Digging Past the Dinosaurs?
Locomotor Trends and Mammalian Survivorship at the K–Pg (Cretaceous/Paleogene) Boundary

A Senior Honors Thesis

Presented in Partial Fulfillment of the Requirements for graduation *with research distinction* in the undergraduate college of The Ohio State University

by

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May 2008

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Abstract

Sixty-five million years ago a bolide approximately 10 km in diameter collided with the Earth. This event triggered global devastation and a mass-extinction event, the Cretaceous-Paleogene (K-Pg) extinction, signaling the end of the "Age of Dinosaurs." Non-avian dinosaurs are the most famous victims of the impact, but other groups such as ammonite cephalopods, angiosperms and mammals were severely affected by the ecological consequences of this catastrophic event. However, there were survivors.

In 2004 Douglas S. Robertson et al. described the geophysical scenario surrounding the impact event including a global thermal pulse lasting 2 to 20 hours caused by infrared radiation (IR) from falling impact ejecta. The authors suggested all terrestrial survivors of the impact event were capable of buffering the resulting 10 kW·m^{-2} of power (the thermal equivalent of an oven on broil) by insulating themselves below ground or underwater. Called the "Sheltering Hypothesis" the hypothesis suggests the survivors of the impact event were morphologically equipped for fossorial or semi-aquatic locomotion.

To test the hypothesis I turned to the mammalian fossil record. Other groups such as arthropods and birds exhibit differential survival patterns, but poor sampling and conservative morphologies make it difficult to test the Robertson hypothesis. Regardless of clade, specific locomotor demands produce predictable post-cranial skeletal structures in mammals that indicate ecological roles in ancient and modern contexts. In order to conduct this study, indicators of locomotor behavior were based on isolated post-crania as the mammalian fossil record near the K-P does not preserve articulated specimens or complete disarticulated specimens.

One of the most reliable indicators of fossorial (digging) behavior is the relative length of the olecranon process of the ulna. Utilizing Ohio State's Higher Vertebrates collections, I first demonstrate extant mammals can be grouped into locomotor guilds based on this feature using linear measurements and linear regression. Unfortunately, complete fossil ulnae are usually not preserved, so a novel proxy based on the length of the semi-lunar notch is described. This proxy is based on correlations to ulnar length based on linear regression analysis. This proxy allows us to understand the locomotor guilds of mammals before and after the K-P impact. Using fossils from the Pioneer Trails Regional Museum in North Dakota and the University of California Museum of Paleontology at Berkeley I compare the locomotor diversity of mammals before and after the impact event.

Preliminary results refute the Robertson hypothesis and suggest mammalian survivorship was more closely related to body size than locomotor guild. Derived adaptations for fossorial or semi-aquatic locomotion are apparent before the boundary including the likely swimmer *Didelphodon vorax*, a large marsupial that went extinct at the boundary. Survivors appear to be scansorial generalists. Future areas of inquiry include incorporating more post-cranial structures and material into the sample, and examining the consequences of a "Lilliputian" mammalian community on extinction recovery patterns throughout the ecosystem.

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-The Rolling Stones
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Introduction

The Cretaceous-Paleogene (K-P) boundary marks the most recent of the "Big Five" mass-extinction events (Sepkoski, 1981). 65.95 million years ago an estimated 70% of species went extinct (Kuiper et al., 2008; Novacek, 2007) leaving behind a devastated ecosystem. Figure 1 shows the relevant geologic time intervals for this discussion. In 1980 Luis Alvarez, Walter Alvarez, Frank Asaro and Helen Michels first proposed the "Impact Hypothesis." The researchers recorded a high (9 parts per billion) concentration of iridium between two limestone formations representing the Late Cretaceous and Paleocene in Gubbio, Italy. They hypothesized the rare element must have an extraterrestrial source, as iridium is exceedingly rare in surface sediments but highly concentrated in asteroids and comets. Alvarez et al. calculated a bolide 10 km in diameter must be the source of the "iridium spike." In 1991 the site of the impact was described on the Yucatan Peninsula of Mexico by Hildebrand, Penfield and company (Alvarez, 1997). The now obscured crater is 65 million years old and bears evidence of shocked quartz, impact breccia and spherules, indicators of a massive impact event (Alvarez, 1997). Since Alvarez et al. first described the iridium spike in Italy, K-P boundary sections have been described all over the world from Denmark to Antarctica (Novacek, 2007). The global iridium spike, shocked quartz and clay spherules reveal an apocalyptic end-Cretaceous world.

The bolide collided with the Yucatan Penninsula and Gulf of Mexico ejecting debris from the impact site and the asteroid into the atmosphere, blotting out the sun, precipitating acid rain and sending tsunamis ripping across the Gulf of Mexico (Alvarez, 1997). The impact site is called the Chicxulub Crater. Such devastating environmental changes presumably drove rapidly increased extinction rates and decreased origination rates during the end-Cretaceous.

Despite the global nature of the extinction, the bolide impact and its environmental

consequences did not affect all groups of organisms with similar severity. In the oceans, the ammonite mollusks went completely extinct along with marine reptiles and as much as 95% of plankton species (Novacek, 2007). On land, 57% of plant species went extinct at the K-Pg and the most popular victims of the extinction, the non-avian dinosaurs, were completely eradicated from the biosphere. Other terrestrial groups, such as the marsupial mammals, were also devastated by the extinction in North America and possibly Asia. However, other mammal groups such as the orders Multituberculata and Eutheria (placental mammals) survived the extinction with higher species diversity than the marsupials. Crocodilians and turtles all survived the K-P without severe decreases in species abundance. The pattern of this differential survivorship, especially in non-marine vertebrates, has not been adequately explained.

The Sheltering Hypothesis

In 2004 Douglas Robertson, Malcolm McKenna, Owen Toon, Sylvia Hope and Jason Lillegraven proposed a model that allowed the immediate selective pressures of the bolide impact to drive differential survival in terrestrial environments. The researchers based their geophysical calculations on a bolide 10-15 km in diameter with a mass of $1\text{-}4\mathrm{x}10^{15}$ arriving at a 45 degree angle to the Earth's surface capable of producing a transient cavity 80-100 km in diameter and a more stable, multi-ring basin 170-200 km in diameter. This crater is the Chicxulub Crater, a gravitational anomaly on the Yucatan Peninsula and under the Gulf of Mexico. They argued the earthquakes, tsunamis and acid rain caused by the impact would have had regional effects, but not the global environmental effects that would drive global extinctions. Instead, the primary selective agent of the impact event was a short-term infrared radiation thermal pulse.

According to the Hildebrand et al (2004) the infrared radiation (IR) flux was a global, 2

to 20 hour long pulse of intense radiation triggered by the particles ejected into the upper

atmosphere by the bolide. These particles would have become incandescent as they traveled

through the upper atmosphere at 7-8 km/s causing the temperature of the upper atmosphere to

rise to 800-1100 K for several hours. Under normal conditions the Earth's surface receives a

solar flux of ~1.4 kW$^.$m-^{2}. Melosh et al. (1990) calculated a thermal flux of 10 kW$^.$m-^{2} was

produced immediately after the impact - the power equivalent of "a domestic oven set on broil".

The most intense thermal energy would have been concentrated within 6000 km of the impact

site and at the antipode of the impact, but the global thermal flux would have been sufficient

across the globe affecting all exposed, terrestrial biota. The thermal flux ignited global wildfires,

creating the ash, soot and charcoal layer that has been globally described from the K-P boundary

of Europe and New Zealand along with the iridium anomaly. Robertson et al. are careful to

emphasize that the primary selective agent driving extinction during the first hours after the

impact was infrared radiation, and not the slightly later effects of the global wildfire (though they

do not discount the selective pressures of such an event).

The IR flux originated from the sky itself, giving unsheltered organisms no safe place to

retreat regardless of their habitat in either dense forest or arid desert. The only safe place to

avoid incineration was below ground or underwater. Soil is a superior insulator against infrared

radiation with a thermal conductivity of 0.0024 to 0.024 W/(m*K) at a density of ~1500 kg/m^3

(Mitchell, 1993). Robertson et al. reasoned that an animal in the most extreme of hypothesized

IR fluxes, ~1000 K for 2 to 20 hours, would only need to burrow 10 cm below the surface of the

Earth to insulate itself during the thermal pulse. Sheltering from heat underground is a strategy

used by modern organisms during forest fires (Boerner, 2006).

Water also acts as an IR insulator with radiant energy dissipated in the surface

micrometers of water. If organisms were further than 6000 km from the impact site, the surface air temperature may have only raised ~10 K. Such a change would allow sheltered organisms to breath without searing their lungs, while the radiation absorbed by organisms not sheltered beneath the soil or water would have been lethal. Animals such as champsosaurs (Choristodera), crocodilians and turtles could have survived the thermal pulse by submerging their bodies while still breathing. This physical scenario makes the IR flux irrelevant to marine ecosystems, as all organisms would have been adequately insulated. Marine ecosystems likely collapsed due to reduced primary productivity during the "nuclear winter" caused by particles suspended in the upper atmosphere, blocking the sun.

Robertson et al. suggest all non-marine vertebrates that survived this IR flux were sheltered below ground or underwater. This does not imply that all survivors capable of IR insulation survived to populate the Cenozoic Earth. The secondary effects of wildfire, acid rain and decreased primary productivity would have also driven extinction, but these secondarily extinct organisms should all have been capable of fossorial (digging) or semi-aquatic (swimming) locomotion, having survived the intense thermal flux.

Testing the Sheltering Hypothesis

In their 2004 paper Robertson et al. listed the non-marine vertebrates that went extinct at the end of the Cretaceous and the non-marine vertebrates that persisted into the Cenozoic (Table 1). The authors posited the "Reasons for Extinction" and "Means for survival" based on the sheltering ability of each group. Of course, these gross aggregates of species cannot account for the diversity of locomotion that may exist within each group; a diversity that has never been fully explored. A fossorial or semi-aquatic mammal has never been described from the Late Cretaceous (except perhaps by Longrich, 2005) though increasing evidence of earlier Mesozoic

mammalian locomotor diversity is becoming abundant (Martin, 2006). Robertson and co-authors are suggesting a locomotor diversity in the Maastrichtian (Late Cretaceous) fauna that has never been demonstrated.

Locomotion is directly connected to post-cranial adaptations. The post-cranial fossil record of non-marine vertebrates in the Late Cretaceous is not well catalogued or well described and has never been placed in an evolutionary context. Further, post-cranial material has never been used to test for locomotor adaptations as the main factor driving differential survival. The reason for this paucity of post-cranial descriptions is the fragmentary nature of the post-cranial record. The Western Interior of North America (New Mexico, Colorado, Wyoming, Montana, North Dakota, Alberta and Saskatchewan) contains all of the terrestrial boundary sections in the world (Figure 2). The most thoroughly examined formations from the region are the Hell Creek and Lance formations from the Late Cretaceous (Maastrichtian) and the Tullock and Ludlow formations from the Paleocene (Puercan). Lithologically these formations are predominantly fine to medium grained fluvial sandstones with occasional coal seams, silt horizons and clay deposits. Such stratigraphic and depositional conditions do not readily preserve articulated post-crania. Post-cranial material is often fragmentary and difficult to assign to taxonomic categories lower than family or even order. However, in the case of the Sheltering Hypothesis, taxonomic categories are not immediately relevant. I am simply interested in identifying the presence of digging or swimming adaptations in the Maastrichtian and Puercan and whether these adaptations affected survivorship.

Based on the poorly understood post-cranial fossil record, I decided to test the Sheltering Hypothesis. First, I had to identify a group of terrestrial vertebrates with 1) a relatively abundant post-cranial fossil record from the Late Cretaceous and Paleocene, 2) differential survival across

the K-P boundary, 3) the potential for locomotor diversity driving survivorship and 4) readily recognized, isolated morphology indicating locomotor adaptation.

Birds exhibit differential survivorship, but the fossil record of the group is very poor and the post-cranial skeletal adaptations to fossorial or semi-aquatic behavior are not well constrained in isolated fossils (Hildebrand and Goslow, 2001). Turtles and crocodilians have a robust fossil record, but do not exhibit readily recognized morphological adaptations to specific locomotor groups especially in isolated post-crania. The ideal group for testing the Sheltering Hypothesis was Class Mammalia.

Mammals in North America have a well-studied fossil record in North America across the K-P (Archibald, 1996; Clemens, 2002; Hunter and Archibald, 2002). Most studies of mammalian survivorship and extinction have focused on the dental fossil record, yielding information on species level trends of survival (Table 2) and geographic radiations. Marsupials nearly go extinct in North America after the Maastrichtian, multituberculates exhibit differential survivorship pattern and eutherians cross into the Puercan with some taxonomic turnover. Mammals also have a prolific post-cranial fossil record that has been underutilized and under described, as post-crania are not readily connected to high taxonomic identifications such as genus and species. Mammals also exhibit consistent, convergent morphologies for derived locomotor groups – or locomotor guilds – that can be identified without a fully articulated skeleton.

Mammalian Post-cranial Adaptations

I considered six possible mammalian locomotor guilds in the Late Cretaceous and Paleocene: Fossorial (diggers), Semi-Aquatic (swimmers), Arboreal (climbers), Scansorial (arboreal and terrestrial), Cursorial (derived runners), and Volant (flyers and gliders). A variety

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of post-cranial indicators including radial head shape, distal phalanx morphology (Macleod and Rose, 1993), the fusion and position of the pelvic girdle (Shockey et al. 2007), ankle structure (Szalay, 1994; Polly, 2007), caudal vertebrae (Qiang, 2006) and the relative length of the ulnar olecranon process (Shockey et al., 2007) can be used to assign fossil mammals to these locomotor categories. Many of these indicators have never been observed or scrutinized in the fragmentary fossils of the Maastrichtian or Puercan mammalian faunas.

For this study I was primarily interested in those post-cranial adaptations directly related to fossorial or semi-aquatic locomotion. The key indicators of digging are long, robust distal phalanges on the manus, a relatively short axial skeleton, a robust pelvic girdle with fused caudal vertebrae, a short neck, reduced eye sockets, short, robust cervical vertebrae and a long olecranon process relative to ulna length (Hildebrand and Goslow, 2001). Adaptations to semi-aquatic behaviors are subtler and include laterally widened, dorso-ventrally flattened caudal vertebrae, long distal phalanges for webbed feet, a generally fusiform body and denser cortical bone (Hildebrand and Goslow, 2001; Thewissen and Fish, 1997). Ideally all of these criteria would be evaluated before arriving at a species' locomotor guild, but the fossil record of mammals in the Western Interior does not allow all of the criteria to be considered. Full pelvic girdles are not preserved and phalanges are not found associated with a manus.

The Ulna

Of all the known morphological indicators enumerated above, the relative length of the olecranon process to the length of the ulna is the most reliable indicator of fossorial locomotion. It therefore became the primary focus of my research on the skeletons of modern and ancient mammals. The ulna, at the most basic biomechanical level, is a lever (Figure 3). The fulcrum is the semi-lunar (trochlear) notch that articulates with the trochlea of the humerus. The ulnar shaft

distal to the semi-lunar notch is the load arm of the lever along with the manus and radius. The shaft sustains the large out-forces exerted by an animal as it interacts with the environment (i.e. moving soil or water, or resisting the substrate running or climbing). The lever arm is the olecranon process, the projection of bone distal to the semi-lunar notch. The olecranon processes is the point of insertion for the triceps, the muscles responsible for extending the forearm and exerting force on the forelimb during digging, running *et cetera*. The longer the olecranon process relative to the length of the ulna, the greater the out-forces exerted by the triceps on the forearm. Diggers have long olecranon processes for moving dense soil. Cursers and arborealists have shorter processes for more rapid but less powerful forearm flexing and volant mammals have extremely small olecranon processes allowing for full extension oat the elbow for expanding the flying or gliding membrane (Hildebrand and Goslow, 2001).

Within the fossorial guild there are several methods of digging, each with specific adaptations. The exceedingly derived diggers such as moles create their tunnels through humeral rotation, pivoting their massive manus on a short, nearly circular humerus. Rotational diggers also have laterally deflected projections on the olecranon process, creating greater surface area for muscular attachments. Such derived adaptations to digging are easily recognized in the fossil record (Hopkins, 2007). Scratch digging is a much more common form of digging among mammals and is more strictly dependent on the length of the olecranon process. Scratch diggers create a burrow or a shallow hole by rapidly extending and flexing the forelimb. Proficient scratch diggers include the armadillo (*Dasypus novemcinctus)* and echidna (*Tachyglossus aculeatus)*.

The relationship between olecranon length and ulnar length has long been recognized and utilized as an indicator of fossorial behavior in large modern and extinct mammals (Shockey et

al., 2007; Van Valkenberg, 1987) but it has rarely been quantified with a large sample size representing a wide range of locomotor guilds and body sizes (Hildebrand and Goslow, 2001). Using mammalian skeletal specimens from the Ohio State Museum of Biological Diversity's Division of Higher Vertebrates and the University of California Museum of Paleontology (UCMP) comparative osteology collection, I generated a sample representing several species from each mammalian locomotor guild and a wide range of body sizes from each guild. The species used in the modern sample are listed on Table 3 with their locomotor guild. The main locomotor guild for each species was identified using ecological and behavior data recorded on the University of Michigan's Animal Diversity Web <http://animaldiversity.ummz.umich.edu>.

The Modern Analogues

In assembling the list of modern species included in this study, emphasis was placed on taxonomic, locomotor, and size diversity. The three modern clades of mammals – Monotremata, Metatheria (marsupials), and Eutheria (placentals) – are each represented in the data set. This diversity is particularly important when comparing modern faunas to the Cretaceous when marsupials were more abundant and diverse in North America than they are today. Cretaceous and Paleocene mammalian faunas also included Allotheria, or the multituberculates, a clade of morphologically distinct mammals with a mixture of derived features such as blade-like premolars and primitive features such as the spiral-like articulation of the humero-ulnar joint (Jenkins and Krause, 1983). Many aspects of the multituberculate post-cranial skeleton place the clade's divergence from therian mammals after the divergence of the monotremes. Adaptations to fossoriality and semi-aquatic behavior in mammals seems consistent regardless of clade (i.e. a long olecranon process), but it is important to consider these adaptations in a phylogentic context as well.

It is also important to note that all semi-aquatic mammals included in this study are also fossorial. *Ondatra zibethicus, Ornithorhynchus anatinus,* and *Castor canadensis* are each "bank burrowers" that forage in or near bodies of freshwater while sleeping and caring for their young in burrowed nests along the shore. In semi-aquatic mammals, propulsive force in the water is created by the hind-feet or the dorso-ventral flexation of the spine and tail (Thewissen and Fish, 1997). The forelimb may be webbed, but is used for steering through the water and excavating the burrow. Therefore, given the trend of coupled fossorial and swimming behavior in the mammalian sample utilized in this study, I predicted the semi-aquatic animals would be closely associated with the fossorial animals, especially when the forelimb was considered isolated from swimming indicators like webbed feet. A cursory review of ecological descriptions of freshwater, semi-aquatic mammals, reveals most are both swimmers and bank-burrows. The same was probably true of semi-aquatic mammals in the Maastrichtian and Puercan.

In this study *Cynocephalus volans* (flying lemur) is considered a volant mammal even through it is more accurately described as a *glissant* or gliding mammal. The flying lemur is among the largest glissant mammals and is capable of gliding over 100 m with minimum loss in altitude (Kuo, 2000). Chiropterans (bats) are the first and only fully volant mammals. While the precise timing of their origination is controversial, bats radiated in the Eocene. Bats were probably not part of either Late Cretaceous or Early Paleocene ecosystems (Rose, 2006). If flying or gliding mammals existed in the Cretaceous, they likely resembled *C. volans* morphologically. Thus this species is associated with the bats for the purpose of this study.

The modern ulna sample also includes a variety of species from the order Rodentia. The most taxonomically diverse order of mammals is also ecologically and morphologically diverse with derived diggers such as *Spermophilus lateralis*, the tawny colored gopher, derived climbers

such as *Sciurus carolinensis*, the gray squirrel, and derived swimmers such as *Castor canadensis*, the beaver. The rodent sample ranges in body size, from the 0.023 kg *Peromyscus leucopus* (white-footed mouse) to the 8 kg *Hystrix brachyura* (Malayan porcupine). Including a range of data from a single order allows a phylogenetic "control" to be introduced into the study. If the rodents share morphological space when plotted, regardless of locomotor guild, then phylogenetic associations will need to be more explicitly considered in the interpretation of the data.

Methods: Olecranon Process and Ulna

Each species is represented by one right ulna, though the left was measured if the right was not available. Using digital calipers accurate to one-hundredth of a millimeter, the olecranon process was measured from the raised proximal margin of the semi-lunar notch to the furthest projecting, proximal-most point on the olecranon process. Ulnar length was measured from the terminus of the styloid process to the terminus of the olecranon process. All subsequent measurements were performed using the same digital calipers.

Results: Olecranon Process and Ulna

Figure 3 shows logarithmic values of olecranon length compared to the logarithmic values of ulnar length with a linear regression for each locomotor guild. A clear separation of predicted guilds is evident from the plot. Fossorial and semi-aquatic animals with high olecranon values cluster together, separate from scansorial, cursorial and arboreal mammals with relatively smaller olecranon processes. The final major group is the volant guild with much reduced olecranon processes and long ulnae relative to body size. This distribution of species is quantitative support to the qualitative observation that a long olecranon indicates a fossorial animal.

The results also indicate adaptations to specific locomotor behavior is consistent across clades, indeed, across the entire Class Mammalia. *Ornithorhynchus anatinus* (duck-billed platypus) is a monotreme, but is closely associated with *O. zibethicus* (muskrat) a placental mammal. The two species converged on similar ecological behavior – semi-aquatic, freshwater foragers – and morphological adaptations despite their phylogenetic remoteness from each other. Similar support for consistent ecomorphology regardless of phylogenetic associations is found in the rodents. Each species in the sample is associated with their locomotor guild rather than other members of the Order Rodentia.

Of all the locomotor guilds under consideration, the arborealists exhibit the smallest R^2 value of 0.64, indicating the regression does not "fit" well and the data points are more scattered. This statistical evidence of arboreal morphological variability is supported by a visible inspection of Figure 3. *Didelphis virginiana* (Virginia opossum) and *Cebus sp.* (capuchin monkey) have similar body sizes, prehensile tails, and arboreal habits, but the olecranon process of the *D. virginiana* is clearly longer, almost associating the species with fossorial animals. The Virginia opossum is a consummate generalist. It spends a great deal of time in the trees, but is equally capable of terrestrial locomotion, and even scratch-digging with its forelimbs. Many arboreal animals are capable of similar generalization of locomotion. Squirrels are infamous scratch burrowers that cache food in the soil. However, none of these arboreal animals are proficient enough at digging to create a burrow deep enough to fully insulate themselves from two to twenty hours of infrared radiation. Olecranon process length is a useful metric for isolating proficient diggers, but does not fully describe arboreal abilities.

Appendix 1 details the absolute lengths and logarithmic lengths of the olecranon process and ulna in each species.

The Ulnar Fossil Record

Isolated mammalian post-cranial material from the Mesozoic or early Paleogene is not well-cataloged by most museums. Most of this material is very small and is found in screen washed samples along with mammalian jaw fragments and teeth. These dental remains are easily assigned to genus and often species. In fact, many species names are tied directly to teeth with no known associated post-crania. Teeth have incredible utility for answering taxonomic questions concerning paleobiogeography, evolutionary rates, and diet and are rapidly catalogued after discovery. Post-cranial material is not as well understood in a taxonomic context, though investigators such as Szalay (1994) have made attempts to use dense post-crania such as the tarsal bones to recognize species. Because most post-crania is not assigned a taxonomic label, it is often placed in a jumble called "miscellaneous post-crania" and never given a specimen number.

One of the primary tasks of this study was to use this jumbled, ostensibly useless isolated post-crania. The first task was separating reptile, fish and dinosaur material from mammalian material. The fossils included in this study are from the Vertebrate Collections at the University of California Museum of Paleontology (UCMP) at the University of California-Berkley and the Vertebrate Collection at the Pioneer Trails Regional Museum (PTRM) in Bowman, ND. The material from the UCMP is predominantly the result of decades of collecting and research by Dr. William Clemens and colleagues in Garfield County and McCone County in eastern Montana with fossils from the latest Maastrichtian and Puercan, effectively straddling the K-P boundary. The PTRM collections are from southwestern North Dakota, collected by Dr. John Hunter, Dean Pearson, and colleagues. The PTRM post-crania included in this examination are restricted to the Maastrichtian. See Figure 4 for the geographic context of these collections. This time-

intensive search for mammalian post-cranial material produced isolated pelvic fragments, distal humeri, proximal femurs, assorted metatarsals and metacarpals, phalanges, vertebrae, radial heads and proximal ulnae. The focus of the search was on the proximal ulnae, though the other post-cranial elements will hopefully be described and utilized in future research.

One of the problems with the ulna (really with all long bones) is its fragility. No complete, isolated ulnae were recovered from either museum. All thirty ulnae were fragments that preserved the semi-lunar notch and a complete olecranon process, but only a small proportion of the shaft (Figure 5 illustrates the common preservation of the ulna from Montana and North Dakota) rendering the relative length of the olecranon process an apparently useless metric for classifying the locomotor guilds of fossil faunas.

Ulna Length Proxy

The second goal of this study was to find a linear measurement on the dense, frequently preserved proximal ulna that scaled proportionally to ulna length. If such a measurement could be found, the length of the olecranon process could be compared to this novel metric and the locomotor diversity of a fragmentary fossil fauna described. Thirteen linear measurements were taken on different aspects of the proximal ulna of each of the modern species used above (Table 3). The description of these measurements are listed and described on Table 4 and Figure 6.

The log values of ulnar length were first plotted and placed in rank order. The linear regression of this line fit well with an R^2 value of 0.984. The rank order of ulnar length did not reflect locomotor type (Figure 7), but does not strictly correlate to body size as small glissant, arboreal and volant mammals have long ulnae relative to body size. Because the body sizes of the fossil mammal are not known, a ulnar/body size comparison was not performed.

After calculating regressions between the collected linear measurements (Appendix 2)

and ulnar length, "Length of the Semilunar notch" was found to have the best-fit ($R^2 = 0.828$) to ulnar length (Figure 8). It also best correlated with the rank order of species based on ulnar length (Figure 9). I concluded that the length of the semi-lunar notch scales proportionally to ulnar length in mammals and can be used as a proxy for ulnar length when the entire bone is not preserved.

Note that the fit of the regression between ulna length and semi-lunar notch length becomes higher ($R^2 = 0.922$) when the "Volant" guild (*C. volans, M. lucifugus* and the unlabled Microchiropteran) is removed from the regression calculation. These animals have exceedingly long ulnae compared to a short semi-lunar notch. There are two morphological features required of flyers that may produce this observation. First, in volant mammals the ulna is disproportionate to the size of the animal as it supports the wing membrane (patagium) when fused with the radius. Bats in particular create a large surface area on the wing by extending the length of the phalanges, radius, ulna and humerus relative to their body size. Second, the length of the semilunar notch reflects the length of the trochlea of the humerus, an articulation that must be tightly locked to support the airfoil of the wing. The necessary lock of the elbow for flight makes the semi-lunar notch more narrow.

With the ulna length proxy identified, the length of the semi-lunar notch was plotted against the length of the olecranon process (Figure 10). As expected, major locomotor guilds differentiate as they did when the olecranon process was compared to the length of the ulna and each guild exhibits different regression equations (Table 5). This represents a simple, novel method of determining the locomotor guild of an extinct mammal based on fragmentary remains.

Applying the Proxy: Locomotor Diversity in the Cretaceous and Paleocene

The length of the olecranon process and length of the semi-lunar notch were collected

from each of the fossil ulnae from UCMP and PTRM vertebrate collections along with locality data describing the age of the site. Only Maastrichtian (Late Cretaceous) and Puercan (Early Paleocene) ulnae are considered here. Figure 11 shows each fauna overlaying the regression lines calculated for each locomotor guild. Regression lines and R^2 values were calculated for each fauna to evaluate the amount of variation within the fauna. The Maastrichtian sample R^2 value is 0.237 indicating a wide variation in olecranon length and therefore a diversity of locomotor guilds during the Late Cretaceous. The Early Paleocene sample has a higher R^2 value (0.704) indicating a better fit for the regression calculation and less variation in the sample and a limited range of locomotor guilds in the Early Paleocene, though this sample is much lower than the Maastrichtian sample.

Discussion

Testing the Sheltering Hypothesis required an analysis of mammalian locomotor diversity that had never been performed on mammalian faunas in the Late Cretaceous or the Early Paleocene. Discussions of diet and diversity are inherent in considering these faunas, but the locomotor adaptations are integral to understanding a mammal's role in its environment, adaptations sometimes referred to as ecomorphology. Historically, mammals during the entire Mesozoic were considered ecomorphologically limited, stereotyped as nocturnal, generalist rat-like or opossum-like animals squeezing into the narrow terrestrial niche left by the dominant dinosaurs (Lillegraven et al., 1979; Rose, 2006). Recent discoveries of exceptionally preserved, articulated skeletons from Mesozoic formations in China have called this stereotype into doubt. *Fruitafossor*, described by Luo and Wible (2005) is clearly a large fossorial mammal from the Jurassic, complete with robust distal phalanges on the manus, a long olecranon process, and fused sacral and caudal vertebrae. *Castorocauda*, described by Qiang et al. (2006) is a Jurassic

semi-aquatic mammal with a broad, beaver-like tail, webbed feet and burrowing adaptations (i.e. a long olecranon). Even a gliding mammal, *Volaticotherium*, has been described from the Jurassic (Meng et al. 2006) revealing mammals took to the air before dinosaurs. These mammals were ecomorphologically derived and clearly occupied specific niches in their Jurassic ecosystem. If these animals had not been so exquisitely preserved, their locomotor derivedness probably would not have been observed as their teeth are not particularly specialized.

The diversity of Mesozic mammals should not be surprising. Non-avian dinosaurs were terrestrial, megafauna. Insectivorous, herbivorous, gumivorous and frugivorous niches, occupied by mammals today, were not monopolized by dinosaurs in the Mesozoic. It is likely mammals were exploiting these resources. Recently discovered new Chinese species demonstrate mammals were diverse ecologically and taxonomically in the Mesozoic occupying niches comparable to modern small-mammal niches.

By proposing the Sheltering Hypothesis and asserting fossorial and semi-aquatic mammals preferentially survived the end-Cretaceous extinction, Robertson et al. (2004) assumed there was a previously undocumented diversity of locomotion in North American mammals. Figure 11 supports this assumption. Mammals in the Late Cretaceous at a range of body sizes are clearly ecomorphologically diverse. For example PTRM 3901 is probably a small, marmoset-sized mammal with fossorial/semi-aquatic adaptations. Several other specimens are tightly associated with the fossorial trendline. Some of the larger specimens (UCMP 127393, UCMP 174601) are closely associated with data recorded for *Didelphis virginiana*, indicating arboreal and terrestrial locomotor types were also present in the Late Cretaceous. Perhaps the most intriguing cluster of ulnae is the group of specimens in the Maastrichtian closely associated with the volant trendline and clustered around the *Cynocephalus volans* data point. All of these

specimens are multituberculates, an order with recognized arboreal affinities (Krause and Jenkins, 1983). Is it possible these arboreal mammals had a membrane similar to the patagium of *C. volans*? A glissant species, *Volaticotherium,* is known from the Jurassic already (Meng et al., 2006). Further investigation is necessary for these specimens. Regardless of the specific insight gained from further research, we can assert with confidence that there was an ecological diversity of Maastrichtian mammals that was previously unsupported.

The Puercan offers a very different mammalian fauna from the Maastrichtian. According to the Sheltering Hypothesis, differential survival of fossorial and semi-aquatic mammals would lead to a Puercan fauna populated by mammals with these locomotor indicators at the range of body sizes exhibited by mammals in the Late Maastrichtian. Locomotor guild should be the primary force of selective extinction pressure, not body size. The Puercan fauna does not demonstrate a wide range of locomotor diversity. Three of the specimens are small and closely associated with scansorial and arboreal mammals like *Glis glis* (dormouse) and *Glaucomys volans* (flying squirrel). UCMP 174458 is a likely fossorial mammal, falling directly on the fossorial regression trend line. The exclusive survival of all derived swimming and burrowing mammals is not supported. There were large, derived diggers and swimmers in the Maastrichtian (see *Didelphodon* discussion) that did not survive. The end-Cretaceous extinction among mammals favored small generalists, curtailing the abundant diversity of the Late Cretaceous faunas. Sheltering didn't matter.

Ecological flexibility and rapid reproduction associated with small body sizes were the premium adaptations favored in survivors. This observation calls into question the Sheltering Hypothesis and the relative importance of the infrared radiation thermal flux as a dominant selective factor driving extinction in the Maastrichtian ecosystem. Subsequent ecological

collapse and limited resources due to "nuclear winter" conditions including reduced biodiversity in plants and arthropods (Wilf et al. 2006) ultimately drove survivorship among mammals. These conditions evidently allowed small mammals to survive.

The survival of small body sizes has been observed before, but has never been placed in an ecological context. These surviving animals were not just small. They were not derived exhibiting no clear morphological indicators of arborality, fossorality *et cetera* in the forelimb. It is possible there was selection for smaller body sizes during the stressful events in the aftermath of the impact. The reduction of body size among survivors during mass extinctions is termed the "Lilliput Effect" and has been observed in surviving faunas as an adaptation for less energy input and more rapid reproduction (Poulin , 1995; Weihong et al. 2006). The Lilliput Effect doesn't necessarily drive speciation, simply the temporary selective pressure for small body sizes. The reoccurrence of pre-extinction body sizes in a fauna indicate the return of more healthful environmental conditions, a possible secondary insight that can be understood with this ulna data.

One issue that arises even through a cursory examination of the data plot is sample size. The Maastrichtian sample clearly contains more data points (25 ulnae) than the Puercan (4). There are several factors driving the smaller Puercan sample size. 1) The Puercan average mammalian body size is smaller than the Maastrichtian. Small long bones are not easily fossilized or collected. Note that no ulna with an olecranon smaller than that of a flying squirrel was sampled. Even the dense proximal ulna is delicate at such small sizes or can be missed during the screen-washing process. 2) The Puercan does not have the density of fossil material found in Maastrichtian localities in the Western Interior. Whether this is a product of depositional, preservational or real biological factors (there weren't that many terrestrial

vertebrates in North America after the end-Cretaceous extinction) is a subject of much debate. 3) The Puercan is frustrating to work in. Because the biota has a smaller body size in the Puercan, much of the information from these localities requires careful screen washing and matrix inspection by microscope. There is more time required to understand only a few data points. Great effort has been exerted trying to identify survivors and extinction among mammals based on the dental record (Archibald, 1996 for example), so the researcher's search image may be biased toward teeth while post-cranial elements are neglected. In this research, I attempted to correct this oversight by sorting unidentified screenwashed material, but I did not have sufficient time to sort through it all.

Didelphodon vorax: A test of sheltering vs. body size

One of the largest mammals in the Late Cretaceous is the badger-sized *Didelphodon vorax*. Large mammalian post-crania from the Maastrichtian can be reasonably associated with this species based on the large size of the mandible, though no complete or partially articulated skeleton is known. *Didelphodon* and its close relatives, the stagodont marsupials, have short, robust mandibles and bulbous premolars similar to *Enhydra* (sea otter). The premolars are often worn to the roots from a hypothesized dense diet of gastropods and bivalves. The *Didelphodon* mandible also has a thick cortex a feature noted in semi-aquatic mammals such as beavers and otters (Longrich, 2005). In the UCMP collections, a large caudal vertebra was identified by a previous researcher as *Didelphodon* based on the large size of the fossil (Figure 12). The vertebra is dorso-ventrally flattened and has laterally widened transverse processes, similar to a beaver's caudal vertebrae (Figure 13). Given this post-cranial evidence, I support the Longrich hypothesis that *Didelphodon* was a semi-aquatic animal.

This species offers a test of the Sheltering Hypothesis, independent of the conclusions

reached by the ulna. *Didelphodon vorax* was one the largest species in the Late Cretaceous. It was also a derived swimmer capable of foraging on the bottom of streams, ponds and rivers for gastropods and bivalves. The dense cortex of the mandible reduces the animals bouyance indicating *Didelphodon* was a competent diver. As it morphologically resembles both *Castor* and *Ornithorhynchus*, it is also reasonable to assert that this animal was a bank-burrower. *Didelphodon* would have been adequately sheltered from the IR pulse according to Robertson et al.'s model either in its burrow or under the first few micrometers of the water. But *Didelphodon* did not survive into the Paleocene; the species goes extinct with the non-avian dinosaurs. Body size is the primary selective pressure acting on this species, not its adaptations to sheltering, supporting the conclusions reached using the olecranon process. Small generalists repopulated the devastated early Cenozoic.

This study represents one aspect of the larger question of terrestrial stability and ecological recovery in the face of mass extinction pressures such as devastated environments, reduced biodiversity and limited resources. Continuing research can help shape conservation policy in the face of the modern anthropogenic "Sixth Mass Extinction," that is driven by extensive changes to the environment. Small generalists were successful species in the face of these pressures in the past. Mammals will likely respond in similar way to modern extinction pressures. Further research will explore how a small, generalized ecosystem recovers and diversifies after the complete collapse of the old order.

Conclusions

1) The relative length of the olecranon process compared to the length of the ulna is a reliable indicator of mammalian locomotor adaptations, especially for separating fossorial mammals from cursorial, arboreal and volant mammals.

2) Semi-lunar notch length is a valuable proxy for ulnar length. This proxy can be used on formerly useless isolated ulnar fragments to understand the ecological diversity of a fossil fauna such as the Maastrichtian or Puercan. Such proxies allow paleobiologists to understand how terrestrial ecosystems diversify and evolve based on both taxonomic diversity and ecomorphogical diversity.

3) The Late Cretaceous mammalian fauna contains a greater locomotor diversity then was previously suspected including clear fossorial, semi-aquatic, arboreal, terrestrial and even glissant mammals. This diversity is consistent with new evidence of Jurassic mammalian diversity.

4) The Sheltering Hypothesis is not supported by this study. A diversity of mammalian locomotion existed in the Late Cretaceous of North America. This diversity was devastated by the K-P extinction. Survivors were small generalists with possible scansorial to arboreal locomotor habits. Body size and ecological flexibility determined successful survivorship rather than derived adaptations to fossorial and semi-aquatic sheltering adaptations.

Areas for Further Research

I briefly discussed that I attempted to take phylogenetic history into account when considering the ulna as an indicator of a specimen's locomotor guild. Further research should

more explicitly address this question with a larger modern sample size including marsupial moles (*Notoryctes typhlops*), African golden moles (i.e. *Eremitalpa granti*), and the naked mole rat (*Heterocephalus glaber)* among others from a variety of guilds and mammalian orders. This would help more rigorously test the locomotor guilds noted with a sample of only 37 species.

While working with the UCMP and PTRM collections I did not focus exclusively on ulnae. I collected data on a variety of post-crania including tarsal bones, humeri, vertebrae, proximal femurs, scapulae and proximal tibias. Each of these will be explored for locomotor indicators so the locomotor diversity of the ulna can be corroborated by independent evidence more rigorous than one caudal vertebra attributed to *Didelphodon*. Particularly promising features include the medial epicondyle and the deltoid tuberosity, of the humerus for fossorial adaptations. The calcaneum may also be a useful indicator of digitigrade and platigrade posture (Polly, 2007), a secondary indicator of locomotor guild. Fossorial and semi-aquatic mammals tend to be platigrade while cursorial or richochetal mammals tend to have digitigrade postures. Distal phalanges have also proven useful through eigenshape analysis for distinguishing guilds (Macleod and Rose, 1993) and should be used when considering K-P boundary faunas. All post-cranial evidence should be brought to bear on both the Sheltering Hyopthesis and, more generally, the diversity of Mesozoic and early Paleogene mammals.
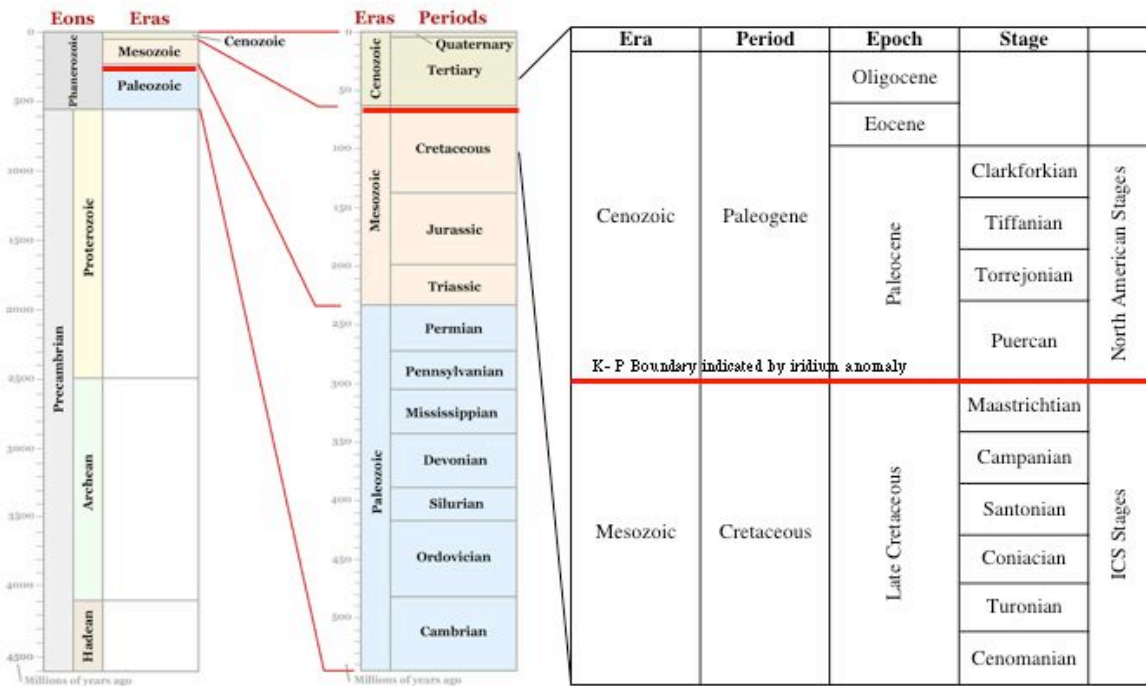
Figure 1. A geologic timescale of time intervals relevant to this discussion (North American Stages = North American Land Mammal Ages (NALMA). All fossils considered in this study are from the Maastrichtian and Puercan stages, as close to the K-Pg boundary iridium anomaly as possible.

NON-MARINE VERTEBRATES THAT BECAME EXTINCT AT THE BEGINNING OF THE CENOZOIC	
A few turtles: one species of aquatic baenid (*Theselus insiliens),* one aquatic species of subgenus *Trionyx*, one aquatic species of indeterminate dermatemydine, and probably the tortiselike dermatmmydid *basilemys sinuosa*(Bug Creek)	Unknown; most turtle groups survived
Azhdarchid pterosaurs	Nonsheltering
Some lizards: most North American teiids	Unknown
Crocodilians: one of six Maastrichtian species in Montana	Unknown; most crocodilians survived
Non-avian dinosaurs	Nonsheltering, except possibly the smallest, for which there is no evidence; loss of plant primary productivity
Archaic birds	Unknown
Some therian mammals: some eutherians (*Gypsonictops)* and most North American marsupials	Unknown

NON-MARINE VERTEBRATES THAT BECAME EXTINCT AT THE BEGINNING OF THE CENOZOIC	
Fishes	Shelter in water, burrows
Amphibians, lizards, amphisbaenians, snakes	Shelter in water, burrows in sediments, soil wood, or beneath rocks
Turtles: Nearly all aquatic lineages	Shelter in water, burrows
Champsosaurs (Choristodera)	Shelter in water
Crocodilians	Shelter in water, burrow
Neornithine birds	Dive, swim, shelter in water, marshlands, burrows, nest in tree holes, termite nests
Monotreme mammals	Semiaquatic or burrowing
Gondwanatherian mammals (Sudamericidae, if separate from multituberculates; extinct later in Cenozoic)	Small size, possibly sheltering behavior
Multituberculate mammals (extinct later in Cenozoic)	Probably sheltering behavior
Dryolestoid mammals (extinct in early Cenozoic)	Small size, probably sheltering behavior
Marsupial mammals (some surviving, especially in some southern landmasses)	Potential burrowers or semi-aquatic
Placental mammals	Potential burrowers or semi-aquatic

Table 1. Adapted from Roberston et al. 2004 this table discusses the sheltering potential of non-marine vertebrates present in the Late Cretaceous.

Figure 2. The K-P boundary in North America. Green indicates Cretaceous Rock, Yellow indicates Paleogene rock. The Western Interior (Montana, North Dakota, Alberta) is the only terrestrial sequence that preserves both sides of the boundary. Image created using North American Tapestry of Time and Terrain <http://nationalatlas.gov/>

Order (infraorder)	Family	Species	Survived K/T
Multituberculata			
	Cimolodontidae		
		Cimolodon nitidus	Yes
	Cimolomyidae		
		Cimolomys gracilis	No
		Meniscoessus robustus	No
	Family indeterminate		
		Cimexomys minor	Yes
		Essonodon browni	No
		Paracimexomys priscus	No
	Neoplagiaulacidae		
		Mesodma formosa	Yes
		Mesodma hensleighti	No
		Mesodma thompsoni	Yes
		? Neoplagiaulax burgessi	Yes
Eutheria			
	Gypsonictopidae		
		Gypsonictops illuminatus	Yes
	Palaeoryctidae		
		Batondon tenuis	Yes
		Cimolestes cerberoides	Yes
		Cimolestes incisus	Yes
		Cimolestes magnus	Yes
		Cimolestes propalaeoryctes	Yes
Metatheria			
	Didelphodontidae		
		Didelphondon vorax	No
	Family indeterminate		
		Glasbius twitchelli	No
	Pediomyidae		
		Pediomys cooki	No
		Pediomys elegans	No
		Pediomys florencae	No
		Pediomys hatcheri	No
		Pediomys krejcii	No
	Peradectidae		
		Alphadon marshi	Yes
		alphadon wilsoni	No
		Protalphadon lulli	No
		Turgidodon rhaister	No

Table 2. Mammalian differential survivorship according to Archibald 1996. Note that marsupials (Metatheria) are particularly devastated by the K-P extinctions and Placentals (Eutheria) relatively unaffected taxonomically.
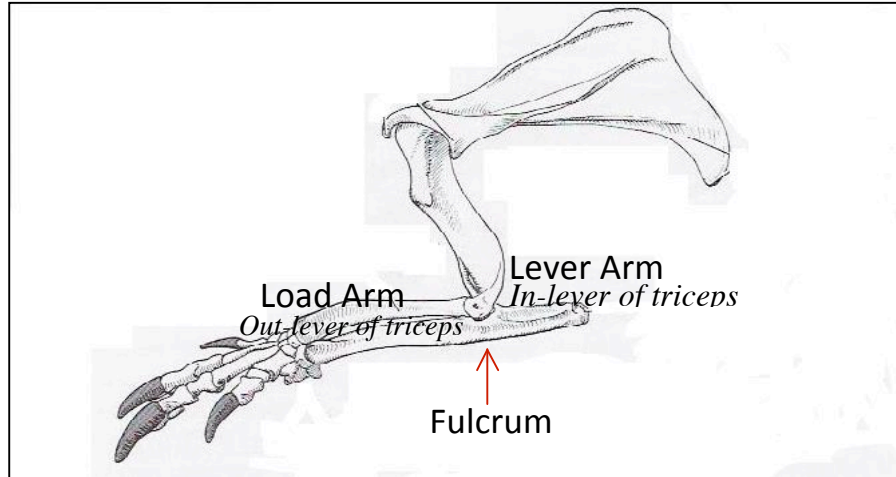
Figure 3. From Hildebrand and Goslow (2001) showing *Dasypus*, a fossorial genus, as a simple lever system. Power can be increased by increasing the length of the lever arm (olecranon process) or by decreasing the length of the load arm (distal ulna).

Species	Abbreviation	Locomotion	Common name
Cebus	CB	A	Capuchin Monkey
Callithrix flavice	*CF*	A	Marmoset
Didelphis virginiana	DV	A	Virgina Opossum
Galago alleni	GA	A	Bushbaby
Glaucomys volans	GV	A	Flying Squirrel
Macaca mulatta	MM	A	Rhesus Monkey
Sciurus carolinensis	SC	A	Gray Squirrel
Acinonyx jubatus	AJ	C	Cheetah
Felis catus	FC	C	Cat
Macropus rufus	MR	C	Red Kangaroo
reoargenteus	UC	C	Gray Fox
Dasypus novemcinctus	DN	F	Armadillo
Hystrix brachyura	HB	F	Porcupine
Mesocricetus auratus	MA	F	Hamster
Marmota flaviventris	MF	F	Marmot
Parascalops breweri	PB	F	Hairy-tailed Mole
Pedetes surdaster	PS	F	Springhare
Scalopus aquaticus	SA	F	Prarie Mole
Spermophilus columbianus	Sco	F	Ground Squirrel
Spermophilus lateralis	SL	F	Gopher
Tachyglossus aculeatus	TA	F	Echidna
Vombatus ursinus	VU	F	Wombat
Glis Glis	GlGl	S	Dormouse
Gulo gulo	GuGu	S	Wolverine
Mustela nivalis	MN	S	Least Weasel
Neotoma magister	NM	S	Woodrat
Neovison vison	NV	S	Mink
Peromyscus leucopus	PL	S	White-footed Mouse
Tupaia glis	TG	S	Tree Shrew
Castor canadensis	CC	SA	Beaver
Ornithorhynchus anatinus	OA	SA	Platypus
Ondatra zibethicus	OZ	SA	Muskrat
Cynocephalus volans	CV	V	Flying Lemur
Suborder Microchiroptera	MC	V	Bat
Myotis lucifugus	ML	V	Little Brown Bat

Table 3. The modern species used as references for locomotor guilds. A = Arboreal, C = Cursorial, F = Fossorial, S = Scansorial, SA = Semi-Aquatic, V = Volant
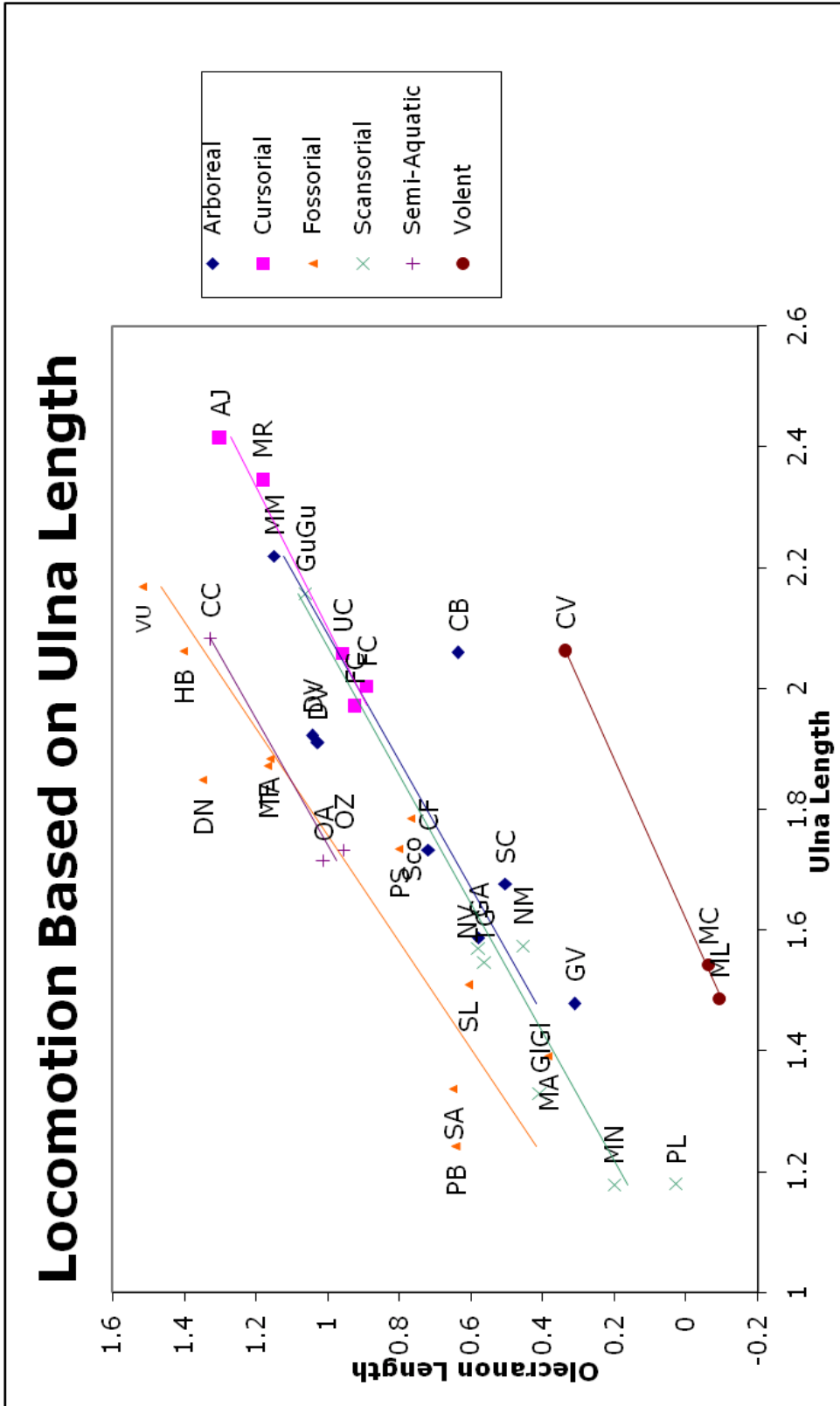
Figure 3. Semi-Aquatic and Fossorial guilds clearly separate from Arboreal, Cursorial, Scansorial and Volant guilds as expected when the olecranon process is considered relative to the length of the forelimb.

Figure 4. The geographic locations for the fossils used in this study. UCMP fossils come from central-eastern Montana and PTRM fossils come from southwestern North Dakota.

Figure 5. Typical preservation of a ~65 million year old mammal ulna (MOR 805). Ulna length (Out-lever) could not be used to evaluate the relative length of the olecranon process (In-lever).

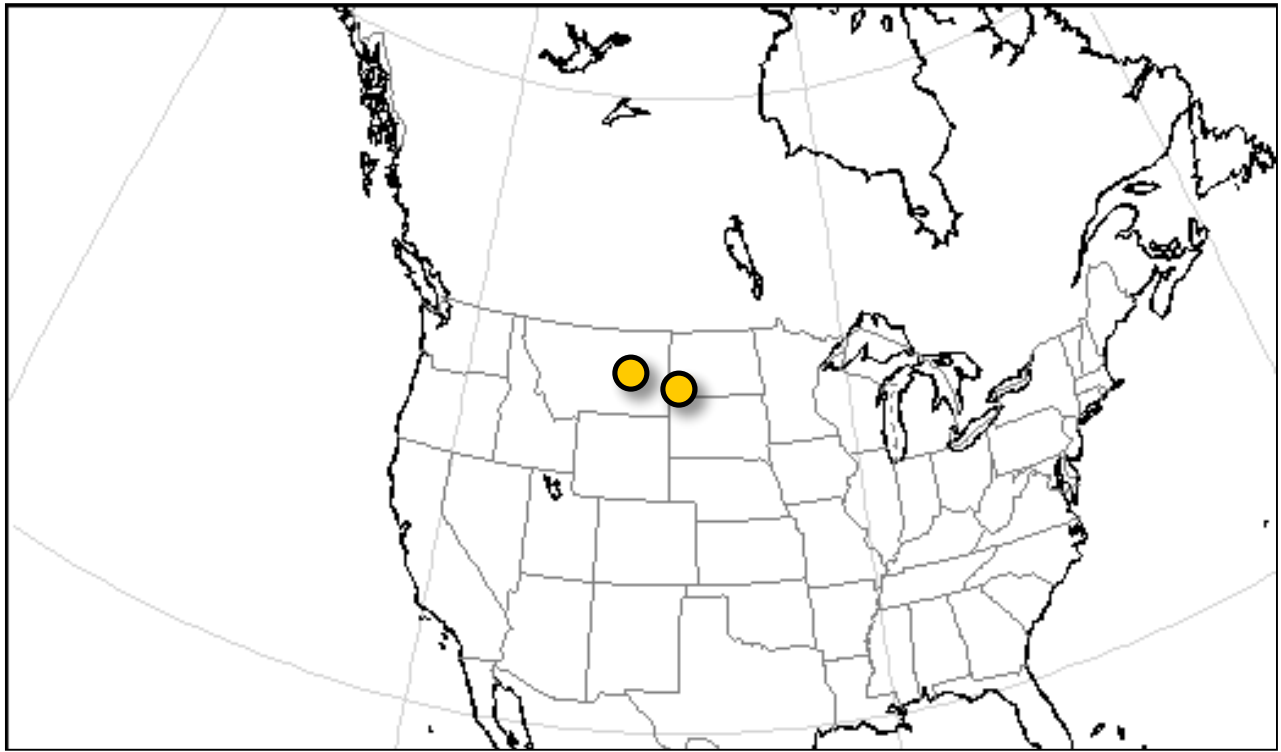| Column letter	Measurement	Description
B	Side	Radial notch is lateral
D	Ulnar Length	Terminal distal end of the styloid process to the terminal proximal end of the olecranon process
E	Olecranon Length	Proximal peak of the semi-lunar notch to the terminal, proximal point of the Olecranon process
F	Depth of Semi-Lunar (SL) Notch	The distance from line connecting the apex of the coronoid process to the apex of the proximal SL notch to the deepest point of the SI notch
G	Length of SL Notch	The tip of the coronoid process to the tip of the proximal semi-lunar notch
H	Width of SL Notch	The widest point connecting the lateral to medial side of the SI notch
I	Shape of SL Notch	The general observed shape
J	Ulna width	Distance from the lowest point of the trochlear notch to the posterior margin of the ulna
K	Width of Coronoid process	Widest lateral to medial line across the coronoid process
L	Width of Proximal process of SL Notch	Widest lateral to medial line across the proximal process of the SI notch.
M	Height of Proximal margin of SL Notch	Distance from medial edge of SL notch to peak of proximal process
N	Height of Coronoid process	Distance from the medial margin of the SL notch to the apex of the coronoid process
O	Radial Notch Height	Distance from proximal to distal margin of the radial notch
P	Radial Notch Width	Distance from the anterior to posterior margin of the radial notch

Table 4. A description of the linear measurements collected from each modern and fossil ulna.

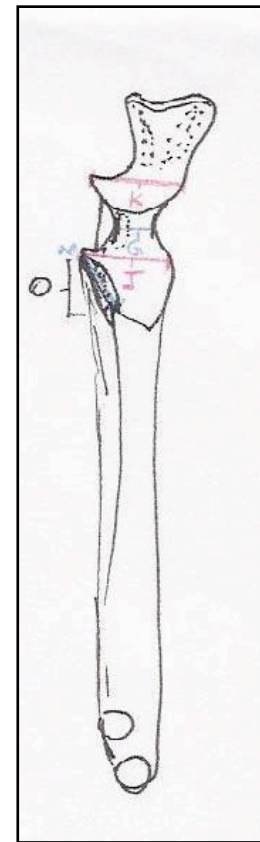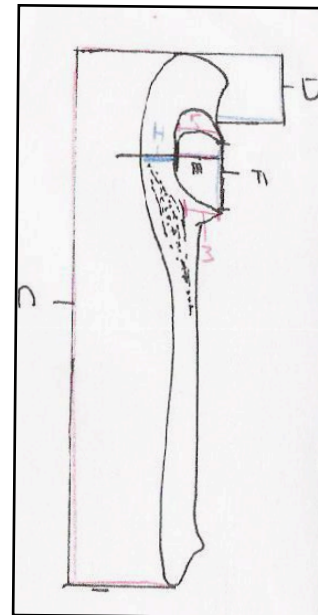**Figure 6.** Sketch of *Didelphis* ulna with measurements detailed.
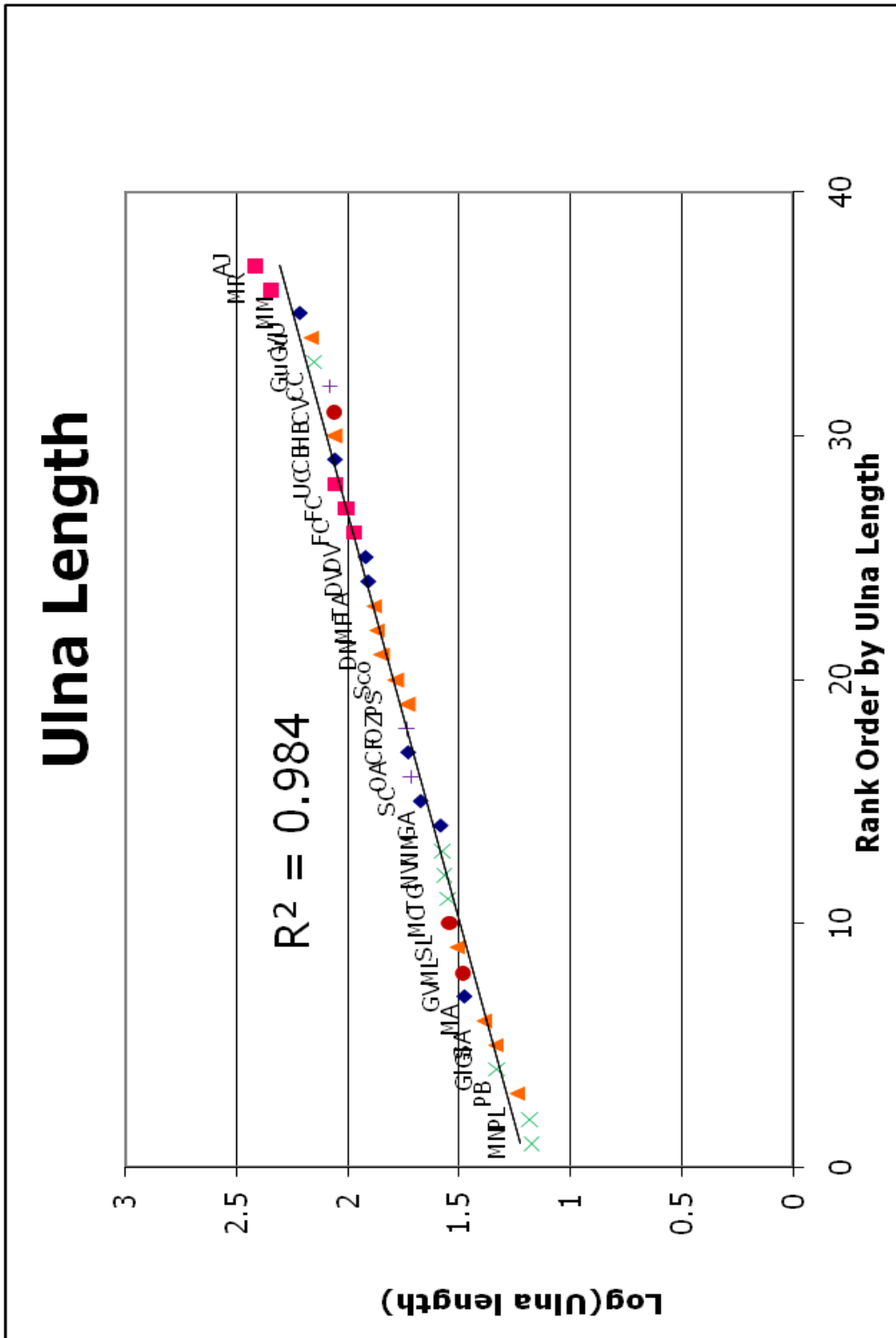
Figure 7. Ulna length does not reflect locomotor guild when placed in rank order. The modern sample represents a near continuum of ulna length when expressed as a logarithmic value.
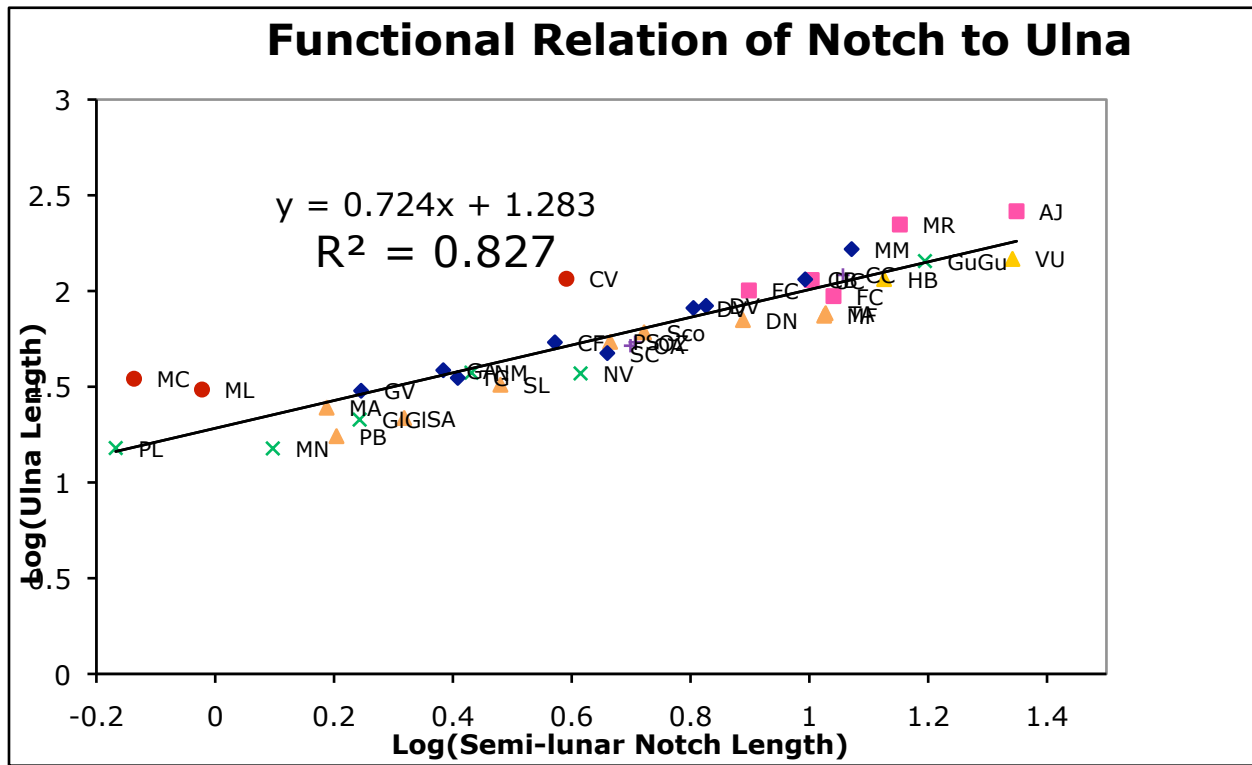
Figure 8. Regression of ulna length and notch length. The "fit" of the data sets was the best of all linear measurements collected from the proximal ulna.
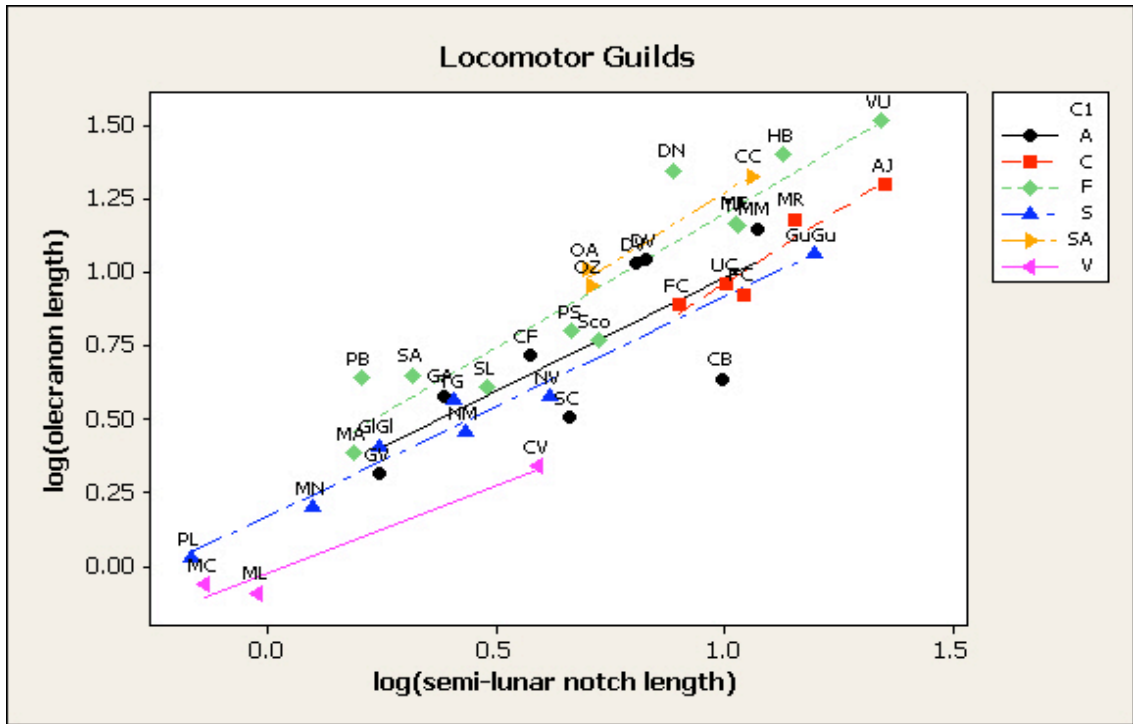
Figure 9. Notch length compared to olecranon length producing a similar graph to Figure 3 which used complete ulna length to isolate locomotor guilds.

Olecranon and Ulna Regressions	Olecranon and Notch Regression
Arboreal	Arboreal
y = 0.9528x - 0.9911	y = 0.7785x + 0.2055
R2 = 0.6404	R2 = 0.5645
Fossorial	Fossorial
y = 1.1279x - 0.9814	y = 0.912x + 0.2875
R2 = 0.8033	R2 = 0.8828
Semi-Aquatic	Semi-Aquatic
y = 0.9476x - 0.6492	y = 0.9709x + 0.3009
R2 = 0.9666	R2 = 0.9746
Cursorial	Cursorial
y = 0.8539x - 0.7931	y = 0.9958x - 0.0332
R2 = 0.9729	R2 = 0.9089
Scansorial	Scansorial
y = 0.9399x - 0.9436	y = 0.7481x + 0.1689
R2 = 0.9347	R2 = 0.9744
Volent	Volant
y = 0.7516x - 1.2134	y = 0.5991x - 0.0241
R2 = 0.9994	R2 = 0.956

Table 5. A comparison of regression equations based on two data sets. Note the differentiation of SA and F in particular from the other guilds.
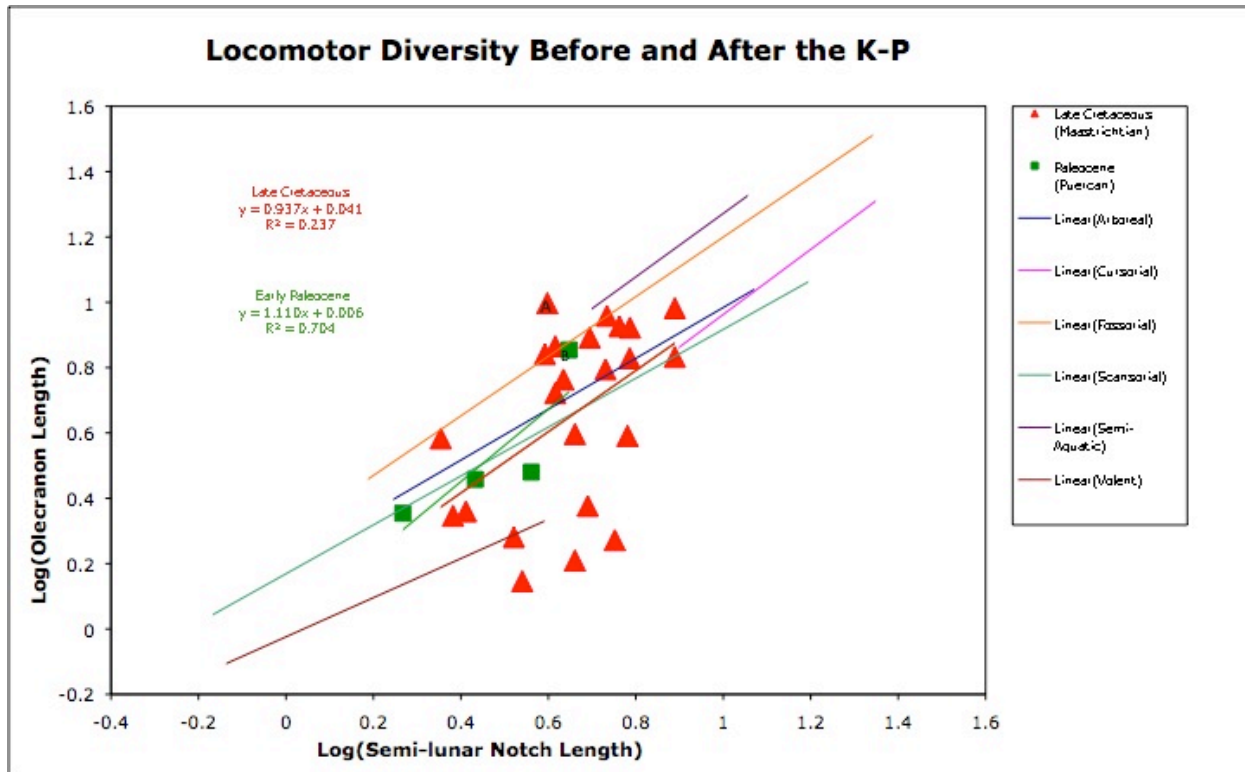
Figure 11. Maastrichtian locomotor diversity compared to Puercan locomotor diversity. The Cretaceous clearly had digging swimming, running, climbing and maybe gliding mammals (A = PTRM 3901). The Puercan had mostly small scansorial mammals (B = UCMP 174458). These data do not support the Sheltering Hypothesis.

Figure 12. The large caudal vertebra of *Didelphodon*

Figure 13. **Castor canadensis *caudal vertebra from an archaeological (Left) and modern (right) context. Scale in cm.***

Species	Body Size	Total Ulnar Length	Olecranon Length	Length of notch	Locomotion	log(Ulna)	log(olec)
Glaucomys volans	0.06538	30.13	2.05	1.76	A	1.48	0.31
Galago alleni	0.323	38.57	3.8	2.42	A	1.59	0.58
Callithrix flavice(?)	0.341	53.93	5.23	3.73	A	1.73	0.72
Sciurus carolinensis	0.54	47.39	3.19	4.57	A	1.68	0.50
Didelphis virginiana	3.35	81.52	10.66	6.38	A	1.91	1.03
Didelphis virginiana	3.35	83.67	11.02	6.7	A	1.92	1.04
Cebus	6.1	115	4.33	9.84	A	2.06	0.64
Macaca mulatta	8	165.5	14.09	11.78	A	2.22	1.15
Felis catus	4.45	100.68	7.79	7.91	C	2.02	0.89
Felis catus	4.45	94.06	8.41	10.98	C	1.97	0.92
Urocyon cinereoargenteus	5.2	114.13	9.1	10.09	C	2.06	0.96
Acinonyx jubatus	53.5	261	19.9	22.32	C	2.42	1.30
Macropus rufus	80	222.48	15.17	14.2	C	2.35	1.18
Parascalops breweri	0.065	17.45	4.38	1.6	F	1.24	0.64
Scalopus aquaticus	0.1035	21.7	4.46	2.08	F	1.34	0.65
Mesocricetus auratus	0.113	24.58	2.43	1.54	F	1.39	0.39
Spermophilus lateralis	0.257	32.38	4.05	3.02	F	1.51	0.61
Spermophilus columbianus	0.576	60.85	5.85	5.27	F	1.78	0.77
Pedetes surdaster	3	54.25	6.33	4.62	F	1.73	0.80
Marmota flaviventris	3.41	74.3	14.68	10.59	F	1.87	1.17
Tachyglossus aculeatus	4.25	76.52	14.47	10.65	F	1.88	1.16
Dasypus novemcinctus	6	70.48	22.22	7.73	F	1.85	1.35
Hystrix brachyura	8	115.39	25.21	13.36	F	2.06	1.40
Vombatus ursinus	50	147.05	32.78	21.97	F	2.17	1.52
Peromyscus leucopus	0.023	15.13	1.07	0.68	S	1.18	0.03
Mustela nivalis	0.0425	15.06	1.59	1.25	S	1.18	0.20
Tupaia glis	0.142	35.17	3.64	2.56	S	1.55	0.56
Glis Glis	0.209	21.3	2.55	1.75	S	1.33	0.41
Neotoma magister	0.2925	37.46	2.85	2.7	S	1.57	0.45
Neovison vison	1.15	37.12	3.78	4.12	S	1.57	0.58
Gulo gulo	19.5	143.33	11.55	15.65	S	2.16	1.06
Ondatra zibethicus	1.1358	53.98	9.01	5.09	SA	1.73	0.95
Ornithorhynchus anatinus	1.55	51.8	10.26	5	SA	1.71	1.01
Castor canadensis	22.5	121.3	21.25	11.39	SA	2.08	1.33
Myotis lucifugus	0.095	30.58	0.81	0.95	V	1.49	-0.09
Suborder Microchiroptera	0.1	34.82	0.87	0.73	V	1.54	-0.06
Cynocephalus volans	1.375	115.85	2.18	3.9	V	2.06	0.34

Appendix 1. Ulna and olecranon measurements and log values from comparative modern species. This data was used to generate Figure 3.

Species	Side	Body Size (kg)	Total Ulnar Length	Olecranon Length	Depth of notch	Length of notch	Width of notch	Ulna width from bottom of notch	Max Width of distal tuberosity	Max Width of Proximal tuberosity	Height of Proximal tub.	Height of Distal Tub.	Radial notch Width	Radial notch Height
Acinonyx jubatus	Right	53.5	261	19.9	12.78	22.32	12.33	12.01	21.28	12.14		4.43		
Callithrix flavice?	Left	0.341	53.93	5.23	2.42	3.73	3.11	3.51	4.53	4.56	2.72	1.3		
Castor canadensis	Right	22.5	121.3	21.25	6.61	11.39	7.82	12.76	7.41	10.88	12.11	8.53	6.12	13.24
Cebus	Left	6.1	115	4.33	5.84	9.84	6.34	7.25	12.4	7.7	5.61	7.2	9.43	6.06
Cynocephalus volans	Left	1.375	115.85	2.18	1.85	3.9	3.74	3.28	6.93	3.76	4.38	3.2	6.36	1.89
Dasypus novemcinctus	Left	6	70.48	22.22	3.88	7.73	6.21	7.72	10.05	7.18	4.41	3.25		
Didelphis virginiana	Right	3.35	83.67	11.02	3.23	6.7	5.21	7.62	5.07	5.06	6.74	2.98	4.18	5.62
Didelphis virginiana	Left	3.35	81.52	10.66	3.3	6.38	4.33	7.23	8.43	5.52	4.28	5.16	6.61	3.48
Felis catus	Right	4.45	94.06	8.41	5.04	10.98	4.47	6.1	4.82	5.22	6.72	7.88	2.23	7.82
Felis catus	Right	4.45	100.68	7.79	4.1	7.91	4.23	6.05	7.61	5.01	4.25	6.6	6.89	4.53
Galago alleni	Left	0.323	38.57	3.8	1.76	2.42	2.11	1.88	2.5	3.43	2.39			
Glaucomys volans	Right	0.065	30.13	2.05	0.91	1.76	0.83	1.27		2.01	1.08	0.45	1.88	0.45
Glis Glis	Right	0.209	21.3	2.55	0.97	1.75	1.53	2	1.96	1.8	2.17	0.86	1.05	0.9
Gulo gulo	Right	19.5	143.33	11.55	9.04	15.65	7.32	11.49	16.92	10.48	12.27	11.61	12.08	4.51
Hystrix brachyura	Right	8	115.39	25.21	7.2	13.36	11.35	10.98	8.35	13.61	11.9	10.73	6.87	15.35
Macaca mulatta	Left	8	165.5	14.09	6.89	11.78	8.4	10.92	7.9	10.56	7.55	8.3	6.7	6.03
Macropus rufus	Left	80	222.48	15.17	5	14.2	17.18	14.43	21.45	18.15	9.14	12.32	13.28	6.8
Marmota flaviventris	Right	3.41	74.3	14.68	4.53	10.59	6.16	6.79	4.7	6.57	6.22	6.21	3.78	4.7
Mesocricetus auratus	Right	0.113	24.58	2.43	0.83	1.54	1.14	2.03	1.97	1.82	1.2	1.01	1.87	1.41
Mustela nivalis	Right	0.043	15.06	1.59	0.97	1.25	0.8	1.24	1.32	1.15	1.23	1.16	1.5	0.55
Myotis lucifugus	Left	0.095	30.58	0.81	0.54	0.95	1.15	0.85	2.13	1.83	0.5	0.68		
Neotoma magister	Left	0.293	37.46	2.85	1.3	2.7	1.72	2.42	1.92	2.81	2.24	1.97	2.25	1.18
Neovison vison	Right	1.15	37.12	3.78	2.12	4.12	2.06	3.05	4.55	3.12	3.18	3.69	4.49	1.94
Ondatra zibethicus	Right	1.136	53.98	9.01	1.86	5.09	2.12	5.22	4.52	5.05	3.21	2.15	1.75	3.72
Ornithorhynchus anatinus	Left	1.55	51.8	10.26	4.11	5	4.42	5.91	4.84	4.58	1.89	1.25		
Parascalops breweri	Left	0.065	17.45	4.38	1.21	1.6	2.05	3.03	1.65	1.25	2.55	1.98	1.79	1.8
Pedetes surdaster	Left	3	54.25	6.33	2.92	4.62	4.8	4.18	3.51	5.46	5.08	3.46	3.22	4.4
Peromyscus leucopus	Left	0.023	15.13	1.07	0.92	0.68	0.74	1.08	1.31	1.24	0.8	1.11	1.18	0.39
Scalopus aquaticus	Left	0.104	21.7	4.46	1.32	2.08	2.7	5.12	1.69	1.6	4.02	1.64	1.48	2
Sciurus carolinensis	Left	0.54	47.39	3.19	2.03	4.57	3.02	3.38	2.62	4.5	4.07	2.1	2.41	2.04
Spermophilus columbianus	Left	0.576	60.85	5.85	3.29	5.27	2.52	3.91	6.32	3.62	4.25	4.42	5.32	1.88
Spermophilus lateralis	Right	0.257	32.38	4.05	1.15	3.02	1.75	2.31	1.84	2.84	1.79	1.82	1.9	2.19
Suborder Microchiroptera	Right	0.1	34.82	0.87	0.51	0.73		0.68			0.45	0.67		
Tachyglossus aculeatus	Right	4.25	76.52	14.47	2.28	10.65	8.24	6.75					7.92	1.54
Tree Shew	Left	0.142	35.17	3.64	2.36	2.56	1.84	1.74						
Urocyon cinereoargenteus	Right	5.2	114.13	9.1	4.83	10.09	4.85	7.57	3.48	4.7	7.29	5.52	8.53	3.28
Vombatus ursinus	Right	50	147.05	32.78	6.46	21.97	20.3	21.3	14.38	14.52	13.65	11.57	10.75	16.05

Appendix 2. Linear measurements of the proximal ulna

Appendix 3: Fossil Measurements

Species	Order?	Stage	Specimen #	Olecranon Length	Length of notch	log(Ulna)	log(length)
UCMP 127378	Multi	Maa	V88907	1.62	4.58	0.661	0.210
UCMP 111152	Mammalia (Multi?)	Maa	V5620	2.38	4.9	0.690	0.377
UCMP 174495	Multi	Maa	V75178	3.83	2.26	0.354	0.583
UCMP 127389	Multi	Maa	V88907	1.87	5.65	0.752	0.272
UCMP 127390	Theria	Maa	V88907	3.95	4.58	0.661	0.597
Temp 1	Theria	Puercan	V74111	2.87	2.71	0.433	0.458
Temp 2	Theria	Puercan	V74111	3.02	3.64	0.561	0.480
UCMP 174400	Multi	Maa	V89092	7.33	4.13	0.616	0.865
UCMP 152012	Condylarthra	Maa	V86031	3.9	6.04	0.781	0.591
UCMP 177834	Multi	Maa	V91051	6.8	7.75	0.889	0.833
UCMP 177835	Multi	Maa	V91051	1.4	3.47	0.540	0.146
UCMP 127393	Multi	Maa	V88909	6.74	6.11	0.786	0.829
UCMP 174530	Multi	Maa	V80092	8.36	6.12	0.787	0.922
UCMP 172370 a	Multi	Maa	V86101	7.79	4.95	0.695	0.892
UCMP 172370b	Multi	Maa	V86101	6.94	3.91	0.592	0.841
UCMP 174247	Multi	Maa	V76144	9.59	7.75	0.889	0.982
UCMP 127386	Theria	Maa	V88905	5.8	4.31	0.634	0.763
UCMP 174601	Theria	Maa	V82060	8.44	5.79	0.763	0.926
UCMP 174588	Multi (eroded meta?)	Maa	V75178	1.91	3.32	0.521	0.281
UCMP 174458	Theria	Puercan	V70206	7.15	4.44	0.647	0.854
UCMP 127375	Theria	Maa	V88908	2.29	2.58	0.412	0.360
UCMP 153025	Theria (Meta)	Maa	V80092	9.09	5.42	0.734	0.959
UCMP D	Multi?	Puercan	V99438	2.26	1.85	0.267	0.354
PTRM #3560		Maa	V92067	6.1	3.71	0.569	0.785
MOR 805		Maa	92028	6.23	5.38	0.731	0.794
PTRM #3681		Maa	V87009	5.27	4.13	0.616	0.722
PTRM #3901		Maa	V98016	9.94	3.96	0.598	0.997
PTRM #3561		Maa	V92067	3.3	2.17	0.336	0.519
PTRM #3690		Maa	V92067	2.22	2.41	0.382	0.346
UCMP 127390		Maa		6	3.44	0.537	0.778

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