

The Extinction of the Multituberculates Outside North America: a Global Approach to
Testing the Competition Model

Thesis

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By

D. Joseph Wood, B.S.

Graduate Program in Evolution, Ecology, and Organismal Biology

The Ohio State University

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Thesis Committee:

John Hunter, Advisor

William Ausich

Laura Kubatko

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Abstract

The hypothesis that the extinction of the Multituberculata largely resulted from competition with early members of the Rodentia, based mainly on fossil-rich sequences in North America, features prominently in the history of early mammals. In this study, I expand the scope of investigation into this subject to include the other two continents where multituberculates made up a significant portion of the community, Europe and Asia. I used diversity measures, percentage richness, taxonomic rates of origination and extinction, and estimates of body size overlap to compare and contrast the replacement patterns on the three continents. In addition to testing hypotheses of multituberculate extinction, I also tested how closely this extinction conforms to the predictions of the incumbent replacement model of competitive faunal replacement. I conclude in this study that, especially in the light of new data, competitive interaction stands as the most likely explanation for the disappearance of the Multituberculata in Europe and North America. I base this conclusion largely on the fact that I observe correlated rates of origination (rodents) and extinction (multituberculates) on both continents. The incumbent replacement model predicts this result and thus provides the best conceptual framework for understanding the global extinction of the multituberculates. I also find that substantial size overlap existed between the Multituberculata and Rodentia of North America and Europe. I infer this to suggest niche overlap and resource competition between these groups. Finally, I conclude that the decimation experienced by

multituberculates at the end of the Cretaceous, especially in Asia, opened up niche space, into which the ancestors of rodents could radiate. These events set the stage for the eventual replacement of multituberculates by rodents in North America and Europe by providing an opportunity for rodents to establish themselves initially in Asia relatively free from competition with multituberculates.

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I thank Mikael Fortelius for access to occurrence data on Paleogene mammals of Europe and Asia compiled from the published literature by him and his students, most notably Majid Mirzaie Ataabadi, at the University of Helsinki. The American Museum of Natural History provided access to specimens. Deborah Weinstein of University of Wisconsin measured specimens on my behalf. Meng Jin of the American Museum of Natural History provided tooth length measurement data. William Ausich and Laura Kubatko of Ohio State University and John Alroy of National Center for Ecological Analysis and Synthesis provided helpful advice on the research presented here. I would like to thank John Hunter for his guidance along the way and for inspiring me to pursue a career in paleontology. I would like to thank the Society of Vertebrate Paleontology for providing me an opportunity to present this work at the 2009 Annual Meeting in Bristol, UK and for awarding me with the Jackson School of Geosciences travel grant to cover costs of attending the meeting. I would also like to thank the Kafe Kerouac in Columbus Ohio, where I spent many hours working on my thesis manuscript. Finally, I would like to thank The Ohio State University for giving me innumerable opportunities to expand my horizons, both academically and personally.

Vita

June 2003.....Hilliard Davidson High School
2007.....B.S. Ohio State University
2006 to present.....Instructor: Columbus Zoo and
Aquarium
2007 to present.....Graduate Teaching Associate,
Department of EEOB

Fields of Study

Major Field: Evolution, Ecology, and Organismal Biology

Paleontology

Paleobiology

Paleoecology

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Chapter 1: Correlation Versus Causality in the Fossil Record: Reexamining the
Extinction of the Multituberculates with Taxonomic Rates of Origination and Extinction

Introduction

One of the most interesting areas of ecological research aims to understand competitive interactions between species or higher taxa. These types of studies can be difficult, however, even when one can directly observe the living organisms in question. Working with extinct taxa magnifies this problem, but paleontologists are uniquely positioned to ask questions about competition because only we have the perspective of deep time. We have the ability to trace the interactions of higher taxa over millions of years rather than just observing the types of interactions that occur within the human life span.

Many paleontologists have focused on the extinction of the Multituberculata as an example of competitive exclusion. They were one of the first groups to rebound after the end-Cretaceous extinction, and they reached high diversity in the Paleocene only to become extinct by the late Eocene (Rose, 2006 p. 56). The assertion put forth by many is that multituberculates shared many characteristics with rodents and were the “herbivorous analogues of rodents” (Rose, 2006 p. 56), so it has been thought probable that rodent diversification and expansion resulted in multituberculate extinction (Jepsen, 1949; Van Valen and Sloan, 1966; Krause, 1986). Rodents are by far the largest order of living mammals in number of species making up roughly forty-two percent of extant

Mammalian species (Wilson and Reeder, 2005 p. 745). They have spread to every continent except Antarctica and have colonized most of the world's islands. Rodents occupy a wide variety of niches and have considerable diversity in body size, shape, and method of locomotion. However, they exhibit remarkable similarity in certain dental and skeletal features, like their self-sharpening incisors, presence of a diastema, and unique structure of the radius and ulna (Nowak, 1999 p. 1244). The traditional scenario involves rodents originating in Asia, then dispersing from there during the Paleocene, and driving multituberculates to extinction wherever they came into contact (Rose, 2006). The questions addressed here are how good is the evidence that rodents contributed to multituberculate extinction, and how does the scenario fit with current ideas about competition between clades? This scenario also does not directly address the replacement of multituberculates in Asia, where they were diverse during the Cretaceous and persisted into the Paleocene, in sympatry with early rodents.

Although speculation concerning the role of rodents in multituberculate extinction stretches back to the late 1800s, the first articulated hypothesis of this nature is that of Jepsen (1949). This paper was the first to enumerate the details of the competition hypothesis that the decline in diversity and relative abundance of multituberculates coincided with the appearance of rodents in North America. Jepsen's ideas that rodents and multituberculates shared morphology reflecting shared feeding preference proved to be influential in the debate over the cause of the multituberculates' extinction but he provided little evidence for this view (Jepsen, 1949). We now understand that members of Rodentia and Multituberculata shared aspects of morphology, both in feeding and locomotor ability. We know that at least some multituberculates used a grinding

mastication method similar to rodents, although the power stroke was effected by retraction rather than protraction (Krause, 1982). The Multituberculata contained ricochetal (Kielan-Jaworowska and Gambaryan, 1994), arboreal (Jenkins and Krause, 1983), and fossorial (Gambaryan and Kielan-Jaworowska, 1997) forms. Van Valen and Sloan (1966) echoed many of Jepsen's ideas, the most important being the implied causal relationship between the coincidental decline of multituberculates and rise of rodents.

Landry (1965) and (1967) took issue with the competition hypothesis and provided some alternative hypotheses for multituberculate extinction that remained unaddressed until Krause's (1986) study. Krause (1986) refuted Landry's (1967) assertion that multituberculates and rodents had different diel patterns as well as the related hypothesis that predation by raptorial birds played a role in the extinction of the multituberculates (Krause, 1986). This paper was in some ways the last word on the competition hypothesis for multituberculate extinction, but it still relied on the same evidence that the decline of the Multituberculata coincided with the rise of the Rodentia and focused on the pattern of replacement in North America. My study intends to provide new lines of evidence with which to evaluate the competition hypothesis by expanding to Europe and Asia and analyzing taxonomic evolutionary rates.

The debate concerning the role of competition in the differential success of clades goes back at least as far as Darwin, who viewed life as a continual struggle for existence with competition being one of, if not the driving force of evolution (Darwin, 1859). The problem is that many contemporary authors question whether these kinds of competitive interactions actually ever occurred anywhere in the fossil record. In the view of these scientists, abiotic factors alone drive macroevolutionary trends, such as major

replacement events. Gould and Calloway (1980) described the Brachiopoda and Mollusca as “two ships that pass in the night”, one on the way in and the other on the way out but not interacting. In their view purely stochastic processes, namely the end-Permian extinction, resulted in the dominance of the Mollusca at the expense of the Brachiopoda (Gould and Calloway, 1980). These authors and others, especially Benton (1987, 2009), are convinced that processes like competition only operate on small time-scales and, therefore, cannot be mechanisms for large-scale trends in evolution, such as clade replacement (for the opposite viewpoint see Briggs, 1998). Benton actually used the case of multituberculates and rodents as an example of a replacement that, when examined in more detail, more closely resembles a passive event where one clade replaced another with little interaction (Benton, 1987).

By now, it seems as if there is no compromise in terms of what paleontologists think about biotic replacements, but does a model exist that can account for the extinction of the multituberculates? We can imagine a spectrum along an axis that represents the importance of biotic interactions in driving macroevolutionary trends. On one end of this spectrum sits the somewhat archaic notion that all replacements are the result of a superiorly adapted group “outcompeting” a less well-adapted group. On the other extreme sits the idea that all replacements boil down to chance. Rosenzweig and McCord deemed this the “stochastic broom” hypothesis because random processes occasionally sweep away an older taxon leaving room for a newer taxon (Rosenzweig and McCord, 1991). They proposed a model of replacement that fits somewhere in the middle of the spectrum and could be applicable to many examples of replacement. They called this

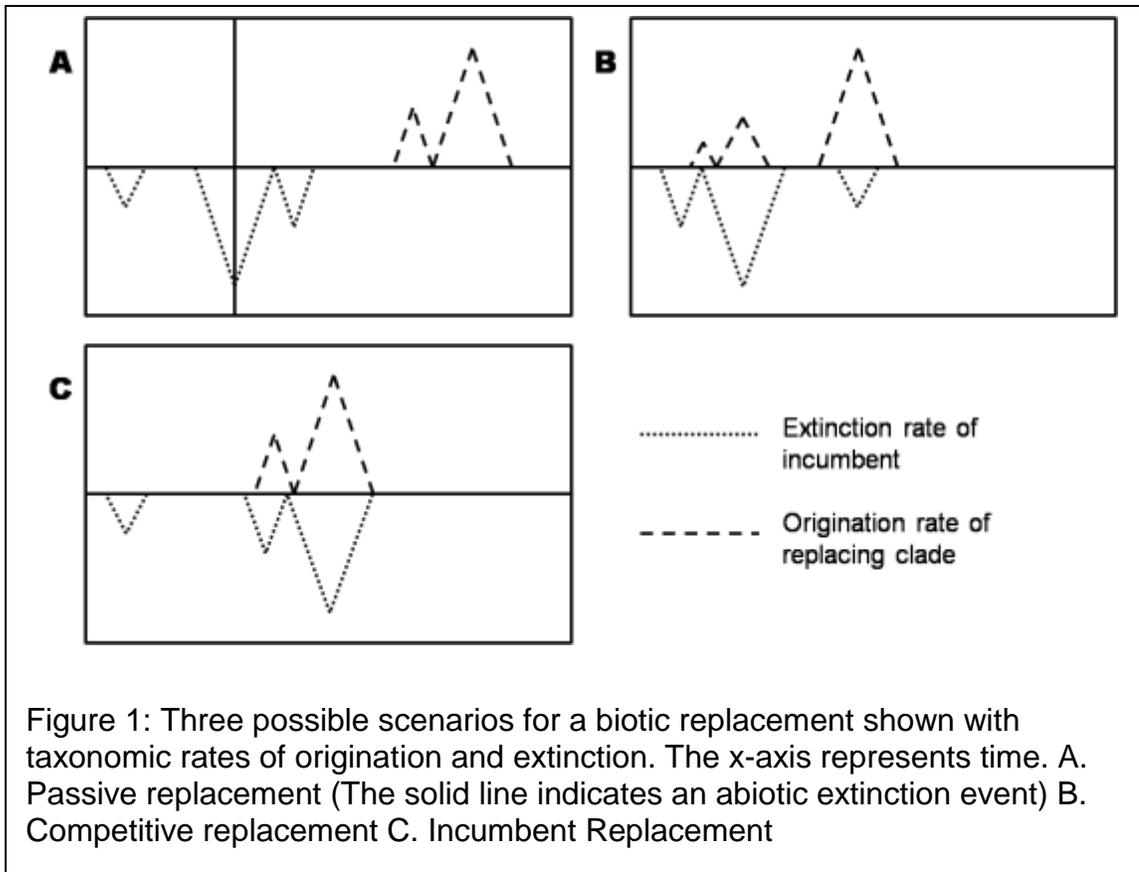
model incumbent replacement and although the authors used turtle evolution as an example, its usefulness for the question of multituberculate extinction becomes apparent.

Taxonomic rates of origination and extinction could help solve a long-standing problem with studies of clade replacement. One problem with studies that attempt to demonstrate competition between two groups of organisms in the fossil record is the difficulty in distinguishing causation from mere correlation. This problem, referred to as the “double wedge” means that, if we wish to test competition hypotheses, we will require more evidence than the fact that one clade declined in diversity while the other clade increased in diversity (Benton, 1987 p. 318). Just because we observe this correlation in diversity of two clades does not necessarily mean they ever actually interacted with one another; therefore, we need a method that allows us to approach the mechanisms that drive clade dynamics more closely. Recently some workers have found ways to evaluate competition hypotheses without appealing solely to diversity measures. Brusatte et al. (2008) used morphological rates of evolution and morphospace occupation/disparity to assess the role of competition in the radiation of early dinosaurs during the Triassic. We propose another approach, using taxonomic rates of origination and extinction, as a means to overcome the problem of the double wedge in the case of the extinction of the multituberculates.

In the incumbent replacement model, replacement is opportunistic, rather than the result of direct competition. The model makes predictions about the taxonomic rates of origination (p) and extinction (q) of the competing taxa. The origination rate of the replacing clade will increase as extinction rate of the incumbent clade increases because it is only after a species of the incumbent clade becomes extinct that a member of the

replacing clade can fill its niche. This is different from other scenarios of replacement like competitive extinction and the stochastic broom. In the competitive extinction model, the extinction rate of the incumbent would increase as a direct result of competition with the replacing clade but the origination rate of the replacing clade would be independent of any taxonomic rates of the incumbent. By contrast, in the stochastic broom model the extinction rate of the incumbent results from some abiotic process and would be independent of the increasing origination rate of the replacing clade. We should be able to distinguish these patterns from each other using available data on the replacement of the multituberculates.

The three hypotheses present three distinctly different patterns, which we can easily distinguish from one another. Figure 1 shows these three patterns. In Figure 1A, a mass extinction event caused by abiotic factors leads to a high extinction rate of a clade. There is a separation in time between this spike in extinction rate and a spike in origination rate of a replacing clade. In Figure 1B, the two clades are not separated in time but the origination rate of the replacing clade shows no correlation with the incumbent clade. This represents the classical competitive exclusion model where the presence of a competing clade directly influences the extinction rate of an incumbent clade. Notice that while the spike in origination and extinction rates may occur at the same time, we see no correlation in their magnitude. Figure 1C shows the expectation of the incumbent replacement model where the rates of origination and extinction are correlated.



In this study, I calculated the taxonomic rates of origination and extinction for multituberculates and rodents as well as several other clades in order to test the pattern of replacement against the three models in Figure 1. I studied the taxonomic rates not just for North America, but also for Europe and Asia to compare the patterns of replacement on all three continents and achieve a clearer picture of the global extinction of the Multituberculata.

Materials and Methods

Data Collection.- The broad scope of this study required the use of multiple sources of data. For occurrences in Europe and Asia, I made use of data compiled at the NOW (Neogene Old World) office for a Paleogene extension of the NOW database of

fossils mammals. For the purposes of this study, I further subjected these occurrence data to checking and updating based on a search by the authors through the primary literature published through 2009. The dataset used here is available from NOW Coordinator Mikael Fortelius (mikael.fortelius@helsinki.fi). Using these data, I generated a matrix of first and last occurrence for all the taxa in the study. Generating a similar first and last occurrence matrix for the North American representatives of the taxa in this study was somewhat easier. Each chapter of the Tertiary Mammals of North America volumes contains an occurrence chart, which were of great use in this study.

When generating the graph of generic diversity for North American multituberculates and rodents, I chose to use the functionality of the Paleobiology Database. Absolute range data were downloaded from the Paleobiology Database on 15 April 2010 using the “analyze taxonomic ranges” function. I used the search terms “Multituberculata” and “Rodentia” and used the time scale criterion “North American Land Mammal Ages”. Because observed stratigraphic ranges of taxa underestimate true ranges, I selected the range estimation method “Strauss and Sadler (1989)”. In this study, I present both raw generic richness as well as adjusted richness incorporating inferred range extensions using the Strauss and Sadler (1989) method (Fig. 2). However, I estimated rates of origination and extinction using raw counts of presence/absence.

For the North American abundance data, I also used the Paleobiology Database. The Paleobiology Database includes a search function for analyzing abundance data, which proved extremely useful for this study. The Paleobiology Database also calculates age estimates for localities using Appearance Event Ordination (AEO) (Alroy, 1994), which I used to arrange abundance data into million year time bins for one of the

analyses. Data for abundance were downloaded from the Paleobiology Database on 2 May, 2009 using the analyze abundance function and the search terms “Multituberculata” and “Rodentia” for the intervals “Paleocene” and “Eocene” and the continent “North America”. For this study, I also wanted to calculate the percent richness of multituberculates in Asia before the end-Cretaceous extinction. I took these data from the faunal lists generated from the literature by John Hunter for Foote et al. (1999).

After collecting the data on first and last occurrence from all sources, I converted these data into a binary matrix of presence and absence for the Paleocene and Early Eocene. I used half-million year bins in order to generate a sufficient number of data points for statistical analysis. If a genus was observed to occur in a given time bin I indicated its presence with a 1 and if the genus was not observed to occur I indicated its absence with a 0. Illustrating presence/absence in this fashion made calculating the taxonomic rates of origination and extinction much simpler.

Taxonomic Rate Analysis.- I used two different methods to calculate the taxonomic rates used in this analysis. For North America, I used the per-taxon rate of origination (p) and extinction (q). I chose this method in part because the fossil occurrence data for North America is of higher quality than from the other two continents in the study. This allowed us to calculate the rates of origination and extinction for many more time slices in order to get a more detailed picture of any patterns. The per-taxon rate is easier to implement in this situation, as it is just the number of origination or extinction events divided by the standing diversity for the time slice divided by time (Simpson, 1944). The fact that all the groups in the study are small mammal orders from the same

time and place mitigates any problems with this particular method. In other words, I was not comparing mammals to clams (Novacek and Norell, 1982).

The European and Asian occurrence data were comparatively lower quality so I used a different rate metric. In this case, I used the Van Valen metric (1984), which is somewhat more complicated but less sensitive to artifacts due to poor sampling and problems with time intervals (Foote, 2001). This method relies on tallying boundary crossers of different types and is computationally more cumbersome than the per-taxon method of calculating origination and extinction rate.

The taxa included in the study were the orders Multituberculata, Rodentia, Plesiadapiformes, Carnivora, and Creodonta. Using the calculated rates of origination and extinction for each of these groups allowed us to test several different hypotheses of interaction between these groups. Workers traditionally implicate rodents as the group responsible for the extinction of the multituberculates so they were an obvious choice to include in the analysis in order to test for correlation between their origination rate and the extinction rate of multituberculates. Some authors (Maas, Krause, and Strait, 1988) have suggested the plesiadapiforms as potential competitors of multituberculates so I included them to look for a relationship between their origination rate and the extinction rate of multituberculates. Additionally, having the origination rate of rodents and plesiadapiforms allowed us to test a sequential competition hypothesis first with Plesiadapiformes and later Rodentia competing with Multituberculata. I combined the creodonts and early carnivorans into one analysis to represent the early carnivorous mammals and use this group as a control. Few, if any, would suggest that rodents were engaged in competition with these early carnivores so investigating correlation between

the taxonomic rates of these two groups provides a contrast to the other analyses. It is conceivable that the calculated rates of origination and extinction of two groups of organisms might show some correlation purely because of their being exposed to the same paleo-environmental conditions or similar preservation artifacts. This autocorrelation could conceivably produce a false signal but including the carnivores in the study gets around this problem.

I used the analyses in this study in order to look for significant correlation concerning any of the sets of taxonomic rates. They serve as a test of the hypothetical scenarios of competition between the taxa in the study. As laid out in my experimental design, two taxa that competed should exhibit a correlation of origination rate in the case of the replacing clade, and extinction rate in the place of the declining clade. Additionally, I predicted that in a competition scenario, origination events in one time bin might not show an immediate effect on the extinction rate. This prediction is justified when one considers that a new group of organisms of a given taxon might not have an instantaneous impact on the ecosystem.

In order to compare the rates of extinction and origination for all the taxa in the study, I placed each set of rates on a time series ranging from the Paleocene through the middle Eocene. The graphs that I generated from this time series serve as a test of the null hypothesis of no interaction between the clades in question. In a competition scenario, I must see a clear relationship between the two rates to suggest that the clades they represent interacted competitively in the past. Analyzing the taxonomic rates in a time series provides more of a signal than simply charting diversity over time and goes some way toward getting around the problem of the double wedge. These time series also

enabled us to analyze the pattern of extinction of the Multituberculata in relation to the rise of the Rodentia and the Paleocene-Eocene Thermal Maximum (PETM). This major climatic event could potentially have been involved in the extinction of the Multituberculata; thus, I think it important to test whether or not the PETM was associated with a spike in extinction of that group.

In addition to the time series graphs of taxonomic rates for the groups in the study, I also looked for significant changes in the extinction and origination rates before and after the addition of rodents to the ecosystem. The before-and-after comparisons help highlight and explain important trends in the replacement of the Multituberculata and shed light on what effect the introduction of rodents had. For the North American data, I used a permutation t-test to determine whether there was a significant difference in mean extinction rate of multituberculates before and after association with rodents. I could only perform a test of this nature on the North American data because the higher quality data provided more data points. The Europe and Asia analyses mainly revolve around the large-scale comparisons of the taxonomic rates before and after rodent invasion.

Krause published the last major study on the subject of multituberculate extinction in 1986, and so it is likely that new data have been published since then that could be useful in this study. For this reason, I chose to recalculate the diversity over time for multituberculates and rodents in all three continents in the study. Since the taxonomic rates are potentially a way to get “behind” the diversity graphs that other workers produced for North America, it is beneficial to have those updated graphs to compare with the rates analyses. For Europe and Asia, generating graphs of diversity over time is informative since this will be new information. In addition to examining diversity over

time, I also chose to examine the relative importance of multituberculates and rodents in faunas over time. I accomplished this by calculating the percent richness for each taxon over time. This information could prove useful when compared with the diversity curves and the taxonomic rate series.

Results

North America.- Figure 2 shows the same double wedge pattern observed by other authors in two ways. Some authors have suggested that the Multituberculata may have been in decline even before the Rodentia invaded North America but this interpretation could be a result of the incompleteness of the fossil record. Figure 2B shows more of an overlap between the two wedges because it takes into account estimates of actual temporal ranges. This probably more closely matches the real pattern of replacement. Figure 3 shows a similar double wedge pattern in percent richness. Multituberculates began to decline in percent richness at the same time as rodents appeared in North America and start their trend towards dominating land mammal faunas. One problem that this graph demonstrates is that multituberculates appear to be nearly absent from mammalian faunas for a period only to reappear around 36 Ma. This demonstrates a gap in my knowledge of the multituberculate record. New discoveries may fill in some of the gaps in my understanding of the extinction of the multituberculates, but they are unlikely to change the general trend shown in Figure 3.

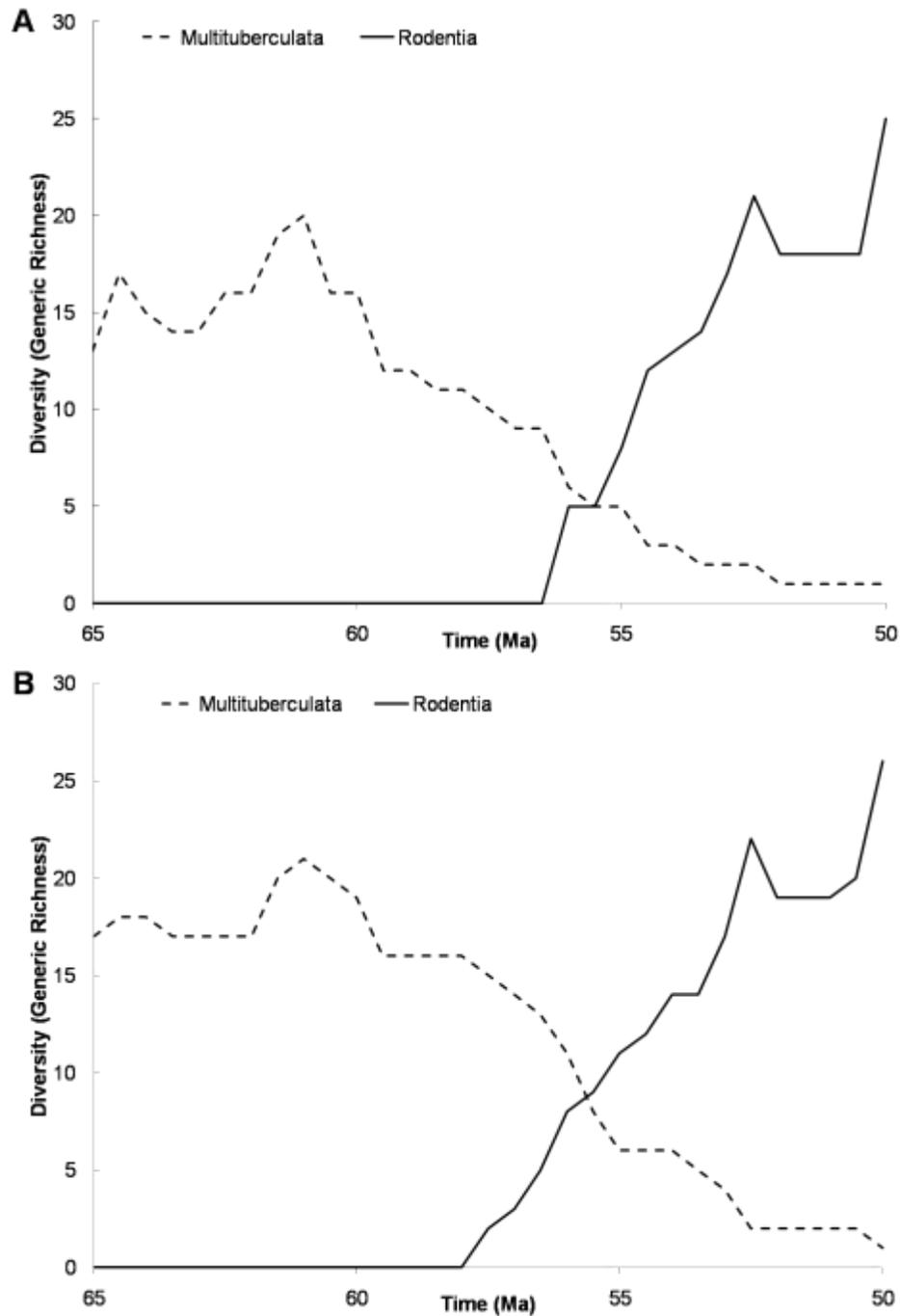
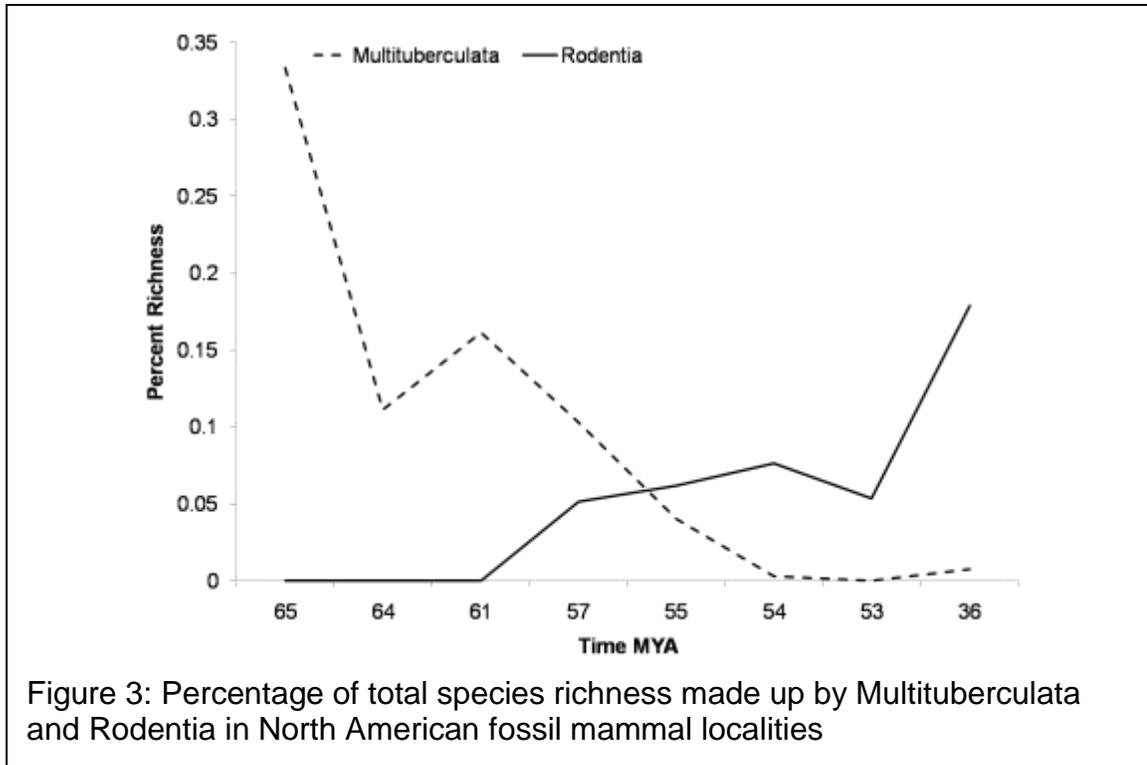


Figure 2: Generic richness of North American Multituberculata and Rodentia. This figure exhibits the classic “double wedge” pattern. A. Raw counts of presence/absence. B. Adjusted for estimates of actual temporal ranges



The results for the analysis of taxonomic rates of North American rodents and multituberculates seem to corroborate the results of the diversity and percent richness analyses. In Figure 4, we can see that the origination rate of the rodents correlates with the extinction rate of the multituberculates in North America. Simple visual inspection shows several isolated spikes in extinction rate for the multituberculates for most of the Paleocene with a much larger cluster of spikes corresponding to the addition of rodents to the ecosystem at the end of the Paleocene. It appears that extinction rates for the multituberculates peaked at the same time that origination rates for rodents peaked.

Additionally, the mean extinction rate for the Multituberculata increased nearly threefold after the rodents' introduction into the ecosystem. The result of a permutation t-

test corroborates this observation. The extinction rate of multituberculates was significantly higher after rodents appeared in the North American record. This result is visible in another format in the before and after comparison in Figure 8. This observation is important in of itself but also because we see the same threefold increase in extinction rate in Europe.

Possibly more telling than the trend in extinction rate of multituberculates is the trend in origination rate. Figure 5 shows the curve of origination rate of rodents that I have already seen. However, here I plot along with it the origination rate for multituberculates in the same interval. The origination rate of multituberculates drops to zero just as I observe the first origination event for rodents. This result is also visible in Figure 8. I observe origination events right up until the first introduction of rodents into the ecosystem but none after that. This result also makes the sharp increase in extinction rate of multituberculates in this period more striking.

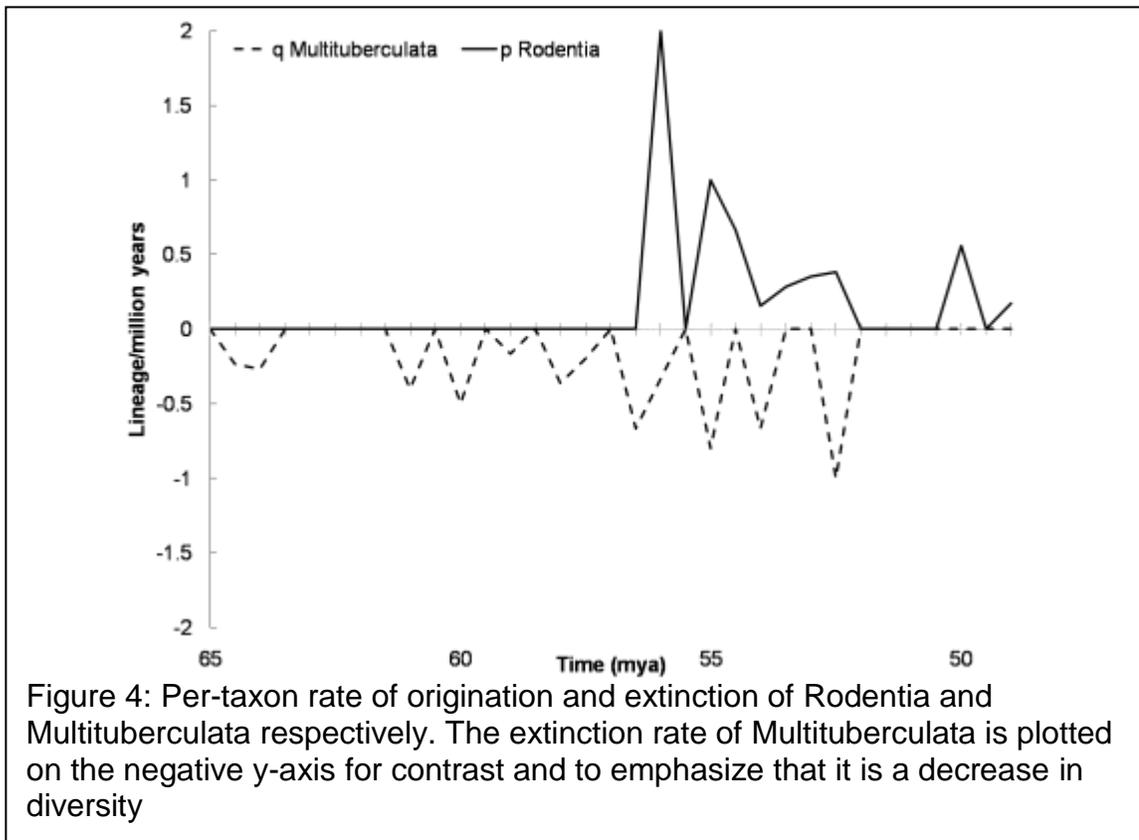
The time series for the North American multituberculates and rodents exhibit some general trends. The point at which the extinction rate for the Multituberculata seems to have begun to spike is at approximately 57 Ma when rodents appeared in North America. It may be more than coincidence that this dramatic change in mean extinction rate occurred after the introduction of rodents to the ecosystem and not a little later in time during the PETM. The mean extinction rate of multituberculates increased threefold with the addition of rodents to the system. A similar phenomenon occurred in Europe according to my analysis (discussed below).

While the analysis of the respective taxonomic rates of North American rodents and multituberculates strongly suggests an incumbent replacement, the analysis

comparing the taxonomic rates for multituberculates and plesiadapiforms is more complicated. Much like in Figure 4, in Figure 6, there seems to be some correlation between peaks of extinction in multituberculates and a purported competitor, in this case plesiadapiforms instead of rodents. The difference is that there does not seem to be as much of a relation between the magnitudes of these peaks. In the right-hand side of the graph where there is a spike in the extinction rate of multituberculates there is no corresponding spike in the origination rate of plesiadapiforms, which appears to remain relatively constant throughout the interval of interest. This lack of correspondence is not consistent with the hypothesis that Plesiadapiformes were the primary cause of the extinction of the Multituberculata but is still consistent with Plesiadapiformes being one of perhaps several competitors of Multituberculata as suggested by Maas et al. (1988).

As I established above, it was necessary to perform an analysis of the origination rate of rodents versus the extinction rate of a group that probably did not interact competitively with rodents. This analysis provides a control group because if significant correlation existed with the taxonomic rates of these two groups it raises the possibility that the correlation I observe elsewhere resulted by temporal autocorrelation. In this study, I chose early carnivores as this control group. Figure 7 fails to show any significant correlation between the origination of rodents and the extinction rate of carnivorans. The peaks of extinction for Carnivora in the graph are actually larger before this group's association with the Rodentia. This result is not surprising but helps corroborate the previously described results. If one observed some correlation between the origination of rodents and carnivorans it would call into question the significance of any correlation observed between the other groups because the taxonomic rates of

origination and extinction of any two groups living in this time and place could conceivably produce a similar relationship. The fact that I see no correlation in these rates for rodents and carnivorans eliminates temporal autocorrelation as a plausible scenario.



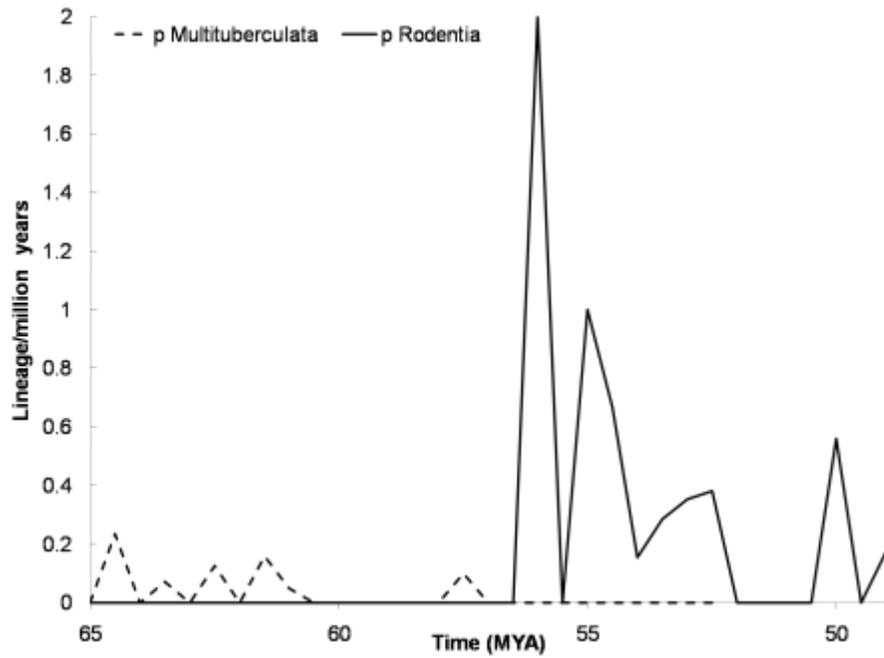


Figure 5: Per-taxon rate of origination for Rodentia and Multituberculata. The origination rate of Multituberculata is plotted on the positive y-axis to emphasize that it is an increase in diversity

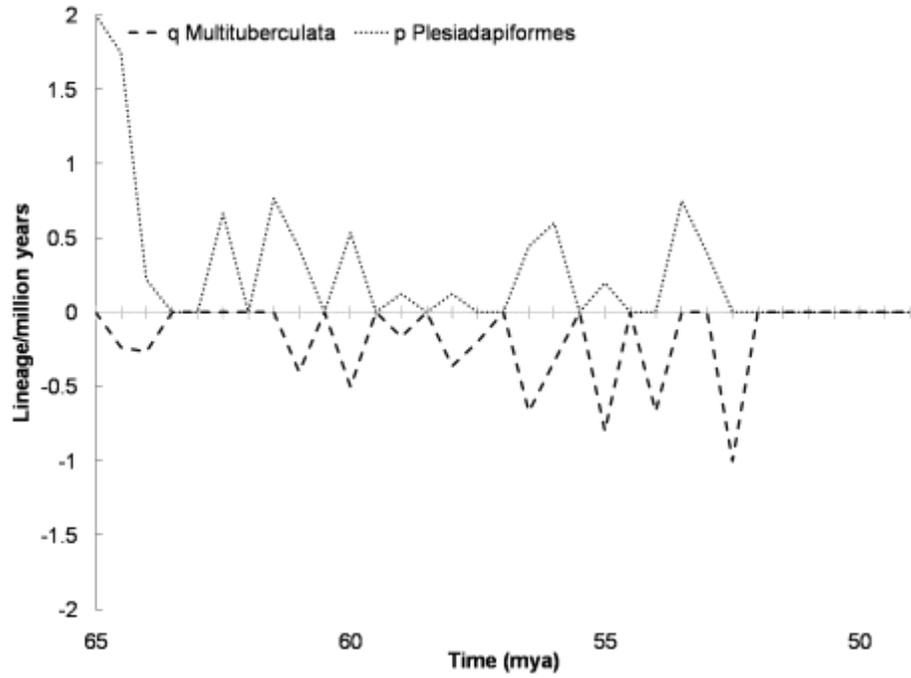
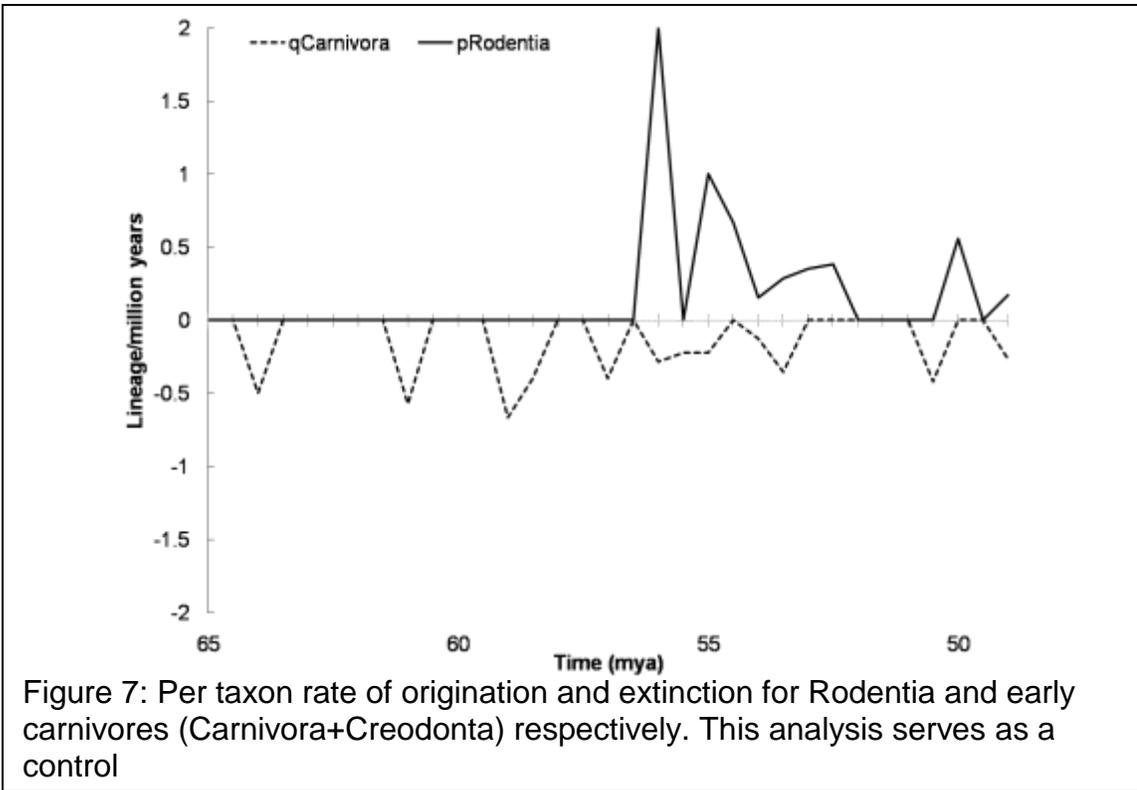
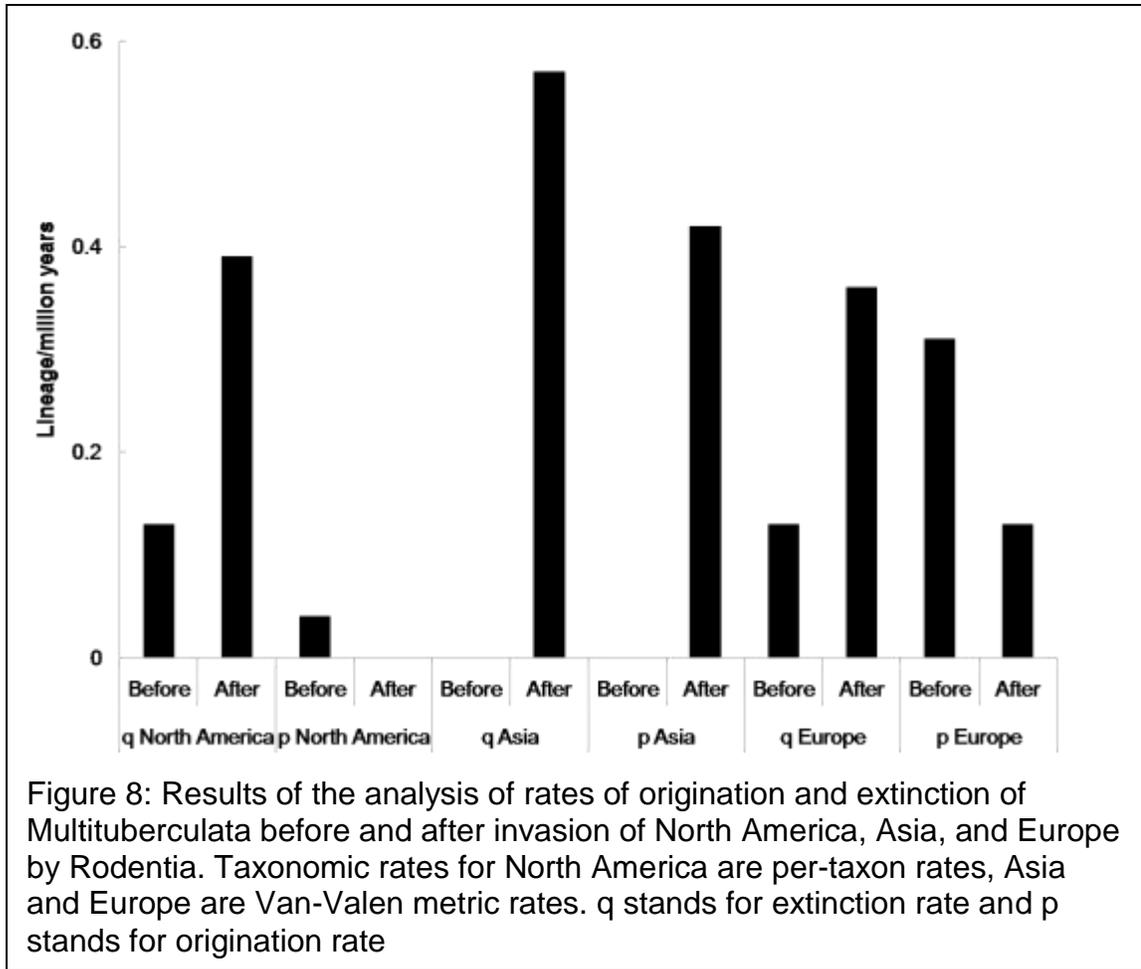


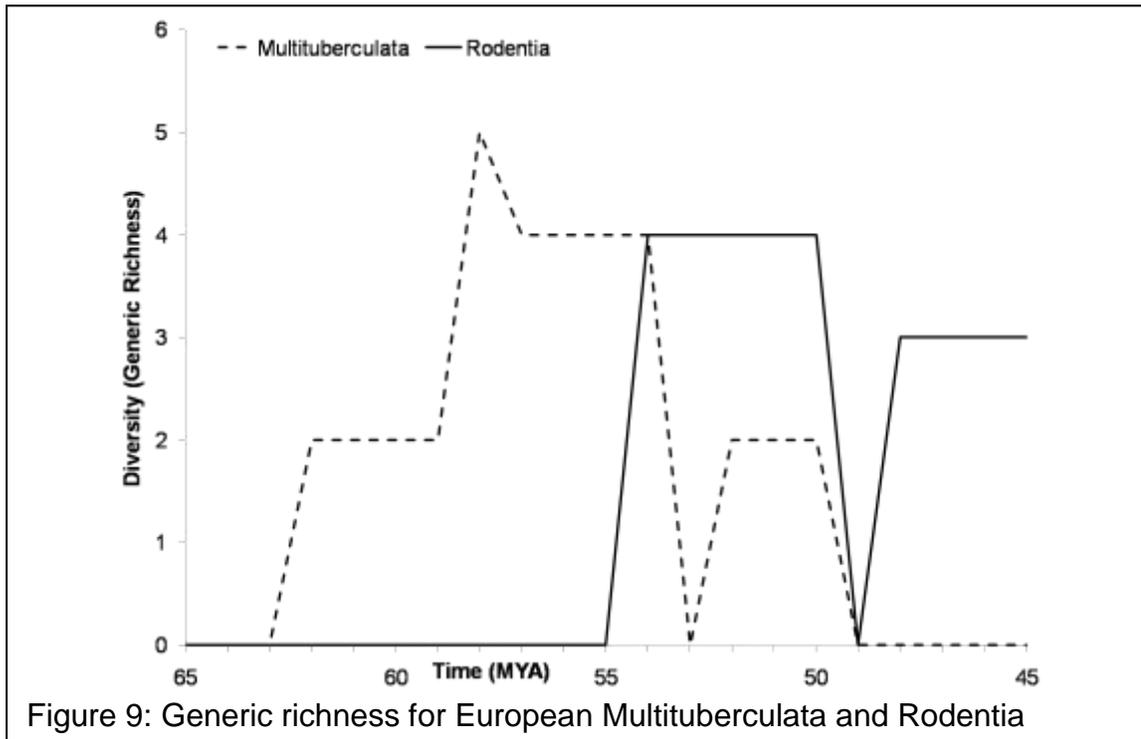
Figure 6: Per taxon rate of origination and extinction for Plesiadapiformes and Multituberculata respectively. Plesiadapiformes has often been suggested as a competitor of Multituberculata

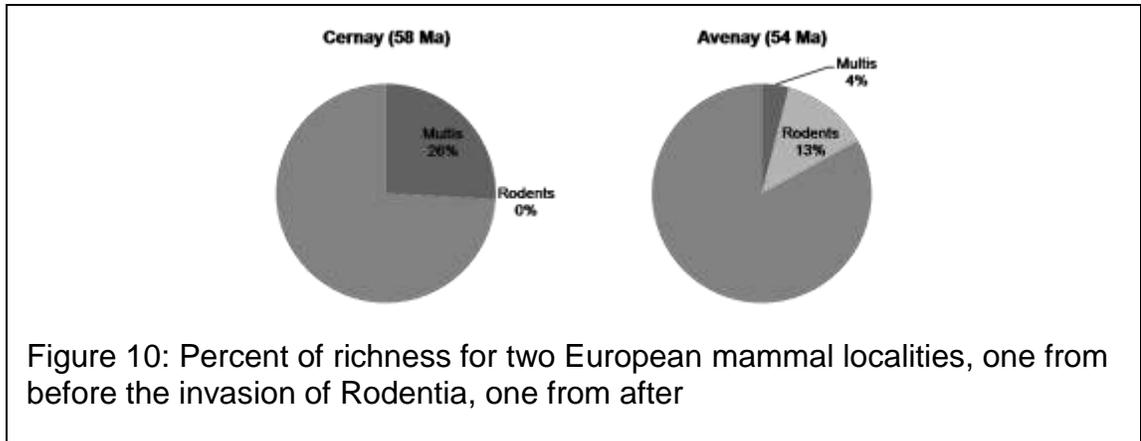




Europe.- The results of the analysis of taxonomic rates of origination and extinction in Europe are somewhat harder to interpret because there are fewer data to incorporate into the study. Nonetheless, I observe some general trends, which point to competition with rodents as a major factor in the extinction of multituberculates in Europe. The diversity curve for European rodents and multituberculates shown in Figure 9 approximates the pattern observed in Figure 2 for North America in that the diversity graph for European multituberculates and rodents exhibits the double wedge pattern. A comparison of the percent richness of multituberculates in Europe before and after

rodents appear shows a sharp decrease in the importance of multituberculates in the ecosystem. Although there is an increase in the total number of species in Figure 10B compared to Figure 10A most of the change in percent richness of multituberculates is due to a decrease in number of species. This shows the same pattern as the other components of the study for Europe. The results of the comparison of the taxonomic rates of origination and extinction of multituberculates before and after the invasion of rodents look remarkably similar for North America and Europe. The relative dearth of data points for Europe as well as Asia means that the time series analysis for the two continents is not very useful. For this reason, I will focus on the before and after comparisons for both.



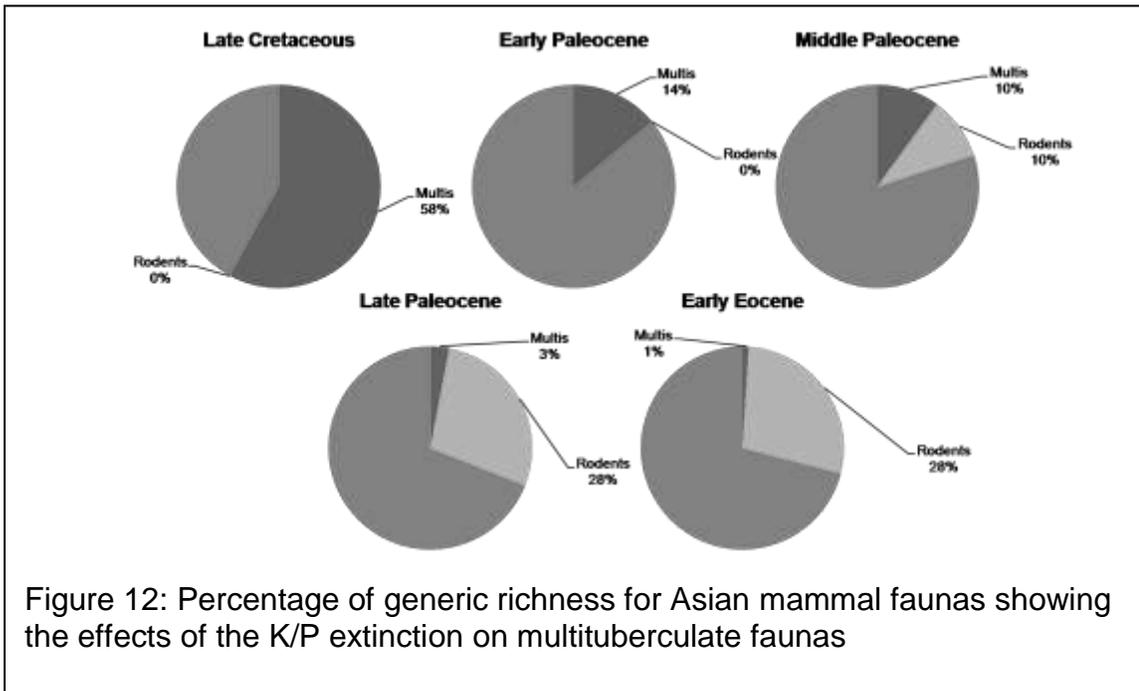
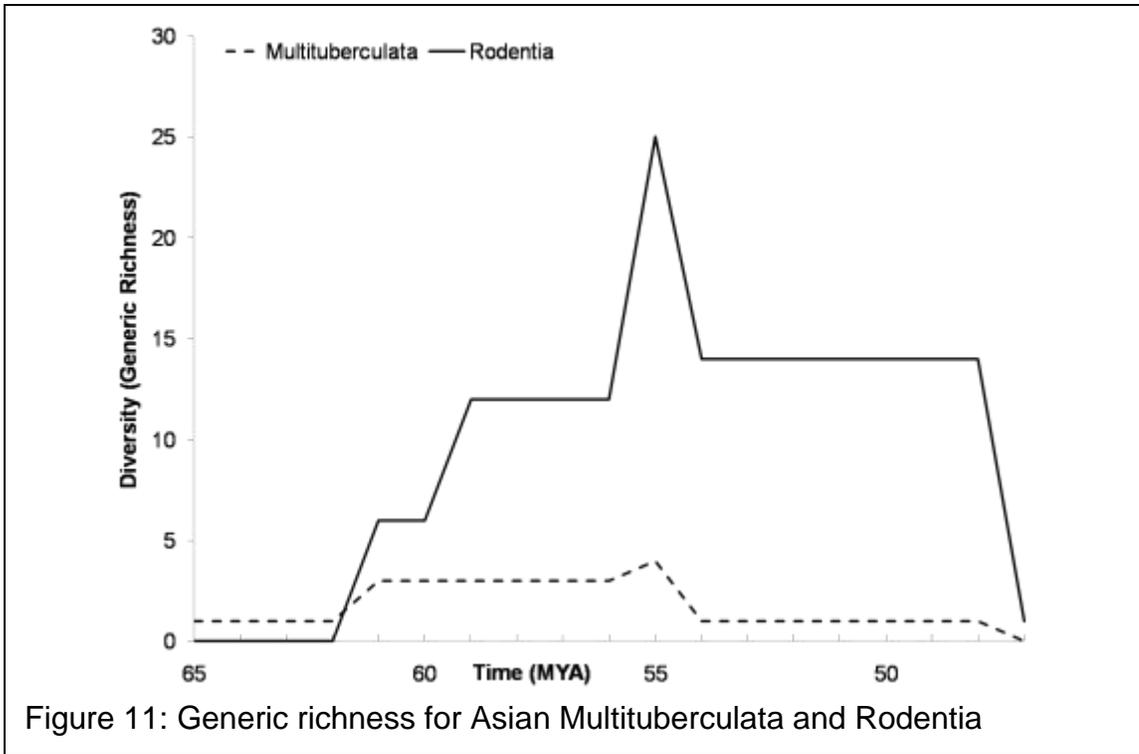


In figure 8, the analyses of extinction rate for the Multituberculata in North America and Europe look similar; and in fact, the figures for each are nearly identical. That said these trends appear to be the same. In Figure 8, we see that, as in North America, there is a threefold increase in the extinction rate of multituberculates in Europe after rodents invade the continent. This observation is even more significant when one considers the fact that these invasion events took place at different times on the different continents.

The results for the analysis of origination rate of European multituberculates before and after association with rodents is different from the same analysis from North America in the actual numbers but the trend is the same. In North America, the origination rate of multituberculates dropped to zero when rodents appeared on the scene but in Europe, their origination rate simply dropped dramatically. The origination rate for the Multituberculata in Europe decreased by a factor of three. I should point out that in Figure 8 the graphs for extinction and origination rates of multituberculates seem to be mirror images of each other. Clearly, the addition of rodents to the ecosystem of Europe

54 Ma had a dramatic effect on multituberculates just as the addition of rodents had on North American multituberculates 57 Ma.

Asia.- Whereas the results of this study seem to suggest that the pattern of replacement of multituberculates by rodents in Europe was similar to the pattern in North America this is not the case for the continent of Asia. I see this immediately in Figure 11, which shows the diversity of these two taxa over time. Rather than showing a trend of increasing diversity of rodents with a corresponding decreasing diversity of multituberculates, the two groups seem to rise and fall in diversity along with each other. This is a very different pattern compared to North America and Europe. The analysis of percent richness over time (Fig. 12) also shows a pattern contrary to the competition hypothesis. The sharpest drop in the percent richness of multituberculates occurred at the K/P boundary where multituberculates went from being the dominant taxon in Asian mammalian faunas to merely one component of these faunas. Furthermore, when rodents appear in the Asian record there is no sharp decrease in percent richness like what I see in North America and Europe.



The before and after analysis (Fig. 8) for Asia appears to show a different trend than what I observed for the other two continents. There is a drastic increase in extinction during the period when multituberculates are associated with rodents. Before rodents appear in Asia, the extinction rate of multituberculates is zero. On the other hand, before rodents appear, the origination rate for multituberculates is similarly zero and subsequently increases dramatically. It seems that the taxonomic rates of origination and extinction for the Asian multituberculates were not inversely tied to the rise of rodents.

Discussion

We can no longer view the extinction of the Multituberculata as a single event. In order to describe this replacement accurately we must begin thinking in terms of three overlapping events. Using this framework comparing and contrasting the disappearance of multituberculates in North America, Europe, and Asia becomes easier. By comparing the replacement events over time and space, I draw several conclusions about not just the causes of multituberculate extinction but also the early evolution of rodents. The results of this study indicate that in North America and Europe, competition with rodents remains a better explanation for the extinction of the multituberculates than alternatives. Furthermore, the Incumbent Replacement Model better describes the replacement pattern on these two continents than other models. Finally, I conclude that rodents cannot be implicated as a major cause in the extinction of multituberculates in Asia. In fact, the lack of analogous competitors may have contributed to open niche space, which the ancestors of rodents exploited, and which contributed to the rise in diversity of the clade.

Determining the main cause or causes of the extinction of a clade comes down to eliminating other potential factors. In the case of multituberculates, I must rule out other

competitors, mass extinction due to climatic or geological events, and stochastic processes before settling on competition with rodents as the prime mover in their extinction. For North America, it is possible to demonstrate that none of these other factors made as significant a contribution to the demise of the multituberculates as the introduction of rodents to mammalian faunas. This result is borne out by the evidence from the taxonomic rates and the timing of events in the replacement pattern.

As the results of the taxonomic rates study show, I cannot rule out competition with plesiadapiforms as a factor in the extinction of multituberculates, as suggested by Maas, Strait, and Krause (1988) who also showed that rodents played a larger role. The multituberculates showed a much larger increase in their rate of extinction at the point that rodents began to diversify in North America. Plesiadapiforms coexisted with multituberculates for a longer period. Only in the second half of this association do I observe a spike in extinction rate for multituberculates. This spike happened to occur when rodents appeared in North America. Furthermore, the largest increases in origination of plesiadapiforms occurred from around 65 Ma to 60 Ma and if this group was the major competitor of multituberculates, I would expect to see the largest increases in origination to coincide with the largest increases in multituberculate extinction. Perhaps later plesiadapiforms came into more direct competition with multituberculates than their ancestors did, and future studies could pursue this question.

My analysis comparing the origination rate of rodents with the extinction rate of early carnivores suggests that the correlation that I see in the other analyses does not result from an autocorrelation effect. These taxonomic rates do not appear to show any kind of correlation at all even though the groups existed in the same time and place and

experienced the same environmental perturbations. Seeing the same strong increase in the extinction rate of early carnivores with the introduction of rodents that I see with multituberculates would force us to consider alternate hypotheses for explaining the extinction of the multituberculates. These hypotheses would involve causes that could affect a broad array of mammal groups not specifically the multituberculates. In the case of early carnivores, I see almost the opposite, which lends further credence to the competition hypotheses.

Many critics of competition hypotheses have posited that the multituberculates perished in a mass extinction event and rodents coincidentally filled the open niche space like Benton (1987: pp 324) when he says “For example, there was a marked drop in diversity (from 9 to 2 species) between the Tiffanian and Clarkforkian Land-Mammal Ages (late Paleocene), which could indicate a mass extinction event”. I can test this hypothesis against what we know about the replacement pattern from the diversity, percent richness, and taxonomic rates analyses. All of these lines of evidence seem to point towards the replacement being an active event driven by competition and against the replacement being a passive event driven by a mass extinction. Implying that climatic or geological events caused the extinction of the multituberculates predicts a more sudden extinction than what I observe in the diversity curves for both North America and Europe. The percent richness data shows the same results. The timing of the replacement pattern is another line of evidence against the mass extinction hypothesis. The most likely candidate for an event responsible for the extinction of the multituberculates would be the Paleocene–Eocene Thermal Maximum (PETM), which occurred approximately 55 Ma (Westerhold, Rohl, McCarren, & Zachos, 2009). The PETM occurred during the period

of replacement. All of the evidence that I collected for this study, especially the taxonomic rates analyses, indicates that the decline of the multituberculates in North America began around 57 Ma, coinciding with the appearance of rodents and not with the PETM. In Europe, the decline in multituberculate diversity began after the PETM and coincides with the migration of rodents, presumably from North America. Clearly, we must invoke another cause than global climatic change to explain the extinction of the Multituberculata from North America and Europe.

The decline in diversity of multituberculates was not a random process and this is apparent from the timing and duration of the replacement. If the multituberculates became extinct purely by stochastic processes, I should expect to see several phenomena not apparent in the results of this study. One could posit that the extinction of this group resulted from a “random walk” of origination and extinction events where purely by chance, the extinction events outnumber the origination events and eventually the clade becomes extinct. In this case, there would be no need to suggest competition as a factor in the extinction, but the data for North America and Europe do not support this scenario. What I observe in North America is actually a sudden decline in multituberculate diversity caused by a dramatic increase in extinction rate coupled with an origination rate of zero. Both of these phenomena coincide with the introduction of rodents into North America. These effects are also evident in the declining percent richness of multituberculates during the period of replacement and the corresponding increase in percent richness of rodents.

In Europe, a similar situation to that in North America is apparent. I observe a threefold increase in the extinction rate of multituberculates and a threefold reduction in

origination rate after rodents appeared in Europe. Stochasticity seems unlikely as a cause for the decline in multituberculate diversity in this case. The fact that the origination and extinction rates are mirror images of each other after the invasion of rodents makes the stochastic broom hypothesis seem even less likely. As with North America, the percent richness data for Europe shows a sudden decrease in prevalence of multituberculates rather than a protracted decline as a stochasticity model would suggest. These data show that many lines of evidence converge on the same conclusion, namely, that competition with rodents is the explanation that best fits the observations about the extinction of the Multituberculata.

After eliminating alternate hypotheses, competition with rodents remains the most likely cause of the extinction of multituberculates. The incumbent replacement model provides the best framework for understanding the competitive interaction between the two groups. The case of the extinction of the multituberculates closely resembles the example of replacement of amphychelydian turtles by cryptodires and pluerodires (Rosenzweig and McCord, 1991). In the turtle example, turtles that could pull their heads into their shells (Cryptodires and Pleurodires) replaced turtles without this feature (amphichelydians) on multiple different continents (Rosenzweig & McCord, 1991). Therapsids seemingly replaced the incumbent pelycosaurs in multiple different regions (Kemp, 2006). I observe a pattern similar to these two examples in the diversity and taxonomic rate analyses for multituberculates and rodents in North America and Europe. The differential timing of the replacements on these continents helps tell the story of how multituberculates became extinct, in large part, because of an origination rate advantage

of rodents. The underlying cause of this advantage is unknown but one might assume that it lies in the biological differences between the two groups.

The story begins in Asia where it seems little or no competition took place between the few multituberculates that existed there in the Paleocene and the earliest rodents. I discuss this issue in more detail later but the important point is that the major turnover event in Asia occurred approximately 61 million years ago when rodents first began their march towards dominance of terrestrial mammalian communities. These rodents then spread to North America at approximately 57 million years ago where I observe the sharp increase in origination rate of rodents related to the sharp increase in extinction rate and cessation of origination in multituberculates. As each species of multituberculate died out, a new species of rodent evolved to fill the empty niche space. Krause produced evidence that rodents and multituberculates occupied overlapping niches by comparing their body size and presumed feeding habits (1986). The process of replacement repeated until all multituberculates were extinct. Rodents eventually migrated to Europe around 54 million years ago and underwent the process of replacing the incumbent multituberculates there as well. The last multituberculate species, *Ectypodus childei*, went extinct near the end of the Eocene in North America (Krishtalka et al., 1982, updated to new time scale by Swisher and Prothero, 1990). It is unclear why this particular species persisted for so long when all of its counterparts succumbed to replacement by rodents.

Whereas I can best describe the extinction of the Multituberculata in Europe and North America as caused by competition with rodents, I cannot say the same for Asia. The replacement pattern there more closely resembles the sort of passive extinction

caused by mass extinction and other stochastic processes described by other authors. This pattern provides a counterexample to the competitive replacement on the other two continents and could lend insight into the evolution of Rodentia. My abundance and diversity analyses show that, while multituberculates were a large and diverse part of Asian mammal communities in the Cretaceous, they never regained that position in the Paleocene. Unlike their North American counterparts, Asian multituberculates did not bounce back after the end-Cretaceous extinction and made up only a small percentage of the diversity in mammalian communities.

I can easily attribute the disappearance of Asian multituberculates to the stochastic broom by observing the rates of origination and extinction of this group before and after the evolution of rodents. These rates seem unrelated to the origination rate of rodents during this period indicating that incumbent replacement was not in operation. The origination rate for Asian multituberculates was zero at the beginning of the Paleocene and actually increased later in the Paleocene after rodents were already gaining in diversity. The Asian multituberculates had an extinction rate of zero before rodents appeared. This rate increased later, but there were so few species of multituberculate that random processes may suffice to explain their demise. The group also appears to have experienced some turnover at around 55 million years ago, which could perhaps relate to the Paleocene–Eocene Thermal Maximum. Overall, it appears that, while important elsewhere, the multituberculates of Asia played a relatively insignificant role in Paleogene faunas and went out with more of a whimper than a bang.

I have provided significant evidence supporting the hypothesis of the role of Rodentia in the extinction of the Multituberculata. Of the continents in my study, only

Asia differs from this interpretation. Perhaps there is some significance to the fact that the only continent where rodents did not compete with multituberculates is the continent where the first rodents evolved as Krause (1986) suggested. I think it plausible that the dearth of multituberculate incumbents in Asia provided an opportunity for a new group of mammals to evolve into the open niche space. Later as this group, the Rodentia, diversified, Asia acted as a staging ground for their invasion of nearby continents that did contain sizable multituberculate populations. I could say then, that a direct cause of the evolution and subsequent dominance of terrestrial mammalian faunas by rodents was the end-Cretaceous extinction, which, in Asia wiped out most of the incumbent multituberculates. The immediate ancestors of rodents exploited this opening to begin the rise to their current position as the largest order of mammals. Regardless of the role they played in the rise of rodents, this study has shown that while the classic hypothesis of multituberculates succumbing to extinction by competition is accurate, the replacement of multituberculates was a complicated and geographically heterogeneous process.

Chapter 2: Kay's Threshold in Living Rodents: Implications for Estimating Niche
Overlap in Extinct Multituberculates and Rodents

Introduction

The story of life on this planet is replete with instances of large and successful clades succumbing to extinction, seemingly due to competition with other clades. The general idea is that new clades possessing some competitive edge ousted the old clades and became their ecological, if not phylogenetic, successors. These kinds of stories make for good pop science, but amongst serious paleontologists, the jury is still very much out as to the role of competition in driving large-scale evolutionary trends, and many questions remain unanswered. My study seeks to answer two of these questions

1. What, if any, examples exist of a well-documented replacement event where competition stands as the most likely explanation?
2. What methods can paleontology use to test a competition hypothesis that circumvents the fact that we cannot observe putative competitive interactions directly?

In this study, I present both a method with which to estimate resource competition between two clades, as well as an example of an assumed competitive interaction in the fossil record, the extinction of the Multituberculata, to which I apply this method.

The Multituberculata existed for over 100 million years making them one of the orders of mammals with the longest geologic range. They survived the end-Cretaceous

extinction and were diverse in the Paleocene, becoming extinct at the end of the Eocene (Rose, 2006 p. 56). Today, the Rodentia makes up the largest order of mammals and enjoys a worldwide distribution (Wilson and Reeder, 2005 p. 745). The hypothesis that the extinction of the multituberculates was related somehow to the evolution of rodents dates to the late 1800s and has many proponents (Krause, 1986; Jepsen, 1949; and Van Valen and Sloan, 1966) as well as many detractors (Benton, 1987; Landry, 1965 and 1967; and Rose, 2006). No consensus exists on the subject of the multituberculate's demise.

At the heart of the issue of what caused the extinction of the Multituberculata lies the philosophical debate concerning the role of ecological processes like competition in clade replacements. On one hand are proponents of competition being a driving force in at least some replacement events (Briggs, 1998; Kemp, 2006; and Rosenzweig and McCord, 1991). Alternatively, there are critics who believe that processes that work on shorter time scales, like competition, have little or no effect at evolutionary time scales (Benton, 2009; Gould and Calloway, 1980). These authors point out that many examples of competitive interactions between clades actually resemble the result of abiotic, stochastic processes instead. In light of this ongoing debate, my study of the extinction of the Multituberculata does more than merely test a classic hypothesis. It also provides either a counterexample to the claim that biotic interactions are unimportant in the history of life, or it dismantles a hypothesis of competition that rests on illusory data.

After identifying an example of a putative competitive interaction to test, we must then devise a method that enables us to test it. I have previously shown that taxonomic rates of origination and extinction provide a means of testing competition models that

avoids certain pitfalls associated with diversity data (Wood and Hunter, in review). Brusatte et al. (2008) used morphospace overlap to investigate the ascendance of the early Dinosauria. They demonstrated a high degree of disparity between early dinosaurs and contemporaneous groups, like the thecodonts and concluded that dinosaurs rose to prominence by chance, rather than because of competitive advantage (Brusatte et al. 2008). One method that Krause (1986) used involved analyzing body mass overlap of some of the multituberculates and rodents present in North America during the replacement event. I think this method holds great promise for understanding the degree of potential niche overlap between these two clades, and this study focuses on it. My study also goes further, by comparing the body masses of all the multituberculates and rodents from the Paleocene and Early Eocene of North America, as well as Europe and Asia.

Krause (1986) found a distinct size overlap between two representative taxa, *Ptilodus*, a multituberculate, and *Paramys*, a rodent. He inferred this to be evidence of potential niche overlap between these clades. In this study I chose to expand the scope of this method to include all rodents and multituberculates from North America, as well as Europe and Asia, the other two continents where multituberculates existed in large numbers of species. I also chose to expand this method of inquiry by finding a way to infer diet from body mass in living rodents and applying this method to extinct rodents and multituberculates.

On the surface, it seems quite obvious that there should be some relationship between body mass and diet preference for a given organism and there seems to be good evidence that size can be used as an indicator of niche allocation (Maurer, 1999, pp. 129-

131). Kay (1975, 1984) and others, (Kay and Hylander, 1978; and Smith and Lee, 1984) provided concrete evidence for the hypothesis that mammals of differing body sizes have differing diet preferences. This observation stems from the distinct physiological demands and foraging costs experienced by mammals at different body masses. Rosenzweig found that prey size correlates with predator size in carnivores (1966). Kay (1975) determined that, among the living primates, those that weigh more than 500g are folivores and those under this threshold are faunivores. Frugivory spans across this threshold. Strait (2001) used the observations of Kay's Threshold to study the diet preference of extinct plesiadapiforms so there is a precedent for a study such as mine. I decided to test for a similar phenomenon in living rodents and apply this knowledge to estimate the diet preferences of the multituberculates and rodents of the Paleocene Holarctic.

Materials and Methods

Using the second volume of Walker's Mammals of the World (Nowak, 1999) I constructed a matrix of body mass and diet preferences for 124 rodent genera. I included at least one representative from each of the families of rodents and at least one representative of each subfamily of the Muridae. This provided a large sample size for the purposes of generating a frequency distribution diagram. Additionally, I produced matrices for the rodent families Muridae and Sciuridae, as well as a matrix for all rodents minus the Sciuridae. I then log-transformed the mass measurements for easier comparison and for other reasons. I placed each taxon into one of three categories insect-seed, mixed feeders, and obligate herbivores and generated frequency distribution diagrams using the log mass measurements and feeding categories. I used the frequency

distribution diagrams to draw conclusions concerning the relationship between body mass and diet preferences.

I chose to generate a frequency distribution for the sciurids and murids to test for phylogenetic bias in the larger sample. It seemed likely that a particular group of rodents could be phylogenetically predisposed to a particular feeding strategy so I considered this an important test. After generating these graphs, I also felt it necessary to generate the frequency distribution diagram without the Sciuridae out of concern for the aforementioned bias.

In order to estimate the body sizes of extinct rodents and multituberculates I collected all the available lower first molar length measurements for these taxa. The North American representatives of the Rodentia and Multituberculata were collected from the Paleobiology Database. The tooth length measurements were downloaded on March 24, 2010. I used the search function “find fossil taxa” and entered the genus names into the “scientific name” field. I found the m1 length measurements under the “morphology” tab. Locality data were collected from NOW (Neogene Old World) office for a Paleogene extension of the NOW database of fossils mammals. For the purposes of this study, I further subjected these occurrence data to checking and updating based on a search by the authors through the primary literature published through 2009. The dataset used here is available from NOW Coordinator Mikael Fortelius (mikael.fortelius@helsinki.fi). I collected some of the tooth length data for the European and Asian taxa from published literature. I collected some of the measurements directly from specimens housed at the American Museum of Natural History. Some tooth

measurements were provided by Meng Jin via personal communication. Appendix B lists the taxa used in this study and the source of the tooth length data.

For purposes of internal consistency, I chose to use the same formula for calculating body mass. This means that some taxa that would otherwise have been included in the study but for which m1 length was not available were left out. The difficulties associated with estimating body mass are well-documented (Creighton, 1980; Martin 1980, 1990; Smith, 1985; Conroy, 1987; Fortelius, 1990; Jungers, 1990) so I chose to use one of the simplest methods for estimating body mass that gives accurate estimates for rodents. Calculating body mass from first molar length generally works for small mammals and molar size in mammals scales isometrically with body size (Martin, 1990 pp. 52-64). The formula for calculating body mass from m1 length, L , is $4.083L^{3.31}$ (Martin, 1990 pp. 57). I log-transformed the estimates of body mass for the extinct taxa for easier comparison to the living taxa. After generating these body mass estimates, I could then compare them with the data from living rodents and categorize the extinct taxa based on their probable diets.

Results

The results of this study indicate a distinct relationship between body mass and diet preference of living rodents. Figure 13 shows this relationship with a frequency distribution. A clear threshold is discernable between 2.5 and 3 in this graph that separates the obligate plant feeders from the insect/seed eaters and the mixed feeders. The threshold roughly corresponds with a mass of 500 grams. Another threshold, although not as distinct, exists between 2.5 and 2 in the graph. Below this point, which corresponds to a body mass of 200 grams, the rodents are much more likely to be insect/seed feeders. As

observed with primates, frugivory seems to range across the size thresholds. Although some rodents eat leaves, unlike the primates used in previous studies (Kay, 1975, 1984) most of the herbivorous rodents feed on grass or tubers.

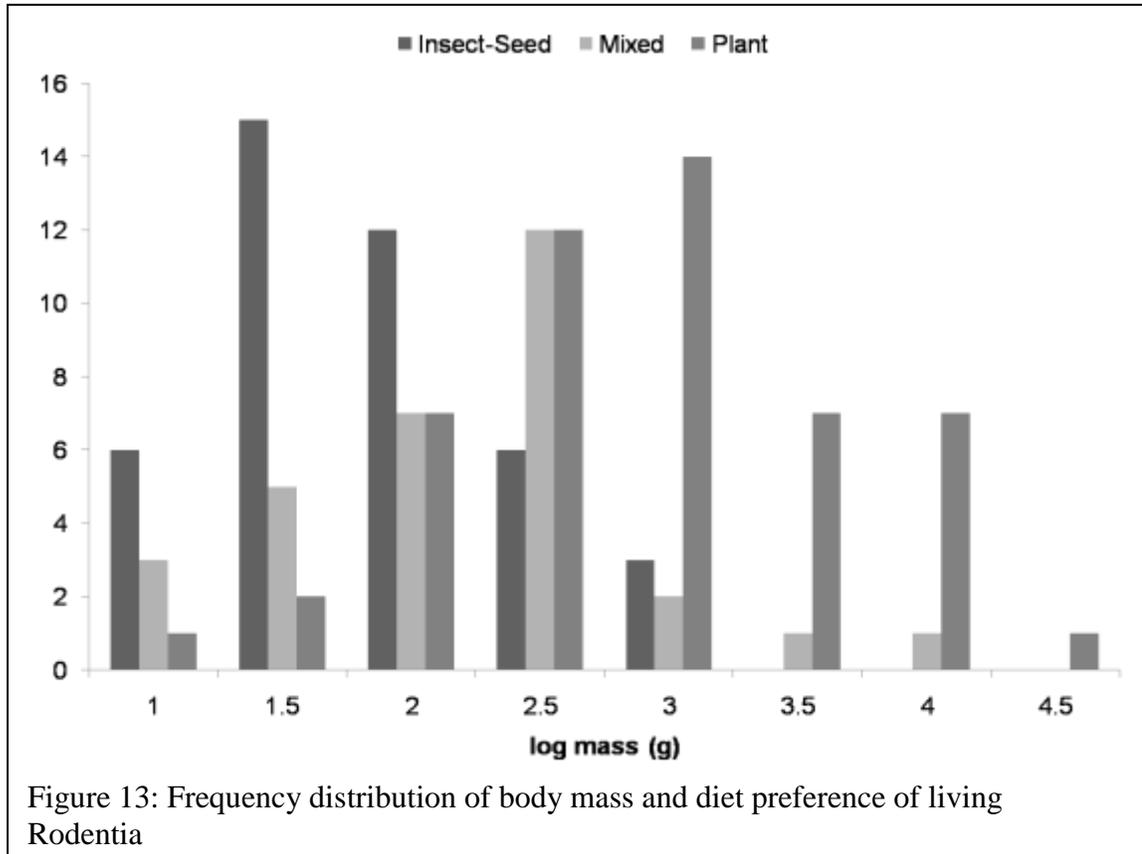
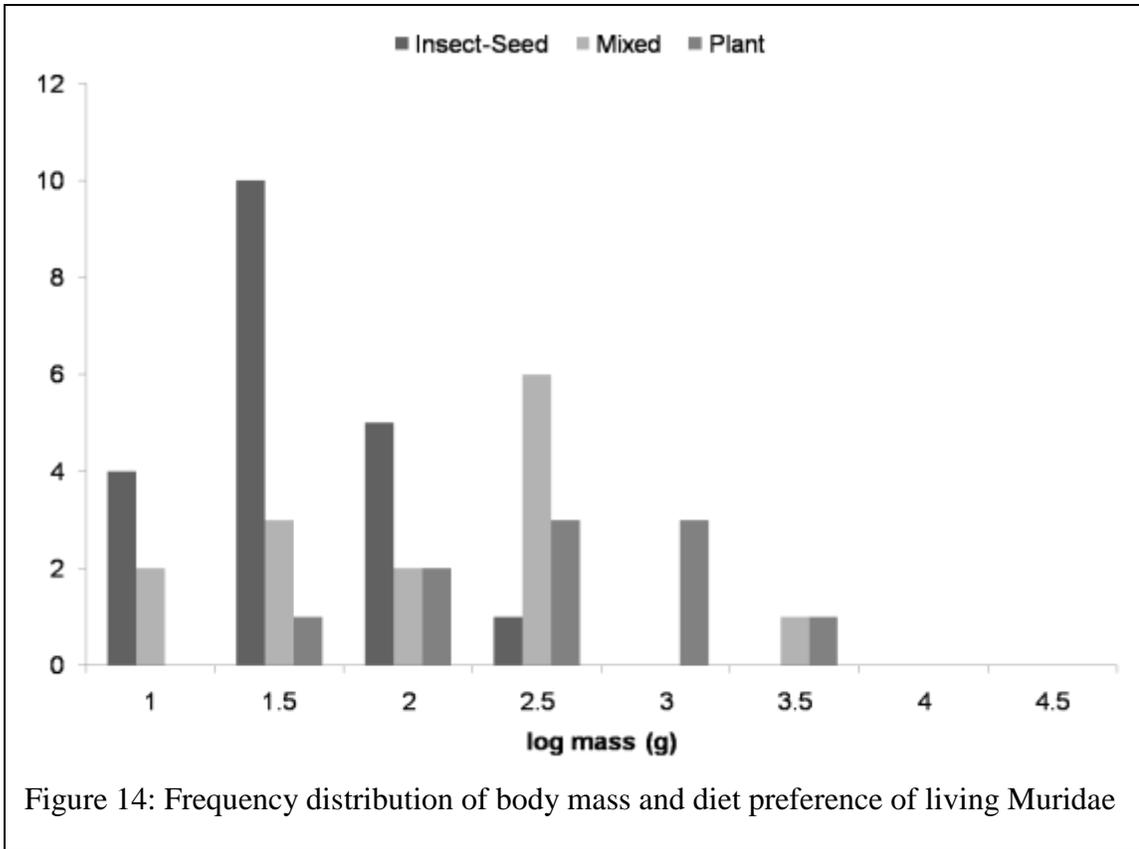


Figure 13: Frequency distribution of body mass and diet preference of living Rodentia

I calculated frequency distributions for two large families of rodents, the Muridae and Sciuridae to test for phylogenetic bias. If either of these groups possessed a strong phylogenetic bias towards a specific diet preference, their frequency distribution would not follow the trend demonstrated in the larger sample. The distribution graph for the murids (Fig. 14) appears to show the same pattern as the larger sample, except that there

are several large carnivorous members of this group that tend to skew the results. Nonetheless, the relationship between body mass and diet preference still holds for the murids, which has the distinction of being the largest rodent family and possessing one of the widest ranges in body mass. I cannot say the same for the sciurids, pictured in Figure 15. The Sciuridae seems to have a strong phylogenetic bias toward faunivory as well as a limited size range compared to the murids. Additionally, the sciurid, *Myosciurus* goes against the trend in the frequency distribution of all rodents in that it is one of the smallest rodents but feeds almost exclusively on the bark of a single species of tree. In light of outliers like this, I chose to make one additional frequency distribution (Fig. 16). This family of rodents does not demonstrate the same pattern of size and diet preference observed in the larger sample of rodents. Even though the frequency distribution of all rodent families follows the predictions of Kay's threshold even with the sciurids included, their inclusion obscures the trends I have previously described. Removal of the Sciuridae tends to reinforce the trends in diet preference and body mass that I observe in the sample of all rodents. A 100% stacked frequency distribution diagram (Fig. 17) also highlights these trends.



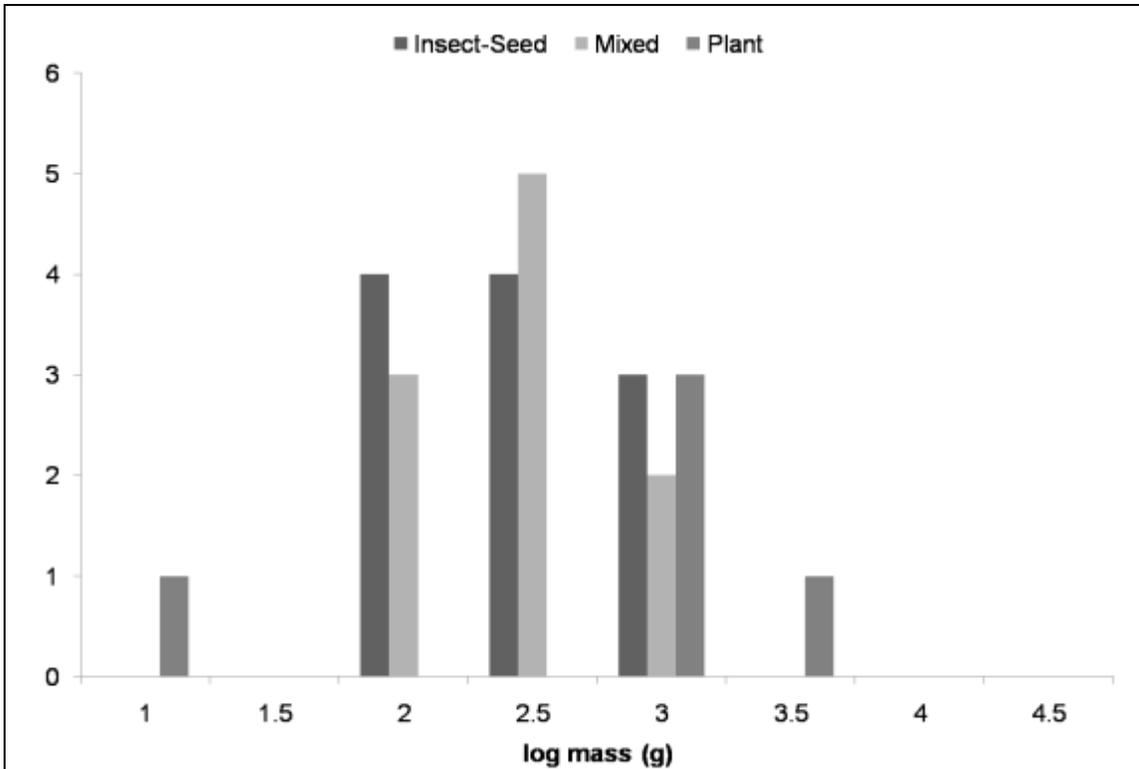


Figure 15: Frequency distribution of body mass and diet preference of living Sciuridae

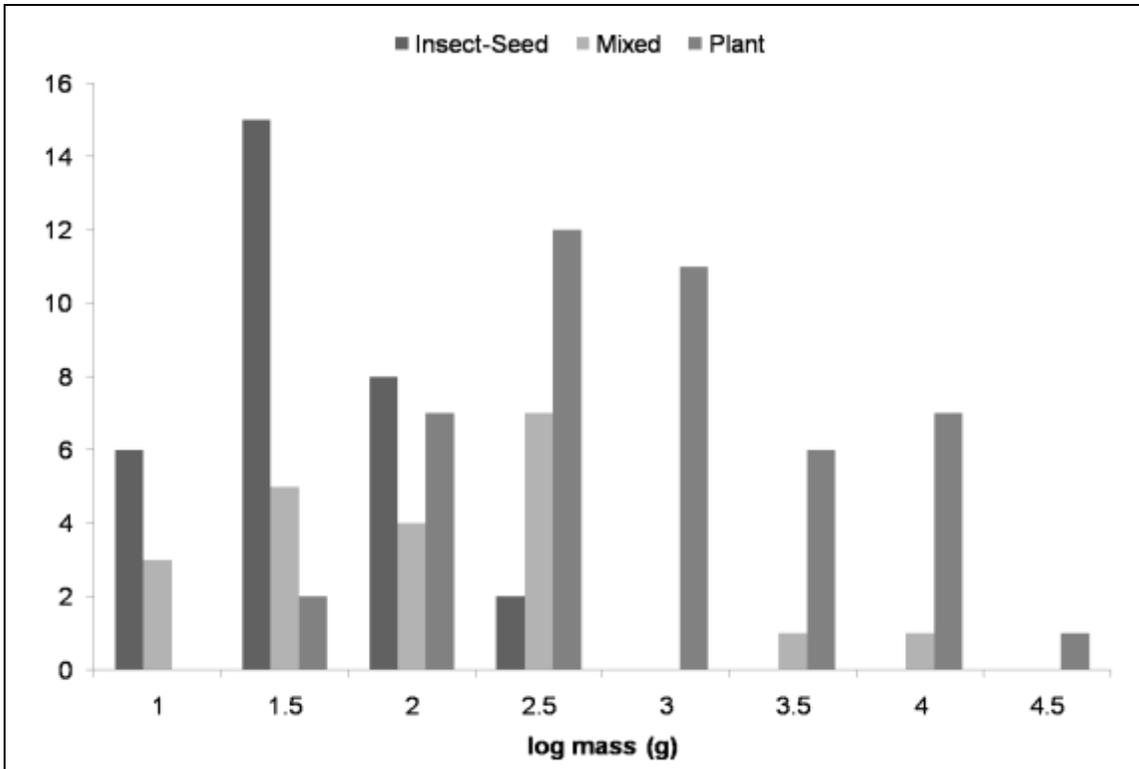


Figure 16: Frequency distribution of body mass and diet preference of living Rodentia minus Sciuridae

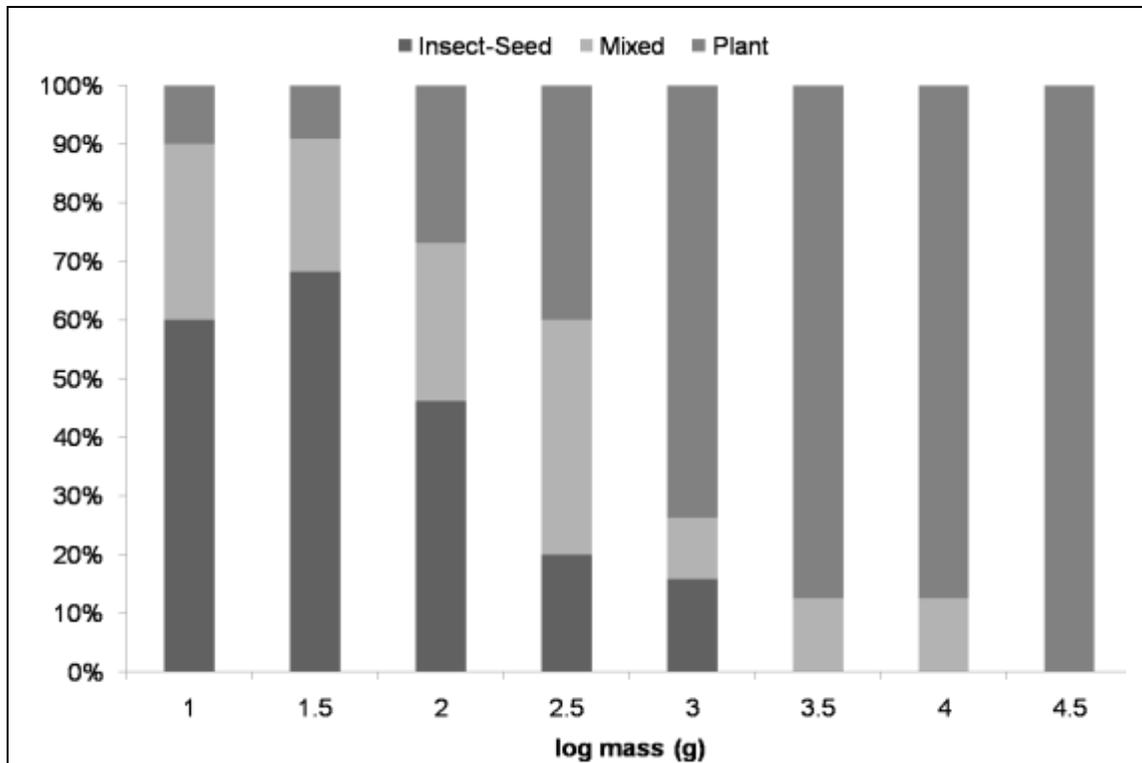


Figure 17: 100% stacked frequency distribution of body mass and diet preference of living Rodentia minus Sciuridae

North America. -The data from body mass estimates have a significant size overlap between the rodents and multituberculates of North America. Table 1 shows the body size estimates and predicted feeding preferences of the multituberculates and rodents of North America. Figures 6-8 show frequency distributions for the body masses of the Multituberculata and Rodentia for three critical periods in the replacement event. Most of the multituberculates and rodents fell into the likely insect/seed eating category but both groups also included several mixed feeders and herbivores. The only area where the multituberculates and rodents did not overlap substantially is at the largest body sizes.

Table 1: First molar length, body size estimates, and diet preference predictions for North American Multituberculata and Rodentia

Multituberculata				Rodentia			
Genus	m1 length	Mass (g)	Inferred Diet	Genus	m1 length	Mass (g)	Inferred Diet
<i>Ectypodus</i>	1.80	29	insect/seed	<i>Alagomys</i>	0.84	2	insect/seed
<i>Parectypodus</i>	2.08	46	insect/seed	<i>Elymys</i>	0.97	4	insect/seed
<i>Microcosmodon</i>	2.08	46	insect/seed	<i>Pauromys</i>	1.23	8	insect/seed
<i>Cimexomys</i>	2.20	56	insect/seed	<i>Mysops</i>	1.33	10	insect/seed
<i>Mesodma</i>	2.30	65	insect/seed	<i>Apatosciuravus</i>	1.42	13	insect/seed
<i>Mimetodon</i>	2.53	89	insect/seed	<i>Microparamys</i>	1.44	14	insect/seed
<i>Baiotomeus</i>	2.58	95	insect/seed	<i>Mattimys</i>	1.46	14	insect/seed
<i>Neoplagiaulax</i>	2.72	113	insect/seed	<i>Lophiparamys</i>	1.48	15	insect/seed
<i>Anconodon</i>	2.90	140	insect/seed	<i>Knightomys</i>	1.73	25	insect/seed
<i>Ptilodus</i>	3.61	291	mixed	<i>Pseudocylindrodon</i>	1.87	33	insect/seed
<i>Stygimys</i>	3.73	325	mixed	<i>Tillomys</i>	1.90	34	insect/seed
<i>Prochetodon</i>	3.78	339	mixed	<i>Dawsonomys</i>	2.10	48	insect/seed
<i>Eucosmodon</i>	5.40	1113	plant	<i>Uriscus</i>	2.18	54	insect/seed
<i>Neoliotomus</i>	7.01	2653	plant	<i>Sciuravus</i>	2.18	54	insect/seed
<i>Catopsalis</i>	12.00	15890	plant	<i>Guanajuatomys</i>	2.30	65	insect/seed
<i>Taeniolabis</i>	19.70	82799	plant	<i>Acritoparamys</i>	2.40	75	insect/seed
				<i>Anomoemys</i>	2.55	91	insect/seed
				<i>Reithroparamys</i>	2.93	145	insect/seed
				<i>Thisbemys</i>	3.33	222	mixed
				<i>Paramys</i>	3.36	229	mixed
				<i>Ischyromys</i>	3.47	255	mixed
				<i>Notoparamys</i>	3.63	296	mixed
				<i>Mytonomys</i>	4.59	648	plant
				<i>Pseudotomus</i>	5.56	1226	plant
				<i>Quadratimus</i>	5.57	1234	plant

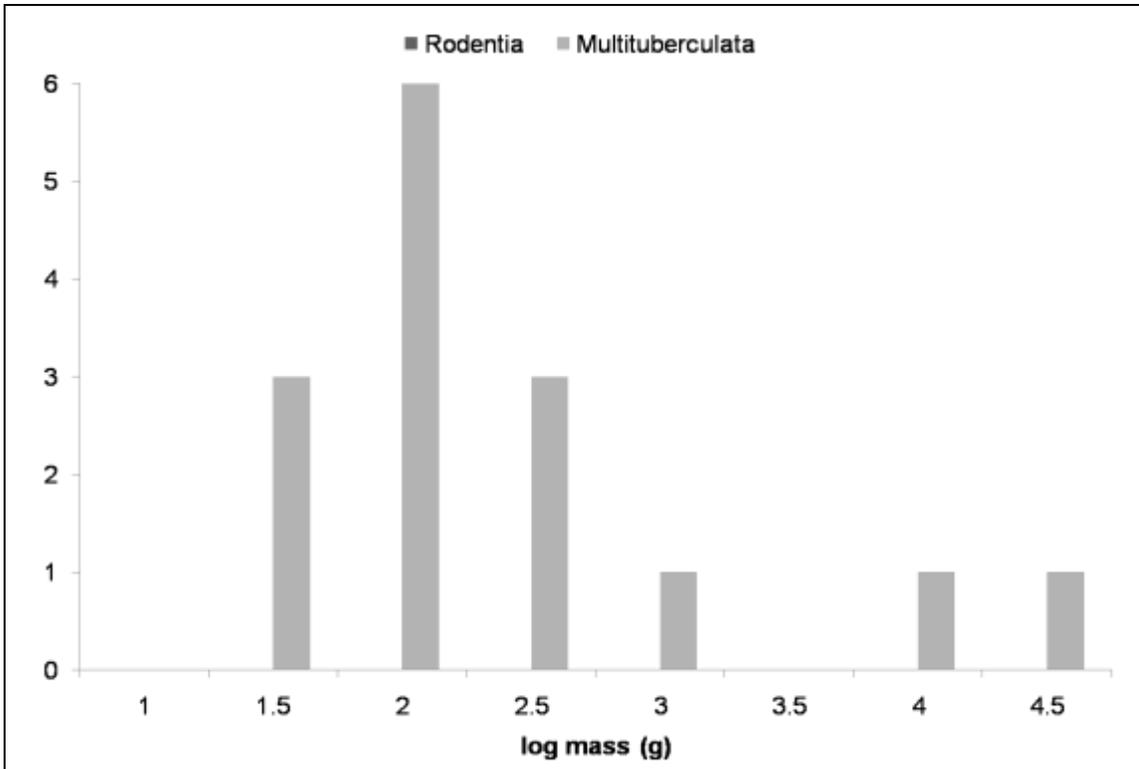


Figure 18: Frequency distribution of body mass estimates of Early Paleocene Multituberculata and Rodentia from North America

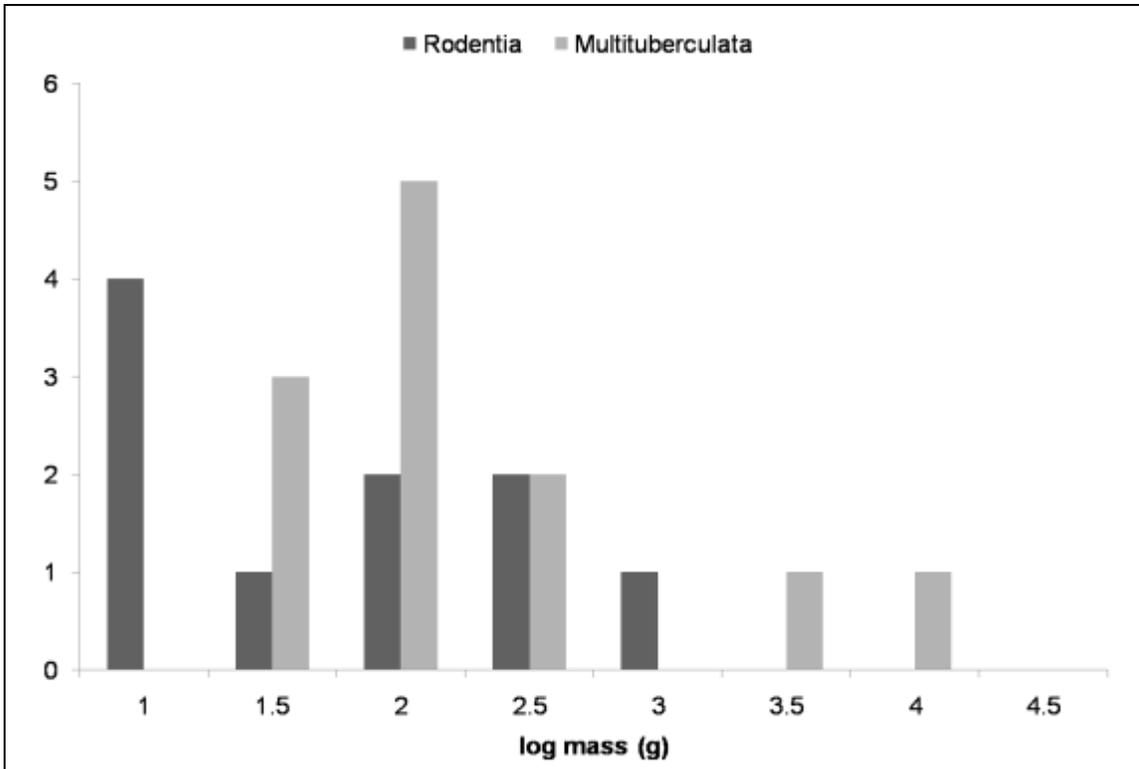


Figure 19: Frequency distribution of body mass estimates of Late Paleocene Multituberculata and Rodentia from North America

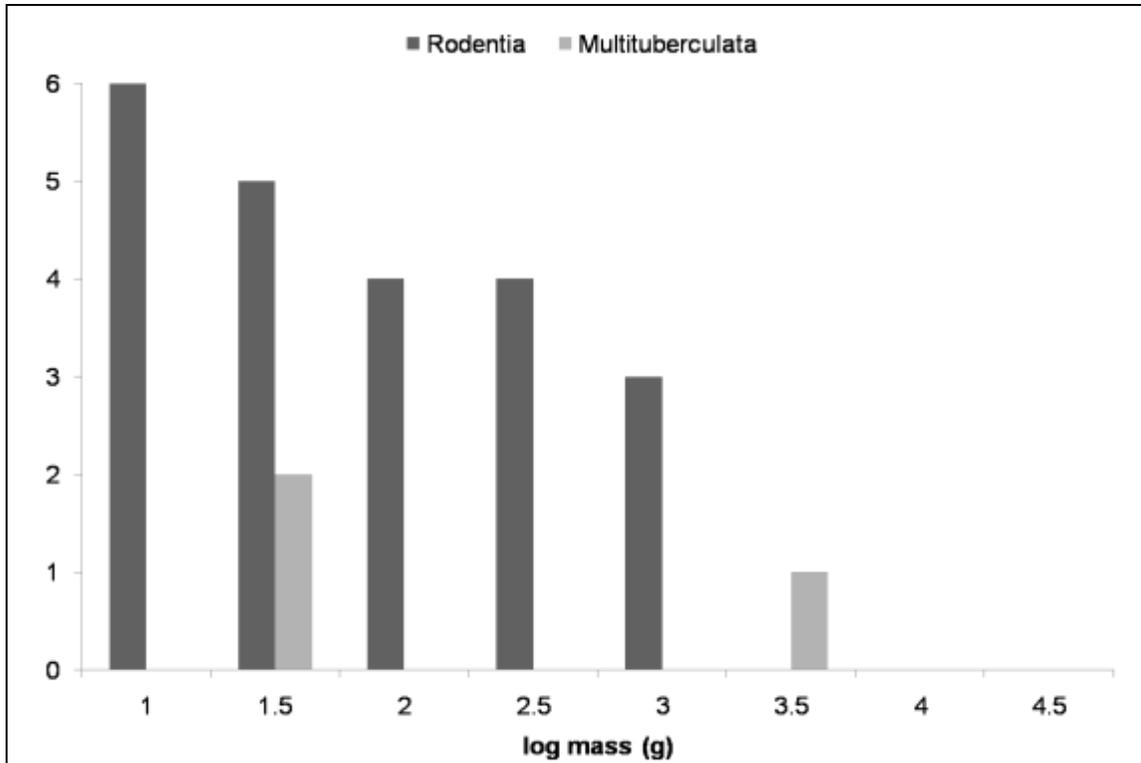


Figure 20: Frequency distribution of body mass estimates of Early Eocene Multituberculata and Rodentia from North America

Europe. -The body size estimates for the Multituberculata and Rodentia of Europe have the same size overlap as their North American counterparts. Because there were so few taxa, I could not produce a frequency distribution as with the North American data. Nonetheless, Table 2 demonstrates the same pattern that I observe in North America. The body size model based on the living taxa predicts that most of the genera of both orders were insect/seed feeders, whereas one genus of each was a mixed feeder. The largest multituberculate, *Boffius*, which was substantially larger than any of the rodents and which I can confidently predict was a herbivore probably went extinct before rodents reached Europe.

Table 2: First molar length, body size estimates, and diet preference predictions for European Multituberculata and Rodentia

Multituberculata				Rodentia			
Genus	m1 length	Mass (g)	Inferred Diet	Genus	m1 length	Mass (g)	Inferred Diet
<i>Ectypodus</i>	1.75	26	insect/seed	<i>Microparamys</i>	1.44	14	insect/seed
<i>Parectypodus</i>	2.35	70	insect/seed	<i>Eogliravus</i>	1.60	19	insect/seed
<i>Hainina</i>	2.54	90	insect/seed	<i>Meldimys</i>	1.90	34	insect/seed
<i>Neoplagiaulax</i>	2.77	121	insect/seed	<i>Protadelomys</i>	2.23	59	insect/seed
<i>Liotomus</i>	3.80	345	mixed	<i>Paramys</i>	3.36	229	mixed
<i>Boffius</i>	15.20	34914	plant				

Asia. -North America and Europe seem to exhibit the same pattern of size overlap in their native multituberculates and rodents, but Asia exhibits the opposite pattern. None of the rodents of Asia were much larger than 100 grams, far below the threshold for herbivory or even omnivory. On the other hand, I consider all but one of the Asian multituberculates to have been herbivores. Table 3 shows the distinct contrast in body mass of the Asian representatives of the Multituberculata and Rodentia.

Table 3: First molar length, body size estimates, and diet preference predictions for Asian Multituberculata and Rodentia

Multituberculata				Rodentia			
Genus	m1 length	Mass (g)	Inferred Diet	Genus	m1 length	Mass (g)	Inferred Diet
<i>Mesodmops</i>	2.35	70	insect/seed	<i>Alagomys</i>	0.75	2	insect/seed
<i>Prionessus</i>	4.83	767	plant	<i>Ivanantonia</i>	0.78	2	insect/seed
<i>Sphenopsalis</i>	8.00	4119	plant	<i>Tribosphenomys</i>	0.90	3	insect/seed
<i>Lambdopsalis</i>	9.03	6164	plant	<i>Bandaomys</i>	1.60	19	insect/seed
				<i>Sharomys</i>	1.70	24	insect/seed
				<i>Ulanomys</i>	1.70	24	insect/seed
				<i>Eomylyus</i>	2.00	41	insect/seed
				<i>Palaeomylyus</i>	2.07	46	insect/seed
				<i>Ardynomys</i>	2.30	65	insect/seed
				<i>Acritoparamys</i>	2.58	95	insect/seed
				<i>Rhombomylyus</i>	2.70	111	insect/seed
				<i>Taishanomys</i>	2.71	112	insect/seed

Discussion

My study demonstrates a strong correlation between body size and diet preference in living rodents that closely mirrors Kay's Threshold for primates. It is reasonable to suggest that this same threshold exists in many groups of small mammals. The fact that Kay's Threshold still applies to rodents, even though they are much more widespread than living primates are and far more speciose suggests that it is applicable to many groups. Many authors have commented on the morphological similarity in the feeding adaptations of rodents and multituberculates. If Kay's Threshold applies to rodents, then I consider it likely that the same Threshold applies to multituberculates. I may now use the insights gained from the study of living rodents to interpret the diet of the extinct multituberculates and rodents and assess the likelihood of niche overlap. I may also compare and contrast the patterns of body mass overlap, or lack thereof, on the three

continents to test the hypothesis that rodents contributed to the extinction of the multituberculates

One independent test of the ability of this body mass/diet preference estimation technique came recently with the discovery of an exceptionally preserved rodent from the Middle Eocene of Germany (Storch and Seiffert, 2007). In addition to preserving virtually all the articulated skeleton and the outline of the rodent's hair, the oil shale of the Messel preserved its last meal. The gut contents of this rodent, *Eogfiravus*, indicate that it ate seeds, fruit, and buds, falling into the insect/seed category in my organizational scheme. I estimate its mass at around 19 grams, well within the insect/seed category. Perhaps more data from independent tests of diet preference in multituberculates and rodents might become available in the future that could potentially corroborate my results.

North America.-The Multituberculata and Rodentia of North America overlapped substantially in body mass. I estimate most representatives of both clades as seed or insect feeders, but both groups also included several mixed feeders and herbivores. It appears that rodents already possessed a substantial range in size even early in their existence. The only discernable difference between the rodents and multituberculates is that the smallest rodents are quite a bit smaller than the smallest multituberculates, and the largest multituberculate is an order of magnitude larger than the largest rodent. This could be due to an overestimation of body mass by my estimation method. Regardless, the diet overlap still existed, even if end members of the two clades might have existed outside the overlapping range. Additionally, as I observe in Figures 18 and 19, the largest of the multituberculates, *Taeniolabis*, went extinct before the invasion of North America

by rodents. Competition with rodents cannot be implicated in the extinction of this particular genus, but remains a good hypothesis for explaining the extinction of, at least, the majority of the multituberculates. Perhaps another group of mammals contributed to the extinction of the largest multituberculates like *Taeniolabis*.

Europe.-The same pattern in the body mass correlation between the North American multituberculates and rodents appears in the data from Europe. Again, most representatives of both clades fall into the insect/seed category indicating significant potential for niche overlap. One member of each clade was probably omnivorous, also indicating potential for niche overlap. None of the rodents appear to match up with the lone herbivore in the group, *Boffius*, meaning that if that genus lived in the same time and place as the rodents, which is not certain, I can assume there was no competition involved. All together, the pattern of niche overlap in Europe appears consistent with the pattern in North America. That these two patterns resemble each other corroborates my previous findings concerning the replacement of the multituberculates by rodents (Wood and Hunter, in review).

Asia.-Whereas the data from body mass estimates of the Multituberculata and Rodentia of North America and Europe indicate potential for niche overlap, no such pattern is apparent for Asia. I estimate all of the Asian rodents in this study as being quite small with the largest weighing only a little over 100g. Meanwhile, all but one of the multituberculates firmly reside in the plant-feeding category. The only multituberculate that overlapped in size with the rodents and fell into the insect/seed category, *Mesodmops*, was the last multituberculate of Asia, appearing around 55 Ma and outliving the other three genera, disappearing around 48 Ma. If anything, the results of this study

demonstrates that the multituberculates were largely unobtrusively present on that continent. Perhaps the absence of smaller, faunivorous and grainivorous multituberculates in Asia provided a window of opportunity for the ancestors of rodents to exploit unoccupied niche space, as suggested by Krause (1986) and, more recently us (Wood and Hunter, in review).

The extinction of the multituberculates provides a useful test of methods for investigating clade interactions. My study demonstrates that it is possible to evaluate, albeit indirectly, competition between organisms in deep time, even though we cannot directly observe them. The results of my diet reconstructions of the Multituberculata and Rodentia of North America and Europe paint a picture of potential niche overlap and competition for food resources between these two orders. My results for Asia indicate little or no evidence for niche overlap between the multituberculates and rodents there. This study suggests that competition with rodents is the best explanation for the disappearance of the multituberculates in Europe and North America. In providing evidence for the competition hypothesis in this specific case, it speaks to the larger issue of the role of biotic interactions driving large-scale faunal turnover. This study alone cannot answer the question of the relative importance of clade interaction and abiotic factors in the history of life, but this study, and my study of taxonomic rates (Wood and Hunter, in review) suggest methods whereby we might test for other examples of competition in the fossil record.

The issue of competitive interactions in the fossil record and their relative importance for driving large-scale evolutionary trends may never be fully resolved. That said, this thesis provides several, quantitative methods, which we can use to investigate

competition without resorting to subjective and antiquated ideas about the superiority of one clade over another. In the specific case of the Multituberculata of North America and Europe, I have laid out an argument, based on several lines of evidence that implicates competition with rodents as the main factor in their extinction. This competition could have been indirect incumbent replacement, or more direct competition resulting from shared diet preferences. Perhaps both types of competition acted simultaneously. The multituberculates in Asia appear to have represented a relic taxon. On that continent, the Multituberculata and Rodentia truly were “ships that passed in the night”.

My thesis also contributes to the larger discussion about competition in the fossil record. An ecological process, competition, did contribute to an evolutionary process, namely clade replacement. Perhaps this is the only example of competition driving an extinction event and all of the other examples one could point to resulted from abiotic factors, but how likely is that? Certainly, this is possible and my example could be the exception that proves the rule, but I expect by applying taxonomic rates analyses and diet reconstructions to other examples of replacement events, we will find other instances where competition played a role.

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Appendix A: Addendum to Chapter 1 Methods

During the course of my thesis work, I endeavored to use any means necessary to answer the questions I posed about the extinction of the multituberculates. This philosophy meant leaving no stone unturned and this manifested itself in my using multiple sources of data. My research philosophy also naturally led to using a wide range of analytical techniques, some of which I deemed inappropriate for inclusion in my actual study. Few precedents exist for using taxonomic rates of origination and extinction to analyze competition in the fossil record so I went through several methods that were less than successful but merit at least a mention. This appendix serves this purpose.

Regression analyses.- The incumbent replacement model predicts a positive relationship between the origination rate of a replacing clade and the extinction rate of an incumbent clade. My initial idea to test for a relationship between the extinction rate of multituberculates and the origination rate of rodents was to use regression analysis. I produced a scatter plot with the extinction rate of multituberculates on the x-axis and the origination rate of rodents on the y-axis and fitted this graph with a trend line. My original assumption was that a trend line with a significant r-squared value would support the incumbent replacement model. This assumption turned out to be somewhat flawed. In addition to a regression model using the taxonomic rates of multituberculates and rodents I also used a partial regression to test the relative importance of the taxonomic rates of multituberculates, rodents, and plesiadapiforms. My rationale being that I might

see a relationship between the origination rates of rodents and plesiadapiforms and the extinction rate of multituberculates. Perhaps the Plesiadapiformes and Rodentia both contributed to the extinction of the Multituberculata.

Correlation analyses.- I also used a method similar to the regression methods, correlation analysis, to test for a significant correlation between the origination rate of rodents and plesiadapiforms and the extinction rate of multituberculates. These analyses possessed the same limitations as the regression analyses and exposed some flawed reasoning on my part. None of these analyses could work because of the nature of my data. The presence/absence data for the taxa in the study were arranged in half-million year bins and I calculated the origination or extinction rate for each bin. For many of the time bins there were no origination or extinction events during that period, meaning the corresponding taxonomic rates were zero. The large number of zeros tended to obscure the results of both regression and correlation analyses. The zero values cluster at the origin and hence give the illusion of a high coefficient of correlation. This makes glean any useful information out of these analyses for this particular study difficult to impossible. Eliminating all the zero values is not a feasible solution for two reasons. First, this would have reduced the number of data points enough to eliminate much of the power of the analysis. Secondly, and more importantly, these zero values actually represent biologically relevant events. If the origination rate of a clade was zero at a given time, that data point cannot be legitimately excluded from the study because that

zero indicates a lack of origination events during that period. Eliminating all the zero values would be arbitrarily tossing out some data points and keeping others.

I should note that these difficulties do not rule out regression and correlation methods as useful tools for other studies of competition in the fossil record. These methods might be appropriate for studies involving much larger clades, for example, brachiopods and bivalves. In this case, many more origination and extinction events occurred at any given time interval, meaning more data points and fewer zeroes. I could easily apply the methodology I used in the taxonomic rates study to investigate the role of competition in the replacement of the Brachiopoda by the Mollusca.

Contingency Analysis.- The other class of analyses I chose not to include in Chapter 1 of this thesis fell victim to the same concerns as the regression-based analyses. Contingency analysis, also sometimes referred to as a crosstabs analysis proves useful in studies with categorical data. My data for the taxonomic rates study can be converted into categorical data. A contingency table calculates how often the two variables fall into the same categories. For instance in the example of my taxonomic rates study, I would predict that whenever extinction rate of multituberculates was high, the origination rate of rodents would also be high. I would also predict that when the extinction rate of multituberculates was zero, the origination rate of rodents would also be zero and so on.

The problem with this type of analysis resembles the problems with regression analyses. Due to the large number of zero values, a contingency table creates the illusion

of a high correlation because the zero values cluster together. This obscures the actual results. Eliminating these zero values poses the same concerns discussed above.

All of the analyses I performed for the sake of the taxonomic rates study that proved unworthy of inclusion in Chapter 1 rested on a faulty assumption about how incumbent replacement would operate. I operated under the premise that extinction events in the incumbent clade would immediately produce increases in origination rate of the replacing clade but nothing in the incumbent replacement model predicts this as the necessary course of events. What the model states is simply that the replacing clade fills vacated niches more quickly than the incumbent clade and this manifests as a correlation between their extinction and origination rates, respectively. This realization led me to the conclusion that a visual inspection of the taxonomic rate graphs would be the best way to draw interpretable results from this study. I finally utilized this approach in Chapter 1.

Appendix B: Data Sources for m1 Measurements

Genus	Reference
<i>Boffius</i>	American Museum of Natural History
<i>Lambdopsalis</i>	American Museum of Natural History
<i>Prionessus</i>	American Museum of Natural History
<i>Ivanantonia</i>	Hartenberger et al. 1997
<i>Protadelomys</i>	Hooker and Weidmann, 2007
<i>Rhombomylus</i>	Meng et al. 2003
<i>Eomylus</i>	Meng et al. 2005
<i>Palaeomylus</i>	Meng et al. 2005
<i>Bandaomys</i>	Meng et al. 2007
<i>Tribosphenomys</i>	Meng et al. 2007
<i>Alagomys</i>	Meng, Jin (pers. comm.)
<i>Sharomys</i>	Meng, Jin (pers. comm.)
<i>Ulanomys</i>	Meng, Jin (pers. comm.)
<i>Acritoparamys</i>	Paleobiology Database
<i>Alagomys</i>	Paleobiology Database
<i>Anconodon</i>	Paleobiology Database
<i>Anomoemys</i>	Paleobiology Database
<i>Apatosciuravus</i>	Paleobiology Database
<i>Ardynomys</i>	Paleobiology Database
<i>Baiotomeus</i>	Paleobiology Database
<i>Catopsalis</i>	Paleobiology Database
<i>Cimexomys</i>	Paleobiology Database
<i>Dawsonomys</i>	Paleobiology Database
<i>Ectypodus</i>	Paleobiology Database
<i>Elymys</i>	Paleobiology Database
<i>Eucosmodon</i>	Paleobiology Database
<i>Guanajuatomys</i>	Paleobiology Database
<i>Ischyromys</i>	Paleobiology Database

Continued

Table 4: Data Sources for m1 Measurements

Table 4 Continued

Genus	Reference
<i>Knightomys</i>	Paleobiology Database
<i>Lophiparamys</i>	Paleobiology Database
<i>Mattimys</i>	Paleobiology Database
<i>Mesodma</i>	Paleobiology Database
<i>Microcosmodon</i>	Paleobiology Database
<i>Microparamys</i>	Paleobiology Database
<i>Mimetodon</i>	Paleobiology Database
<i>Mysops</i>	Paleobiology Database
<i>Mytonomys</i>	Paleobiology Database
<i>Neoliotomus</i>	Paleobiology Database
<i>Neoplagiaulax</i>	Paleobiology Database
<i>Notoparamys</i>	Paleobiology Database
<i>Paramys</i>	Paleobiology Database
<i>Parectypodus</i>	Paleobiology Database
<i>Pauromys</i>	Paleobiology Database
<i>Prochetodon</i>	Paleobiology Database
<i>Pseudocylindrodon</i>	Paleobiology Database
<i>Pseudotomus</i>	Paleobiology Database
<i>Ptilodus</i>	Paleobiology Database
<i>Quadratimus</i>	Paleobiology Database
<i>Reithroparamys</i>	Paleobiology Database
<i>Sciuravus</i>	Paleobiology Database
<i>Stygimys</i>	Paleobiology Database
<i>Taeniolabis</i>	Paleobiology Database
<i>Thisbemys</i>	Paleobiology Database
<i>Tillomys</i>	Paleobiology Database
<i>Uriscus</i>	Paleobiology Database
<i>Meldimys</i>	Rana et al. 2008
<i>Eogiliravus</i>	Storch and Seiffert, 2007
<i>Acritoparamys</i>	Tong and Dawson, 1995
<i>Taishanomys</i>	Tong and Dawson, 1995
<i>Mesodmops</i>	Tong and Wang 1994
<i>Hainina</i>	Vianey-Liaud, 1986
<i>Liotomus</i>	Vianey-Liaud, 1986
<i>Neoplagiaulax</i>	Vianey-Liaud, 1986
<i>Sphenopsalis</i>	Walter, Granger, and Simpson, 1928