Rhinocerotinae is opposite of the expected pattern of Bergmann's Rule. My data suggest that other factors, besides climatic cooling, also need to be considered in mammalian body size evolution across the Eocene-Oligocene boundary.

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I. Introduction

The Eocene – Oligocene transition (EOT, ~33.7 Ma), which correlates with the boundary between the Chadronian and Orellan North American Land Mammal 'Ages' (NALMA) (Prothero 1995; see discussion in Biostratigraphy section), was a time of global cooling (Zachos et al., 2001) that saw a drop in mean annual temperature (MAT) of approximately 8.2±3.1°C in Wyoming, South Dakota, and Nebraska (Zanazzi et al. 2007). This drop in temperature seems to have coincided with a change in the environment that is preserved in the White River sequence[1] of Wyoming, South Dakota, and Nebraska. Specifically, the vegetation shifted from woodlands to grasslands (Evanoff et al. 1992; Retallack 1986, 1992; Terry 2001) with exception of northeastern Colorado which Hembree and Hasiotis (2007) have hypothesized shifted from grasslands to woodlands. As the environment changed, organisms need to adapt to the new conditions, disperse to other regions, or face extinction (Meynecke 2004).

Previous studies on terrestrial mammalian faunas spanning the EOT have focused on changes in the community structure. In North America, Stucky (1992) found that the diversity of mammalian predators remained stable, although soricomorph insectivores replaced erinaceomorph insectivores, and true carnivores replaced creodonts. Herbivorous mammals increased in diversity, increased the height of their molar crowns, and developed more robust co-ossified metapodials and elongated limbs, all three of which are hypothesized adaptations for more efficient food processing and living in more open habitats. In the Plains of North America, Prothero and Heaton (1996) looked for morphologic changes over the EOT in mammalian taxa and

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[1] Formation in Wyoming and Colorado, Group in South Dakota and Nebraska, see Stratigraphic Range section

concluded that most species remained static and only size changes were noted in a few species such as *Miniochoerus*. In Europe, the changes at the EOT were more pronounced, with a drop in total number of species in Britain (Hooker 1992), and faunal turnover in mammalian faunas of France such that rodents became more important to diversity relative to ungulates (Lengendre 1986; Legendre and Hartenberger 1992). However, in the Fayum, Africa, there did not seem to have been any dramatic extinction event or faunal turnover associated with the EOT (Rasmussen et al. 1992). Zanazzi and Kohn (2008) looked at the changes in diet and habitat for specific ungulate taxa from the White River sequence and concluded that only *Leptomeryx* changed its habitat (see below for more *Leptomeryx* results and *Subhyracodon* results). The present study concentrates on the change in body size at different taxonomic levels in faunal assemblages of Rhinocerotinae (subfamily and genus levels) and *Leptomeryx* (species lineage levels) recovered from the White River sequence cropping out in northeastern Colorado, eastern Wyoming, western South Dakota, and western Nebraska.

Following Bergmann's Rule – the hypothesis that larger species in a genus will inhabit cooler climates or higher latitudes (interspecific; Bergmann 1847 as translated in James 1970), and that larger populations in a lineage will inhabit cooler climates or higher latitudes (intraspecific; Mayr 1956, 1963) – an increase in body size is predicted for most mammals during the EOT when climate cooled (Zanazzi et al. 2007). Bergmann's Rule has been recognized in a variety of modern mammalian taxa, ranging from Artiodactyla to Cetacea, Carnivora, Hyracoidea, Rodentia, Lagomorpha, Primates, Insectivora, and Monotremata (Meiri and Dayan 2003; Ashton et a. 2000; and references therein). Using dental measurements as a proxy for body size, I compare Chadronian-aged specimens of the small artiodactyl *Leptomeryx* and the perissodactyl subfamily Rhinocerotinae with their

Orellan counterparts. Teeth were used in preference over post-cranial bones because they can be identified to genus and species level, whereas postcranial elements generally cannot unless they are found in association with cranial and dental remains. Additionally teeth are typically more numerous in the fossil record than diagnostic post-cranial bones.

I chose to study rhinocerotines and *Leptomeryx* because they were abundant during late Eocene and early Oligocene time, as evidenced by their large sample size in numerous North American fossil vertebrate collections (compared to other mammals similar in size), and equations for their body mass estimates are readily available (e.g. Damuth 1990, Fortelius 1990; Janis 1990). Even though Bergmann's Rule has been examined more often in carnivores than herbivores (Klein and Scott 1989; Klein 1986; Dayan et al. 1991; Meiri et al. 2007; Meiri et al. 2004; Meiri and Dayan 2003; McNab 1971; Ashton et al. 2000), carnivores are rarer in the fossil record than herbivores such as rhinocerotines and *Leptomeryx*. Davis (1981) looked at Bergmann's Rule for some modern artiodactyls (e.g. gazelle, fallow deer, aurochs, wild goat, and wild boar), but modern perissodactyls have not been analyzed for Bergmann's Rule. The rarity (small population sizes) and low diversity of living perissodactyls, such as zebras, tapirs, and rhinos, in the wild (IUCN 2009) may be one reason for the lack of analysis. Bergmann's Rule is not expected to apply to non-wild populations (i.e. zoo and domesticated animals such as horses) due to artificial breeding and living in microhabitats (Davis 1981). With the possible exception of zebras, Bergmann's rule cannot easily be tested on today's populations of perissodactyls for the above reasons. During the Eocene and Oligocene, rhinocerotines were relatively common and abundant with multiple lineages (Prothero 2005), providing a unique opportunity to examine populations of perissodactyls with respect to Bergmann's rule during a time of climatic cooling.

All specimens utilized in my study are from the White River sequence of the High Plains (northeastern Colorado, Nebraska, Wyoming, and South Dakota) (Figure 1), from ~40.5°N to ~44.25°N latitude, which should reduce latitudinal influence on body size. Due to small sample size (<30) for most datasets, non-parametric statistics such as Mann-Whitney U and Kolmogorov-Smirnov tests were utilized to estimate the amount of difference in various dental measurements between Chadronian and Orellan populations of *Leptomeryx* and rhinocerotines.

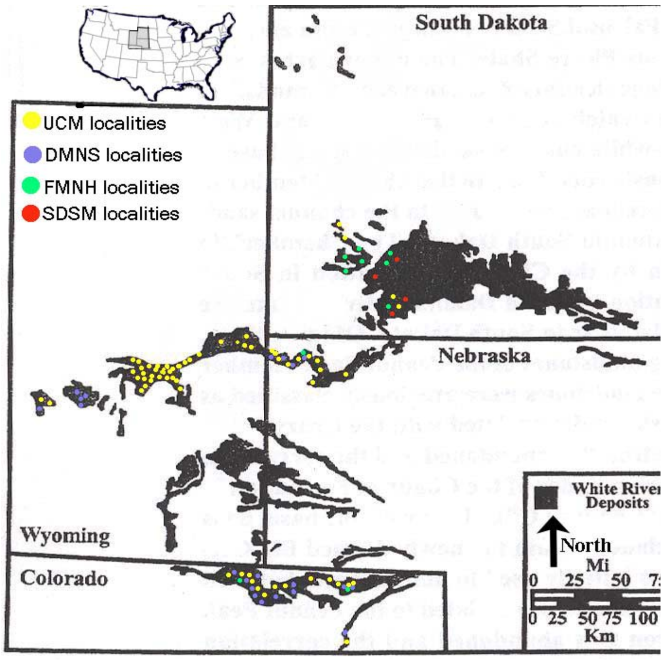

Figure 1. White River outcrop and specimen locations in the four states of my study area: South Dakota, Wyoming, Nebraska, and Colorado. Circles represent general locations where specimens came from based upon databases at the particular institution. Modified from Terry (2001).

To date, few studies have tested Bergmann's Rule on North American fossil land mammals, and no studies have specifically looked at *Leptomeryx* or rhinocerotines. The conclusions of this research will provide a direction for future research on modern and fossil ungulates and will add to the body of literature concerning the biotic impacts of climate and environmental change.

1. The Eocene – Oligocene Cooling Event

On a worldwide scale, the Eocene – Oligocene transition (EOT, ~33.7 Ma Prothero et al. 2004; Berggren et al. 1995) marked a major cooling event (Zanazzi et al. 2007). Although climatic cooling started approximately 50 Ma during the Duchesnean NALMA, there was a marked decrease in temperature near the Eocene – Oligocene boundary of approximately 8°C (Zanazzi et al. 2007) that lasted approximately 400,000 years and is hypothesized to have been initiated by the sudden appearance of large continental ice sheets on Antarctica (Zachos et al. 1992; Zachos et al. 2007; Hambrey et al. 1991). The decrease in temperature during the EOT, estimated using oxygen and carbon isotope ratios, was larger on land than in the marine record (~8°C on continental North America *versus* 2-3° in the oceans; Lear et al. 2000; Zachos et al. 1994), despite the hypothesis that the continental climatic transition occurred up to 400,000 years after the climatic transition in the marine realm (Zanazzi et al. 2007).

In the marine record, there was a noticeable faunal change around the boundary between middle and late Eocene time, (~40 Ma, P14/P15 foraminifera zone boundary, Keller et al. 1992; and NP17/NP18 calcareous nannoplankton biochronal boundary; Aubry 1992). In the terrestrial realm, there were less noticeable faunal changes amongst mammalian taxa across the EOT, although reduction in body size was noted for some taxa (e.g.*Miniochoerus*, *Palaeolagus*) (Prothero and Heaton 1996, Alroy 1998). The terrestrial animals that seemed most affected by the climate change at the EOT were amphibians and snails that had larger faunal turnovers across the EOT (Hutchison 1992; Evanoff 1990).

Numerous studies have looked at the changes in aridity and temperature across the EOT. Many have found a decrease in temperature and increase in aridity to various degrees (e.g. Retallack 1986; Hutchison 1992; Zanazzi et al. 2007), suggesting an ecosystem transition from woodland to grassland (Evanoff et al. 1992; Retallack 1986, 1992; Terry 2001). On average, the western Plains states of Wyoming, South Dakota, and Nebraska saw a temperature decrease of approximately 8°C based upon isotope data (Zanazzi et al. 2007), although these authors noted no resolvable change in aridity. The mean annual temperature (MAT) in the Chadronian (latest Eocene) in the Big Badlands area was around 15.6°C (60°F) based upon analyses of lateritic weathering of the underlying sediments (Clark et al. 1967). Winter temperature is estimated to have been mostly above freezing due to the presence of small alligators in the Chadronian (Clark et al. 1967). According to oxygen isotope analysis, the mean annual range in temperature (MART), and hence seasonality, in these three states may have increased, but not significantly (Zanazzi et al. 2007).

The Big Badlands area in South Dakota also preserved evidence for groundwater lakes and ponds, mostly restricted to the Chadronian with very few in the Orellan (Evans and Welzenbach 1998). The Chadronian is estimated to have been more humid than the Orellan, with mean annual rainfall decreasing from a range of approximately 500 to 700 mm in the Chadronian to a range of approximately 500 to 600 mm in the Orellan (Retallack 1992). Further south in Nebraska, the mean annual precipitation (MAP) decreased from approximately 852 mm in the late Eocene (35.3 Ma) to 260 mm in the early Oligocene (30.3 Ma), based upon study of chemical weathering and calcic horizons of paleosols (Sheldon and Retallack 2004). In the Douglas area of Wyoming, the gastropod fauna suggests an increase in aridity with only a minor decrease in temperature near the EOT (Evanoff et al. 1992). A shift from fluvial deposits in the Chadron Member (Chadronian) to eolian deposits in the Brule Member (Orellan) near Douglas, Wyoming also suggests a change to more arid conditions (Evanoff et al. 1992). In contrast, paleosol analyses of Chadronian-Orellan exposures of the White River Formation in northeastern Colorado seem to indicate a contrasting environmental change at the EOT. Based upon analyses of paleovegetation and rhizoliths, the White River exposures around Logan County changed from grasslands and shrublands during the late Chadronian to savannahs and woodlands during Orellan time (Hembree and Hasiotis 2007). However, similar to the other exposures of the White River Group, the amount of soil moisture decreased as did the water table based upon paleosol data (Hembree and Hasiotis 2007).

Although the cooling at the EOT was worldwide (Miller et al. 1987), the amount of cooling, precipitation changes, and biotic reactions to the cooling cannot be assumed to be uniform. My study uses specimens from multiple states (Colorado, Wyoming, South Dakota, and Nebraska) in order to test whether there were differences among the states in the amount or direction of body size change.

2. *Bergmann's Rule*

Bergmann (1847, as translated by James 1970) first proposed the hypothesis that two species or two populations of homeothermic animals that differ only in body size, the smaller-sized population will live in warmer climates while the larger-sized population will live in colder climates. This idea, coined Bergmann's Rule, incorporates relative temperature as the independent, climatic variable in the rule. Although Bergmann (1847) did correlate temperature to latitude, many subsequent studies have used latitude as a proxy for temperature (e.g. Blackburn et al. 1999; McNab 1971; Meiri et al. 2004). Subsequently, there have been two main discussions regarding testing the validity of Bergmann's Rule. One is whether the rule should be applied to only intraspecific populations (individuals within a given population or taxon) or interspecific populations (multiple species or populations within a higher taxon) (Blackburn et al. 1999; Mayr 1956, 1963; Rensch, 1938). The second concern is whether the mechanism that Bergmann (1847) first proposed to explain Bergmann's Rule (decrease of volume to surface area ratio decreases heat loss; discussed below) is necessarily part of the rule (Geist 1990; Blackburn et al. 1999; Mayr 1956). Both Mayr (1956) and Rensch (1938) stated that the interpretation of the rule as intraspecific was not Bergmann's original intent, and that their definition of the rule as intraspecific was based upon subsequent studies. For instance, Mayr (1958) stated "It has long been known, for instance, that the validity of the so-called ecological rules (Bergmann's rule, Allen's rule, etc.), so far as it exists at all, is restricted to intraspecific variation" (p.167). Rensch (1938) similarly noted "…within a Rassenkreis [complexes of races] of warm-blooded animals the races living in colder climates are generally larger than the races living in warmer regions" (p. 282).

In modern studies, the intraspecific variation of Bergmann's Rule is used within the species; either individuals are treated as data points and are measured and plotted *versus* temperature (or latitude) with a negative slope (positive for latitude) of the best-fit line indicating compliance with Bergmann's Rule (Freckleton et al. 2003); or populations of races are compared to each other (Mary 1956, 1963). In contrast, the interspecific variation compares the average body mass of multiple closely related species across temperature gradients (Bergmann 1847as translated in James 1970); the interspecific variation can also be studied by comparing the average body mass of communities across a temperature gradient (Blackburn and Hawkins 2004). These are the strict biological definitions. However, when looking at Bergmann's Rule in the paleontological record, the definitions must be modified to take into account the uncertainties of the relationships among fossil species, which are identified by morphological characters preserved in the fossils and do not necessarily correlate with biological species. Often in paleontological collections, specimens are fragmentary and cannot be identified to species level, and consequently are simply identified as genus or even subfamily. Due to the inability to identify biological species in the fossil record, the intraspecific variation of Bergmann's Rule can be used for a lineage of closely related species, genera, and maybe at its broadest definition, subfamily. In this study, I am using two species-lineages of *Leptomeryx*, the subfamily Rhinocerotinae, and the genus *Subhyracodon* to test the occurrence of Bergmann's Rule at the intraspecific level. Specifically I am asking: do individuals of *Leptomeryx* and Rhinocerotinae lineages get larger across the Eocene – Oligocene boundary as temperatures cooled?

Bergmann (1847) did not specify whether he was looking at mean annual, winter minimum, or summer maximum temperature. Other studies have since been more specific with regard to the relationship between temperature and Bergmann's Rule, for instance: mean annual temperature (MAT) (Rodríguez et al. 2008; Brown and Lee 1968; Smith et al. 1995); minimum winter/January temperature (Meiri et al. 2007; Yom-Tov and Geffen 2006; Davis 1977); mean summer/July temperature (Davis 1977; Smith et al. 1995). Yom-Tov and Geffen (2006) found that species did not follow Bergmann's Rule when minimum January temperature was used, but did follow the rule when using maximum June temperature, whereas Rensch (1939, as translated in Mayr 1956) found the bird *Parus montanus* did follow Bergmann's Rule when temperatures from the coldest months were used but not when MAT was used. Here I use MAT because previous studies that have examined the change in temperatures over the EOT have estimated MAT (Zanazzi et al. 2007)

In Bergmann's (1847) original paper, he gave a mechanism for this phenomenon: an increase in size would cause a decrease in the surface area to volume ratio of the animal and hence decrease the amount of body heat lost (Bergmann 1847, as translated by James 1970). This mechanism, by itself, does not seem to be correct (Geist 1987, 1990; Ashton et al. 2000; McNab 1971), and some have thrown out the whole rule because of it (Geist 1990, 1987). However, invalidating Bergmann's Rule because the mechanism seems incorrect would be equivalent to throwing out all of Darwin's ideas on evolution because he got the mode of transmission wrong. Therefore, many researchers (Blackburn et al. 1999; Mayr 1956, 1963; Rensch 1938; Dayan 1991; Rodríguez et al. 2008; Blackburn and Hawkins 2004) decided that the rule should be interpreted in only the empirical sense, and that the mechanism should not be part of the rule. Of course, they concluded that the determination of the mechanism is an important area of study. Other hypothesized mechanisms for an inverse relationship between body size and temperature/latitude have been proposed. One hypothesis states that larger animals generally retain more fat and therefore have a greater resistance to starvation and a greater fasting endurance. This enables larger animals to subsist with the smaller annual food source at higher latitudes (Blackburn et al. 1999; Ashton et al. 2000). Mass might not be the primary trait affected by temperature, but could possibly be coupled with another trait that is affected by temperature of latitude (Blackburn et al. 1999). Life-history characteristics such as delayed maturity, larger offspring, and litter size may be such traits (Ashton et al. 2000). Some mechanisms predict larger body mass in the middle latitudes, in which case we would see Bergmann's Rule in the lower latitudes (smaller animals in the lower latitude/hotter climates with larger animals in the middle latitude/cooler climates) but would see the inverse in the high latitudes (smaller animals in the higher latitudes colder climates with larger animals in the middle latitude warmer climates). These mechanisms include an increase in the duration of the productivity pulse and hence more resources in middle latitudes (Geist 1987; Blackburn et al. 1999), and a combination of available resources and competition for those resources (Ashton et al. 2000; Blackburn and Hawkins 2004). It has also been hypothesized that the change in body size may not be influenced by only temperature, but also by precipitation and humidity (Yom-Tov and Geffen 2006).

Theoretical models predict that, based upon heat loss, relatively small-bodied species will follow Bergmann's Rule more so than relatively large-bodied species because increasing fur density in larger species should be a more effective insulation than increasing body size, whereas smaller species should compensate for changes in temperature with an increase in body size (Steudel et al. 1994). However, Meiri and Dayan (2003) observed the opposite to be true in mammals (larger mammals with a mass > 0.5 kilograms conformed to Bergmann's Rule more so than small mammals whose mass < 0.5 kilograms) (Meiri and Dayan 2003). In looking at intraspecific populations, Freckleton et al. (2003) similarly observed that larger mammals (mass > 0.16 kilograms) better conform to Bergmann's Rule. Conversely, Blackburn and Hawkins (2004), who looked at communities of mammals, found that relatively small-bodied species follow the interspecific version of Bergmann's rule more strongly than relatively large-bodied species. Ashton et al. (2000) found broad support for Bergmann's Rule for mammals regardless of body size. The discrepancies in these results could be because the studies are looking at different variations of Bergmann's Rule. For example, Meiri and Dayan (2003), Freckleton et al. (2003), and Ashton et al. (2000) looked at the intraspecific variation, whereas Blackburn and Hawkins (2004) looked at the interspecific variation. Additionally, the boundaries between large and small body size are not standardized and have been placed at different masses. Meiri and Dayan (2003), Ashton et al. (2000), and Frekleton et al. (2003) looked at numerous studies that reported on a variety of mammals including Artiodactyla, Cetacea, Carnivora, Hyracoidea, Rodentia, Lagomorpha, Primates, Insectivora, and Monotremata. Blackburn and Hawkins (2004) looked at all of the mammals in the communities.

Test of the applicability of Bergmann's Rule in non-homeothermic animals found that salamanders, turtles, and ostracodes follow the rule, while lizards and snakes follow the inverse and frogs do not seem to trend in either direction (Ashton 2002; Ashton and Feldman 2003; Hunt and Roy 2006). Other studies have examined whether the ranges in body sizes of the taxa of interest affect the probability of a taxon following the rule (Ashton et al. 2000; Meiri and Dayan 2003; Blackburn and Hawkins 2004). Within Mammalia, species living in microclimates such as burrowers are not as affected by differences in temperatures as are other mammals, and therefore are not expected to follow Bergmann's Rule (Mayr 1956, 1963; Meiri and Dayan 2003), although some studies have found that certain burrowing genera do follow Bergmann's Rule (Brown and Lee 1969). Mammals that hibernate or go into torpor also can be challenging to interpret in terms of Bergmann's Rule because they behaviorally avoid extremely cold ambient temperatures (Meiri and Dayan 2003; Blackburn and Hawkins 2004). However, Panteleev et al. (1998) found "that Bergmann's ecogeographic rule is equally applicable to hibernating species, including marmots".

Bergmann's Rule has also been examined over temporal intervals in the geologic past to determine whether body size change corresponded to past climatic change (e.g. Gingerich 2003; Klein and Scott 1989; Klein 1986; Davis 1981; Wilson 2005). Gingerich (2003) observed a change in the size of the mammalian 'condylarth' genera *Ectocion* and *Copecion* that inversely correlated with a significant temperature increase at the Paleocene-Eocene boundary (coined the Paleocene-Eocene Thermal Maximum of PETM). Klein and Scott (1989) studied spotted hyenas (*Crocuta crocuta)* during the Pleistocene glacial and interglacial intervals and similarly noted an inverse relationship between body size and temperature in which spotted hyenas were larger during glacial intervals and smaller during interglacials, confirming Bergmann's Rule. Further, Davis (1981) reported a decrease in body size of fox, wild boar, gazelle, and goat in the area now known as Israel at the end of the Pleistocene epoch during global warming; however, body size of fallow deer did not show any trend. Wilson (2005), studying the interspecific variation of Bergmann's Rule, looked at the mammalian fauna of the latest Cretaceous Hell Creek Formation in northeastern Montana and found that the ratio of large-sized mammalian species relative to small-sized mammalian species increased during cool periods and decreased during warm periods, following Bergmann's Rule.

Bergmann's Rule has also been used as a paleothermometer, wherein a change in body size of fossil mammals is used as a proxy for paleotemperature (e.g. Davis 1981, 1977; Klein 1986; Klein and Scott 1989; Gingerich 2003). Klein (1986) tried to quantify the correlation of body size to temperature in modern carnivores so as to use the equations to estimate paleotemperatures (body size of carnivores was inferred from mean carnassial tooth length). Klein and Scott (1988) and Gingerich (2003) used similar equations to estimate temperature change, but concluded that their results did not match with temperature estimates based upon other paleobiological, geomorphic, and stable isotope data. Caution should be taken in using Bergmann's Rule to estimate past temperature change for a few reasons. The mechanism of Bergmann's Rule is not known with certainty and different taxa are not expected to respond to environmental change in the same way. In addition, fossil species that evolved at the same time may well have responded in different ways to the same climatic change, and the populations of a particular species with different geographic locations may have dissimilar responses (Dayan et al. 1991). Therefore, caution should be taken in using Bergmann's Rule to estimate past temperature change. More research is needed in order to demonstrate the utility of this technique.

I am using Bergmann's Rule in the relative sense, with no implied mechanism, and at the intraspecific level (within a lineage of the subfamily Rhinocerotinae and within species-lineages of *Leptomeryx*). The Rhinocerotinae are considered large mammals whose mass ranged from approximately 238 kg to 517 kg (Damuth 1990). In contrast, *Leptomeryx* are much smaller, weighing approximately 3.0 kg to 3.2 kg (Damuth 1990), but these artiodactyls would still fall within the large-bodied category of Freckleton et al. (2003) (mass>0.16 kg) and Meiri and Dayan (2003) (mass>0.5 kg). However, I am following Legendre's (1986) divisions for body-size – small <0.5 kg; 0.5 kg < medium < 8 kg; and large > 8kg – because his study also looked at body size during the late Eocene and Oligocene. Specifically, I test whether the two Chadronian-Orellan spanning lineages of *Leptomeryx* (it is hypothesized that *L. speciosus* evolved into *L. evansi* (Heaton and Emry 1996); and *L. mammifer* evolved into *L. exilis* (Korth and Diamond 2002)) and the subfamily Rhinocerotinae (lineage contains two genera in the Chadronian, one genus in the Orellan) followed Bergmann's Rule and became larger with the decreasing temperature that others have associated with the Eocene-Oligocene transition (EOT).

3. *Background to Biostratigraphy*

The Chadronian North American Land Mammal 'Age' (NALMA) which corresponds to latest Eocene time (Prothero 1995) derives its name from the Chadron Formation of northwestern Nebraska and southwestern South Dakota (Wood et al., 1941). An age range of 37-33.7 Ma is based upon magnetostratigraphy and ^{40}Ar/^{39}Ar ages of the many tuffs used to correlate the magnetochrons with the Berggren et al. (1995) time scale (Prothero and Emry 2004). The Chadronian was originally considered to be earliest Oligocene, but Berggren et al. (1995) subsequently revised the age of the Eocene/Oligocene boundary based upon the European marine record, while Prothero and Swisher (1992) revised the age of the Chadronian/Orellan boundary. Both revisions moved the Chadronian from the Early Oligocene to the Late Eocene (Prothero 1995) (Figure 2). The revised ^{40}Ar/^{39}Ar calibrations place the Chadronian in magnetochrons C16n to C13n (Prothero and Swisher 1992).

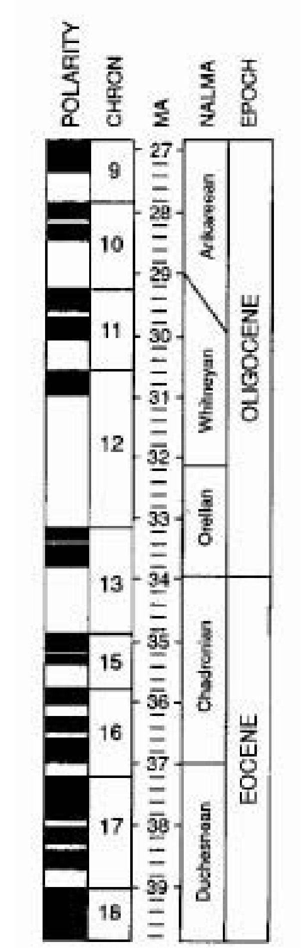

Figure 2. Timescale and correlation of the Duchesnean to the Arikareean NALMA (Eocene-Oligocene Epochs) to magnetostratigraphy and ^{40}Ar/^{39}Ar dating, from Prothero and Swisher 1992.

The Chadronian was originally defined as the time interval when *Mesohippus* and titanotheres coexisted (Wood et al., 1941). A revised definition published by Prothero and Emry (1996) used the first appearance datum (FAD) of *Bathygenys* (Order: Artiodactyla) to define the beginning of the Chadronian with artiodactyl taxa *Merycoidodon dunagani* (oreodont) and *Archaeotherium* (entelodont) and the carnivore *Brachyrhynchocyon dodgei* as characterizing taxa. The use of these taxa is based upon their occurrence in the Little Egypt Local Fauna in the Trans-Pecos region of Texas (Vieja Group) and from the Flagstaff Rim Area (White River Formation: Chadron Member) in Wyoming (Prothero and Emry 1996). The Chadronian is subdivided into four biostratigraphic zones: Earliest Chadronian, Late Early Chadronian, Middle Chadronian, and Late Chadronian (Prothero and Emry 1996, 2004). These zones have been radiometrically dated using $^{40}Ar/^{39}Ar$ dating and are correlated to the Geomagnetic Polarity Time Scale (Prothero and Emry 2004, 1996).

Latest Eocene-aged specimens measured in this study come from localities of Middle and Late Chadronian age of the White River sequence. The type section for the Middle Chadronian *Leptomeryx mammifer* Interval Zone is at the main Flagstaff Rim section, Wyoming (Prothero and Emry 2004). The Middle Chadronian correlates with magnetochrons C15n-C15r, and is approximately a million years in duration, from 34.7 to 35.7 Ma (Prothero and Emry 1996, 2004). The Late Chadronian *Miniochoerus chadronensis* Interval Zone correlates to magnetochrons C13r-C15n, ranging in age from 34.7 to 33.7 Ma, and its type section is in the Boner Ranch section of Wyoming (Prothero and Emry 1996, 2004).

The end of the Chadronian, and hence beginning of the Orellan NALMA, is traditionally defined by the last appearance of brontotheres (=titantotheres). However, due to the low abundance of brontotheres directly before the boundary, Prothero and Whittlesey (1998) redefined the end of the Chadronian, and therefore the onset of the

Orellan, as the *Hypertragulus calcaractus* Interval Zone, characterized by the FAD of the artiodactyls *Hypertragulus calcaratus* and secondarily by FADs of *Leptomeryx evansi* (artiodactyl)*, Palaeolagus intermedius* (rabbit), and *Miniochoerus chadronensis* (oreodont)*,* and last appearance datum (LAD) of *Poebrotherium eximium* (camel) and *Miohippus grandis* (horse).

The Chadronian – Orellan boundary lies approximately seven meters above the '5 tuff' ash layer at Douglas, Wyoming, as well as at the persistent white layer (also known as the purplish-white layer and the PWL) ash layer near Lusk, Wyoming (Prothero and Whittlesey 1998). The Chadronian – Orellan boundary near Douglas, WY occurs in magnetochron C13r, about halfway between the boundary of magnetochron C13r and C13n and the '5 tuff' and PWL ash layers (Prothero and Whittlesey 1998), and gives an age close to the Eocene – Oligocene boundary of 33.7 Ma (Prothero and Emry 2004).

The Orellan NALMA, once thought to represent the middle Oligocene, is now considered to be earliest Oligocene (Berggren et al. 1995) (Figure 2). The Orellan occurs between the Chadronian (ending in latest Eocene ~33.7 Ma, Prothero and Whittlesey 1998), and the Whitneyan NALMA (beginning ~32.0 Ma, Prothero and Whittlesey 1998), and is named for the fauna contained within the Orella member of the Brule Formation of northwestern Nebraska, southwestern South Dakota, and eastern Wyoming (Prothero and Emry 2004). The first appearance of the artiodactyl *Hypertragulus calcaratus* was chosen to define the beginning of the Orellan because there are no known occurrences of *Hypertragulus* in the Chadronian part of the White River Group, and this species appears suddenly at the onset of the Orellan with no reliable reported finds from the Chadronian (Prothero and Whittlesey 1998, Prothero and Emry

1996). The magnetostratigraphy shows that the lower boundary of the Orellan falls within the upper part of magnetochron C13r, while its upper boundary occurs in the middle of magnetochron C12r (Swisher and Prothero 1990).

The Orellan is also subdivided into four biostratigraphic zones: Earliest Orellan, Late Early Orellan, Early Late Orellan, and Latest Orellan (Prothero and Whittlesey 1998). The specimens used in my research come from all four biostratigraphic zones. Earliest Orellan is known as the *Hypertragulus calcaratus* Interval Zone, named after the species that marks the beginning of the Orellan (Prothero and Emry 2004). The type section for the Earliest Orellan is at the Reno Ranch East section in Converse County, Wyoming (Prothero and Whittlesey 1998). The biostratigraphic zone falls in the later part of magnetochron C13r and the earliest part of magnetochron C13n and ranges in age from 33.7 to 33.4 Ma (Prothero and Emry 2004). The Late Early Orellan, type section Boner Ranch section of Wyoming, is the *Miniochoerus affinis* Interval Zone (Prothero and Whittlesey 1998) and is within magnetochron C13n ranging in age from 33.4 to 33.1 Ma (Prothero and Emry 2004). The Early Late Orellan, *Miniochoerus gracilis* Interval Zone, also has its type section at Boner Ranch in Wyoming (Prothero and Whittlesey 1998); it began in the latest magnetochron C13n, ended in the early part of magnetochron C12r, and lasted just over half a million years from 33.1 to 32.5 Ma (Prothero and Whittlesey 1998, Prothero and Emry 2004). The Latest Orellan is designated the *Merycoidodon bullatus* Interval Zone with the type section located on the east side of Sheep Mountain Table in South Dakota. This zone falls within the early part of magnetochron C12r, and its age ranged from 32.0 to 32.5 Ma.

The Whitneyan NALMA (middle Oligocene, ~31.0 Ma to 30.0Ma) occurs after the Orellan (Prothero and Whittlesey, 1998) (Figure 2). Magnetostratigraphy places the lower boundary within the middle of magnetochron C12r, while the upper boundary is at the top of magnetochron C11n. My research does not use specimens from the Whitneyan because they are too young to be relevant for my study of mammalian size change associated with the climate change at the Eocene–Oligocene transition.

4. *Sedimentology and Stratigraphy*

The White River sequence (Figure 3) consists of stream-channel sandstones, fresh-water limestone deposits, sheet-flood deposits, volcanic ash beds, and eolian deposits (Wanless 1922) deposited during the upper Eocene and lower Oligocene in the Great Plains and central Rocky Mountains, including Colorado, Nebraska, Wyoming, South Dakota, North Dakota, and Montana (Larson and Evanoff 1998). When deposited, the White River sequence covered an area of approximately 400,000 km^2 and has a thickness ranging from a feather edge to greater than 300 meters (Larson and Evanoff 1998). The non-volcanic, non-carbonate sediments are derived from the unroofing of the Black Hills uplift (Evans and Welzenbach 1998; Evans 1999). The limestone deposits are found in only the Chadronian sediments (Evans and Welzenbach 1998). The volcanic sediments are thicker to the west, indicating the source to be from the west; specifically, Larson and Evanoff (1998) considered the volcanoes in the Great Basin of eastern Nevada and western Utah to be the primary source for the ash deposited in the White River sequence.

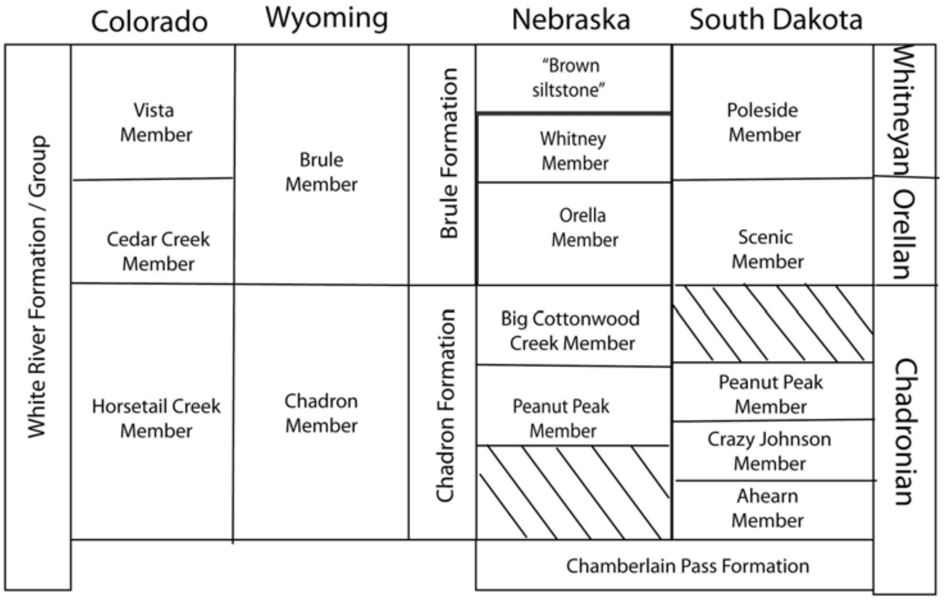

Figure 3. Stratigraphic Column of the White River sequence in the four states of my area of study. Colorado and Wyoming are separate from Nebraska and South Dakota because of the stratagraphic nomenclature (based on Galbreath 1953, Evanoff et al. 1992, Terry and LaGarry 1998, Terry 1998, and others). Not drawn to scale, all boundaries relationships are approximate. Hashed boxes represent

Originally defined as a Formation (Meek and Hayden 1857), the White River sequence is now usually regarded as a Group, except in Wyoming (Emry 1973; Evanoff 1990; Evanoff et al. 1992) and northeastern Colorado (Galbreath 1953; Hembree and Hasiotis 2007) where it remains a formation. The White River Group consists of three formations: the Chamberlain Pass Formation, the Chadron Formation, and the Brule Formation (Terry 1998, Terry and LaGarry 1998, Evans and Welzenbach 1998; Evans 1999) spanning the length of the Chadronian and Orellan (~5 Ma). None of the specimens used in this study came from the Chamberlain Pass Formation, and consequently this formation is not discussed any further. In Wyoming, the White River Formation consists of the Chadron and Brule Members (Evanoff 1990; Evanoff et al. 1992). In Colorado, the White River Formation consists of the Horsetail Creek, Cedar Creek, and Vista Members (Galbreath 1953).

The early Oligocene (Orellan and Whitneyan– aged) Brule Formation cropping out in Nebraska and South Dakota, (restricted to a member of the White River Formation in Wyoming by Evanoff et al. 1992) is the stratigraphically highest formation of the White River Group. Darton named the formation in 1899, although no type section was designated (Darton 1899). The formation consists of interbedded siltstone and sandstone overlaid by siltstone (LaGarry 1998) with interstratified ash layers (Evans and Welzenbach 1998). In the eastern side of the Brule Formation's geographical range, Nebraska and South Dakota, the Brule Formation is approximately 177 and 137 meters thick respectfully (Evans and Welzenbach 1998). The upper boundary of the Brule Formation, and hence the White River Group, is the abrupt unconformity between the overlaying sandstones of the Arikareean-aged Arikaree Formation (late Oligocene and early Miocene) and the underlying siltstones of the "brown siltstone" member (LaGarry 1998).

The latest Eocene (Chadronian– aged) Chadron Formation of Nebraska and South Dakota (considered a member of the White River Formation in Wyoming by Evanoff et al. 1992) is stratigraphically below the Brule Formation (Darton 1899, Galbreath 1953, Hoganson et al. 1998, Terry and LaGarry 1998). Darton (1899) also named this formation, and once again did not designate a type section. In 1929, Osborn designated the type section on Bear Creek, northwest of the town of Scenic (Harksen and Macdonald 1969a). Due to the fact that the type section does not show all of the Chadron Formation, Harksen and Macdonald (1969b) suggested that a section three miles to the southeast of the type section be considered a reference section as it is the closest outcrop that preserves the entirety of the Chadron Formation (Harksen and Macdonald, 1969b). On whole, the Chadron Formation has fewer volcanic clastics

(Larson and Evanoff 1998) and more lacustrine sediments that the overlying Brule Formation (Evans and Welzenbach 1998).

I discuss Nebraska, South Dakota, Wyoming, and Colorado in more detail below because the specimens used in this study come from these states.

a. Nebraska

In Nebraska, the Brule Formation is subdivided into three members (in order of youngest to oldest): "brown siltstone" member; Whitney Member; and the Orella Member. The Orella Member (Orellan in age) consists of sandstone sheets, massive and laminated volcaniclastic clayey siltstones, occasional volcaniclastic silty claystones, and volcanic ash (Swinehart et al. 1985; LaGarry 1998). The Whitney Member and the "brown siltstone" member (originally included in the Gering Formation by Vondra et al. (1969), but now considered to be part of the Brule Formation (Swinehart et al. 1985)) are mainly Whitneyan (middle Oligocene) in age (Wood et al., 1941). Therefore, any specimens from the Whitney Member or the overlying "brown siltstone" member are too young to be used in this study.

Terry and LaGarry (1998) revised and redescribed the Chadron Formation of Nebraska, naming a new member the Big Cottonwood Creek Member, which sits on top of, and intertongues with the Peanut Peak Member. The Big Cottonwood Creek Member contains pedogenic and lacustrine limestone interbeds, as well as pedogenic calcrete, gypsum, and volcanic ash within volcaniclastic silty claystones and sandstones (Terry and LaGarry 1998). The Big Cottonwood Creek Member extends into South Dakota to the town of Oelrichs, but does not extend to the Big Badlands of South Dakota (Terry 1998). The rest of the Formation consists of claystones and mudstones with areas of sandstones and conglomerates underlying the claystones and mudstones

(Swinehart 1985). There are also layers of rhyolitic and rhyodactic tuffs throughout the Chadron Formation (Larson and Evanoff 1998)

b. South Dakota

In South Dakota, the Brule Formation contains the lower Scenic Member and the upper Poleslide Member. The Scenic Member (Orellan in age) is similar to the Orella Member of Nebraska except the Scenic member also contains abundant nodules (LaGarry 1998; Retallack 1983). The magnetostratigraphy shows the Scenic Member starting near the end of magnetochron C13n and ending in the first half of chron magnetoC12r (Prothero & Swisher 1992). The Poleside Member (end of Chron C12r to beginning of C11n, Prothero and Swisher 1992) contains fossils belonging to the Whitneyan NALMA (Schultz and Stout 1955; Retallack 1983) and because the Whitneyan NALMA is too young to be included in the is study that focuses on the EOT,, no specimens from the Poleside Member of the Brule Formation were measured. The upper contact of the Brule Formation in South Dakota is at the base of the white Rockyford Ash Member of the Sharps Formation (Harksen and Macdonald 1969b).

The Chadron Formation fills paleovalleys and blankets the surrounding area of the paleovalleys (Evans 1999; Evans and Welzenbach 1998; Terry 1998). The paleovalleys cut through the underlying early Chadronian–age Chamberlain Pass Formation and Interior Zone Paleosol and the Crecaceous– aged Yellow Mounds Paleosol and Pierre shale (Terry 1998; Evans 1999). Inside the paleovalleys the sediments progress through three members named by Clark (1954), with the standard section in the Big Badlands by the south fork of Indian Creek, Pennington County, South Dakota (Clark 1954). The lowest Ahearn Member is multistory, pebbly, sandstone rich channel fills; the middle is the transitional Crazy Johnson Member consisting of massive clays with intermittent limestone bands; and the Peanut Peak Member, a single-storey, avulsion-dominated sandstone with limestone lenses tops off and the paleovalleys and surrounding floodplains (Evans 1999; Terry 1998). Due to this backfilling of paleovalleys, the thickness of the Chadron Formation ranges from approximately 2.5 meters (8 feet, Clark et al. 1967) to approximately 55 meters (180ft, Harksen and Macdonald 1969a).

c. Wyoming

In the Douglas area of Wyoming, the White River Formation can be separated into the Brule and Chadron Members. The Brule Member consists of sandy mudstones and sandy siltstones with occasional ribbon sandstones and conglomeratic sheet sandstones and layers of glass-rich tuff (Evanoff et al. 1992). Similar to the Brule Formation in South Dakota, the Brule Member in Wyoming starts near the end of magnetochron C13n and ends in the middle of magnetochron C12r, making it Orellan in age (Evanoff et al. 1992). In the Douglas area of Wyoming, the Chadron Member (Chadronian–aged) consists of clayey mudstones, typically nodular sandy mudstones, thin sheet sandstones, and many thick ribbon sandstones (Evanoff et al. 1992).

Farther west, in the Flagstaff Rim area of Wyoming, the deposited White River Formation is only of Chadronian age and cannot be differentiated into members although it can be divided into two parts based on lithology (Emry 1973). The lower part consists of interbedded silty claystones separated by tongues of conglomeratic sandstone while the upper part consists of massive tuffaceous siltstones with occasional thin lenses of claystone and thick lenses of coarse channel sandstones (Emry 1973). The White River Formation near Flagstaff Rim has a maximum thickness of 243 meters (800 feet) (Emry 1973).

d. Colorado

The oldest White River Formation unit in Colorado, the Chadronian-aged Horsetail Creek Member, sits unconformably on Cretaceous rocks and in some places is separated by overlying the Cedar Creek Member by an erosional unconformity. The Horsetail Creek Member was considered the Horsetail Creek facies of the Chadron Formation by Wood et.al (1941) (Wood et al., 1941). Similar to other Chadronian strata of the White River sequence, the Horesetail Creek Member contains beds of lacustrine limestone with interfingering siltstone (Galbreath 1953). The Orellan-aged Cedar Creek Member overlays the Horestail Creek Member and consists of channel deposits of fine-grained sandstones interfingering with massive, coarser sandstone, progressively thinning, and capped by a massive siltstones (Galbreath 1953). Galbreath (1953) proposed the name 'Cedar Creek Member' for the strata containing fossils of Orellan age. The stratigraphically highest member of the White River Formation in Colorado is the Vista Member. Although the Vista Member can lithologicially be separated from the underlying Cedar Creek Member, the boundary was chosen arbitrarily and has no real stratigraphic significance (Galbreath 1953). Instead, Galbreath (1953) proposed this member for deposits of Whitneyan (middle Oligocene) age fauna in Logan County Colorado (Galbreath 1953). Because my study does not include fossils from the Whitneyan NALMA, no fossils from the Vista Member of the White River Formation of Colorado were measured. The member is simply noted here for completeness.

5. *Mammalian Taxa used in this study*

As discussed in Section II, Bergmann's Rule has been supported more in large-bodied animals than to small-bodied animals (Meiri and Dayan 2003, Frekleton et al.

2003). In order to test whether the intraspecific variation of Bergmann's Rule is evident in a temporal sequence from latest Eocene through earliest Oligocene time (Chadronian – Orellan NALMA), I analyzed the large-bodied perissodactyl Rhinocerotinae (*Trigonias* and *Subhyracodon*), and the small-bodied, though more abundant, artiodactyl (cloven-hoofed mammal) *Leptomeryx*.

a. Rhinocerotinae

Rhinoceroses were chosen as the representative for large-bodied mammals because they are the largest mammal found in the Orellan and are only second in size to brontotheres in the Chadronian (Prothero 2005). They are also the most common large (>100kg) mammals from White River Orellan strata (Mead and Wall 1998a), and are very abundant in the museum collections of the Denver Museum of Nature & Science and the University of Colorado Museum of Natural History. *Subhyracodon* is the only genus of rhinocerotids that crossed the Chadronian – Orellan boundary and is found in Orellan strata according to Prothero (2005). The genus *Amphicaenopus* also crossed the Chadronian – Orellan boundary, but no specimens have been found in Orellan strata although some have been found in the overlying Whitneyan strata (Prothero 2005). This genus is rare and therefore was not included in my study. The genus *Trigonias* has been found only in Chadronian strata and was included in my study of the Rhinocerotinae subfamily population. There are difficulties in differentiating between check teeth dentitions of *Subhyracodon* and *Trigonias* as explained below.

The subtribe Caenopina in the subfamily Rhinocerotinae contains seven genera: *Prohyracodon*, *Trigonias*, *Amphicaenopus*, *Subhyracodon*, *Epiaceratherium*, *Ronzotherium*, and *Moschoedestes* (McKenna and Bell 1997), two of which were used in my study – S*ubhyracodon* and T*rigonias*. The two genera differ postcranially, specifically *Subhyracodon* has lost the 5th metacarpal while the more primitive *Trigonias* still retains it. The two genera also show differences in the skull (Scott 1941), and in the presence (or absence) of the anterior teeth. In particular, *Trigonias* retains all anterior teeth except for the lower canine while *Subhyracodon* has lost both canines and the upper and lower 3rd incisor. The challenge with identifying an individual as belonging to either genus occurs when only cheek teeth are preserved because the cheek teeth by themselves are indistinguishable for these two genera. This is partly due to the similarity in size of the cheek teeth (Scott 1941) as well as the variability of the morphology of the premolars of *Trigonias* (Prothero 2005). Previously, fragmentary specimens from both *Trigonias* and *Subhyracodon* specimens were placed in the genus *Caenopus*. The genus *Caenopus* was sunk into *Trigonias* and *Subhyracodon* by Prothero (2005) as most specimens referred to *Caenopus* are actually either *Trigonias* or *Subhyracodon*. Specimens only identified to Rhinocerotinae indet. were also include in this study because of their inclusion in the subfamily Rhinocerotinae.

i. Subhyracodon

Brandt (1878) initially erected the name S*ubhyracodon* as a subgenus in the genus *Aceratherium* based upon the species *A. mite*, *A. occidentale* (originally placed in the extant genus *Rhinoceros*), and *A. quadriplicatum* (Prothero 2005). In 1927, H. E. Wood raised *Subhyracodon* from subgenus to genus rank (Wood, H. E. 1927). The type species for the genus *Subhyracodon* is *S. occidentalis*. Currently, three species of *Subhyracodon* are recognized: *S. occidentalis*, *S. mitis*, and *S. kewi* (Prothero 2005). However only two of these – *S. occidentalis* and *S. mitis* – fall into my temporal and geographic range.

S. occidentalis, the larger of the two species, lived from the late Chadronian to the late Orellan. Most specimens have been found in the Plains states (Colorado to North

Dakota) and in the Rocky Mountains of Wyoming, although a specimen has been documented in Mississippi (Prothero 2005). The smaller species, *S. mitis*, has a shorter time span from the late Chadronian to the early Orellan with a geographic range from Colorado and Nebraska to Montana, and therefore overlapping the range of *S. occidentalis* (Prothero 2005).

Subhyracodon was a small to medium rhinoceros (Prothero 2005) which had a body mass greater than 100kg (Mead and Wall 1998a). They were a hornless rhino and a selective mixed feeder that probably consumed high-fiber vegetation and succulent browse, based on dental and skull morphology (Mead and Wall 1998a, 1998b). The genus has been excavated from former stream margins, near-stream floodplains, and in the dry floodplain deposits further from streams, and therefore probably occupied riparian forests and the surrounding wooded habitats in the Orellan (Retallack 1983; Clark et al. 1967). Zanazzi and Kohn (2008) interpreted δ^{13}C values of *Subhyracodon* enamel to indicate a preference for the open plains and/or xeric areas.

ii. Trigonias

F.A. Lucas (1900) erected the genus *Trigonias*, based upon USNM 3924 from the Eocene of South Dakota as the type specimen and *Trigonias osborni* as the type species (Lucas 1900). The original paper lists the age as Miocene, specifically found in the Lower Titanotherium Beds which is now considered to be part of the Chadron Formation and hence Chadronian in age (Schultz and Stout 1955.) Gregory and Cook (1928) named additional species based upon specimens gathered at the *Trigonias* Beds Quarry in Weld County, Colorado. In 1931, Wood studied the same specimens as Gregory and Cook (1928) and synonymized three species, while naming one new species (Wood 1931). Also in 1931, W. D. Matthew published a paper stating, "There is every reason to believe on ecologic and other grounds that this series [from the *Trigonias* Beds Quarry] represents one genus and one species…" (Matthew, 1931, p.5). A decade later, Scott (1941) published a monograph where he discussed this controversy and recognized two species *T. osborni* and *T. taylori*, and one subspecies *Trigonias osborni wellsi* from the Colorado and South Dakota material (Scott 1941). More recently, Prothero (1998) stated that there are only two valid species, the type *T. osborni* and the much larger *T. wellsi*. The *Trigonias* specimens that I measured for this study were identified as *Trigonias* sp. or *Trigonias osborni*.

The first appearance of *Trigonias* questionably occurred in the Duchesnean NALMA (middle Eocene; precedes the Chadronian; Robinson et al. 2004). However, by the Chadronian, *Trigonias* was quite common in the Great Plains (Scott 1941). By the Orellan, *Trigonias* had gone extinct while *Subhyracodon* did not and hence became the most common rhinocerotid in North America (Prothero 2005). The north to south range for *Trigonias* is from Canada to Colorado. *Trigonias* ranged from the Plains region to California (Prothero 2005).

Trigonias fossils have been excavated from stream channels and near-stream deposits (Retallack 1983). They were medium sized for rhinoceroses (Prothero 2005) with short, heavy limbs and perhaps semi-aquatic (Clark et al. 1967), although $\delta^{18}O$ values (N=1) do not support a semi-aquatic lifestyle (Zanazzi and Kohn 2008). There are no known body mass estimates specifically for the genus *Trigonias*.

b. Leptomeryx

I chose the genus *Leptomeryx* as a representative of medium-bodied mammal because of its abundance in the White River Formation/Group. Second only to oreodonts, the most common mammals in the Orellan are the smaller deerlike

Leptomeryx and *Hypertragulus* (Prothero and Whittlesey 1998). In the Badlands of Dakota *Leptomeryx* specimens are much more abundant than *Hypertragulus* (Webb 1998).

Leptomeryx is a small hornless artiodactyl first described by Leidy (1853). This taxon ranges from the Duchesnean (late middle Eocene) to the Arikareean (Early Miocene) (Metais and Vislobokova). There are two lineages of *Leptomeryx* that are differentiated by the shape of the posterolophid on the third lower molar (Heaton and Emry 1996; Korth and Diamond 2002) (Figure 4). The posterolophid of the *L. yoderi* – *L. mammifer* – *L. exilis* lineage (Y/M) has an elongated and narrow entoconulid that is lower than the entoconid and gently slopes posteriorly. This creates a shallow valley with the entoconulid and hypoconulid. In contrast, the posterolophid of the *L. speciosus* – *L. evansi* lineage (S/E) has a rounded entoconulid that is as high as the entoconid and sharply slopes posteriorly creating a deep valley between the entoconulid and hypoconulid (Figure 4). Although *L. yoderi* is not listed as part of the S/E lineage, *L. yoderi* is hypothesized to be the ancestor of *L. speciosus* as well, based upon stratigraphic distribution of *L. yoderi* and *L. speciosus* at Flagstaff Rim in Wyoming (Heaton and Emry 1996).

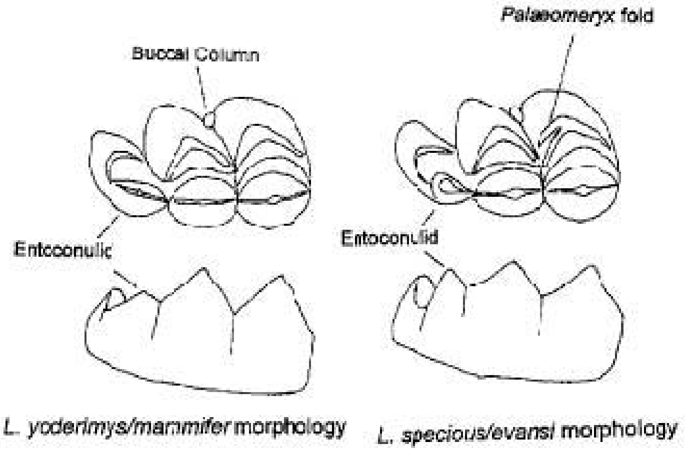

Figure 4. Differing morphologies of the lower left third molars for the two *Leptomeryx* lineages, occulsal view on top, lingual view on the bottom, from Diamond and Korth (2000).

The differentiation of species within the Y/M lineage is partly based upon size and partly based upon age; the early to middle Chadronian-aged *L. yoderi* is smaller than the middle to late Chadronian-aged *L. mammifer*, which in turn is larger than the Orellan-aged *L. exilis* (Heaton and Emry 1996; Korth and Diamond 2002). At Flagstaff Rim in Wyoming, one of *L. yoderi's* descendents, *L. mammifer* is limited to, and the index fossil for, the Middle Chadronian biostratigraphic interval (Prothero and Emry 2004). However, even though some researchers have stated that the *Leptomeryx* Y/M lineage died out in the Chadronian (Heaton and Emry 1996), this cannot be accurate because *L. exilis*, which clearly belongs to the Y/M lineage on the basis of its m3 posterolopid morphology, has been found in Orellan and Whitneyan-aged strata in Nebraska, South Dakota, Colorado, and Wyoming (Korth and Diamond 2002, this research). Korth and Diamond (2002) also consider the Whitneyan species *L. obliquidens* to be descended from this lineage. *L. obliquidens* is differentiated from *L. exilis* by its larger size.

Differentiation of the species of the S/E lineage is based upon morphology, which is consistent with the differences in age. Individuals with the S/E entoconulid from the Chadronian belonging to *L. speciosus* have a small percentage of individuals with paleomeryx folds, while individuals with the S/E entoconulid from the Orellan assigned to *L. evansi* have a much higher percentage of paleomeryx folds. Paleomeryx folds are small lophs that extend posteriorly off of the protoconid and run down the posterior slope of the protoconid; they are found only in individuals within the S/E lineage (Korth and Diamond 2002; see figure 4). Korth and Diamond (2002) also noted that *L. evansi* specimens possessed a paleomeryx fold on all of the m1s, 90% of the m2s, and 83% of the m3s. Korth and Diamond (2002) identified a second species from the Orellan with the S/E entoconulid – *L. elissae*; this species lacks paleomeryx folds on all of its lower molars, making it difficult to identify unless the complete molar row is present. Heaton and Emry (1996) also used the labial ridge posterior to the protoconid on p3 to differentiate between *L. evansi* and *L. speciosus*. However, Korth and Diamond (2002) found this character to be extremely variable and not useful for differentiating species.

Leptomeryx were small (rabbit–sized), deer-like, hornless, browsing ruminant artiodactyls (Wall and Collins 1998, Webb 1998). During the Orellan, *Leptomeryx* probably lived in savannas and grassy woodlands on terraces or floodplain areas away from streams (Retallack 1983), although a few specimens have been found in near-stream deposits of the lower nodular zone of the Brule Formation in the Badlands (Clark et al. 1967). *Leptomeryx* was most likely an active runner on dry ground that entered forests and streams, but preferred the open plains (Clark et al. 1967). There is an indication based upon $\delta^{13}C$ values that through the EOT, *Leptomeryx* changed its preferred habitat from woodlands to grasslands (Zanazzi and Kohn 2008). Dentally, *Leptomeryx* specimens from the Chadronian have less occlusal enamel than specimens from the Orellan (Mathis 2008), possibly indicating a change in feeding habit from soft leaves to coarse grass.

II. Materials and Methods

Dental Abbreviations used in this study include:

L – Left side of jaw or maxilla
R – Right side of jaw or maxilla

N_C – Sample size of Chadronian specimens
N_O – Sample size of Orellan specimens

Uppers – 1st premolar: P1
2nd premolar: P2
4th premolar: P4
1st molar: M1
2nd molar: M2
3rd molar: M3

Lowers – 1st premolar: p1
2nd premolar: p2
4th premolar: p4
1st molar: m1
2nd molar: m2
3rd molar: m3

Institutional Abbreviations used in this study include:

UCM – University of Colorado at Boulder Museum of Natural History
DMNS – Denver Museum of Nature & Science
FMNH – Field Museum of Natural History
SDSM – South Dakota School of Mines and Technology Geology Museum

Artiodactyl terminology (Figure 5) comes from Heaton and Emry (1996).

Perissodactyl dental terminology (Figure 6) follows Hooker (1989).

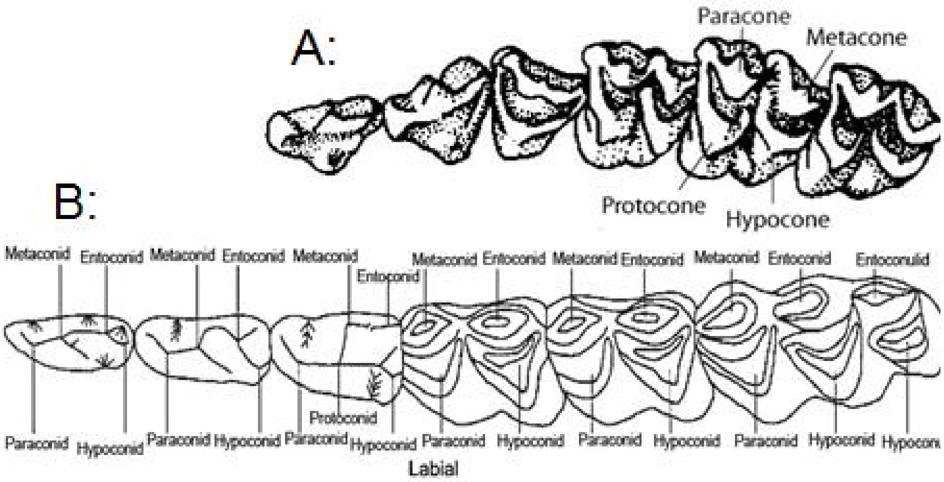

Figure 5. Cusp terminology of *Leptomeryx* (Artiodactyla); A: Upper right dentition picture, modified from Webb (1998). B: Cusp terminology for the lower left dentition of *Leptomeryx*, from Heaton and Emry (1996)

I only used dental measurements in this study because of the ability to identify teeth to a lower taxonomic level with more certainty than postcranial material, and because teeth are more often preserved (and therefore more abundant) than diagnostic bones, including the skull.

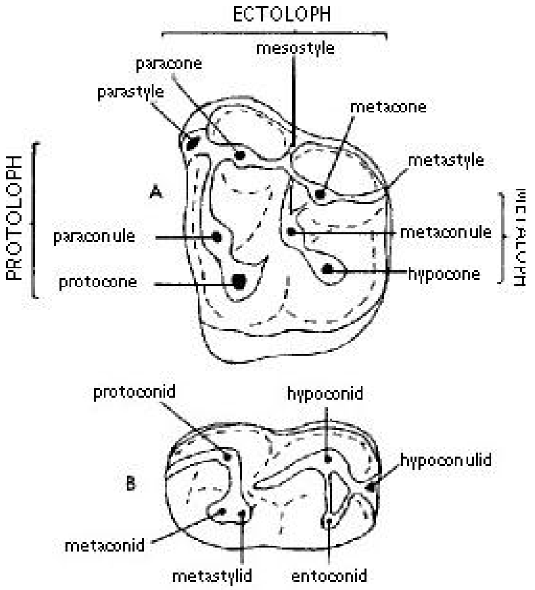

Figure 6. Cusp and loph terminology for Perissodactyla, modified from Hooker (1989) A: Upper left molar; B: Lower right molar

The *Leptomeryx* and Rhinocerotinae specimens used in this study were collected by field parties from the University of Colorado Museum of Natural History (UCM) in Boulder, the Denver Museum of Nature & Science (DMNS), the Field Museum of Natural History (FMNH) in Chicago, and the South Dakota School of Mines and Technology (SDSM) in

Rapid City over the course of many decades and are housed in four museum collections: UCM, DMNS, FMNH, and SDSM. The *Leptomeryx* specimens came from all four museums, with the most specimens coming from UCM, followed by DMNS, then FMNH and SDSM (Appendix 2). The specimens housed at UCM are from the Chadron Member and Brule Member of the White River Fm. in Wyoming; the Chadron and Orella Members of the Brule Fm. in Nebraska; the Cedar Creek and Horsetail Creek Members of the White River Fm. in Colorado; and the Scenic Member of the Brule Fm. in South Dakota. The DMNS specimens were collected from the Chadron Member of the White River Fm. in Wyoming; the Chadron Formation of Nebraska; the Cedar Creek and Horsetail Creek Members of the White River Formation of Colorado; and the Chadron Member of White River Fm. in Wyoming. The FMNH specimens were collected from the Brule Formation of Nebraska and the Peanut Peak and Crazy Johnson Members of the Chadron Formation of South Dakota. The SDSM specimens were collected from the Chadron Formation in South Dakota.

The Rhinocerotinae specimens also came from all four museums, with *Trigonias* specimens coming from UCM, DMNS, and FMNH and *Subhyracodon* specimens coming from UCM, DMNS, and SDSM (Appendix 3). Specimens identified only down to the subfamily (Rhinocerotinae) or identified as *Caenopus* (nomen dubium) came from DMNS, SDSM, and UCM. The specimens housed at UCM are from the Chadron Fm. and the Orella Member of White River Fm. in Nebraska; the Brule Member of the White River Fm. in Wyoming; the Horsetail Creek Member of White River Fm. in Colorado; and the Scenic Member of the Brule Formation in South Dakota. The DMNS specimens come from the Horsetail Creek and Cedar Creek Members of the White River

Formation in Colorado. The FMNH specimens were collected from the Chadron Formation, and the Peanut Peak, the Crazy Johnson, and Ahearn Members of the Chadron Formation in South Dakota, and the Horsetail Creek Member of the White River Fm. in Colorado. The SDSM specimens were collected from the Brule Formation and the Scenic Member of the Brule Formation, and the Chadron Formation in South Dakota.

For the rhinoceratine specimens from DMNS and UCM, digital calipers with a maximum measurement of 120 mm and a 0.01 mm resolution were used to take length and width measurements. The rhinoceratine specimens from FMNH were measured with a metric dial caliper with a 0.05 resolution. All of the *Leptomeryx* specimens were measured using digital calipers. There were a few specimens where the M2/m2 length could not be accurately measured with the calipers; for these specimens, a SPOT camera and associated computer software were used to determine the length. In order to make sure that the computer and calipers would give equivalent measurements, I used the computer to measure certain *Leptomeryx* specimens that could also be accurately measured with digital calipers and compared the results.

For this study, I took the following eight measurements of upper and lower dentitions of the rhinoceratine taxa *Trigonias*, *Subhyracodon*, and Rhinocerotinae indet.: length and width of right and left m2 and M2; length of the right and left molar tooth rows; and length of the right and left post-canine tooth row. Maximal values for each dimension were used following Damuth (1990). The m2 width is the widest point of the tooth measured through the apices of the metaconid and protoconid (Figure 7a). The m2 length was measured from the point of contact between m1 and m2 to the point of contact between m2 and m3 (Figure 7b); for worn teeth, where the contact is a line and not a point, the measurement is from the middle of the contact line between the teeth. The length of the lower molar row (m1-m3) was measured from the contact between p4 and m1 to the posterior margin of m3 (Figure 7d). The length of the post-canine tooth row (p1-m3) – the longest measurement – was measured from the anterior margin of the p1 to the posterior margin of the m3 (Figure 7c+d). However, due to the size limitations of the calipers, the post-canine tooth row was measured in two parts - the molars and the premolars – which were simply added together. I used the anterior margin in the rhinocerotids length of the lower molar row as the posterior margin when measuring the premolar row (Figure 7c) in order to limit the amount of overlaps and/or gaps.

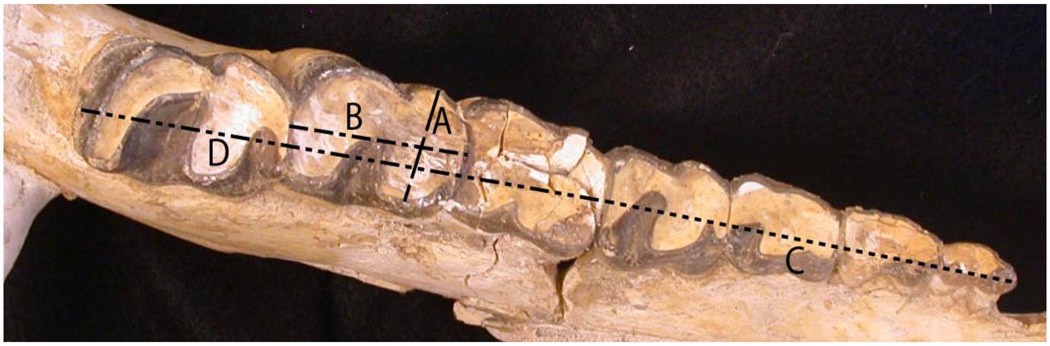

Figure 7. Lower dentition measurements of Rhinocerotinae (UCM 89771); A (dashed): m2 width; B (two dashes one dot): m2 length; C (dots): premolar row; D (one dash two dots): molar row. Post-canine tooth row is the molar row plus the premolar row (D + C).

With regard to measurements on the upper dentition, the M2 length is the length of the ectoloph, parallel with the line of the loph (Figure 8b), whereas the M2 width is the widest distance from the apices of the paracone and the protocone (protoloph) (Figure 8a). The upper molar row length (M1-M3) is the widest part from the anterior margin of the ectoloph of the first molar to the posterior margin of the M3 hypocone

(Figure 8d). The length of the upper post-canine tooth row (P1-M3) is defined here as the longest distance from the anterior margin of the first premolar to the posterior margin of the M3 hypocone (Figure 8c+d). Due to the size limitations of the calipers that I used, the post-canine tooth row was measured in two parts - the molars and the premolars – and these two measurements were simply added together. I used the anterior margin in the rhinoceratines' molar row length as the posterior margin when measuring the premolar row (Figure 8c) in order to limit the amount of overlaps and/or gaps. However, due to small sample size, I was not able to use the lower post-canine tooth row in my statistical analysis.

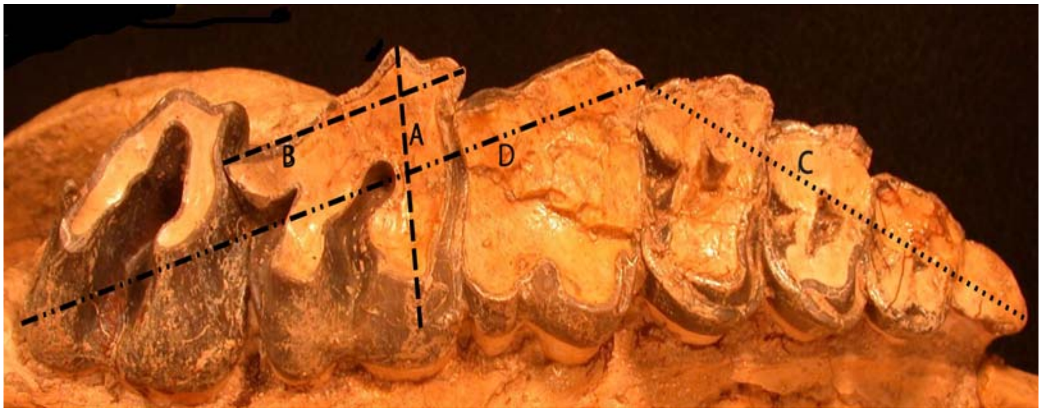

Figure 8. Upper dentition measurements of Rhinocerotinae (UCM 89765); A (dashed): m2 width; B (two dashes one dot): m2 length; C (dots): premolar row; D (one dash two dots): molar row. Post-canine tooth row is the molar row plus the premolar row (D + C).

For *Leptomeryx*, measurements were similar to those of the rhinocerotines. Specifically, I measured length and width of right and left m2 and M2, length of the upper and lower molar tooth row, and length of the upper and lower post-canine tooth row. The m2 width is the greatest transverse width through the protoconid and metaconid apices (Figures 9a). The M2 width is the greatest transverse width through the apies of the protocone and paracone (Figure 10a). The length of m2 is the longest distance measured along the lingual side of the tooth through the apices of the metaconid and entoconid (Figure 9b, which is similar to Heaton and Emry 1996), whereas the M2 length is the longest distance as measured through the paracone and metacone (Figure 10b). The lower molar row length (m1-m3) is measured from the anterior margin of the metaconid on m1 to the most posterior margin of the m3 through the hypoconulid (Figure 9d). The length of the upper molar row (M1-M3) is the distance from the anterior margin of the paracone on M1 to the posterior margin of the metacone on M3 (Figure 10d). Due to presence of a diastema between p1 and p2 and the caniniform morphology of p1, the lower cheek teeth row is defined here as the distance from the anterior margin of p2 to the posterior margin of the m3 measured through the hypoconulid (Figure 9c). The length of the upper cheek tooth row is the distance from the anterior margin of P2 to the posterior margin of the metacone on M3 (Figure 10c). However, due to small sample size, I was not able to use the post canine tooth row measurements in my statistical analysis, leaving a maximum of 12 variables for statistical analysis.

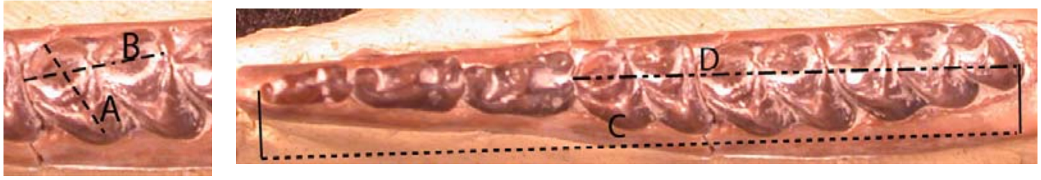

Figure 9. Lower dentition measurements of *Leptomeryx* (UCM 87459); A (dashed): m2 width; B (two dashes one dot): m2 length; C (dots): post-canine row; D (one dash two dots): molar row.

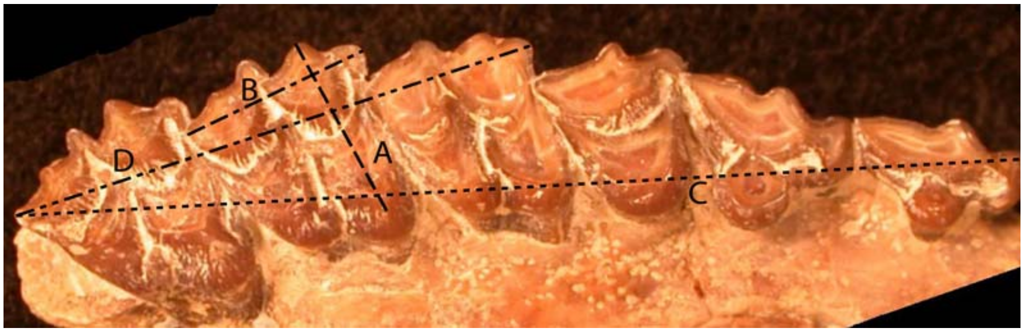

Figure 10. Upper dentition measurements of *Leptomeryx* (UCM 87475); A (dashes): M2 width; B (two dashes one dot): M2 length; C (dots): post-canine row; D (one dash two dots): molar row.

The 16 possible measurements are: right M2 width (RM2 w); right M2length (R M2 l); right upper molar row length (RM1-3); right upper post-canine row length (RP1-M3 or RP2-M3); left M2 width (RM2 w); left M2 length (RM2 l); left upper molar row length (RM1-3); left upper post-canine row length (RP1-M3 or RP2-M3); right m2 width (Rm2 w); right m2 length (Rm2 l); right lower molar row length (Rm1-3); right post-canine row length (Rp1-m3 or Rp2-m3); left m2 width (Rm2 w); left m2 length (Rm2 l); left lower molar row length (Rm1-3); left post-canine row length (Rp1-m3 or Rp2-m3).

Some of these measurements are not independent of each other; however a correlation of the measurements show that although all four measurement (second molar width and length, molar row length, post-canine row length) in each post-canine tooth row (right upper, right lower, left upper, left lower) are highly correlated, they are not necessarily correlated to any of the other post-canine tooth rows. For the *Leptomeryx* this is probably due to the fragmentary nature of most of the specimens; most of the specimens containing teeth from the right side did not preserve teeth on the left side and vice versa, similarly specimens where the mandible was preserved often did not have the skull preserved. The rhinocerotines often had both sides of the jaw or skull preserved, although there were not many skulls with associated jaws, and there is a high correlation between the left and the right sides but not the upper and lower dentitions. Therefore, I am looking at multiple sample populations of Chadronian and Orellan *Leptomeryx* and rhinocerotines.

1. Age Categories

Specimens of *Trigonias* and *Subhyracodon* were subdivided into four age categories based upon tooth eruption and wear. These categories are arbitrarily based on the second molar since that is the only tooth I studied individually. These categories are also objective in that each specimen can clearly be place in the appropriate category. In the youngest individuals (juveniles), M2/m2 were not erupted and consequently these specimens were not measured for this study and are not figured. The youngest group used in my study was the adolescent/young adult age class. These individuals bore a fully erupted M2/m2, but either M3/m3 had not yet erupted or it had erupted but lacked wear (Figure 11). The middle group – adults – had wear on M3/m3 but M2/m2 still retained a semblance of the loph pattern, pi-shape on the uppers and the V and backwards J patterns on the lower molars (Figure 12). The third group comprised the oldest individuals – the seniors – bore M2/m2s that were worn down to the dentine and there was no enamel left on the occlusal surface of the M2/m2s (Figure 13).

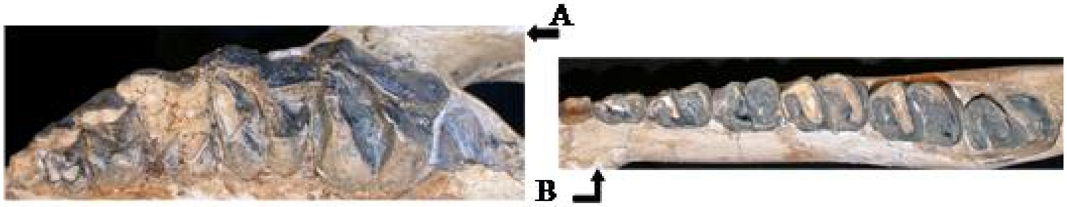

Figure 11. Adolescent Rhinocerotinae, A: upper dentition (UCM 43697), notice the minimal wear on M2 and the erupting M3; B: lower dentition (UCM 87461), notice the lack of wear on /m2 and that /m3 is just erupting.

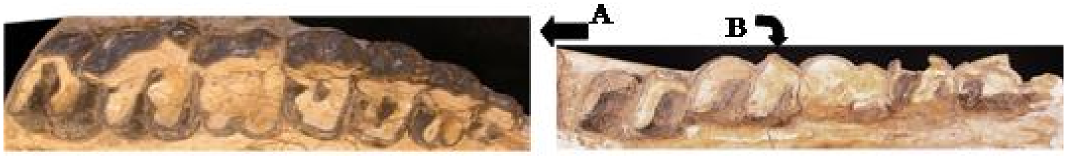

Figure 12. Adult Rhinocerotinae; A: upper dentition (UCM 68915), notice the pi-shape is still on M2; B: lower dentition (UCM 68913), notice the upside-down ‘v’ is still visible on the m2.

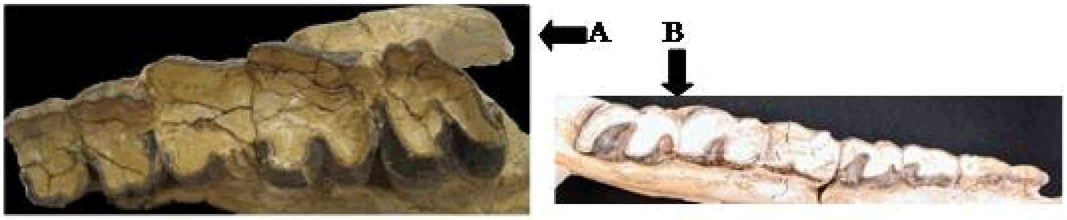

Figure 13. Senior Rhinocerotinae; A: upper dentition (DMNS 1860), notice the pi-shape of M2 is no longer visible; B: lower dentition (UCM 89771), notice the upside-down ‘v’ is no longer visible on the m2.

As with the rhinocerotines, specimens of *Leptomeryx* were initially divided into four age groups – juvenile, adolescent, adult, and senior. The juveniles were not measured because the second molar had not yet erupted, and consequently I did not include figures of them. The adolescents were identified as those individuals with a fully erupted M2/m2, but not a fully erupted M3/m3, or if fully erupted, it was absolutely unworn (Figure 14). If the M3/m3 was not present, the age of the individual at death was subjectively based upon the wear of M2/m2. The adults had a fully erupted M3/m3 that showed wear, but still retained the posterior lake between the metacone and hypocone on M2, and the hypoconid and entoconid on m2 (Figure 15). The teeth of seniors were worn down to the point that there was no longer a lake between the metacone and hypocone on M2 and between the hypoconid and entoconid for m2 (Figure 16). These wear stages are similar to the wear stages defined by Clark and Guensburg (1970), with their infant and juvenile stages equating to my (unmeasured) juvenile group. Their adolescence stage equates with my adolescent group. These authors' young adulthood and middle age stages fall into my adult group, as do some individuals of their senility stage because I used the elimination of the posterior lake of m2 instead of the m1 as the means for differentiating between adults and seniors.

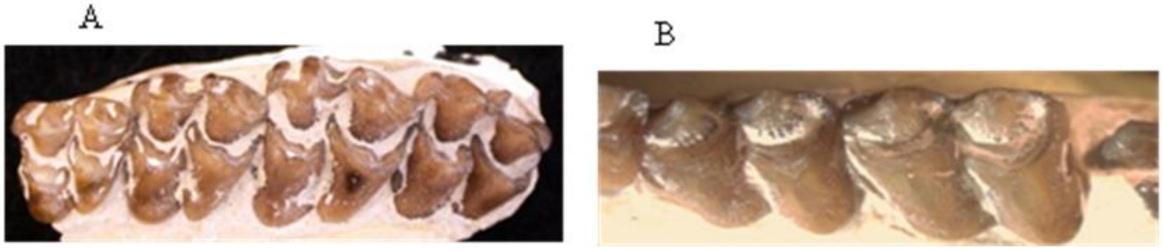

Figure 14. Juvenile *Leptomeryx*. A: upper dentition (UCM 87494), notice that M3 has no wear; B: lower dentition (UCM 87461), notice that m3 is not fully erupted.

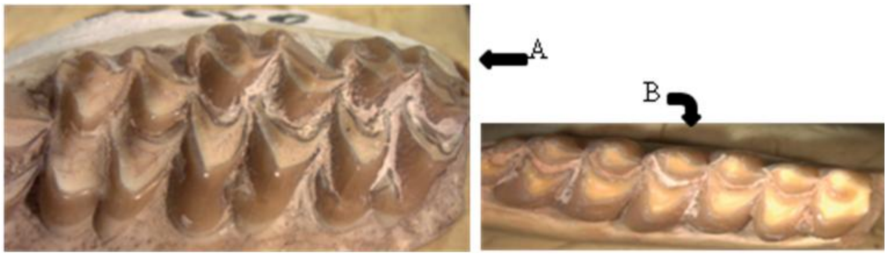

Figure 15. Adult *Leptomeryx*. A: upper dentition (UCM 52288); B: lower dentition UCM (20947).

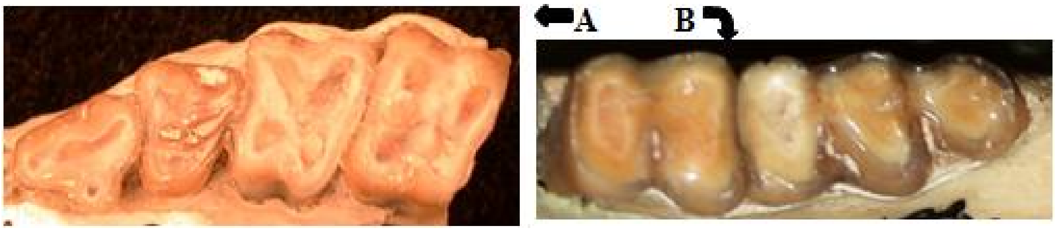

Figure 16. Senior *Leptomeryx*. A: upper dentition (UCM 36015); B: lower dentition (UCM 20781), noticed on both pictures the teeth are worn flat.

2. *Methods for Estimating Body Mass*

Weight-bearing, postcranial bones generally give more accurate body mass estimates than teeth (Damuth and MacFadden 1990), which may undergo selection for differences in function/dietary type and digestive physiology (Damuth 1990; Janis 1990). Teeth are, however, directly related to food processing and therefore indirectly related to metabolic rate and body mass (Fortelius 1990). Also, with morphologically similar, closely related species, precise relative sizes can be determined regardless of the imprecision of the absolute body mass estimates (Fortelius 1990). Since I am interested in only relative changes and not absolute changes, the use of teeth, which are more abundant, diagnostic, and hence more likely to be identifiable to genus and species level (Damuth 1990), is appropriate.

Within the tooth row, the second molar (M2/m2) was used in this study in preference to the first and third molar because of its high correlation to body mass (Janis 1990; Fortelius 1990; Alroy 2008). The m2 was chosen over the M2 following Alroy (2008). Length was chosen over width and area because width has a strong dietary component to it that length does not have, and width is more affected by age and wear than is length (Damuth 1990; Fortelius 1990). I tried to use equations derived from morphologically similar and closely related extant mammals. *Leptomeryx* has no living descendents, so I used a general selenodont browser equation from Damuth (1990) to estimate its body mass from the measurements of m2 length ($\log_{10} body\ mass\ (g) = 3.41 \log_{10} m2\ length (mm) + 0.72$). I chose this equation because the regression equation using this variable has a high r^2 value (r^2= 0.94), the results produced similar estimates to other equations that used the same variable (Janis 1990) and to equations that use other variables (Damuth 1990), and because the m2 length has the largest sample size for *Leptomeryx*. For the Rhinocerotinae, the two equations for estimating body mass based on m2 length from Damuth (1990) and Janis

(1990) did not produce similar estimates with each other or with other body mass estimates based upon other dental variables from Damuth (1990), Janis (1990) and Fortelius (1990). For completeness, both are calculated and compared here. Damuth's (1990) equation ($\log_{10} body\ mass(kg) = 3.010 \log_{10} \frac{m2\ length(mm)}{10} + 1.216$) is general for nonselenodonts (r^2=0.97), while Janis's (1990) equation ($\log_{10} body\ mass\ (g) = 2.98 \log_{10} m2\ length\ (mm) + 1.11$) is for perissodactyls plus hyracoids (r^2=0.986). I converted all body mass estimates to kilograms.

3. Statistical Methods

All statistical hypotheses were computed using the free online software program P.A.S.T. (PAlaeontological STatistics[2]; Hammer et al. 2009); univariate statistics were computed using JMP 8.

For my statistical analysis, I used two non-parametric tests due to small sample size (N<30) and because not all of my sample populations fit normal curves (Davis 2002; Hammer et al. 2009). The Mann-Whitney U test compares the medians of two sample populations with the null hypothesis of equivalence, in this case the medians between the Chadronian population and the Orellan population for the same variable (e.g. m2 length). This test is valid for samples sets of any distribution, but is not valid for sample sets smaller than seven individuals ($N < 7$) (Davis 2002; Hammer et al. 2009). The Kolmogorov-Smirnov test compares the distributions of two sample populations, but unlike the Mann-Whitney U test, the Kolmogorov-Smirnov test can be used for samples of any size (Davis 2002; Hammer et al. 2009), although I did not run the test if a

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[2] http://folk.uio.no/ohammer/past/

sample size included fewer than three specimens. A total of 446 *Leptomeryx* and 205 Rhinocerotinae specimens were measured, although due to incompleteness of many specimens, not all could be used in every statistical analysis. The sample size for each analysis is listed in the appropriate table (Tables 2-11). Even though the upper and lower post-canine tooth row and the left upper molar row of *Leptomeryx* were measured, the sample sizes ($N_C \leq 2$) were too small to be included in the statistical analysis. However, these measurements are included in Appendix 1 for the sake of completeness and in the hopes that future researchers may find them useful. All significance levels are at the 95% confidence interval (CI), unless otherwise stated.

Since I am using non-parametric, rank-based statistical tests, all p-values based upon body mass estimates will be the same as the p-values based upon the actual measurements of the teeth. Therefore, only p-values for the dental measurements are given. Results for body mass are given in kilograms with two standard deviations.

III. Results

1. *Leptomeryx*

To increase the sample size for *Leptomeryx*, I used a combined dataset of both the right and left jaws. If both sides of the jaw were preserved from the same individual, I used measurements from only the left side to prevent replication in the datasets. I chose the left side because I have more measurements of individuals with just the left jaw preserved. Prior to combining the samples, I tested for significant differences in size between the medians of the right and left sides. Results presented in Table 1 verify that there are no significant size differences between teeth from the left and right side within the Chadronian and Orellan datasets.

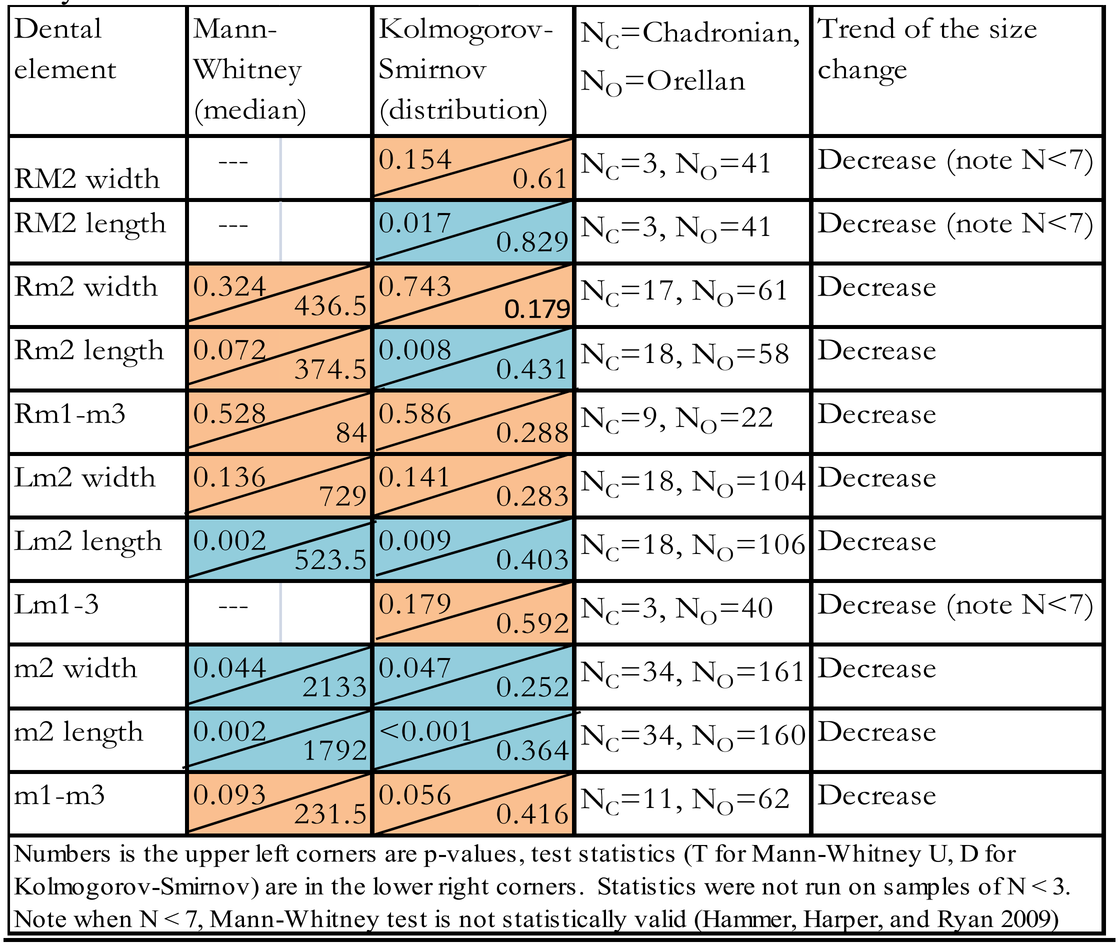
Table 1: Comparison of the right and left sides of the skull and jaws in all *Leptomeryx* used in this study

NALMA	M2 width	M2 length	M1-3 length	m2 width	m2 length	m1-3 length
Chadronian	p=0.7593 T=83 N_R=20, N_L=9	p=0.3384 T=76.5 N_R=22, N_L=9	p=0.1147 D=0.8333 N_R=6, N_L=2	p=0.7732 T= 585.5 N_R=33, N_L=37	p=0.9779 T=660 N_R=34, N_L=39	p=0.9755 D=0.2308 N_R=13, N_L=5
Orellan	p=0.6149 T=1367 N_R=46, N_L=63	p=0.2197 T=1180 N_R=45, N_L=61	p=0.1614 T=353 N_R=28, N_L=32	p=0.8234 T=6698 N_R=94, N_L=145	p=0.6526 T=6662 N_R=92, N_L=150	p=0.3334 T=515 N_R=26, N_L=46

All p-values based upon Mann-Whitney U comparison of median test except for N < 7 samples (upper and lower molar row of the Chadronian specimens), where the Kolmogorov-Smirnov comparison of distributions test was used. T is the test statistic for the Mann-Whitney U test; D is the test statistic for the Kolmogorov – Smirnov test.

Each of the two lineages of *Leptomeryx* were analyzed separately to test the intraspecific variation of Bergmann's Rule in *Leptomeryx*. Table 2 shows the results for the *L. speciosus* – *L. evansi* lineage; Table 3 shows the results for the *L. mammifer* – *exilis* lineage.

Table 2: Statistical analysis of dental elements of *L. speciosus – L. evansi* used in this study



Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
RM2 width	---	0.154 0.61	N_C=3, N_O=41	Decrease (note N<7)
RM2 length	---	0.017 0.829	N_C=3, N_O=41	Decrease (note N<7)
Rm2 width	0.324 436.5	0.743 0.179	N_C=17, N_O=61	Decrease
Rm2 length	0.072 374.5	0.008 0.431	N_C=18, N_O=58	Decrease
Rm1-m3	0.528 84	0.586 0.288	N_C=9, N_O=22	Decrease
Lm2 width	0.136 729	0.141 0.283	N_C=18, N_O=104	Decrease
Lm2 length	0.002 523.5	0.009 0.403	N_C=18, N_O=106	Decrease
Lm1-3	---	0.179 0.592	N_C=3, N_O=40	Decrease (note N<7)
m2 width	0.044 2133	0.047 0.252	N_C=34, N_O=161	Decrease
m2 length	0.002 1792	<0.001 0.364	N_C=34, N_O=160	Decrease
m1-m3	0.093 231.5	0.056 0.416	N_C=11, N_O=62	Decrease

Numbers is the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Statistics were not run on samples of N < 3. Note when N < 7, Mann-Whitney test is not statistically valid (Hammer, Harper, and Ryan 2009)

Table 3: Statistical analysis of dental elements of *L. mammifer* – *L. exilis* lineage used in this study

Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
Rm2 width	---	0.152 0.152	$N_C=5$, $N_O=7$	Decrease (note N<7)
Rm2 length	---	0.010 0.857	$N_C=5$, $N_O=7$	Decrease (note N<7)
Lm2 width	---	0.188 0.523	$N_C=5$, $N_O=13$	Decrease (note N<7)
Lm2 length	---	0.003 0.857	$N_C=5$, $N_O=14$	Decrease (note N<7)
m2 width	0.099 62	0.021 0.550	$N_C=10$, $N_O=20$	Decrease
m2 length	<<0.001 18	<<0.001 0.86	$N_C=10$, $N_O=21$	Decrease

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Statistics were not run on samples of $N < 3$. Note for $N < 7$, Mann-Whitney test is not statistically valid (Hammer, Harper, and Ryan 2009).

In the *L. speciosus* – *L. evansi* lineage only eight variables (11 including the combined datasets) could be compared due to small sample size; these are: RM2 width and length, R and L2 width and length, R and Lm1-3 (Table 2). The length of the RM2 showed a significant difference in the distributions of the Chadronian and Orellan datasets, while the width of the same tooth did not. However, because the sample size for each Chadronian dataset is tiny (N=3), neither result is very conclusive. Further, combining the right and left sides of the upper dentition would only add a single data point to my Chadronian dataset bringing my sample size to four, which is still too small for a reliable statistical analysis. In the lower dentition, only the m2 length showed a significant difference, although there is a significant difference in the distribution of the Rm2 length but not the median. When the sample size is increased by combining the right and left sides, and using the lefts for individuals that preserved both sides, there is significant change in both the m2 width and length. The lower molar row does not show a significant difference at the 95% CI, but does at the 90% CI. All of the 11 results from dental measurements trend towards decreased size in the *L. speciosus – L. evansi* lineage across the Chadronian-Orellan boundary.

Only the m2 width and length could be analyzed from the *L. mammifer – exilis* lineage (Table 3). Separately, both the right and left side saw a significant change in the distribution of the length but not the width. Combined (i.e. both sides), there was a significant change in the length and distribution of the width, but not the median of the width at the 95% CI; there is significant change in the median of the width at the 90% CI. All of these comparisons have a small Chadronian sample size ($N \leq 10$), which may account for why there is only a significant change in length but not width for the *L. mammifer – L. exilis* lineage. This is also seen in the left m2 of the *L. speciosus – L. evansi* lineage, but not *Leptomeryx* as a whole.

A recent study suggests that the vegetation of Colorado from the Chadronian to the Orellan responded in the opposite fashion (grassland to woodlands) to the other White River areas (Hembree and Hasiotis 2007, see EOT chapter). Another recent paper (Zanazzi and Kohn 2008) suggests that *Leptomeryx*, as a genus, may have changed its diet in South Dakota, Nebraska, and Wyoming (no specimens in their study came from Colorado) Therefore, I analyzed the specimens from Colorado separately from the specimens from South Dakota, Nebraska, and Wyoming combined (Tables 4 and 5). Due to small sample size, I combined the two lineages and included specimens that could only be identified to genus level. The mixing of two lineages means I am not testing Bergmann's Rule with this analysis, but rather just looking at body size change in *Leptomeryx* in two areas with difference vegetation changes. For Colorado specimens, only the left m2 width and length and the combined m2 width and length datasets are compared due to small sample size (Table 4). All four comparisons show significant differences between the Colorado Chadronian dataset and the Colorado Orellan dataset, reflecting a decrease in size. The non-Colorado dataset (South Dakota, Nebraska, and Wyoming) also shows a statistically significant change in size in those four variables, as well as in six other variables: RM2 width, Rm2 width and length, and the combined datasets variables M2 width and length, and m1-m3 (Table 5). All of the variables trended towards a size decrease including RM2 length, RM1-M3, LM2 width and length, Rm1-m3, Lm1-m3, and the combined dataset variable M1-M3, which were not statistically significantly different.

Table 4: Statistical analysis of dental elements of Colorado *Leptomeryx* used in this study

Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
Lm2 width	0.019 64	0.025 0.025	$N_C=14$, $N_O=18$	Decrease
Lm2 length	0.001 38	<0.001 0.680	$N_C=14$, $N_O=19$	Decrease
m2 width	0.021 134.5	0.037 0.037	$N_C=16$, $N_O=29$	Decrease
m2 length	<0.001 69	<0.001 0.650	$N_C=16$, $N_O=30$	Decrease

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Statistical analyses were not run on samples of N < 3.

Table 5: Statistical analysis of dental elements of non-Colorado *Leptomeryx* used in this study

Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
RM2 width	0.037 249.5	0.041 0.38	N_C=17, N_O=45	Decrease
RM2 length	0.084 302	0.468 0.224	N_C=19, N_O=44	Decrease
RM1-M3	---	0.482 0.352	N_C=6, N_O=27	Decrease (note N < 7)
LM2 width	0.234 186	0.227 0.269	N_C=8, N_O=63	Decrease
LM2 length	0.771 228	0.966 0.176	N_C=8, N_O=61	Decrease
Rm2 width	0.023 916	0.025 0.303	N_C=31, N_O=82	Decrease
Rm2 length	<0.001 601.5	<0.001 0.45	N_C=32, N_O=80	Decrease
Rm1-m3	0.112 96	0.197 0.357	N_C=13, N_O=22	Decrease
Lm2 width	0.002 880	0.013 0.349	N_C=23, N_O=128	Decrease
Lm2 length	<0.001 830.5	0.001 0.416	N_C=25, N_O=132	Decrease
Lm1-3	---	0.278 0.476	N_C=4, N_O=41	Decrease (note N < 7)
M2 width	0.004 789.5	0.005 0.373	N_C=25, N_O=101	Decrease
M2 length	0.029 948	0.113 0.253	N_C=27, N_O=97	Decrease
M1-M3	0.097 113	0.105 0.458	N_C=7, N_O=53	Decrease
m2 width	<<0.001 3441	0.001 0.306	N_C=52, N=206	Decrease
m2 length	<<0.001 2892	<<0.001 0.403	N_C=55, N=208	Decrease
m1-m3	0.015 328	0.008 0.434	N_C=17, N=63	Decrease

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Statistics were not run on samples of N < 3. Note when N < 7, Mann-Whitney test is not statistically valid (Hammer, Harper, and Ryan 2009).

I also separately ran the adult specimens to determine if the age and wear of the specimen would bias my results. This analysis included both of the lineages combined and the results are located in Appendix 1. I did not perform a statistical analysis of only the adolescents or seniors due to the small Chadronian sample size for both (largest Chadronian sample size for adolescents, (N=4, for seniors N=3), but my adult results show that age and wear did not bias my analyses.

Figure 17 shows box plots of the body mass estimates of the genus *Leptomeryx* and Table 6 shows a numerical comparison of the univariate statistics of the body mass of *Leptomeryx* estimated using m2 length and the following equation (Damuth 1990):

$$\log_{10} body\ mass\ (g) = 3.41 \log_{10} m2\ length(mm) + 0.72$$

Once again, when specimens had both left and right jaws or maxillae preserved, m2 measurements from the left jaw were chosen in preference to the right. As shown, the high maximum values for the right Chadronian and left Orellan samples are due to outliers that fall at and beyond, respectfully, the 99% CI. Based upon the combined Chadronian dataset, the average mass of Chadronian individuals of *Leptomeryx* is 4.09 kg ± 2.15 kg. In contrast, the average mass in kilograms based upon the combined Orellan dataset of m2 length is 3.14 kg ± 1.61 kg. These values are slightly higher than the 2.5 kg reported by Zanazzi and Kohn (2008), but these authors estimated the body mass of *Leptomeryx* using that reported by Janis (1982) for the contemporaneous hornless artiodactyl *Hypertragulus*. However, the body mass estimates that I calculated for *Leptomeryx* are similar to those of *L. evansi* reported by Damuth (1990). In comparing my body mass estimates for Chadronian and Orellan *Leptomeryx*, there was a 23% decrease in mean body mass (approximately one kilogram) across the EOT, although the ranges still overlap.

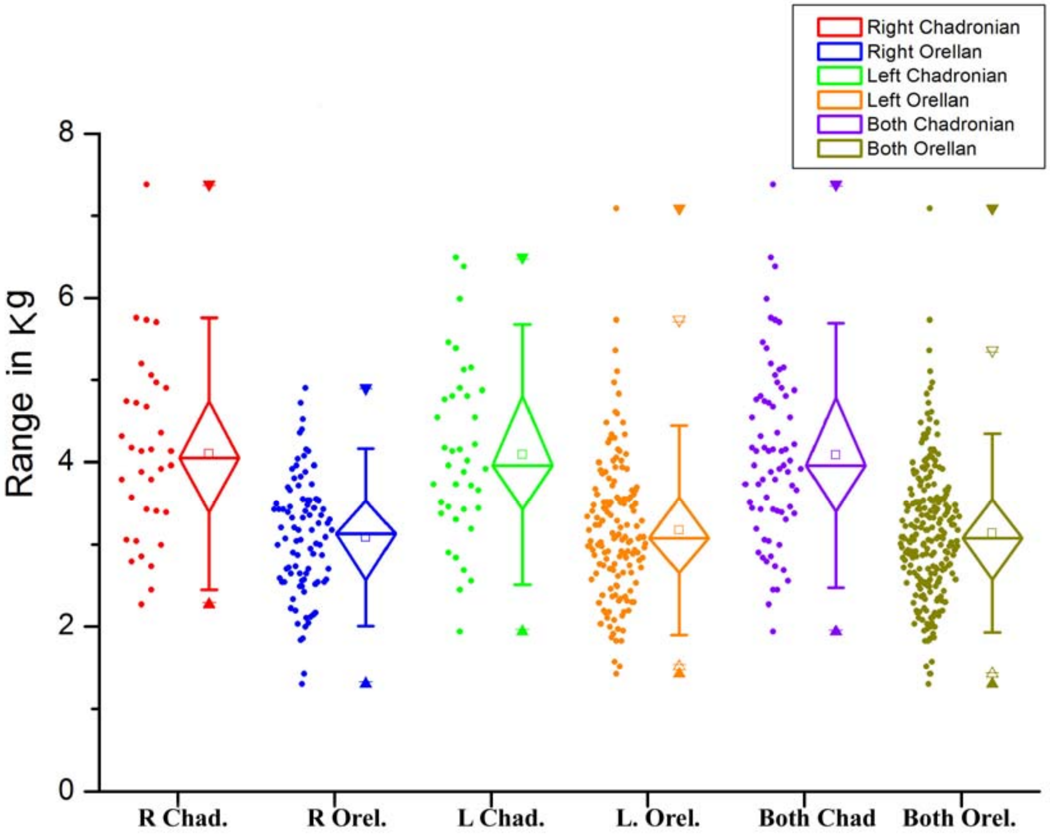


Figure 17. Diamond box and dot plot of *Leptomeryx* body mass estimates (in kilograms) based upon m2 length measurements. The dot plots show the distribution of the data points. The ends of the whiskers on the diamond box plots are 1.5 standard deviations away from the mean (the hollow box in the diamond). The diamonds' endpoints are at the 25th and 75th percentile and the horizontal line inside the diamond is the median. The solid triangles above and below the box plot show the minimum and maximum values, while the hollow triangles with a line through them show the 99% and 1% confidence intervals. Figure made with OriginPro8.

Table 6: Univariate body mass estimates of *Leptomeryx* based on m2 length

Univariate Statistic	Rm2 length Chadronian	Rm2 length Orellan	Lm2 length Chadronian	Lm2 length Orellan	Both sides m2 length Chadronian	Both sides m2 length Orellan
N	34	92	39	150	72	238
Minimum	2.27	1.30	1.94	1.42	1.94	1.30
Maximum	7.38	4.90	6.49	7.09	7.38	7.09
Mean	4.10	3.09	4.09	3.17	4.09	3.14
Std. error	0.19	0.07	0.17	0.07	0.13	0.05
Variance	1.22	0.52	1.12	0.72	1.16	0.65
Std. dev.	1.10	0.72	1.06	0.85	1.07	0.81
Median	4.05	3.13	3.96	3.08	3.96	3.08
25 percentile	3.31	2.56	3.43	2.65	3.39	2.57
75 percentile	4.78	3.53	4.81	3.58	4.80	3.55
$\log_{10} \mathit{body\ mass}\ (g) = 3.41 \log_{10} \mathit{m2\ length} + 0.72$ (Damuth 1990) all mass values have been converted to kg						

2. *Rhinocerotinae*

I am considering the subfamily Rhinocerotinae a lineage in the broadest sense. Fragmentary fossils (such as when only the cheek teeth are preserved) preclude identification to the genus level for many specimens. Also, the two genera of the subfamily that I use here did have a common ancestor. However, due to the mixing of two genera, this may not be an accurate test of Bergmann's Rule (more on this in Discussions).

Similar to both lineages of *Leptomeryx*, the Rhinocerotinae show a trend towards decreasing size (see Table 7). The change was statistically significant in 10 of the 16 variables that I measured, which are: RM2 and LM2 and m2 width and length, RM1-3 and LM1-3. Differences between Chadronian and Orellan rhinocerotines in length of the right and left upper post-canine tooth row (P1-M3) as well as the right and left lower molar row were not statistically significant, but did show a trend towards a decrease.

Sample size (N<7) for length of the lower post-canine tooth row was small, precluding use of the Mann-Whitney U test. However, the distributions (Kolmogorov-Smirnov test) of the Chadronian and Orellan lower post-canine tooth row datasets were not significantly different, but they did trend towards an increase in size. This result contrasts the other results, but must be treated with caution given the small Orellan sample size (N =3 for both right and left). I did not combine the right and left sides of the Rhinocerotinae because most of the individuals measured included both right and left jaws. Therefore, inclusion of both right and left sides would effectively double the same size, but would represent only half the number of individuals.

Table 7: Statistical analysis of dental elements of all Rhinocerotinae used in this study

Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
RM2 width	0.002 199	<0.001 0.618	$N_C=55$, $N_O=15$	Decrease
RM2 length	0.006 221	<0.001 0.576	$N_C=55$, $N_O=15$	Decrease
RM1-M3	0.020 107	0.006 0.545	$N_C=33$, $N_O=12$	Decrease
RP1-M3	0.855 105	0.916 0.200	$N_C=22$, $N_O=10$	Decrease
LM2 width	<0.001 141	<0.001 0.621	$N_C=53$, $N_O=15$	Decrease
LM2 length	0.008 205.5	0.005 0.492	$N_C=55$, $N_O=14$	Decrease
LM1-M3	0.002 0.636	0.001 0.636	$N_C=33$, $N_O=11$	Decrease
LP1-M3	0.560 113	0.285 0.346	$N_C=26$, $N_O=10$	Decrease
Rm2 width	0.002 419	0.017 0.017	$N_C=82$, $N_O=19$	Decrease
Rm2 length	0.026 555.5	0.015 0.382	$N_C=87$, $N_O=19$	Decrease
Rm1-m3	0.333 272	0.529 0.225	$N_C=47$, $N_O=14$	Decrease
Rp1-m3	---	0.759 0.381	$N_C=14$, $N_O=3$	Increase (note N<7)
Lm2 width	<0.001 305.5	<<0.001 0.577	$N_C=78$, $N_O=18$	Decrease
Lm2 length	0.005 439.5	0.011 0.403	$N_C=85$, $N_O=18$	Decrease
Lm1-3	0.483 289	0.530 0.240	$N_C=51$, $N_O=13$	Decrease
Lp1-m3	---	0.824 0.360	$N_C=13$, $N_O=3$	Increase (note N<7)

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Statistical analyses were not run on samples of N < 3. Note of N < 7, Mann-Whitney test is not statically valid (Hammer, Harper, and Ryan 2009).

As mentioned above, a recent study suggests that Colorado had a different vegetation change across the EOT than in other states (Hembree and Hasiotis 2007); therefore, I ran the data excluding the Colorado specimens (Table 8). I was not able to run just the Colorado samples because there was only one Orellan specimen from Colorado. In order to attain a sample size of seven, I combined right and left jaws, giving preferential treatment to the left side for individuals that preserved both. Only the m2 had enough data points to make a comparison. Neither the width nor the length showed a statistically significant change in distribution; the median could only be compared in the m2 width sample and showed no statistically significant change; there is, however, a trend towards an increase in size.

Table 8: Statistical analysis of dental elements of non-Colorado Rhinocerotinae used in this study

Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
m2 width	0.162 51.5	0.137 0.466	N_C=7, N_O=23	Increase
m2 length	---	0.627 0.319	N_C=6, N_O=23	Increase (note N<7)

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners.. Note of N < 7, Mann-Whitney test is not statically valid (Hammer, Harper, and Ryan 2009).

When only adult specimens were compared, all of the p-values increased from all of the Rhinocerotinae comparisons (Table 7), except for the left lower molar row and post-canine tooth row which had lower p-values that their counterparts in all of the Rhinocerotinae statistical analysis, although they were still not statistically significant (Table 9). The increase in p-values leaves only the width of all of the second molars as statistically significant at the 95% CI, although the lower left second molar length and the upper molar row lengths are statistically significant at the 90% CI. The adolescents and seniors were not analyzed by themselves due to the absence of Orellan seniors and small sample size or Orellan adolescents (N=5).

Table 9: Statistical analysis of dental elements of all adult Rhinocerotinae used in this study

Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N=Orellan	Trend of the size change
RM2 width	0.009 37	0.001 0.703	N_C=13, N=14	Decrease
RM2 length	0.182 63	0.062 0.478	N_C=14, N=13	Decrease
RM1-M3	0.091 38	0.083 0.492	N_C=11, N=12	Decrease
RP1-M3	0.838 42	0.980 0.200	N_C=9, N=10	Decrease
LM2 width	0.008 32	0.002 0.692	N_C=13, N=13	Decrease
LM2 length	0.115 58	0.048 0.495	N_C=14, N=13	Decrease
LM1-M3	0.081 33	0.028 0.583	N_C=12, N=10	Decrease
LP1-M3	0.804 50	0.525 0.333	N_C=12, N=9	Decrease
Rm2 width	0.036 127	0.054 0.414	N_C=30, N=14	Decrease
Rm2 length	0.121 159	0.039 0.429	N_C=32, N=14	Decrease
Rm1-m3	0.348 148	0.474 0.269	N_C=28, N=13	Decrease
Rp1-m3	---	0.826 0.367	N_C=10, N=3	Increase (note N<7)
Lm2 width	0.002 104	<0.001 0.613	N_C=32, N=15	Decrease
Lm2 length	0.065 170	0.132 0.345	N_C=34, N=15	Decrease
Lm1-3	0.177 131	0.155 0.367	N_C=30, N=12	Decrease
Lp1-m3	---	0.534 0.500	N_C=6, N=3	Increase (note N<7)

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Note of N < 7, Mann-Whitney test is not statically valid (Hammer, Harper, and Ryan 2009).

Unlike the subfamily Rhinocerotinae, which may not be testing Bergmann's Rule, the genus *Subhyracodon* is a valid test of the intraspecific variation of Bergmann's Rule. After combining the right and left sides, giving preferential treatment to the left side, there were enough data points of m2 width and length to test the genus *Subhyracodon* by itself (Table 10). Similar to specimens outside of Colorado, there was no statistically significant change in distribution across the EOT; the median could only be compared in the m2 width sample and showed no statistically significant change. Although the change is not statistically significant, once again the measurements trend towards an increase in body size across the EOT.

Table 10: Statistical analysis of dental elements of *Subhyracodon* used in this study

Dental element	Mann-Whitney (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
m2 width	0.353 55.5	0.344 0.381	N_C=7, N_O=21	Increase
m2 length	---	0.767 0.286	N_C=6, N_O=21	Increase (note N<7)

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Note of N < 7, Mann-Whitney test is not statically valid (Hammer, Harper, and Ryan 2009).

Body mass of the subfamily Rhinocerotinae was estimated from the right m2, due to its slightly larger sample size over the left side (see Table 7 for sample sizes). Because there are differences in body mass estimates depending on whether you use the equation of Janis (1990) or that of Damuth (1990), and because estimates are unreliable for rhinocerotids (Fortelius 1990), I report estimated body masses calculated from both Janis (1990) and Damuth (1990) (Figure 18 and Table 11). The equation from Janis (1990) is:

$$\log_{10} body\ mass(kg) = 3.010\log_{10}\frac{m2\ length(mm)}{10} + 1.216$$

Whereas the equation from Damuth (1990) is:

$$\log_{10} body\ mass\ (g) = 2.98\log_{10} m2\ length\ (mm) + 1.11$$

Using the equation from Janis (1990), the estimated average body mass of Rhinocerotinae (including *Subhyracodon*, *Trigonias* and Rhinocerotinae indet.) based upon my Chadronian dataset is 834.41 kg, and for the Orellan rhinos, the mean body mass is 724.16 kg. In comparison, the equation from Damuth (1990) gives a mean mass estimate of 600.13 kg for the Chadronian rhinocerotines and for the Orellan, the mean body mass is 521.59 kg. There is a body mass decrease of about 13% regardless of whose equation is used (110.25 kg using Damuth, 1990, *versus* 78.54 kg using Janis 1990). These mean body mass results are much higher than values given by Zanazzi and Kohn (2008) for *Trigonias* and *Subhyracodon* (250 kg for both). However, these authors took their body mass values from Janis (1982) who listed the now invalid taxon *Caenopus* (see chapter Taxa Studied: Rhinocerotinae) as 250kg, but unfortunately did not include her calculations of body mass. Even with the decrease in body mass among rhinocerotines across the EOT, the range recorded by the Orellan specimens falls within the range of the Chadronian dataset, as can be seen in Figure 18.

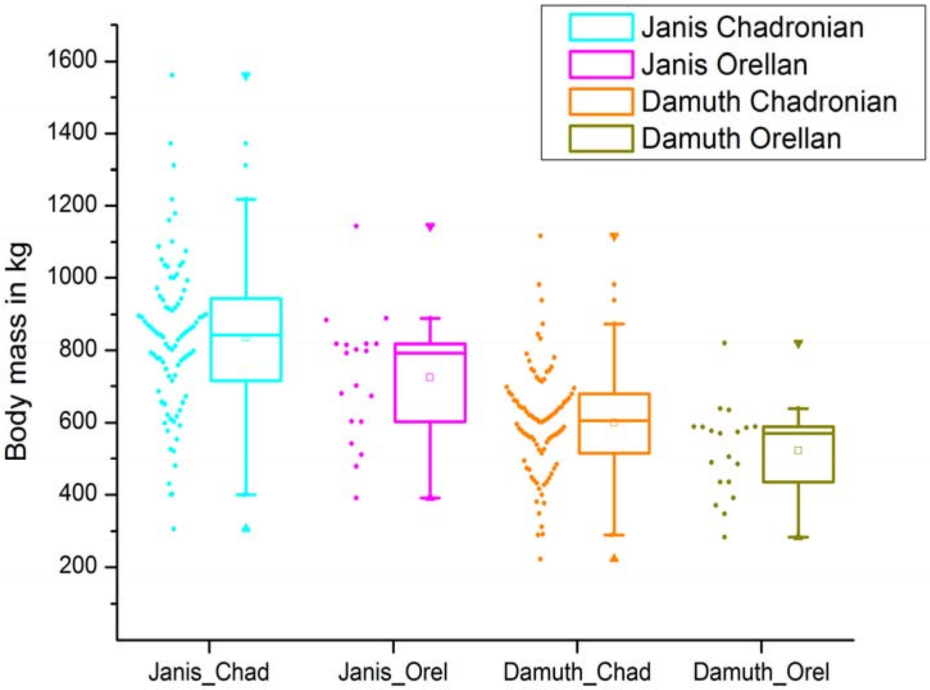


Figure 18. Box and dot plot of Rhinocerotinae body mass estimates (in kilograms) based upon equations from Janis (1990) and Damuth (1990) that utilize m2 length measurements. The dot plots show the distribution of the data points. The ends of the whiskers on the box plots are 1.5 standard deviations away from the mean (the hollow box inside the square). The squares' endpoints are at the 25th and 75th percentile and the horizontal line inside the square is the median. The solid triangles above and below the box plot show the minimum and maximum values as well as the 1% and 99% confidence intervals. Figure made using OriginPro8.

Table 11: Univariate body mass estimates of Rhinocerotinae based on right m2 length

Univariate Statistic	Chadronian (Janis)	Orellan (Janis)	Chadronian (Damuth)	Orellan (Damuth)
N	87	19	87	19
Minimum	306.56	390.79	222.77	283.29
Maximum	1561.17	1143.52	1116.20	820.13
Mean	834.41	724.16	600.13	521.59
Std. error	22.89	40.59	16.31	28.96
Variance	45597.11	31307.00	23134.39	15931.74
Std. dev.	213.53	176.94	152.10	126.22
Median	842.52	792.13	606.10	570.20
25 percentile	715.14	602.96	515.30	435.21
75 percentile	944.45	818.07	678.65	588.68

All body mass estimates calculated using the right m2 length and converted in kg.

Equation from Janis (1990):

$$\log_{10} body\ mass(kg) = 3.010\log_{10}\frac{m2\ length(mm)}{10} + 1.216$$

Equation from Damuth (1990):

$$\log_{10} body\ mass\ (g) = 2.98\log_{10} m2\ length\ (mm) + 1.11$$

IV. Discussion and Conclusions

Based upon the dramatic decrease in mean annual temperatures (MAT) reported for the EOT by Zanazzi et al. (2007), I predicted that both species-lineages of *Leptomeryx* and members of the Rhinocerotinae would increase in body size across the EOT. This prediction follows from Bergmann's Rule, which states that an increase in body size will occur within a mammalian lineage as temperatures become cooler. However, in measuring 446 *Leptomeryx* and 205 rhinocerotine (including *Subhyracodon*, *Trigonias,* and Rhinocerotinae gen. indet.) specimens from both sides of the EOT, my study does not support Bergmann's Rule for the small artiodactyl *Leptomeryx* (at the lineage or generic level), nor does the study support Bergmann's Rule for the subfamily Rhinocerotinae. The m2 length and width of the rhinocerotine genus *Subhyracodon* does show a statistically non-significant trend towards an increase in body size across the EOT, but the sample size was small (N=7 for Chadronian m2 width and N=6 for Chadronian m2 length). My results for *Leptomeryx* agree with Heaton and Emry (1996) as well as Korth and Diamond (2001), both of whom stated that the Orellan species of *Leptomeryx* were relatively smaller than their Chadronian predecessors were, although neither study quantified this size difference. My study builds upon these earlier works by quantifying the size change in the genus as a whole; the Orellan species of *Leptomeryx* were on average approximately 23% smaller than their Chadronian predecessors.

It is difficult to test Bergmann's Rule in the strict sense in the paleontological record due to the uncertainty of the relationships among fossils species. Whereas in the modern record it can be easy to tell two rhinocerotine genera from each other, it can be very difficult in the fossil record. Species in the paleontological sense are morphologic species, meaning there is some difference in morphology, while biological species are defined as an interbreeding population able to produce viable offspring (Queiroz 2007). It is impossible to know if two morphologic species, such as *L. speciosus* and *L.mammifer*, are two biologic species. It is also difficult to know the gender of the fossil which can cause problems in species that are sexual dimorphic. Another problem with looking at Bergmann's Rule in the paleontological record is that sample sizes are smaller than in modern biological studies.

The statistically significant decrease in body size in Rhinocerotinae for some dental measurements may not be accurately testing Bergmann's Rule and are biased. As mentioned earlier in the section on Bergmann's Rule, there is no reason to expect different animals to respond to climate change in the same way. By mixing two closely related, but different genera I could be obscuring the actual changes that occurred in either genus. This is probably the case with *Trigonias* going extinct at the end of the Chadronian and *Subhyracodon* surviving into the Orellan. Therefore, my results for the subfamily Rhinocerotinae may be an artifact of extinction. According to Prothero (2005), *Trigonias* was a small to medium-sized rhinocerotid, while *Subhyracodon* was small-sized, although the size ranges overlap for most dental variables. The extinction of the larger-bodied *Trigonias* at the Chadronian-Orellan boundary could explain why we see a decrease in body size in rhinocerotines in Orellan time (hypothesized explanations for the extinction of *Trigonias* at the EOT are discussed below). In contrast, *Subhyracodon* does not show a statistically significant change in body size (inferred from dental measurements), although the sample size is small (N_C=7, N_O=21). This is the only unbiased assessment of Bergmann's Rule for rhinocerotines because it is a single lineage crossing the EOT. Although two species of *Subhyracodon* have been found in my study area, due to the size ranges I believe all of my specimens to be from one species.

This study merely tests the validity of Bergmann's Rule for the two species-lineages of *Leptomeryx*, the subfamily Rhinocerotinae, and the genus *Subhyracodon* during the EOT; these results cannot be used in invalidate Bergmann's Rule as a whole. In light of my results that do not demonstrate Bergmann's Rule within these two taxa during the EOT, alternative explanations for the trend towards decreasing body size must be considered. For instance, minimum January temperature or maximum July temperature may be correlated to body size changes instead of MAT (Rensch 1939, as translated in Mayr 1956; Yom-Tov and Geffen 2006). Other factors that may have affected the body size of *Leptomeryx* and rhinocerotines include changes in precipitation and other shifts in the environment that can alter the vegetation and ecosystems. It is important to note that the environment consists of many factors, and therefore one environmental variable such as MAT may not be the only cause for a change in body size, but it may still be an important factor.

The particular temperature variable used can also influence the likelihood of an organism to follow Bergmann's Rule. As mentioned in the chapter on Bergmann's Rule, Bergmann (1847) did not state which temperature to which he was referring (e.g., MAT *versus* maximum summer *versus* minimum winter, etc.), although some subsequent studies use the MAT (e.g. Rodriguez et al. 2008; Brown and Lee 1968; Smith et al. 1995), which I have done as well. Body size clines may follow other temperature variables, such as minimum winter and maximum summer, but this remains to be shown for the Eocene – Oligocene transition.

Precipitation and humidity directly affect annual food productivity pulse, which, in turn, affects body size in herbivorous mammals (Geist 1987; Gingerich 2003). Yom-Tov and Geffen (2006), Blackburn and Hawkins (2004), and Burnett (1983) found precipitation to be positively correlated with body size. As concluded by Retallack (1986, 1992), Hutchison (1992), Sheldon and Retallack (2004), and Hembree and Hasiotis (2007), there is evidence for a decrease in precipitation across the Chadronian – Orellan boundary which may explain the change in vegetation from woodland to grassland that has been hypothesized for my study area (Evanoff et al. 1992; Retallack 1986, 1992; Terry 2001). Therefore, it is possible this decrease in body size in *Leptomeryx* and the subfamily Rhinocerotinae is correlated to the decrease in precipitation. Isotope analyses suggest that *Leptomeryx* changed its habitat preference from woodlands to grasslands, and possibly started to incorporate more C_4 plants (Zanazzi and Kohn 2008), thereby decreasing their nutritional intake (Barbehenn et al. 2004). Because body size is partly dependant on access to quality food (Geist 1987; Gingerich 2003), the decrease in body mass of *Leptomeryx* may be due to a decrease in nutritional intake as a result of feeding on C_4 plants. It is interesting to note though that despite ecological differences between Colorado and the rest of the Great Plains (Hembree and Hasiotis 2007) under analysis, statistical trends in body size change of the Colorado *Leptomeryx* parallel the trend observed in the South Dakota, Nebraska, and Wyoming dataset, and when the datasets from all four states are analyzed. *Leptomeryx* from all areas trend towards decreased body size across the Chadronian–Orellan (Eocene–Oligocene) boundary.

In contrast, *Subhyracodon*, for which there is no isotopic evidence for changing habitat or feeding preference (Zanazzi and Kohn 2008), did not show a significant change in body size. The rhinocerotine *Trigonias*, hypothesized as semi-aquatic based upon short stocky limb bones and fossil occurrence in fluvial sediments (Clark et al. 1967), went extinct at the E–O boundary (Prothero 2005), which may be the result of habitat loss (i.e., moist woodlands or forests). This hypothesis has also been suggested for the extinction of the large brontothere *Brontops* (Zanzaai and Kohn 2008).

As mentioned above (see Taxa Studied section), the occlusal enamel of *Leptomeryx* increased over the EOT (Mathis 2008), which could correspond to a change in diet. It is reasonable to suggest that *Leptomeryx* and the rhinocerotines may have adapted to the changing environment with morphologic changes more so than body size change. Using the evolution of horses in North America as a parallel (MacFadden, 1992), I would expect to see an increase in tooth crown height (more hypsodont dentition) and longer, more slender limbs with fewer toes in both *Leptomeryx* and rhinocerotines with a change from a relatively closed woodland habitat to more open grassland environment. We do see the extinction of the more primitive, 5-toed *Trigonias* while the not quite so primitive 3-toed *Subhyracodon* survived the EOT.

Geist (1987) hypothesized that for smaller mammals an increase in fur length or density is more energy efficient to stay warm than an increase in body size. Using a different model, Steudel et al. (1994) found that small animals have little leeway for changing fur length or density. It is possible that *Leptomeryx* compensated for the decrease in temperature by increasing the density or length of its fur, but unfortunately, this is not feasible to test in the paleontological record. Although mammalian body fossils of hair, fur, and skin impressions have been found at Jurassic (Ji et al. 2006) and

Cretaceous (Ji et al. 2002) aged localities, they are rare, and as far as I am aware, there are no fossils of hair for mammals crossing the EOT in North America.

Sexual dimorphism can obscure body size patterns and changes. If one sex if larger than the other sex, a difference in the proportion of males to females (such as just females on one side of the boundary and just males on the other side) could bias the results. However, I do not think that any of the groups I looked at are sexually dimorphic. None of my samples produced bimodal curves, which you would expect to see in a dimorphic population. Also, most rhinocerotine genera are known to not be sexually dimorphic (Prothero 2005).

1. *Future Research*

Future research areas include increasing the sample size of the rhinocerotine *Subhyracodon* in order to determine if the non-statistically significant trend of size increase is an artifact of small sample size. This will be made challenging by the observation that cheek teeth of *Subhyracodon* are very similar to those of *Trigonias*, and complete dentitions and skulls (with anterior teeth preserved) are necessary to distinguish these two genera. Further, a comprehensive review of Eocene and Oligocene rhinocerotines would need to be completed to differentiate specimens in other museum collections. Another area of future research is to use post-cranial material, especially weight-bearing elements such as femora and humeri, to estimate body mass, instead of the teeth. Finding a statistically valid sample size for the use of post-cranial material to test the intraspecific variation of Bergmann's Rule will be difficult; however, certain groups of mammals have a skeletal element or two that are diagnostic (i.e. complete limb bones) and could be used to test the intraspecific variation of Bergmann's Rule (Scott, 1990). In a different direction, future research should look at the climatic and environmental variables other than MAT to test whether they may be related to the decrease in body mass of *Leptomeryx* and the rhinocerotines.

As mentioned above, climatic and environmental changes at the EOT may be manifested in changes in dental and postcranial morphology more so than in body size evolution. Analyses of the tooth crown height can help to determine if the taxa changed their diet and add to those ecologic studies that are based upon isotopic analysis (e.g., Zanazzi and Kohn 2008). Analyses of the post-cranial elements can add to the body of literature on habitat preferences by providing insight into changes in locomotion.

This future research will help us to understand how mammals reacted to climatic and environmental changes in the past. Understanding the past is key to predicting the future. As such, understanding morphologic change (including body size) in mammalian taxa that span past intervals of climate change will help us to predict biotic changes in mammals due to climatic and environmental changes going on today.

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VI. Appendix 1.

Statistical analysis of dental elements of all adult *Leptomeryx* used in this study

Dental element	Mann-Whitney U (median)	Kolmogorov-Smirnov (distribution)	N_C=Chadronian, N_O=Orellan	Trend of the size change
RM2 width	0.074 243.5	0.081 0.35	$N_C=17$, $N_O=41$	Decrease
RM2 length	0.206 301.5	0.541 0.214	$N_C=19$, $N_O=40$	Decrease
RM1-M3	---	0.482 0.482	$N_C=6$, $N_O=27$	Decrease (note N<7)
LM2 width	0.163 178	0.241 0.241	$N_C=9$, $N_O=56$	Decrease
LM2 length	0.346 194.5	0.699 0.241	$N_C=9$, $N_O=54$	Decrease
Rm2 width	0.057 928	0.068 0.272	$N_C=29$, $N_O=84$	Decrease
Rm2 length	<0.001 605	<0.001 0.429	$N_C=30$, $N_O=82$	Decrease
Rm1-m3	0.212 111	0.390 0.3	$N_C=12$, $N_O=25$	Decrease
Lm2 width	0.015 1544	0.038 0.265	$N_C=34$, $N_O=125$	Decrease
Lm2 length	<<0.001 1128	<<0.001 0.449	$N_C=36$, $N_O=120$	Decrease
Lm1-3	---	0.033 0.683	$N_C=4$, $N_O=45$	Decrease (note N<7)
M2 width	0.005 745	0.003 0.386	$N_C=26$, $N_O=90$	Decrease
M2 length	0.029 871	0.147 0.241	$N_C=28$, $N_O=86$	Decrease
M1-M3	0.037 114	0.033 0.512	$N_C=8$, $N_O=53$	Decrease
m2 width	0.001 4549	0.003 0.255	$N_C=61$, $N_O=205$	Decrease
m2 length	<<0.001 3314	<<0.001 0.407	$N_C=64$, $N_O=208$	Decrease
m1-m3	0.008 321.5	0.007 0.449	$N_C=16$, $N_O=70$	Decrease

Numbers in the upper left corners are p-values, test statistics (T for Mann-Whitney U, D for Kolmogorov-Smirnov) are in the lower right corners. Statistical analyses were not run on samples of N < 3. Note when N < 7, Mann-Whitney test is not statistical

VII. Appendix 2.

***Table 1: Measurements of lower dentition* of Leptomeryx**

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
DMNS 10936		5.39	7.16							Chadronian	WY	adult
DMNS 10937		5.42	6.98							Chadronian	WY	adult
DMNS 11545				24.22						Chadronian	WY	adult
DMNS 12267	*evansi*					5.08	6.61			Oligocene	CO	adult
DMNS 12268		4.65	6.76							Oligocene	CO	adolescent
DMNS 12509	*speciosus*	5.05	7.09	22.55						Chadronian	WY	adult
DMNS 14170	*mammifer*					5.51	8.03			Chadronian	CO	adolescent
DMNS 17339		5.43	7.77							Chadronian	WY	adolescent
DMNS 17493	*evansi*					5.06	7.08			Chadronian	WY	adult
DMNS 17593	*evansi*	6.31	7.08	25.45						Chadronian	WY	senior
DMNS 23056		5.42	6.43							Chadronian	NE	adult
DMNS 23057						5.84	7.54			Chadronian	NE	adolescent
DMNS 23528	*speciosus*	5.83	7.18	23.31						Chadronian	WY	adult
DMNS 2422		5.81	7.56							Chadronian	WY	adult
DMNS 27694	*speciosus*					5.32	6.62			Chadronian	NE	adult
DMNS 27695	*speciosus*	5.24	6.47							Chadronian	NE	adult
DMNS 29224	*?elissae*					4.33	5.56			Orellan	CO	adult
DMNS 29230		4.07	5.17							Orellan	CO	adult
DMNS 30289	*elissae*					3.93	5.17	17.60		Oligocene	CO	adult
DMNS 34800	*speciosus*					5.51				Chadronian	CO	adult
DMNS 3757	*elissae*	5.25	6.63	21.83	37.28					Orellan	CO	adult
DMNS 41050		5.42	7.36	23.72						Chadronian	WY	adult
DMNS 41055		5.48	6.77	23.37						Chadronian	WY	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
DMNS 41056						5.62	7.09			Chadronian	WY	adult
DMNS 43205						5.42	6.96			Chadronian	CO	adult
DMNS 43836	*speciosus*					6.14	7.37			Chadronian	CO	adult
DMNS 45279						4.61	6.33			Chadronian	WY	adult
DMNS 45280						5.15	6.14			Chadronian	WY	adult
DMNS 45281	*speciosus*					5.04	6.55			Chadronian	CO	adult
DMNS 45283	*speciosus*					4.79	6.23			Chadronian	CO	adult
DMNS 45284	*speciosus*					5.26	6.71			Chadronian	CO	adult
DMNS 45341		5.21	5.93							Chadronian	WY	adult
DMNS 45342	*speciosus*	5.57	6.94							Chadronian	CO	adult
DMNS 47634							5.66			Chadronian	CO	adult
DMNS 5081						6.20	7.42	24.23		Chadronian	WY	adult
DMNS 5082		5.29	7.43			5.17	7.11	24.47		Chadronian	WY	adult
DMNS 5085						6.25	8.07			Chadronian	WY	adult
DMNS 661						5.88	6.86			Chadronian	NE	adult
DMNS 6746	*mammifer*	4.48	7.07							Chadronian	CO	adolescent
FMNH PM 14456	*speciosus*	4.80	6.06	21.13	38.83					Chadronian	SD	adult
FMNH PM 20765		5.47	7.46	24.57						Chadronian	SD	adult
FMNH PM 26252	*speciosus*					5.99	7.43			Chadronian	SD	adult
FMNH PM 44530		5.58	7.33	24.50						Chadronian	SD	adult
FMNH PM 49791		4.40	6.67	21.88						Chadronian	SD	adult
FMNH UM 1031	*evansi*					4.84	6.48	22.34	39.12	Orellan	NE	adult
FMNH UM 1032	*evansi*	5.13	6.94	23.19						Orellan	NE	adult
FMNH UM 1034	*evansi*	5.47	6.85	22.41						Orellan	NE	adult
FMNH UM 1035	*evansi*	5.49	6.24	22.19						Orellan	NE	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
FMNH UM 1036	*evansi*	5.49	6.54	22.26						Orellan	NE	adult
FMNH UM 1037	*evansi*	5.78	7.26	24.30						Orellan	NE	adult
FMNH UM 1038	*evansi*	5.37	6.68	22.49						Orellan	NE	adult
FMNH UM 1074	*evansi*					5.34	6.51	23.21		Orellan	NE	adult
FMNH UM 1076	*evansi*					5.17	6.76	22.18		Orellan	NE	adult
FMNH UM 1077	*exilis*					5.02	6.00	21.20		Orellan	NE	adult
FMNH UM 1079	*evansi*					5.22	6.23	21.74		Orellan	NE	adult
FMNH UM 943	*evansi*					5.41	6.88	22.80	39.32	Orellan	NE	adult
SDSMT 42801						5.30	6.37	21.86		Chadronian	SD	senior
SDSMT 75362	*speciosus*	5.22	6.30	22.33	38.27					Chadronian	SD	adult
UCM 101123	*evansi*					4.92	6.09			Oligocene	CO	adult
UCM 101399						5.56	6.61	23.08		Orellan	WY	adult
UCM 101428		5.87	6.84			5.91	7.05			Orellan	WY	adult
UCM 101435	*evansi*	5.47	6.49	21.45						Orellan	NE	adult
UCM 101437		5.31	6.69			5.14	6.82	22.10	39.13	Orellan	WY	adult
UCM 101814	*exilis*	5.21	7.08							Orellan	WY	adult
UCM 101815		5.28	6.96							Chadronian	WY	adult
UCM 101816						5.40	7.27			Chadronian	WY	adult
UCM 101889	*elissae*	4.80	6.20	20.28						Orellan	NE	adult
UCM 101890	*evansi*	5.48	6.56	22.27						Orellan	NE	adult
UCM 101907						4.64	5.94			Orellan	WY	adult
UCM 101908						5.40	6.41			Orellan	WY	adult
UCM 101909						5.20	6.44			Orellan	WY	adult
UCM 101910						5.38	6.64			Orellan	WY	adult
UCM 19854	*evansi*					4.93	5.82	19.00		Orellan	CO	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 19875	*elissae*					4.30	5.78			Orellan	CO	adult
UCM 20776						5.75	7.24			Orellan	CO	adult
UCM 20778						4.59	6.15			Orellan	CO	adult
UCM 20779						4.34	5.95			Orellan	CO	adult
UCM 20780							6.01			Orellan	CO	adult
UCM 20781						4.41	5.74			Orellan	CO	senior
UCM 20865		5.27	6.73							Orellan	CO	adult
UCM 20867	*evansi*					5.56	7.08	23.39		Orellan	CO	adult
UCM 20869		5.18	6.76							Orellan	CO	adult
UCM 20871		4.67	5.98							Orellan	CO	adult
UCM 20872	*evansi*					5.36	6.58			Orellan	CO	adult
UCM 20873	*evansi*	5.54	6.70	22.16						Orellan	CO	adult
UCM 20882		4.01	5.04							Orellan	CO	adult
UCM 20912	*elissae*					4.33	5.32			Orellan	CO	adult
UCM 20931						5.34	6.05			Orellan	CO	adult
UCM 20932	*evansi*					5.00	6.36	21.06		Orellan	CO	adult
UCM 20947	*exilis*	5.12	5.75	19.73						Orellan	CO	adult
UCM 20948	*exilis*					4.93	6.20	20.35		Orellan	CO	adult
UCM 21690	*evansi*	5.52	7.35							Orellan	SD	adult
UCM 21693	*evansi*						6.27			Orellan	SD	adult
UCM 21694	*evansi*					5.18	6.27			Orellan	SD	adult
UCM 21695	*exilis*	4.61	5.74	19.83						Orellan	SD	adolescent
UCM 21700						4.78	5.56			Orellan	SD	adult
UCM 21704	*evansi*	5.48	6.67							Orellan	SD	adult
UCM 21705	*evansi*	5.51	6.59							Orellan	SD	senior

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 21707	*evansi*	5.04	6.48							Orellan	SD	adult
UCM 21713	*evansi*	4.48	5.59							Orellan	SD	adult
UCM 21723	*evansi*					5.48	6.93	22.98		Orellan	SD	adult
UCM 21726	*evansi*					5.24	7.01	23.11		Orellan	SD	adult
UCM 21728	*evansi*	5.18	6.65							Orellan	SD	adult
UCM 21730	*evansi*					5.31	6.42			Orellan	SD	adult
UCM 21737		4.73	5.89							Orellan	SD	adult
UCM 21787	*evansi*					5.40	6.82	22.80		Orellan	SD	adult
UCM 21834	*evansi*					5.41	6.57			Orellan	SD	adult
UCM 21842	*evansi*	4.80								Orellan	SD	adult
UCM 22047	*speciosus*					5.17	7.39			Chadronian	CO	adult
UCM 22639	*evansi*					4.78	5.86			Orellan	SD	adult
UCM 22640	*exilis*					4.71	6.12	19.91		Orellan	SD	adult
UCM 22662		5.04	6.43							Orellan	SD	adult
UCM 22674	*evansi*					5.89	7.63			Orellan	SD	adult
UCM 23024						5.83	6.79			Orellan	SD	senior
UCM 23025	*evansi*					5.61	6.21			Orellan	SD	senior
UCM 23026	*evansi*					5.62	6.95	23.29		Orellan	SD	adult
UCM 23027	*evansi*	5.38	7.20	23.42						Orellan	SD	adult
UCM 23029	*evansi*	5.41	6.69	23.58						Orellan	SD	adult
UCM 23035	*evansi*					5.42	7.14			Orellan	SD	adult
UCM 23036	*evansi*	5.16	6.69							Orellan	SD	adult
UCM 23089	*evansi*	5.42	6.90	23.71	42.13					Orellan	CO	adult
UCM 35907	*evansi*					5.28	6.97	23.33		Orellan	NE	adult
UCM 35908	*evansi*					5.25	7.15			Orellan	NE	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 35909	*evansi*					4.90	6.58	22.72		Orellan	NE	adult
UCM 35910	*evansi*	5.06								Orellan	NE	adult
UCM 35911							5.85			Orellan	NE	senior
UCM 35912			5.57							Orellan	NE	adult
UCM 35913		4.97	5.81							Orellan	NE	adult
UCM 35914	*exilis*					5.21	6.36	21.00		Orellan	NE	adult
UCM 35915	*elissae*					4.76	6.01			Orellan	NE	adult
UCM 35916	*elissae*					4.96	6.77			Orellan	NE	adult
UCM 35917	*elissae*						6.97			Orellan	NE	adult
UCM 35918	*elissae*					5.25	6.10			Orellan	NE	adult
UCM 35919	*evansi*					4.80	6.49			Orellan	NE	adult
UCM 35920						5.24	6.35			Orellan	NE	adult
UCM 35924		4.91	6.24							Orellan	NE	adult
UCM 35925	*evansi*					4.90	6.67			Orellan	NE	adolescent
UCM 35926		5.29	6.35							Orellan	NE	adult
UCM 35927						5.18	6.37			Orellan	NE	adult
UCM 35928							6.72			Orellan	NE	adult
UCM 35929	*evansi*					5.17	6.38			Orellan	NE	adult
UCM 35930	*evansi*	4.89	6.63							Orellan	NE	adult
UCM 35931	*evansi*	5.40	6.98							Orellan	NE	adult
UCM 35933		4.98	6.13							Orellan	NE	adult
UCM 35934		4.76	5.87							Orellan	NE	adult
UCM 35935	*evansi*	5.11	6.40							Orellan	NE	adult
UCM 35937	*evansi*					5.67	6.69			Orellan	NE	adult
UCM 35938	*exilis*					5.27	6.43			Orellan	NE	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 35941	*evansi*					5.47	6.45			Orellan	NE	adult
UCM 35942						5.27	6.49			Orellan	NE	adult
UCM 35943		4.68	6.13							Orellan	NE	adult
UCM 35944	*evansi*	4.70	6.47							Orellan	NE	adolescent
UCM 35946	*exilis*	4.72	6.13							Orellan	NE	adult
UCM 35950		4.88	6.13							Orellan	NE	adult
UCM 35953	*evansi*	4.67	6.75							Orellan	NE	adolescent
UCM 35955						4.62	5.87			Orellan	NE	adolescent
UCM 35956						5.18	6.39			Orellan	NE	adult
UCM 38466	*evansi*					5.43	6.83	22.53	40.57	Orellan	WY	adult
UCM 38470	*evansi*					5.38	6.84	23.23		Orellan	WY	adult
UCM 38508	*evansi*	5.57	6.91							Orellan	NE	adult
UCM 38512						5.26	5.87			Orellan	NE	adult
UCM 38633						5.15	7.17			Orellan	NE	adult
UCM 38635						5.35	6.31			Orellan	NE	adult
UCM 39177	*elissae*					5.15	6.46	21.90		Orellan	??	adult
UCM 39893		5.52	8.38							Chadronian	WY	adult
UCM 39896		6.31	7.79							Chadronian	WY	senior
UCM 39908	*mammifer*					5.07	6.86			Chadronian	CO	adult
UCM 39909	*mammifer*					4.78	6.94			Chadronian	CO	adult
UCM 41469	*exilis*	4.63	6.09	20.19						Orellan	NE	adult
UCM 41471	*evansi*					5.06	6.74			Orellan	NE	adolescent
UCM 41472	*exilis*					4.63	5.80			Orellan	NE	adult
UCM 41475		4.77	6.15							Orellan	NE	adult
UCM 41477		5.23	6.16							Orellan	NE	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 41478	*exilis*					4.89	6.39			Orellan	NE	adult
UCM 41479	*exilis*					5.15	7.12			Orellan	NE	adult
UCM 41693	*evansi*					5.25	6.32			Orellan	NE	adult
UCM 41740	*evansi*					5.10	6.74	22.29		Orellan	WY	adult
UCM 42480	*elissae*					4.92	6.49	21.32		Orellan	WY	adult
UCM 42507	*exilis*						7.24			Orellan	WY	adult
UCM 42517	*evansi*					4.91	6.07	20.05		Orellan	WY	adult
UCM 42535						4.24	5.67			Orellan	CO	adult
UCM 45053	*evansi*					5.50	7.29			Orellan	WY	adolescent
UCM 45139		5.14	7.07							Chadronian	WY	adult
UCM 45144	*mammifer*	5.55	7.78							Chadronian	WY	adult
UCM 45146						5.07	6.74			Chadronian	WY	adult
UCM 45147						5.10	6.82			Chadronian	WY	adult
UCM 45149	*mammifer*	5.48	7.50							Chadronian	WY	adult
UCM 45152							7.01			Chadronian	WY	adult
UCM 45158	*speciosus*		6.68							Chadronian	WY	adult
UCM 45192	*elissae*					5.22	7.03			Orellan	WY	adult
UCM 47033	*mammifer*					5.26	7.53			Chadronian	WY	adult
UCM 47133	*evansi*					5.32	6.61			Orellan	WY	adult
UCM 47134	*evansi*					5.35	6.71	22.51		Orellan	WY	adult
UCM 47142	*evansi*	5.36	6.71							Orellan	WY	adult
UCM 47143	*evansi*	5.07	6.26							Orellan	WY	adult
UCM 47144	*evansi*					5.26	6.94			Orellan	WY	adolescent
UCM 47145	*evansi*					5.25	6.45			Orellan	WY	adult
UCM 47146	*evansi*					5.08	6.68			Orellan	WY	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 47147	*evansi*					5.18	6.33			Orellan	WY	senior
UCM 47262	*exilis*					4.69	5.69	19.32		Orellan	NE	adult
UCM 47265	*evansi*					5.03	6.70			Orellan	NE	adolescent
UCM 47267	*evansi*					5.44	6.00			Orellan	NE	adult
UCM 47268	*elissae*					4.80	5.96	19.39		Orellan	NE	adult
UCM 47388	*speciosus*	4.54	6.46	21.80						Chadronian	WY	adult
UCM 47404	*speciosus*	5.33	7.35							Chadronian	WY	adult
UCM 47412	*evansi*					5.92	7.52			Orellan	WY	adult
UCM 47494		4.87	6.24							Orellan	WY	adult
UCM 47499	*evansi*	5.34	6.96	23.29						Orellan	WY	adult
UCM 47971		5.88	7.18							Orellan	NE	adult
UCM 48036	*evansi*					5.74	7.78			Orellan	WY	adult
UCM 48038						4.73	5.60			Orellan	WY	senior
UCM 48040		4.79	5.71							Orellan	WY	adult
UCM 48041		4.65	6.62							Orellan	WY	adult
UCM 48661	*evansi*					5.26	6.34			Orellan	WY	adult
UCM 48665	*evansi*	5.31	6.35							Orellan	WY	adult
UCM 48666	*evansi*					4.81	6.24			Orellan	WY	adult
UCM 48838	*mammifer*	4.51	6.89							Chadronian	WY	adult
UCM 49291		5.13	5.83							Orellan	NE	adult
UCM 50138	*evansi*	5.27	6.11							Orellan	NE	adult
UCM 52257	*evansi*					5.37	6.58	23.02		Orellan	WY	adult
UCM 52258	*evansi*	4.68	6.36							Orellan	WY	adolescent
UCM 52281						5.03	6.70			Chadronian	WY	adult
UCM 52286	*mammifer*					5.42	7.07			Chadronian	WY	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 52412	*exilis*					4.65	6.48			Orellan	WY	adult
UCM 52413	*evansi*					4.78	6.74	21.84		Orellan	WY	adult
UCM 52414	*evansi*	5.13	6.46							Orellan	WY	adult
UCM 52415	*evansi*					5.24	6.52			Orellan	WY	adolescent
UCM 52416	*evansi*	5.41	6.65							Orellan	WY	adult
UCM 52417	*evansi*					5.19	6.85			Orellan	WY	adult
UCM 52418		4.95	6.43							Orellan	WY	senior
UCM 52419						5.06	5.96			Orellan	WY	senior
UCM 52420	*evansi*	5.11	6.75	22.51						Orellan	WY	adult
UCM 52421	*evansi*					5.20	5.98			Orellan	WY	adult
UCM 52422	*exilis*					5.17	6.28			Orellan	WY	adult
UCM 52450						6.31	7.27			Chadronian	WY	adult
UCM 53460	*elissae*					4.91	6.28	21.42		Orellan	NE	adult
UCM 53473	*mammifer*	5.35	6.69							Chadronian	WY	adult
UCM 53495	*evansi*					5.34	6.63	22.48		Orellan	WY	adult
UCM 53497	*evansi*					5.09	6.25			Orellan	WY	adult
UCM 53648	*evansi*	5.01	6.56							Orellan	WY	adult
UCM 54376						4.73	5.71			Orellan	WY	adult
UCM 54385	*speciosus*						6.06			Chadronian	WY	adult
UCM 54418	*speciosus*					5.35	7.39			Chadronian	CO	adult
UCM 54419	*speciosus*					4.86	6.98	23.33		Chadronian	CO	adult
UCM 54420	*speciosus*					4.84	6.85			Chadronian	CO	adult
UCM 54421	*speciosus*					5.72	7.64			Chadronian	CO	adult
UCM 57045	*evansi*					5.26	6.90			Orellan	NE	adult
UCM 57046		5.09	5.85							Orellan	NE	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 57063	*exilis*					5.06	5.64	21.12		Orellan	NE	adult
UCM 57064	*evansi*	5.39	6.86							Orellan	NE	adult
UCM 57065	*evansi*	4.95	6.04							Orellan	NE	adult
UCM 57066						4.23	5.26			Orellan	NE	adult
UCM 57627	*exilis*	5.14	6.25							Orellan	NE	adult
UCM 57630	*elissae*	4.91	6.15	20.83						Orellan	NE	adult
UCM 57631						5.35				Orellan	NE	adult
UCM 57640	*evansi*					5.08	6.76			Orellan	NE	adult
UCM 57680		5.12	6.54							Orellan	WY	adult
UCM 57682	*evansi*			22.54						Orellan	WY	adult
UCM 57683						5.06	6.54	21.25	38.49	Orellan	WY	adult
UCM 57684	*evansi*	5.78	7.07	24.96						Orellan	WY	adult
UCM 57686						4.98	6.33			Orellan	WY	adult
UCM 57687	*evansi*	5.77	7.02							Orellan	WY	adult
UCM 57688	*exilis*					5.23	6.42			Orellan	WY	adult
UCM 57691						5.24	6.42			Orellan	WY	adult
UCM 57692	*evansi*					5.22	6.49	21.69		Orellan	WY	adult
UCM 67271	*exilis*	5.02	6.20	21.16						Orellan	WY	adult
UCM 67277	*evansi*					5.49	6.47	21.72		Orellan	WY	adult
UCM 67279	*evansi*	4.85	6.54							Orellan	WY	adolescent
UCM 67311	*evansi*					5.26	7.17			Orellan	WY	adult
UCM 67342						5.54	6.66			Chadronian	WY	adult
UCM 67343	*speciosus*					5.02	6.69	22.04		Chadronian	WY	adult
UCM 72066	*evansi*	5.02	6.26	21.50						Chadronian	WY	adult
UCM 72067	*evansi*	5.10	6.34							Chadronian	WY	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 87125	*evansi*					4.69	5.86	20.57		Orellan	WY	adult
UCM 87126	*evansi*					5.05	6.76			Orellan	WY	adult
UCM 87127	*evansi*					4.87	7.30			Orellan	WY	adolescent
UCM 87130	*evansi*					4.95				Orellan	WY	adolescent
UCM 87306	*evansi*	5.29	6.37							Orellan	WY	adult
UCM 87313	*evansi*					4.24	6.38			Orellan	WY	adult
UCM 87316	*evansi*					4.88	6.24			Orellan	WY	adult
UCM 87318	*evansi*					5.25	6.65			Orellan	WY	adult
UCM 87320	*evansi*					4.35	6.73			Orellan	WY	adult
UCM 87328	*evansi*					5.15	6.76			Orellan	WY	adult
UCM 87332	*evansi*					5.02	6.73			Orellan	WY	adolescent
UCM 87334	*evansi*					5.34	7.01			Orellan	WY	adult
UCM 87458	*evansi*					4.99	6.37	21.21	34.00	Orellan	NE	adolescent
UCM 87459	*evansi*					5.44	7.07	23.12	39.89	Orellan	NE	adult
UCM 87460	*evansi*	5.24		23.03	40.00					Orellan	NE	adult
UCM 87461	*evansi*					5.13	6.96			Orellan	NE	adolescent
UCM 87462	*evansi*	4.90	6.09	20.52						Orellan	NE	adult
UCM 87463	*evansi*					5.10	6.38			Orellan	NE	adult
UCM 87484	*elissae*	5.16	6.20		40.00	5.18	6.18	21.34	37.59	Orellan	NE	adult
UCM 87485	*evansi*					4.97	6.74	23.02		Orellan	NE	adult
UCM 87486	*evansi*					5.32	6.77			Orellan	NE	adult
UCM 87619	*evansi*	5.21	6.82	23.15						Orellan	SD	adult
UCM 87620	*evansi*					5.34	6.79			Orellan	SD	adult
UCM 87623		5.18	6.75							Orellan	SD	adult
UCM 87624	*evansi*					5.87	7.46			Orellan	SD	adult

Specimen #	species	Rm2w	Rm2l	Rm1-m3	Rp2-m3	Lm2w	Lm2l	Lm1-m3	Lp2-m3	NALMA	State	Age
UCM 87625	*evansi*	5.36	6.69							Orellan	SD	adult
UCM 90690	*evansi*					5.15	6.72	22.01		Orellan	WY	adult
UCM 90691	*evansi*					4.80	6.21			Orellan	WY	adolescent
UCM 90937	*evansi*					5.72	7.40			Orellan	SD	adult
UCM 90939	*evansi*	5.69	7.43							Orellan	SD	adolescent
UCM 90941	*evansi*					5.10	7.00			Orellan	SD	adolescent
UCM 91034	*elissae*	4.73	6.14							Orellan	CO	adult
UCM 96280	*evansi*	5.13	6.59							Orellan	???	adult
UCM 98885	*evansi*	5.67	6.98							Orellan	NE	adult
UCM 98887						4.88	5.95			Orellan	NE	adult
UCM 99164						5.03	6.68			Orellan	WY	adult
UCM 99370	*evansi*					4.54	6.46			Orellan	CO	adult
UCM 99395		5.31	6.89			6.31	7.67			Eocene	WY	adult
FMNH UC 1406	*evansi*						8.28	25.30		Orellan	NE	adult
FMNH UM 988	*evansi*	5.55	6.72			5.46	6.56	22.53		Orellan	NE	adult
DMNS 41057						5.82	7.88			Chadronian	WY	adult

Table 2: Measurements of upper dentition of Leptomeryx

Specimen #	Species	RM2w	RM2l	RM1-M3	RP2-M4	LM2w	LM2l	LM1-M3	LP2-M4	NALMA	State	Age
DMNS 17330						8.58	7.41			Chadronian	WY	adult
DMNS 17333						9.20	8.00	21.41		Chadronian	WY	adult
DMNS 17341		8.75	7.26							Chadronian	WY	adult
DMNS 17492						8.50	6.73			Chadronian	WY	adult

Specimen #	Species	RM2w	RM2l	RM1-M3	RP2-M4	LM2w	LM2l	LM1-M3	LP2-M4	NALMA	State	Age
DMNS 17501		7.67	6.96							Chadronian	WY	adult
DMNS 17584	*evansi*					7.95	6.81			Chadronian	WY	adult
DMNS 27992		8.14	6.79							Chadronian	CO	adult
DMNS 41057		9.01	7.80							Chadronian	WY	adolescent
DMNS 44302		8.78	7.81							Chadronian	CO	adolescent
DMNS 48257						9.37	7.73	22.04		Chadronian	CO	adult
DMNS 52571		8.43	7.02							Chadronian	WY	adult
DMNS 6051		8.82	7.60	21.19						Chadronian	WY	adult
FMNH PM 14455		7.69	6.23	18.26	35.14					Chadronian	SD	adult
FMNH UM 1008	*evansi*	8.25	7.21	20.06	36.95					Orellan	NE	adult
FMNH UM 1009	*evansi*	7.94	7.00	20.28	36.67					Orellan	NE	adult
FMNH UM 1010	*evansi*	8.15	6.47	18.73						Orellan	NE	adult
FMNH UM 1012	*evansi*	9.06	7.29	20.39						Orellan	NE	adult
FMNH UM 1020	*evansi*					7.84	6.26	18.45	34.79	Orellan	NE	adult
FMNH UM 1021	*evansi*					8.14	7.43			Orellan	NE	adult
SDSMT 40331		7.52	7.25							Chadronian	SD	adolescent
SDSMT 56707						7.10	5.94			Chadronian	SD	adult
UCM 101906		7.69	6.08							Chadronian	WY	adult
UCM 101912		8.40	6.83							Chadronian	WY	adult
UCM 20774		7.82	6.73	19.17						Orellan	CO	adult
UCM 21788		7.66	6.69							Orellan	SD	adolescent
UCM 21789						7.98	7.20	20.21		Orellan	SD	adult
UCM 21790								20.04		Orellan	SD	adult
UCM 21791		7.84	7.35	19.85						Orellan	SD	adult
UCM 21792						7.87	6.70	18.71		Orellan	SD	adult

Specimen #	Species	RM2w	RM2l	RM1-M3	RP2-M4	LM2w	LM2l	LM1-M3	LP2-M4	NALMA	State	Age
UCM 21795						7.50	6.45			Orellan	SD	adult
UCM 21796		7.71	6.67	18.58						Orellan	SD	adult
UCM 21801		7.38	6.35							Orellan	SD	adult
UCM 21804						7.27	7.07			Orellan	SD	adolescent
UCM 21808		7.44								Orellan	SD	adult
UCM 21811						7.71	6.83			Orellan	SD	adolescent
UCM 21832		8.25	7.38	19.71						Orellan	SD	adult
UCM 21838						8.63	7.54			Orellan	SD	adult
UCM 22628						7.89	6.27			Orellan	SD	adult
UCM 22633		7.85	6.62							Orellan	SD	adult
UCM 22634						7.25	5.71			Orellan	SD	adult
UCM 22635						7.15	6.21			Orellan	SD	adult
UCM 22638						7.68	6.93			Orellan	SD	adult
UCM 35986	*exilis*	7.71	6.91	19.03						Orellan	NE	adolescent
UCM 35987	*evansi*	7.86	6.51							Orellan	NE	adult
UCM 35990	*evansi*					7.41	6.16	17.41		Orellan	NE	adult
UCM 35991	*evansi*					7.72	6.20	18.59		Orellan	NE	adult
UCM 35992	*evansi*					7.26	6.81			Orellan	NE	adult
UCM 35995	*evansi*		7.50	22.94						Orellan	NE	adult
UCM 35997						7.82	6.49			Orellan	NE	adult
UCM 36000	*evansi*					7.71	6.21			Orellan	NE	adult
UCM 36001	*exilis*					7.13	6.18	17.32		Orellan	NE	adult
UCM 36002						7.21	6.28			Orellan	NE	adult
UCM 36003	*evansi*					7.13	6.88			Orellan	NE	adolescent
UCM 36004	*exilis*					8.21	6.73	19.01		Orellan	NE	adult

Specimen #	Species	RM2w	RM2l	RM1-M3	RP2-M4	LM2w	LM2l	LM1-M3	LP2-M4	NALMA	State	Age
UCM 36006		7.47	5.94							Orellan	NE	senior
UCM 36009		7.83	6.22	17.71						Orellan	NE	adult
UCM 36012	*evansi*	8.02	6.81							Orellan	NE	adult
UCM 36013	*evansi*	6.65	6.26	17.13						Orellan	NE	adult
UCM 36014	*evansi*					7.45	5.83	16.85		Orellan	NE	adult
UCM 36015						7.09	5.25			Orellan	NE	senior
UCM 38467		8.31	7.53	19.93						Orellan	WY	adult
UCM 38644	*evansi*					6.31	5.42			Orellan	NE	adult
UCM 38645	*evansi*	6.99	6.44							Orellan	NE	adult
UCM 39175		8.81	7.20	20.11	37.68					Orellan	??	adult
UCM 39176						8.84	7.47	20.59		Orellan	??	adult
UCM 39895						7.31	6.34			Chadronian	WY	adult
UCM 41487						7.66	6.74	19.11		Orellan	NE	adult
UCM 41488						7.23	6.83			Orellan	NE	adolescent
UCM 41491						8.17				Orellan	NE	adult
UCM 41710		7.07	6.17							Orellan	NE	adult
UCM 41736	*evansi*					8.13	7.13			Orellan	WY	adult
UCM 41737	*evansi*	7.99	6.87	19.73						Orellan	WY	adult
UCM 41739	*evansi*	7.08	6.54							Orellan	WY	adult
UCM 42479	*evansi*	8.92	7.67			8.77	7.76	20.88		Orellan	WY	adult
UCM 42534						8.02	6.67	18.27		Orellan	CO	adult
UCM 45116	*speciosus*	8.37	7.44							Chadronian	WY	adult
UCM 45117		9.12	7.95	21.14						Chadronian	WY	adult
UCM 45143		8.17	6.54	19.63						Chadronian	WY	adult
UCM 47126	*evansi*					7.77	6.27	18.79		Orellan	WY	adult

Specimen #	Species	RM2w	RM2l	RM1-M3	RP2-M4	LM2w	LM2l	LM1-M3	LP2-M4	NALMA	State	Age
UCM 47127	*evansi*					6.70	6.01			Orellan	WY	adult
UCM 47131	*evansi*					7.48	6.40			Orellan	WY	adult
UCM 47132	*evansi*					7.92	6.73			Orellan	WY	adult
UCM 47269						7.79	6.52			Orellan	NE	adult
UCM 47386		8.51	7.49	21.79						Chadronian	WY	adult
UCM 48037	*evansi*	8.02	6.54	19.40		7.99	6.71	19.86		Orellan	WY	adult
UCM 48658	*evansi*					7.91	6.40	18.50		Orellan	WY	adult
UCM 48659	*evansi*					7.82	6.93			Orellan	WY	adolescent
UCM 48722	*evansi*	6.95	6.06	17.01						Orellan	WY	adult
UCM 50137	*evansi*					7.49	6.66			Orellan	NE	adult
UCM 50140		9.05	7.63							Chadronian	WY	adult
UCM 52254						9.10	6.74			Orellan	WY	adult
UCM 52255	*evansi*					7.88	6.95			Orellan	WY	adult
UCM 52256	*evansi*					8.94	7.24	21.32		Orellan	WY	adult
UCM 52288	*evansi*	8.48	6.79	18.57		8.54	7.01	18.42		Orellan	WY	adult
UCM 52289	*evansi*					8.20	6.83	19.26		Orellan	WY	adult
UCM 52290	*evansi*	8.86	7.65	21.55						Orellan	WY	adult
UCM 52406	*evansi*					7.91	6.49	19.41	36.05	Orellan	WY	adult
UCM 52408	*evansi*					7.76	6.44	18.53		Orellan	WY	adult
UCM 52409	*evansi*					7.97	6.71	18.77		Orellan	WY	adult
UCM 52410	*evansi*	7.27	6.89							Orellan	WY	adult
UCM 52411	*evansi*					8.49	7.29			Orellan	WY	adult
UCM 53482		7.79	6.50							Orellan	WY	adult
UCM 53500		9.11	6.87	20.11						Orellan	WY	adult
UCM 54207	*evansi*					7.84	6.41	18.31		Orellan	WY	adult

Specimen #	Species	RM2w	RM2l	RM1-M3	RP2-M4	LM2w	LM2l	LM1-M3	LP2-M4	NALMA	State	Age
UCM 54377	*evansi*					8.04		20.09		Orellan	WY	adult
UCM 54386	*evansi*					8.55	7.15	20.82		Orellan	WY	adult
UCM 54401	*speciosus*	8.11	7.45							Chadronian	CO	adult
UCM 67264	*evansi*					8.00				Orellan	WY	adult
UCM 67276						7.65	6.30	18.06		Orellan	WY	adult
UCM 72062						7.94	6.57			Orellan	WY	adult
UCM 72065	*evansi*	8.40	7.16							Orellan	WY	adult
UCM 87248		7.65	6.89	19.24						Chadronian	WY	adult
UCM 87249						8.03	6.72			Chadronian	WY	adult
UCM 87250			6.73							Chadronian	WY	adult
UCM 87302		8.41	6.69							Chadronian	WY	adult
UCM 87303						8.19	6.65			Chadronian	WY	adult
UCM 87304			6.49							Chadronian	WY	adult
UCM 87474	*evansi*	7.40	6.56	17.77		7.38	6.58	17.62	32.26	Orellan	NE	adult
UCM 87475	*evansi*	8.45	7.31	20.23		8.45	7.28	20.22	37.58	Orellan	NE	adult
UCM 87476	*evansi*	7.79	6.73	18.75	38.83					Orellan	NE	adult
UCM 87477	*evansi*	8.64	6.97							Orellan	NE	adult
UCM 87491	*evansi*	9.22	7.58	21.97		9.40	6.93			Orellan	NE	adult
UCM 87492		7.50								Orellan	NE	adult
UCM 87493						7.61	6.81			Orellan	NE	adolescent
UCM 87494	*evansi*	7.81	7.04							Orellan	NE	adolescent
UCM 87621		8.56	7.56	21.38						Orellan	SD	adult
UCM 90692	*evansi*					8.39	6.79	18.87	34.89	Orellan	WY	adult
UCM 90938						8.53	7.66			Orellan	SD	adult
UCM 91553						7.86	6.82	19.29		Orellan	SD	adult

Specimen #	Species	RM2w	RM2l	RM1-M3	RP2-M4	LM2w	LM2l	LM1-M3	LP2-M4	NALMA	State	Age
FMNH UC 1406	*evansi*	8.54	7.52	21.12	40.07		8.10	21.87	39.52	Orellan	NE	adult
FMNH UM 988	*evansi*	8.31	6.49	19.01	35.66	8.24	6.55	18.99	35.65	Orellan	NE	adult
DMNS 41057		8.90	7.86							Chadronian	WY	adult
UCM 52253	*evansi*	7.84	6.62	18.50						Orellan	WY	adult
UCM 87128	*evansi*	7.63	6.12							Orellan	WY	adult
UCM 87483	*evansi*	6.56	5.65							Orellan	NE	adolescent

VIII. Appendix 3.

Table 1: Measurements of lower dentition of Rhinocerotinae (**Trigonias, Subhyracodon,** ***and Rhinocerotinae indet.)***

Specimen #	Genus	Rm2w	Rm2l	Rm1-m3	Rp1-m3	Lm2w	L m2l	Lm1-m3	Lp1-m3	NALMA	State	Age
DMNS 1026	*Trigonias*									Chadronian	CO	adolescent
DMNS 1028	*Trigonias*	23.85	33.22	101.05	182.59	22.65	33.97	100.35		Chadronian	CO	adult
DMNS 1029	*Trigonias*	28.42	36.20	106.95	186.66	27.51	36.43	105.48	185.47	Chadronian	CO	senior
DMNS 1037	*Trigonias*	26.59	36.24	110.92	195.57	27.05	36.41	114.40		Chadronian	CO	adult
DMNS 1038	*Trigonias*	27.00	37.30	111.78		27.89	38.58	109.08		Chadronian	CO	senior
DMNS 1046	*Trigonias*	26.40	42.83			26.34	39.35			Chadronian	CO	adolescent
DMNS 11005	*Subhyracodon*					22.09	32.97			Chadronian	NE	adult
DMNS 11007	*Subhyracodon*	23.37	32.17							Chadronian	NE	adult
DMNS 11009	*Subhyracodon*	23.81	35.84							Chadronian	NE	adult
DMNS 11010	*Subhyracodon*					21.84				Chadronian	NE	adolescent
DMNS 1510	*Trigonias*	26.40	36.45	109.60		22.18	37.43	109.44	194.60	Chadronian	CO	senior
DMNS 24800	*Subhyracodon*	27.06	40.09			26.62	40.77			Chadronian	CO	adolescent
DMNS 2653	*Trigonias*	26.51	37.79	109.53	182.72	26.18	36.77	109.85	185.53	Chadronian	CO	adult
DMNS 2658	*Trigonias*	25.12	37.74			24.28	38.81			Chadronian	CO	adolescent
DMNS 2661	*Trigonias*	30.44	36.15							Chadronian	CO	adult
DMNS 2665	*Trigonias*	28.69	36.32	110.24	190.81	28.06	36.22	108.53	202.31	Chadronian	CO	adult
DMNS 2666	*Trigonias*	27.83	37.67	109.65		26.90	38.10	111.69		Chadronian	CO	adult
DMNS 2667	*Trigonias*					28.69	35.96	103.52		Chadronian	CO	senior

Specimen #	Genus	Rm2w	Rm2l	Rm1-m3	Rp1-m3	Lm2w	L m2l	Lm1-m3	Lp1-m3	NALMA	State	Age
DMNS 2668	*Trigonias*	28.19	36.53							Chadronian	CO	senior
DMNS 2669	*Trigonias*	28.53	37.05	109.99		28.75	36.50	112.84		Chadronian	CO	adult
DMNS 2670	*Trigonias*	27.34	37.69	113.82	199.86	26.91	37.56	111.67	196.08	Chadronian	CO	adult
DMNS 2674	*Trigonias*					25.64	37.83	110.52		Chadronian	CO	adult
DMNS 2675	*Trigonias*					19.97	32.27	91.36		Chadronian	CO	adolescent
DMNS 2683	*Trigonias*	27.23	36.78							Chadronian	CO	adolescent
DMNS 2684	*Trigonias*	25.26	36.12	106.34						Chadronian	CO	senior
DMNS 2685	*Trigonias*	30.30	35.23	107.71		29.72	37.22	113.31	204.14	Chadronian	CO	senior
DMNS 2686	*Trigonias*	25.57	38.07							Chadronian	CO	adolescent
DMNS 2687	*Trigonias*	26.80	36.60			27.16	35.85			Chadronian	CO	adolescent
DMNS 2688	*Trigonias*	28.63	38.48			29.00	38.92			Chadronian	CO	adolescent
DMNS 2690	*Trigonias*	24.15	33.36			24.24	34.65			Chadronian	CO	adolescent
DMNS 2693	*Trigonias*	23.58	32.89	103.40	191.68	23.10	35.54	104.73	185.92	Chadronian	CO	adult
DMNS 2694	*Trigonias*	25.21	36.02			24.21	37.60			Chadronian	CO	adolescent
DMNS 2695	*Trigonias*	25.72	37.03	114.36		27.56	35.17	111.85		Chadronian	CO	adult
DMNS 2705	*Trigonias*	26.43	34.04	101.26		27.84	34.03	100.99		Chadronian	CO	senior
DMNS 2706	*Trigonias*		29.59	99.08			29.28	93.10		Chadronian	CO	senior
DMNS 2707	*Trigonias*	28.07	41.13							Chadronian	CO	adolescent
DMNS 2710	*Trigonias*					22.52	32.14	94.93		Chadronian	CO	adult
DMNS 2712	*Trigonias*					25.60	34.82	102.94		Chadronian	CO	adolescent
DMNS 2713	*Trigonias*	21.43	31.52							Chadronian	CO	adolescent
DMNS 2719	*Trigonias*	26.69	36.01	106.15						Chadronian	CO	adult
DMNS 2720	*Trigonias*					26.59	34.28	105.73		Chadronian	CO	adult
DMNS 2721	*Trigonias*	27.46	37.24							Chadronian	CO	adolescent
DMNS 2723	*Trigonias*						27.30			Chadronian	CO	adolescent

Specimen #	Genus	Rm2w	Rm2l	Rm1-m3	Rp1-m3	Lm2w	L m2l	Lm1-m3	Lp1-m3	NALMA	State	Age
DMNS 2724	*Trigonias*					26.07	39.18			Chadronian	CO	adolescent
DMNS 2725	*Trigonias*					27.34	35.69			Chadronian	CO	adult
DMNS 338	*Trigonias*	24.86	35.71							Chadronian	CO	adolescent
DMNS 37317	*Trigonias*	26.57	37.16				38.28			Chadronian	CO	senior
DMNS 412	*Trigonias*	28.93	38.71	113.26		29.45	38.44	112.24		Chadronian	CO	adult
DMNS 414	*Trigonias*									Chadronian	CO	adult
DMNS 415	*Trigonias*	29.72	39.16	96.86		26.95	37.78	107.08		Chadronian	CO	adult
DMNS 418	*Trigonias*	26.63	40.42	113.07		27.52	39.26	110.87		Chadronian	CO	senior
DMNS 422	*Trigonias*	25.77	38.05			25.45	35.37			Chadronian	CO	adolescent
DMNS 4414	*Trigonias*	23.81	33.42							Chadronian	CO	adolescent
DMNS 4415	*Trigonias*	25.22	34.30	100.50						Chadronian	CO	adult
DMNS 4420	*Trigonias*					28.92	35.82	112.08		Chadronian	CO	adult
DMNS 4421	*Trigonias*	26.44	37.71	112.50	196.19					Chadronian	CO	adult
DMNS 4422	*Trigonias*		33.94	103.73						Chadronian	CO	adult
DMNS 4423	*Trigonias*	26.77	38.01							Chadronian	CO	adolescent
DMNS 4424	*Trigonias*	27.04	39.58	113.89						Chadronian	CO	adult
DMNS 4426	*Trigonias*	24.23	37.95							Chadronian	CO	adolescent
DMNS 4428	*Trigonias*	28.69	35.54							Chadronian	CO	adolescent
DMNS 4430	*Trigonias*					29.27	37.85			Chadronian	CO	adolescent
DMNS 4431	*Trigonias*					32.06	40.18			Chadronian	CO	adolescent
DMNS 4432	*Trigonias*					27.45	35.81			Chadronian	CO	adolescent
DMNS 4537	*Trigonias*					26.36	39.15	111.24		Chadronian	CO	adult
DMNS 4538	*Trigonias*	24.75	34.54	103.80	189.13	26.34	35.16	103.26	184.52	Chadronian	CO	senior
DMNS 4540	*Trigonias*					25.53	38.03	109.43	193.86	Chadronian	CO	adult

Specimen #	Genus	Rm2w	Rm2l	Rm1-m3	Rp1-m3	Lm2w	L m2l	Lm1-m3	Lp1-m3	NALMA	State	Age
DMNS 54830	*Trigonias*					23.29	33.31	98.02		Chadronian	CO	adult
DMNS 875	*Trigonias*	27.80	37.52	105.56	198.23		38.44	105.15	194.20	Chadronian	CO	senior
DMNS 887	*Trigonias*	25.72	36.98			25.59	37.38			Chadronian	CO	adolescent
DMNS 888	*Trigonias*	24.60	36.38			28.05	37.69			Chadronian	CO	adolescent
DMNS 888	*Trigonias*	26.36	39.69			29.13	39.31			Chadronian	CO	adolescent
DMNS 890	*Trigonias*	22.93	33.02	100.59	178.73	22.67	33.26	101.26		Chadronian	CO	adult
DMNS 891	*Trigonias*	27.24	37.47	112.89		25.86	40.41	112.16		Chadronian	CO	senior
FMNH PM 14418	*Trigonias*	28.50	41.34	122.37		27.46	41.36	120.49	207.70	Chadronian	SD	
FMNH PM 14557	*Trigonias*	27.65	38.35	109.31	180.71	27.54	29.02	114.50	202.06	Chadronian	CO	
FMNH PM 49903	*Trigonias*					18.06	28.50	88.10		Chadronian	SD	
SDSMT 2655	*Subhyracodon*	25.67	37.57	112.76		25.35	36.52	114.41		Orellan	SD	adolescent
SDSMT 30115	*Subhyracodon*	23.11	31.33	93.92	178.43	22.76	31.85	94.10	179.18	Orellan	SD	adult
SDSMT 3649	*Subhyracodon*	20.77	30.64	94.93		20.80	31.30	95.46		Orellan	SD	adult
SDSMT 38819	*Subhyracodon*					25.39	35.00			Orellan	SD	adult
SDSMT 38820	*Subhyracodon*	26.75	36.57	107.50	197.94	25.22	35.54	108.76	199.80	Orellan	SD	adult
SDSMT 39296	*Subhyracodon*	27.77	36.23	105.57		26.88	38.88	108.28		Orellan	SD	adult
SDSMT 48099	*Subhyracodon*	27.31	34.32	110.16		24.57	31.96	100.15		Orellan	SD	adult

Specimen #	Genus	Rm2w	Rm2l	Rm1-m3	Rp1-m3	Lm2w	L m2l	Lm1-m3	Lp1-m3	NALMA	State	Age
SDSMT 50453	*Subhyracodon*	24.01	34.80	103.45		24.50	33.83	103.03		Orellan	SD	adult
SDSMT 52893	*Subhyracodon*	25.68	37.64	111.13		23.50	36.88	113.44		Orellan	SD	adult
SDSMT 60870	*Subhyracodon*	21.32	30.68	91.85						Chadronian	SD	adult
SDSMT 62303	*Subhyracodon*	25.12	36.62	108.97		24.36	36.59	109.83		Orellan	SD	adult
SDSMT 73340	*Subhyracodon*	22.09	31.93							Orellan	SD	adult
SDSMT 73579	*Subhyracodon*	23.78	33.09							Orellan	SD	adolescent
SDSMT 77476	*Subhyracodon*	25.22	36.62	108.97		24.36	36.59	109.83		Orellan	SD	adult
SDSMT 78175	*Subhyracodon*	25.07	33.10	99.12		24.29	31.48	96.82		Orellan	SD	adult
SDSMT 7980	*Subhyracodon*	24.47	36.61	108.55	209.11	26.63	37.50	115.36	214.17	Orellan	SD	adult
SDSMT 82000	*Subhyracodon*	26.08	36.32	104.58		27.05	36.44	105.00		Orellan	SD	adult
UCM 20488	*Subhyracodon*	20.20	28.91	90.97			29.43	84.49		Chadronian	CO	adult
UCM 20494A	*Trigonias*	27.54	40.25	113.54		29.05	37.00	111.39		Chadronian	CO	adolescent
UCM 20494B	*Trigonias*	27.03	39.54	115.88		27.36	40.75	116.54		Chadronian	CO	adolescent
UCM 20657						30.36	37.54	111.95		Chadronian	CO	adult
UCM 20659		26.92	40.93							Orellan	NE	adolescent
UCM 22995	*Subhyracodon*					24.38	34.71			Orellan	SD	adult

Specimen #	Genus	Rm2w	Rm2l	Rm1-m3	Rp1-m3	Lm2w	L m2l	Lm1-m3	Lp1-m3	NALMA	State	Age
UCM 38479	*Subhyracodon*					23.09	30.25			Orellan	WY	adult
UCM 43698	*Trigonias*	28.15	33.65	106.27		30.76	33.67	100.50	180.65	Chadronian	CO	adult
UCM 57644	*Subhyracodon*	18.65	28.65							Orellan	WY	adolescent
UCM 68913	*Trigonias*	26.45	39.61	119.20	205.12	28.56	39.78	119.13		Chadronian	CO	adult
UCM 73384	*Subhyracodon*	21.07	34.43							Orellan	NE	adolescent
UCM 73385	*Subhyracodon*					20.73	32.75			Orellan	NE	adolescent
UCM 73386	*Trigonias*					27.70	40.47			Chadronian	CO	adult
UCM 73387	*Trigonias*					29.03	41.29			Chadronian	CO	
UCM 86803			31.62			20.47	30.09			Chadronian	CO	adolescent
UCM 86808		24.19	32.61			24.58	35.46			Chadronian	CO	adolescent
UCM 86809		28.16	37.12			29.56	39.22			Chadronian	CO	adolescent
UCM 89768						28.20	35.47			Chadronian	CO	adult
UCM 89771		27.16	36.92	106.30		26.22	36.02	103.85		Chadronian	CO	senior
UCM 89772		30.13	39.27	114.15		28.99	40.01	115.42		Chadronian	CO	adult
UCM 89773		25.32	34.01			25.29	35.68			Chadronian	CO	adolescent
UCM 89774		30.10	43.48			30.17	42.81			Chadronian	CO	adolescent
UCM 89775		24.30	33.09			23.23	33.06			Chadronian	CO	adolescent
UCM 89776		27.72	36.02			27.60	35.89			Chadronian	CO	adolescent
UCM 89777						23.78	35.58	102.21		Chadronian	CO	senior
UCM 89778		28.81	41.80				42.47			Chadronian	CO	adolescent
UCM 89779			35.26	106.65			34.99	103.39		Chadronian	CO	adult
UCM 89780		25.66	39.79			25.25	39.56			Chadronian	CO	adolescent
UCM 89781		27.89	39.15							Chadronian	CO	adolescent
UCM 89783		29.03	39.05	112.61	203.74	26.06	39.10	113.65		Chadronian	CO	adult
UCM 89786		26.06	38.41			26.25	37.97			Chadronian	CO	adolescent

Specimen #	Genus	Rm2w	Rm2l	Rm1-m3	Rp1-m3	Lm2w	L m2l	Lm1-m3	Lp1-m3	NALMA	State	Age
UCM 89789		27.16	37.28	107.09		26.77	37.99	105.46		Chadronian	CO	adult
UCM 89792		25.79	26.43			25.30	34.81			Chadronian	CO	adolescent
UCM 90514						28.55	40.06			Chadronian	CO	adolescent
UCM 90520		24.95								Chadronian	CO	adolescent
UCM 90522		30.68	45.39	129.81						Chadronian	CO	adolescent
UCM 90527			35.02	100.81						Chadronian	CO	senior
UCM 90528		27.13	35.91	108.75						Chadronian	CO	adult
UCM 90535		22.87	28.87							Chadronian	CO	adolescent
UCM 90538		26.49	36.89	107.48		27.18	31.60	101.05		Chadronian	CO	adult
UCM 90542			38.19	109.53			38.22	112.34		Chadronian	CO	senior
UCM 90543		26.89	37.38	111.79		27.21	36.58	110.87		Chadronian	CO	adult
UCM 96982		30.85	38.77			28.85	38.03	110.58		Chadronian	CO	adult
UCM 98237		26.66	36.38	120.59						Orellan	NE	adult
UCM 98745	*Subhyracodon*					21.06	30.13			Orellan		adolescent

Table 2: Measurements of upper dentition of Rhinocerotinae (**Trigonias, Subhyracodon,** ***and Rhinocerotinae indet.)***

Specimen #	Genus	RM2w	RM2l	RM1-M3	RP1-M3	LM2w	LM2l	LM1-M3	LP1-M3	NALMA	State	Age
(SDSMT) 07CPG075	*Subhyracodon*	43.06	41.40	109.96	205.57	43.45	40.76	109.93	203.13	Orellan	SD	adult
DMNS 1026	*Trigonias*	43.76	45.74			46.32	46.01			Chadronian	CO	adolescent
DMNS 1029	*Trigonias*	51.49	44.63	115.51	201.03	56.33	44.46	113.14	198.11	Chadronian	CO	senior
DMNS 1050	*Trigonias*	46.48	47.67			45.86	48.43			Chadronian	CO	adolescent
DMNS 1051	*Trigonias*	49.28	47.38			51.55	47.77			Chadronian	CO	adolescent
DMNS 1052	*Trigonias*	48.93	47.49			48.11	46.62			Chadronian	CO	adolescent

Specimen #	Genus	RM2w	RM2l	RM1-M3	RP1-M3	LM2w	LM2l	LM1-M3	LP1-M3	NALMA	State	Age
DMNS 1053	*Trigonias*	48.59	47.33	122.04	219.77		47.51	121.58	217.06	Chadronian	CO	adolescent
DMNS 1054	*Trigonias*	51.74	46.43	116.50	204.04	51.20	44.56	120.25	208.87	Chadronian	CO	senior
DMNS 1054	*Trigonias*	52.37	46.52	116.63	200.76	51.03	44.75	120.26	210.28	Chadronian	CO	senior
DMNS 1055	*Trigonias*	48.69	48.82			46.70	45.77			Chadronian	CO	adolescent
DMNS 1056	*Trigonias*	46.86	47.49	118.17	208.13	47.00	48.34	118.43	94.63	Chadronian	CO	adult
DMNS 10774	*Subhyracodon*	44.46	41.83							Orellan	CO	adult
DMNS 121	*Subhyracodon*	41.62	39.00							Chadronian	NE	adolescent
DMNS 1283	*Trigonias*	47.52	42.16	109.72		46.49	39.69	106.35		Chadronian	CO	senior
DMNS 1284	*Trigonias*	48.61	42.31	112.59	200.26	48.56	42.33	114.42	200.33	Chadronian	CO	senior
DMNS 1445	*Trigonias*	47.89	48.37			46.80	47.92			Chadronian	CO	adolescent
DMNS 1503	*Trigonias*	50.55	42.14	116.91	208.40	50.13	42.61	116.55	206.09	Chadronian	CO	senior
DMNS 1504	*Trigonias*	52.15	48.78			50.68	48.64			Chadronian	CO	adolescent
DMNS 1507	*Trigonias*	50.56	36.82	118.56	208.64	48.41	39.76	115.10	212.29	Chadronian	CO	senior
DMNS 1512	*Trigonias*	49.14	45.05			44.94	44.84			Chadronian	CO	adolescent
DMNS 1513	*Trigonias*	40.42	41.40			42.14	44.58			Chadronian	CO	adolescent
DMNS 1517	*Trigonias*	50.35	44.86	112.88		49.02	43.96	117.87		Chadronian	CO	senior
DMNS 1746	*Trigonias*	51.12	50.68	123.06		51.07	52.22	121.55	216.90	Chadronian	CO	adult
DMNS 1850	*Trigonias*	40.16	34.99	93.20	175.88	39.47	35.73	97.56	175.99	Chadronian	CO	adult
DMNS 1850	*Trigonias*	40.05	35.91	93.76	175.74	39.31	36.92	97.40	175.84	Chadronian	CO	senior
DMNS 1854	*Trigonias*	47.46	48.86	118.85	212.65	48.86	47.33	120.48	213.06	Chadronian	CO	adult
DMNS 1856	*Trigonias*	47.59	44.64	110.63		47.00	45.64	109.91	200.96	Chadronian	CO	senior
DMNS 1860	*Trigonias*					45.89	42.48	112.41		Chadronian	CO	senior
DMNS 1861	*Trigonias*	46.18	44.05	111.79		46.64	45.24	113.68		Chadronian	CO	senior
DMNS 414	*Trigonias*	47.62	46.47	111.93	193.41	48.88	46.51	112.70	191.16	Chadronian	CO	adult

Specimen #	Genus	RM2w	RM2l	RM1-M3	RP1-M3	LM2w	LM2l	LM1-M3	LP1-M3	NALMA	State	Age
DMNS 420	*Trigonias*	50.18	44.38	115.01		47.66	43.35	116.44	206.30	Chadronian	CO	adult
DMNS 421	*Trigonias*	50.17	44.69	116.11		49.79	41.95	116.14		Chadronian	CO	senior
DMNS 422	*Trigonias*	45.69	43.27			44.91	42.87			Chadronian	CO	adolescent
DMNS 876	*Trigonias*	52.18	46.55	121.22	216.72	55.31	47.36	125.77	223.10	Chadronian	CO	senior
DMNS 878	*Trigonias*	55.12	48.85	112.83	214.98	54.99	48.67	120.60	221.68	Chadronian	CO	adult
DMNS 879	*Trigonias*	51.99	46.93	116.52	210.26	51.54	46.04	116.53	208.81	Chadronian	CO	senior
DMNS 880	*Trigonias*	45.37	46.02	118.23		45.05	45.52	113.95		Chadronian	CO	senior
DMNS 884	*Trigonias*	45.42	45.56	109.41	205.33	45.20	44.54	111.18	198.49	Chadronian	CO	adult
DMNS 886	*Trigonias*	48.11	42.62	110.03	199.40	47.01	42.47	109.16	197.66	Chadronian	CO	adult
DMNS 895	*Trigonias*	41.41	48.31			43.40	48.52			Chadronian	CO	adolescent
DMNS 897	*Trigonias*	51.10	48.50	117.67	194.82	51.22	47.41	119.42	213.45	Chadronian	CO	senior
DMNS 949	*Trigonias*	50.32	47.49	118.94	203.15	51.33	48.18	121.29	209.44	Chadronian	CO	adult
DMNS 953	*Trigonias*	51.93	46.04	115.68	196.47	52.23	46.55	118.93	197.71	Chadronian	CO	senior
DMNS 954	*Trigonias*	48.76	47.36			47.57	46.72			Chadronian	CO	adolescent
DMNS 995	*Trigonias*	48.02	46.15			47.63	47.28			Chadronian	CO	adolescent
FMNH 44706	*Trigonias*					35.00	34.45			Chadronian	SD	
FMNH P 15772	*Trigonias*	48.25	46.94			47.04	47.05			Chadronian	SD	
FMNH PM 14557	*Trigonias*	49.95	45.50	116.20	210.25	49.90	47.72	119.39	219.41	Chadronian	CO	
FMNH PM 49917	*Trigonias*	32.75	33.02							Chadronian	SD	
FMNH PM 50167	*Trigonias*						39.32			Chadronian	CO	
FMNH UC 375	*Trigonias*	40.95	46.19	123.90						Chadronian	SD	

Specimen #	Genus	RM2w	RM2l	RM1-M3	RP1-M3	LM2w	LM2l	LM1-M3	LP1-M3	NALMA	State	Age
SDSMT 2996	*Subhyracodon*	49.40	44.63	117.18	203.59	46.17	43.75			Orellan	SD	adult
SDSMT 30115	*Subhyracodon*	42.85	39.53	102.92	196.24	43.51	38.81	103.94	197.89	Orellan	SD	adult
SDSMT 3649	*Subhyracodon*	41.77	36.93			39.24	36.72			Orellan	SD	adult
SDSMT 38813	*Subhyracodon*					42.39	45.21	114.19	210.14	Orellan	SD	adult
SDSMT 38814	*Subhyracodon*	42.12	44.00	112.03		42.36	44.86	113.54		Orellan	SD	adult
SDSMT 39311	*Subhyracodon*	44.43	44.22	109.15	200.00	45.25	43.63	110.59	207.84	Orellan	SD	adult
SDSMT 40407	*Subhyracodon*	44.51	41.93	109.23	208.38	45.56	43.49	112.59	210.64	Orellan	SD	adult
SDSMT 50354	*Subhyracodon*	41.52	40.68	106.85	201.34	43.49	41.75	109.70	198.59	Orellan	SD	adult
SDSMT 52932	*Subhyracodon*	43.93	44.50	109.32	209.73	44.93	44.33	111.22	210.04	Orellan	SD	adult
SDSMT 601	*Subhyracodon*	42.35	42.41	107.34		42.33	42.78	108.82	201.50	Orellan	SD	adult
SDSMT 7972	*Subhyracodon*	46.49	49.35	125.20	234.51	47.85	47.51			Orellan	SD	adult
SDSMT 82001	*Subhyracodon*	42.75	40.35	102.92	192.88	43.45	42.12	102.10	193.75	Orellan	SD	adult
UCM 20488	*Subhyracodon*						33.95	88.52	167.82	Chadronian	CO	adult
UCM 20494A	*Trigonias*	48.96	46.80	120.19		50.99	47.65	120.42		Chadronian	CO	adolescent
UCM 20494B	*Trigonias*	48.03	47.59	111.30		47.45	46.30			Chadronian	CO	adolescent

Specimen #	Genus	RM2w	RM2l	RM1-M3	RP1-M3	LM2w	LM2l	LM1-M3	LP1-M3	NALMA	State	Age
UCM 20516		37.62	38.92			39.72	39.44			Chadronian	CO	adult
UCM 22761	*Subhyracodon*	41.49	41.32							Orellan	SD	adolescent
UCM 43697	*Trigonias*	52.28	49.50			50.00	47.96			Chadronian	CO	adolescent
UCM 43698	*Trigonias*									Chadronian	CO	adult
UCM 48395	*Subhyracodon*					40.65	38.43	107.49	207.56	Orellan	WY	adolescent
UCM 68915	*Trigonias*	46.30	45.50			47.37	46.70			Chadronian	CO	adult
UCM 87233	*Subhyracodon*	49.53	49.05	119.08	226.45					Orellan	NE	adult
UCM 89752		49.22	47.57			50.18	49.46			Chadronian	CO	adolescent
UCM 89755		41.46	44.76			45.47	45.09			Chadronian	CO	adolescent
UCM 89758		45.70	42.45			46.41	41.61			Chadronian	CO	adolescent
UCM 89765	*Trigonias*	51.66	49.07	125.21	218.24	52.28	47.81	123.69	216.00	Chadronian	CO	adult