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Causes of lineage decline in the Aplodontidae: Testing for the influence of physical and biological change

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Abstract

This study documents diversity decline in a once-speciose rodent clade, the family Aplodontidae, and evaluates the potential influence of three commonly suggested controls on diversity: climate change, floral change, and competitive interactions. Aplodontids first appeared in the late Eocene, diversified during the early Oligocene, declined precipitously at the end of the Oligocene such that standing diversity was only about 5 species during the early Miocene, peaked again in the early middle Miocene, then declined through the late Miocene, and are entirely absent from the Pliocene and early Pleistocene fossil record. This long term pattern culminated in the survival of a single extant species, *Aplodontia rufa*, the mountain beaver. The species' richness and body size distribution through time were compared with the timing of climatic changes as inferred from global oxygen isotope curves, with the rise of grasslands as inferred from phytolith and other stable isotope studies, and with fluctuating diversity of potential competitors as inferred from published stratigraphic and geographic distributions. The timing of global climate change is decoupled from the diversity fluctuations and seems not to have been a proximate cause. Rise of grasslands and the increasing dominance of C_4 vegetation correlates with diversity decline in the late Oligocene and late Miocene, but data are sparse, and more work will be required to determine the mechanism driving this relationship. Examination of potential mammalian competitors (sciurids and castorids) finds no evidence for competitive replacement of aplodontids. It is difficult to ascribe the fluctuations in aplodontid diversity to a single cause. The explanation likely involves vegetation changes associated with the spread of grasslands, but there is some variation in diversity that cannot be explained by the vegetation, at least using the proxies employed here. Climate and competition are less consistent with the available data. The reasons for the decline of aplodontids in the late Oligocene and the late Miocene apparently involved the interaction of multiple physical and biological causes, coupled with the chance events that underlie any evolutionary process.

Keywords: Rodentia; Paleoecology; Terrestrial environment; Biodiversity; Ecosystems; Climate change

1. Introduction

Many studies have sought to identify the causes behind apparent changes in mammalian diversity through time. A recent body of literature has focused in particular on the evidence (or lack of evidence) for the importance of climate in driving mammalian diversity dynamics (Prothero, 1999; Alroy et al., 2000; Barnosky and Carrasco, 2002). In general, studies that consider all mammalian taxa at once have found little relationship between changes in global climate and diversity dynamics. It is unclear whether the individualistic responses of ecologically disparate groups of mammals

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tend to "average out" climate responses, or if there genuinely is no response of these organisms to climate. Furthermore, it is possible that the responses of organisms to climate are mediated through some other aspect of environmental change, such as climate-driven habitat change. Barnosky (2001) has suggested that the influence of climate on organisms will only be visible at a regional scale. While local or regional terrestrial climate signals that span long periods of time can be difficult to obtain, habitat proxies are available that may offer some insight into the relationship between the environment and animal diversity. Some authors (i.e. Alroy et al., 2000) have suggested that, rather than climate, biological interactions such as competition, predation, and coevolution may be more important in driving large-scale diversity patterns. These processes are inherently observable only at a small taxonomic scale, and may contribute to the randomness often apparent (Van Valen, 1973; Raup, 1975, 1977, 1985) in diversity dynamics on a large scale. Here I focus on diversity dynamics within a single lineage, taking into account the differences among taxa in ecology (and hence how they respond to their environment) to examine whether there is a response to physical environmental change or biological changes at a narrow taxonomic scale.

The Aplodontidae are a group of rodents represented in modern ecosystems by only a single species, but in the past were much more diverse, both taxonomically (Fig. 1) and morphologically (Fig. 2). The reasons for the decline of this clade from its peak diversity in the early Miocene to its present depauperate state are unknown, although Shotwell (1958) speculated about the possible role of habitat specialization in shaping the changes in geographic distribution of the clade through time. This group also provides an ideal system for looking at the relative importance of the physical environment and biological interactions in shaping macroevolutionary patterns. Here I use recently refined phylogenies and ecological intepretations of aplodontids to examine the three major causes that typically are invoked to explain diversity fluctuations – climate, vegetation change, and competition – to determine whether a within-lineage study will reveal a clearer relationship between mammalian diversity dynamics and external causes than has been apparent by meta-analyses. Understanding more about which of these causes may have been most important in the decline of this once-diverse clade is of general interest in informing us about the process of lineage extinction.

Taxonomic diversity patterns in the Aplodontidae are shown in Fig. 1, illustrating the history of each of the major ecomorphological (and taxonomic) groups, the prosciurines, ansomyines, allomyines, meniscomyines, aplodontines, and mylagaulids. Basal, brachydont aplodontids are common, widespread members of communities in North America during the late Oligocene and early Miocene. These smaller forms go extinct by the end of the middle Miocene. Middle and late Miocene diversity of aplodontids is dominated by mylagaulids, although aplodontines are also present. Shotwell (1958) pointed out the limited geographic distribution of aplodontines (limited to the northwestern U.S.) as compared with mylagaulids (known throughout North America) in the middle and late Miocene as possible evidence that mylagaulids were more arid-adapted, and hence better able to exist in the drier habitats that predominated in North America during the latter half of the Miocene. Mylagaulids, however, decline through the late Miocene and go extinct just

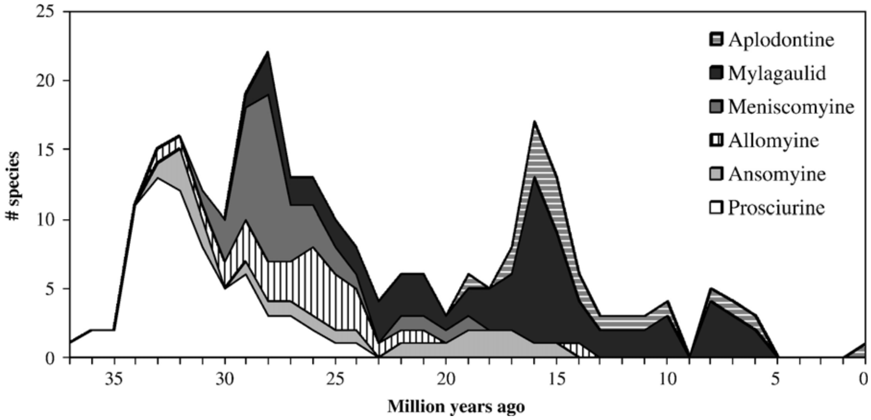

Fig. 1. Species diversity of aplodontids through the duration of the lineage. Total diversity is divided up among the six morphological groups considered in this study.

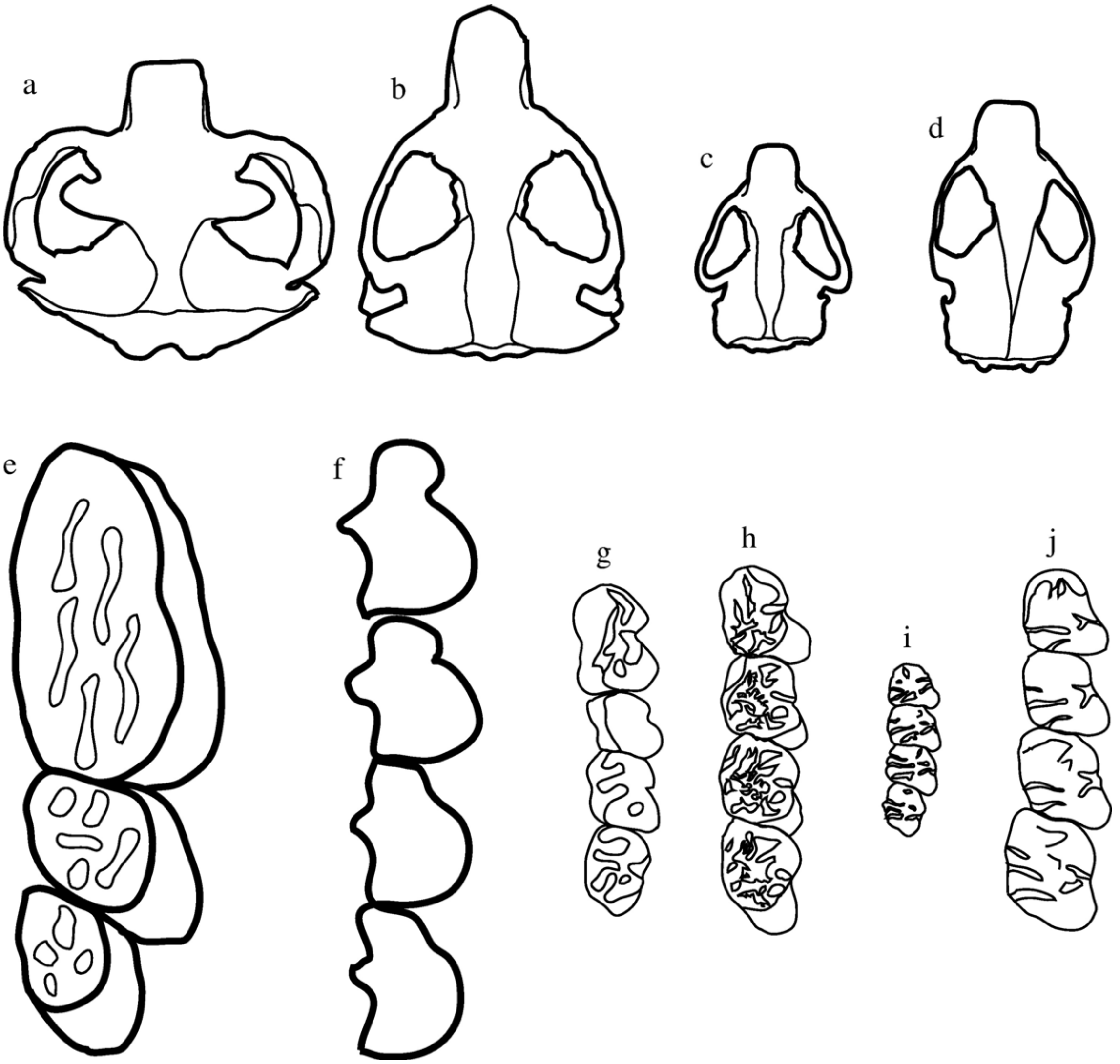

Fig. 2. Morphological diversity among fossil and living aplodontids. Representative lower dentitions are shown for all six groups, and skulls for four of the six. Well-preserved skulls were not available for allomyines and ansomyines. a–d. skulls of aplodontids. a. Mylagaulid. b. Aplodontine. c. Meniscomyine. d. Prosciurine. e–j. lower dentitions of aplodontids. e. Mylagaulid. f. Aplodontine. g. Meniscomyine. h. Allomyine. i. Ansomyine. j. “Prosciurine.”

before the beginning of the Pliocene. Aplodontids are not even represented through most of the Pliocene and Pleistocene, and the single extant species, *Aplodontia rufa*, does not appear in the fossil record until the latest Pleistocene deposits at Potter Creek Cave, CA.

2. Methods

2.1. General approach

The general methodology was to first examine whether any obvious sampling biases influence the shape of the diversity curve through time. I then compared the timing of diversity fluctuations and morphological change to timing of global climate change; to floral change; and to changes in diversity, distribution, and morphology of taxa that are possible competitors for the same resources. The role of climate and vegetation change in diversity dynamics of aplodontids was tested using the regression of diversity and body size values against proxies for vegetation and climate. Testing competitive replacement is more difficult. Geographic ranges, relative timing of diversity changes, and approximate body sizes of aplodontid fossil taxa and their most likely competitors were used to provide a first approximation of whether there is any reason to believe that diversity dynamics could be driven by competition; i.e., if potential competitors fluctuated inversely in diversity at the same place and time, the hypothesis of competition cannot be ruled out and geographic and morphological patterns would need to be examined. If results are consistent with competition, however, a great deal more detail would be necessary to definitively demonstrate competitive interactions between involved taxa. Such definitive demonstration is onerous for fossil taxa, in some cases impossible, and is not attempted here. Rather, I am only attempting to determine whether patterns of diversity, morphology, and geographic distribution in the aplodontid lineage might be consistent with the idea that competition could offer a general explanation for diversity changes apparent at the level of the entire clade. In short, the methodology allows rejecting competition as an explanation if occurrence patterns of taxa do not fit predictions, and highlights pairs of taxa that may have interacted competitively, but it does not provide a means for demonstrating that competition did operate.

The efficacy of this approach has been demonstrated by past studies that have shown evidence of competition and competitive replacement in the fossil record (Krause, 1986; Van Valkenburgh, 1999). In general, demonstrating competitive replacement is easier than demonstrating competition; thus here I focus on looking for patterns that would suggest competitive replacement. In competitive replacement, one clade is replaced entirely by another as a result of the superior competitive ability of the second clade. Such is suggested to be the case with the replacement of multituberculates by rodents (Krause, 1986), wherein the superior reproductive capacity of rodents seems to have given them a competitive advantage in filling many of the small herbivore niches. For a hypothesis of competitive replacement, the replacing clade is postulated to have an inherent advantage over the clade being replaced, so the prediction is that, whenever the two groups occur together, the replacing clade will essentially always “win” over the other, forcing it out of its previous niche space. Translated to the fossil record, this appears as an inverse correlation in abundance between members of the two clades through time.

2.2. Included taxa and phylogenetic context

The list of taxa with ages, occurrences, and morphological dimensions is provided in Appendix A. Occurrence data and ages are known for all species of Holarctic squirrels, castorids, and aplodontids. The analysis includes 105 species of aplodontids, which have been set in phylogenetic context by detailed work reported elsewhere (Hopkins, 2005b). In brief, most species are known from North America, but the analysis also includes species from Europe and Asia.

2.3. Sources of occurrence data

All occurrences of aplodontid rodents were collected from a comprehensive survey of the systematic literature. These data were accumulated in the course of a complete systematic study of aplodontid rodents (Hopkins, 2005b). The data on sciurids and castorids were accumulated primarily from 4 databases of mammalian occurrence data: The Paleobiology Database (http://paleodb.org/, downloaded February 22, 2005 using the higher taxon name ‘Rodentia’), MIOMAP (Carrasco et al., 2005; http://miomap.berkeley.edu), the Neogene of the Old World (NOW) database (http://www.helsinki.fi/science/now/), and FAUNMAP (http://www.museum.state.il.us/research/faunmap/). All Holarctic occurrences of sciurids and castorids were drawn from these databases. Additional taxa were referred to in the taxonomic indices of these databases; these taxa were also located and added to the list. Finally, a search of GeoRef yielded a few additional, recently-published species not yet incorporated into these databases. Sciurids from Africa and South America are not included in the analysis, as they could not have influenced evolution in aplodontids, which are an exclusively Holarctic clade throughout their history. The taxonomy was reconciled in cases where databases disagreed about the same occurrences. For each species, a list of localities was assembled from which it had been published. All known fossil occurrences were noted, except in the cases of extremely common, widespread species, in which some localities were excluded if they provided no new information about the geographic or temporal range of a species. Commonness may provide a useful ecological indicator, but issues of taphonomic bias make it a difficult parameter to measure consistently, so simple geographic and temporal ranges are used here. Finally, all modern species were added using the list from Wilson and Reeder (1993). Modern species with no fossil record, however, were not used in the comparisons of diversity and disparity through time, nor in the studies of co-occurrence, as the complete knowledge we have of the modern record of rodents is not comparable to preceding intervals, which are recorded only in the fossil record.

This study endeavors to use the most recent taxonomy, although some inadvertent errors may be present. While I am confident that I have not excluded a significant number of species, I did not spend a great deal of effort trying to make certain of the generic assignments of included species. In particular, there are several taxa among both sciurids and castorids for which generic affinities are uncertain, including several species that could be placed in two or more different genera, depending on the taxonomic authority used. The genus associated with a particular species does not make a difference to my results, given the methods applied here. The genera to which castorid and sciurid species are assigned should not, however, be considered to represent a studied taxonomic opinion; that is not the objective of this study.

2.4. Stratigraphic and geographic ranges

Stratigraphic ranges of taxa used for diversity counts were determined from published information about the age of the deposits from which the specimens were recovered. In general the age assignments take into account biostratigraphic, biochronologic, magnetostratigraphic and geochronologic lines of evidence, although the relative weight of each kind of evidence varies dramatically from taxon to taxon. Age assignments for North American Land Mammal Ages follow Woodburne (2004). For European taxa, MN and MP zone ages were taken from the databases or from the original publications (in cases where taxa were not found in the databases). Those zones were converted to numerical ages using the correlations presented in Agustí et al. (2001) (for Neogene ages) and using the following estimates for Paleogene mammal zones: MP 21 = 33.7–32 Ma, MP 22 = 32–30 Ma, MP 23 = 30–28.7 Ma, MP 25 = 29–28 Ma, MP 28 = 26–25 Ma, MP 29 = 25–24 Ma, MP 30 = 25–23.8 Ma. The ages of Paleogene mammal zones are not well constrained so the possible age ranges for those zones should be regarded as maxima.

Because most taxa are found at only a single locality or in a single local fauna, they occur only in a restricted part of the temporal range to which they are assigned. For those taxa that occur in multiple localities or faunas, the range used here spans from the earliest possible date for its occurrence to the latest possible date. Therefore, the stratigraphic range of some taxa may be overestimated, especially those that come from poorly-dated localities. At the same time, the incompleteness of the fossil record, particularly of small mammals, causes underestimation of the true total temporal span of species. Although there is no better way to estimate the true temporal range of a species, all analyzed taxa are subject to similar biases, justifying comparisons between time intervals and taxa as long as the temporal averaging constraints are taken into account in interpretations. With the exception of a very few of the included species, the potential overestimation of the stratigraphic range due to imprecise knowledge of locality ages is roughly 1 million years or less. Data are lumped into million year bins for analysis of diversity and morphology through time, so small errors or imprecision in locality ages should not significantly bias diversity estimates.

The geographic distributions of species are reported to the level of state or province (for North American and Chinese occurrences) or country (for other Asian and European occurrences). The geographic resolution is thus rough; however, especially for species published 100 years ago or more, this is often the best that is possible. Spatially averaging at this scale is appropriate for this study because the goal is to understand trends that manifest from the subcontinental to continental scale. However, several nuances of such spatial averaging are important to recognize. It may obscure the fact that a group of species occurring in the same state never actually lived together. This could represent a biologically meaningful habitat partitioning; however, it could also represent taphonomic differences between those localities. The net effect of lumping occurrences by geographic areas resembling U.S. states is to overestimate co-occurrence. A main impact on this study is that spatial averaging decreases the likelihood of type I error (incorrect rejection of the null hypothesis) in looking for evidence of competitive exclusion. An implicit assumption of this spatial averaging method is that geographic ranges of species are considered to be constant throughout the temporal range of a taxon, with any observed range changes through the time attributed to sampling biases. While constancy of geographic range clearly is not the case in nature, the assumption does not present a major problem for this study because the geographic and stratigraphic ranges of almost all included species are extremely limited, so relatively little averaging is taking place. In a few cases apparent range shifts through time do occur. Whether these are biologically significant or represent sampling biases are discussed in appropriate sections below.

2.5. Sampling error and the fossil record of aplodontids

In order to assess the potential impact of sampling bias on the diversity of aplodontids, locality data from

MIOMAP (Carrasco et al., 2005) were used to compare the number of known localities in a million year bin and the number of North American aplodontid species occurring within that bin. While the MIOMAP database primarily uses North American Land Mammal Age bins, the database also includes data on the actual minimum and maximum age ranges of localities. These more precise data were used to bin the numbers of localities into million year intervals using the same methodology as was used for aplodontid taxa, above. This approach provides the greatest possible correspondence between the sampling data and the diversity data. Assembling the data to perform this analysis for the entire dataset is not presently feasible, but the MIOMAP database includes all of the North American taxa, which is a reasonable subset for examining the question of sampling bias. Numbers of localities were regressed against numbers of taxa, with the expectation of high correlation if sampling biases were influencing the number of species. Because the locality counts and diversity values are serially correlated, the two were differenced and compared as well. Other methods of sampling correction commonly applied in paleontological analyses, such as rarefaction and weighting by occurrences, were not possible given the nature of the data. Correction of diversity data by utilizing counts of ghost lineages was rejected because of the problem of "backweighting" of diversity in clades (like the Aplodontidae) that have poor modern representation. Because ghost lineages are corrected but zombie lineages (those that persist beyond their last fossil occurrence) are not, diversity is actually significantly skewed relative to real values by such a correction. This problem is discussed in detail by Lane et al. (2005).

2.6. Climate and aplodontid diversity

Because aplodontids have a Holarctic distribution, I use a climate proxy that estimates global avererage temperature. This proxy is provided by $\delta^{18}O$ time-series composited from several Pacific ocean-sediment cores (Zachos et al., 2001). The time-series spans the Cenozoic, with actual data points occurring at intervals as fine as a few thousand years. In order to bin the oxygen-isotope data at the same resolution as the faunal data, all oxygen isotope values for a given million year bin are averaged to derive an average value for that bin; this value is used as a proxy for global temperature. The influence of climate on aplodontid diversity is assessed in a simple way by linear regression of aplodontid species diversity against $\delta^{18}O$ for each of the million year time bins. Because $\delta^{18}O$ is negatively correlated with temperature, a negative correlation with oxygen isotope values is equivalent to a positive correlation with global temperature, and vice versa. The relationship is also tested within each of the six major ecomorphological groups, "Prosciurinae", "Allomyinae", Ansomyinae, "Meniscomyinae", Aplodontinae, and Mylagaulidae (see the Competitive Exclusion section below for a discussion of how these groups were defined). Both the $\delta^{18}O$ and the species richness values were significantly serially correlated (except in the allomyines), a problem which can create artifactual correlations when serially correlated values are compared using linear regression. To remove this serial correlation, the values were differenced prior to running correlation analyses. As first-order differencing is only a crude way of removing serial correlation, a Hildreth-Lu procedure was applied to the undifferenced values; this approach corrects for autocorrelation in the residuals of first-order differencing. In this case, a nonlinear fit algorithm is applied to finding the terms of the following equation as applies to the variables of interest:

$$Y_{\mathrm{i}} = rY_{i-1} + a(1-r) + b(X_i - rX_{i-1})$$

where Y is the species richness, X is the $\delta^{18}O$ value, and r, a, and b are parameters of the nonlinear fit. Both approaches were effective in removing serial correlation.

Because climate may influence aplodontids without being linearly related to species richness, I also explored other potential biotic effects. Changing body size has been recognized as an ecological response to climate (Brown and Lee, 1969; Smith et al., 1995; Hadly, 1997; Hadly et al., 1998). To test for this phenomenon on a higher taxonomic scale, the mean body size of aplodontids, and of members of each clade, is regressed against $\delta^{18}O$ value for each of the million year bins. There was no significant serial correlation apparent in the morphological data, so these values were not differenced, with the exception of the Allomyinae, as addressed below, in the Results section.

2.7. Floral change and aplodontid diversity

Global vegetation patterns have changed dramatically in the last 30 million years, during the waxing and waning of aplodontid diversity. The spread of grasslands and the rise in dominance of C_4 grasses have both taken place during the second half of the Cenozoic. In order to examine the possibility that changing vegetation drove the dynamics of diversity in these small herbivores, two vegetation proxies were used from published studies, both from the Great Plains of North America. Plant phytoliths have been used (Strömberg, 2004) to detect the rise in abundance of grasses at the beginning of the Miocene; these are hypothesized to be primarily C_3 grasses until late in the Miocene, when C_4 grasses became more predominant. The proportion of grass phytoliths, while not an exact correlate of the proportion of grasses on the landscape, provides an approximation of the relative abundance of grasses in Great Plains ecosystems. As a vegetation proxy I used the proportion of grass phytoliths through time provided by Strömberg (2004). I compared that proportion to species richness of aplodontids from the Great Plains per million year bin, as well as to estimated average body size of Great Plains aplodontids per bin. Phytolith data are available for the time interval from 34 to 18 Ma.

To examine whether the rise of more arid-adapted C_4 grasses corresponds with changes in aplodontid diversity, I employed isotope data that has been reported by Fox and Koch (2003), who used stable isotopes of carbon to estimate the proportion of C_4 grasses in the Great Plains through the Neogene. They used the $\delta^{13}C$ value of soil carbonates to provide an estimate of the proportion of vegetation using the C_4 photosynthetic pathway (Fox and Koch, 2003). plotted the average value of $\delta^{13}C$ for a given million year bin against the diversity of Great Plains aplodontids, as well as their average body size. These data are available for the time span from 23 Ma to the present. For these analyses the subgroups of aplodontids are not examined individually, because there are too few species known from the North American Great Plains. The vegetation history of other regions within the range of aplodontids is not so well-known, and cannot be examined in this fashion. Furthermore, the Great Plains have a longer, better published, more diverse, and more continuous record of aplodontids than any other area in their range, with the possible exception of the northern Great Basin. Hence, they are more likely than any other region to show tight links between vegetation and diversity within this clade.

2.8. Competitive replacement

In general, examining the fossil record for signs of competitive replacement requires: (1) identification of potential competitors; (2) assignment of fossil taxa into ecological groups; and (3) determining whether certain predictions are upheld concerning patterns of diversity, geography, and morphology in purportedly competing clades.

2.8.1. Assigning aplodontids to ecological groups

I categorized aplodontids into five ecological subgroups defined on inferred paleoecology as interpreted from dental morphology, cranial morphology, and inferred body size (Table 1). These groups are taxonomic as well, though not all are monophyletic. Because each group is a lineage or section of a lineage with coherent morphology, they act as ecologically consistent evolutionary units. For ecological categories of individual species, see Appendix A. These five groups are: (1) the "prosciurines" (a paraphyletic basal group), (2) the ansomyines (sensu Hopkins, 2004) and the allomyines (sensu Korth, 1994) taken together, (3) the meniscomyines (sensu Korth, 1994), (4) the aplodontines, and (5) the mylagaulids. The five groups are defined primarily on dental and skull morphology that relates to dietary preference; additionally, all are either monophyletic clades or paraphyletic basal groups (Hopkins, 2005b), and hence have a degree of evolutionary consistency. Examples of dental and skull morphology (where available) for each of these groups are shown in Fig. 2. Prosciurines are relatively small brachydont aplodontids. Only a few postcrania are available to reconstruct their ecology, and the known skeletal material is little different from that of their paramyid ancestors, or of squirrels, which are closely related to aplodontids. None have the dental modifications (crenulate enamel in the basins of the teeth) indicative of arboreal frugivory as in flying squirrels or some primates (i.e. *Arapahovius*, Savage and Waters, 1978). For these reasons, prosciurines are considered to be non-flying squirrel analogs. Ansomyines and allomyines resemble each other in dental morphology, although they appear to have derived their dental attributes independently, as they are mutually monophyletic, and derive from ancestors with relatively simple dentition (Hopkins, 2005b). Both have increased complexity of crests and crenulation in the cheek teeth, and both are relatively small in size (Fig. 2). Based on dental morphology and size, their ecological niches may have overlapped with those of tree squirrels, ground squirrels, or flying squirrels. Meniscomyines are small, apparently fossorial (Hopkins, 2006), and mesodont;

Table 1
Groups of potential competitors used in the study of competitive replacement

	Aplodontid group(s)	Competing group(s)
Case 1	"Prosciurinae"	Tree squirrels, ground squirrels
Case 2	"Allomyinae," Ansomyinae	Flying squirrels, tree squirrels, ground squirrels
Case 3	"Meniscomyinae"	Tree squirrels, ground squirrels
Case 4	Aplodontinae	Aquatic castorids (Castorinae, Castoroidinae)
Case 5	Mylagaulidae	Fossorial castorids (Palaeocastorinae, *Rhizospalax*)

they are extremely diverse for a very brief interval of time in the late Miocene. Based on size and dental morphology they reasonably could overlap in ecology both tree squirrels and ground squirrels; however, the fossorial adaptations would make ground squirrels a more likely analog. Aplodontines, including the modern *A. rufa*, originate from among the small meniscomyines, but become larger during the Plio-Pleistocene, such that the modern species is often over a kilogram in body mass (Carraway and Verts, 1993). These hypsodonts, fossorial rodents are never particularly diverse among the Aplodontidae, and are limited to the northern Great Basin and Northern Rocky Mountains throughout their fossil history. Their ecological niches may have overlapped with those of aquatic castorids. Mylagaulids are relatively large, hypsodont, fossorial aplodontids found throughout western North America in the middle and late Miocene, with morphology and body size resembling that of extinct fossorial castorids.

2.8.2. Assigning potential competitors to ecological groups

In addition to aplodontid ecological groups, I also grouped potential competitors into 6 groups: tree squirrels, ground squirrels, flying squirrels, aquatic castorids, fossorial castorids, and castorids of indeterminate ecology. These ecological groupings, like those of aplodontids, are recognizable in both dental morphology and body size, as well as some aspects of postcranial morphology. The ecological categories into which taxa are placed are shown in Appendix A. Squirrel ecology may be reflected in the morphology of the dentary (de Bruijn, 1999). Ground squirrels tend to have shallower mandibles with more anteriorly-projecting incisors, while tree squirrels generally have a deeper diastema with a more dorsally-projecting incisor. Extinct taxa are assigned to tree squirrel and ground squirrel groups on the basis of this morphology. Flying squirrels are members of a discrete clade of squirrels, and have the cranial and dental characters (particularly crenulate, complex occlusal surfaces of cheek teeth) diagnostic of the modern members of the clade essentially from the time of their first appearance. Thus all members of the Petauristinae are assumed to be ecologically similar to modern flying squirrels. With essentially no postcranial remains of fossil petauristines, this is the best approximation that can be made. Given the uncertainty of the ecological distinctions between tree and ground squirrels, both groups are compared in all cases where one or the other is posited to compete with a given aplodontid taxon.

The ecological role of fossil castorids has been the subject of much more study. A number of taxa, including *Palaeocastor*, *Euhapsis*, and *Fossorcastor*, have left skeletal remains which clearly indicate that they were fossorial. *Palaeocastor* has actually been found inside fossil burrows (Martin and Bennett, 1977). For this study, all members of the Palaeocastorinae (sensu Korth, 2001) are considered to be fossorial on the basis of those taxa from the group with known fossorial ecology. Additionally, *Rhizospalax poirrieri* from the late Oligocene of Europe is a highly fossorial castorid of unrelated ancestry; morphologically, it bears a strong resemblance to *Euhapsis* or some mid-sized mylagaulids. Other castorid groups, including *Steneofiber*, *Dipoides*, and *Castoroides*, have been demonstrated to have skeletal morphology (particularly the morphology of the tail vertebrae) consistent with aquatic adaptation (Hugueney and Escuillie, 1996; Rybczynski, 2003). Enough evidence is present (Rybczynski, 2003) to say with some certainty that all members of the subfamilies Castorinae and Castoroidinae (sensu Korth, 2001) were aquatic. More difficult to classify with certainty are the basal castorids classified by Korth (2001) into the Agnotocastorinae. While some authors (Hugueney and Escuillie, 1996) have suggested these taxa were likely aquatic, Rybczynski (2003) hypothesized on the basis of a phylogenetic analysis that castorids were primitively fossorial, and hence that most of the Agnotocastorinae should be considered fossorial. Because this suggestion is based on character reconstruction using a very unstable and poorly resolved phylogenetic analysis, these taxa are treated as ecologically *incertae sedis*, of questionable ecology, and compared with hypothesized competitors of both fossorial and aquatic castorids.

2.8.3. Inclusion of body mass for inferring ecological groupings

Body mass is one of the three most important aspects of paleoecology to quantify (body mass, diet, and habitat) in determining the potential for competition (Morgan et al., 1995; Viranta, 1996); therefore part of the ecological assignment of the various aplodontid groups and their competitors is based on estimates of body mass — more similarly sized taxa are expected to be more likely competitors. To estimate body mass, toothrow length was used as a proxy. Hopkins (2005b) provides the detailed rationale for this, with the following summary providing salient details of the method. Lower toothrow length (LTRL), the anteroposterior measurement of the lower cheek tooth row, is a good proxy for body size in rodents, especially in non-muroids (Hopkins, 2005b). Because lower teeth were not known for many of the species included here, upper toothrow length (UTRL) was also measured, and used as a proxy for those taxa for which LTRL could not be measured. UTRL is highly correlated to LTRL ($p < 0.0001$, $R^2 = 0.98$), and hence can be used to estimate LTRL for purposes of comparison using the regression equation LTRL = (1.055272*UTRL) − 0.05735. Data on toothrow measurements were derived primarily from the original publications of the species. Where possible, actual specimens from the University of California Museum of Paleontology (UCMP) and the University of California Museum of Vertebrate Zoology (MVZ) were measured with Mituoyo Digimatic CD-6″CS digital calipers. For many species, no specimens were available in these museums; in this case, the measurements were taken from a survey of the literature. If no complete toothrows were available, they were assembled from adding up the lengths of the individual teeth. Where some toothrow positions were not represented, measurements of the alveoli were used. The difference between the length of the toothrow and the length of the alveolar row is very small relative to the variation within a species in toothrow length, so this is unlikely to create substantial error. At least 1 of the two toothrow measurements is known for 83% of the taxa included in the analysis. LTRL, the measurement used in all the statistical comparisons of morphology, is known for 75% of the taxa. It has been inferred from UTRL for an additional 8% of the included taxa.

Most of the measurements used for species in this study are of individual specimens, not averaged from large samples of many individuals. While problems could arise if these individuals are not representative of the species as a whole, the data are used only to create a broad-scale picture of the size disparity of taxa through time. To indicate the uncertainty in the data, values are only reported to two significant digits. The original data are frequently more precise than the values reported here, especially for specimens measured in the museums, but this resolution gives information only about the individual being measured. These measurements are used to represent entire species, and, to the precision that they are reported, are reasonable representatives of the populations from which they are derived.

2.8.4. Identifying potential competitors

Putative competitors with aplodontids are listed in Table 1. The comparison of these clades is not a definite statement about habitat and diet of the groups; rather, the listed clades of sciurids and castorids represent the only groups of small mammals that are of the right size, dental morphology, and in some cases selected postcranial morphology to overlap in ecological niche even broadly with fossil aplodontids. Put another way, if aplodontids are not competitively replaced by the rodent groups listed in Table 1, there are no morphologically closer candidates for competitors, so it would be unlikely that competition could explain their demise. While there remains the possibility of replacement by some other clade (such as ants, known to compete with desert rodents: Valone et al., 1994; Schooley et al., 2000), such hypotheses would be untestable given the difficulty of reconstructing ecological similarity between two such disparate groups and the miniscule probability of preserving good samples of two such groups in the same fossil record.

2.8.5. Predictions of competitive replacement

As Krause (1986) explained, if there is competition, a pattern like that shown in Fig. 3 should be apparent, with the following four predictions holding true. (1) The inferior competitor will decline in diversity as the superior competitor increases in diversity, (2) the inferior competitor must be present prior to the superior one, or it would never diversify. (3) A relatively small period of overlap is necessary to demonstrate that the two coexisted over an amount of time long enough for competitive replacement to occur. However, long term overlap should not occur because if one clade is competitively superior, competitive replacement is the inevitable result. (4) The two purported competitors must overlap geographically, because otherwise they could not compete.

2.8.6. Criteria that preclude rejecting competitive replacement

Operationally, I determine whether all four criteria noted above are fulfilled for each purported competing pair by first looking for overlaps in ecological groups in

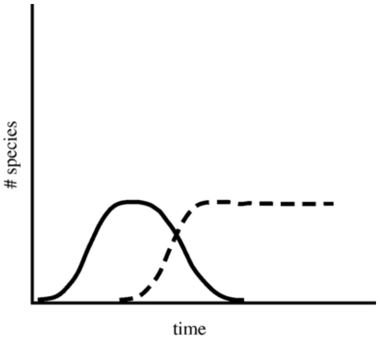

Fig. 3. Pattern of diversity that should be observed in the case of competitive replacement of one group by another. The solid line represents the “inferior” competitor, which is present first. The dashed line represents the “superior” competitor, arriving after the first group has become established. The diversification of this second group drives a decline in the first group, resulting, in this case, in its extinction.

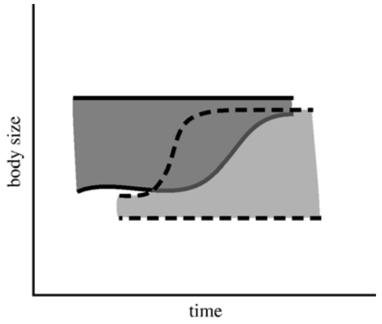

Fig. 4. Pattern of morphological change that should be observed in the case of competitive replacement. The first group (solid lines and dark gray fill) occupies some initial range of sizes. The "superior" competitor (dashed lines and light gray fill) moves into that size range, driving the "inferior" competitor into a narrower range of sizes, or into a new morphospace.

space and time. Then, for groups which at face value exhibit the requisite pattern of spatiotemporal overlap, I trace the pattern of body size overlap through time. Body size is estimated from tooth row length (see above). This metric has the advantages of being quantifiable and, because it reflects body size, of allowing examination of patterns at an ecologically more refined scale than simple taxonomic comparisons. Generally, competition is expected to be most intense between animals of similar size (Hutchinson, 1959; Bowers and Brown, 1982). Hence, competitive replacement predicts that the inferior competitor will be in a given size range first, and that range will be taken over by the superior competitor, in a pattern like that shown in Fig. 4. The clade being outcompeted is expected to be forced to alter its morphology, or go extinct. Thus, the superior competitor would be expected to either remain in the same morphospace through time or to expand into an increasingly large morphospace, while the inferior competitor would be expected to be "forced" out of its previous morphospace as the superior competitor moved in. The two clades must be similar in size by a ratio of less than 1.2:1 (an approximate value for limiting similarity; see Hutchinson, 1959; Schoener, 1965; Simberloff and Boecklen, 1981 for more discussion of this value) over some period of time to fit the predictions of competitive replacement. If all these conditions were met, the next step would be to look at similar proxies for overlap in habitat and diet, the two other critical ecological parameters; however, as none of the potential competitors with aplodontids show all the predicted patterns for geographic and temporal overlap, diversity dynamics, and changes in body size ranges, habitat and diet of potential competitors are not addressed in this study.

3. Results

3.1. Sampling bias results

The regression between number of sites and number of North American aplodontids (shown in Fig. 5a) is not significant ($p=0.55$), indicating that diversity as a whole is not related to the number of sites. After differencing, the regression revealed a significant relationship (Fig. 5b, $p=0.02$). However, sampling apparently explains only a very small part of the variance ($R^2=0.20$) in aplodontid diversity, and the significance depends entirely on two points, 28–27 Ma and 17–16 Ma. Removing either of these points results in an insignificant relationship. This result suggests that better sampling may contribute to the inflated diversity for those two intervals, but it seems unlikely that sampling issues entirely explain those two peaks in view of the low R^2. This conclusion is borne out by the fact that these two times of greatest diversity in the simple species richness counts correspond to the times of major diversification events according to Hopkins (2005b).

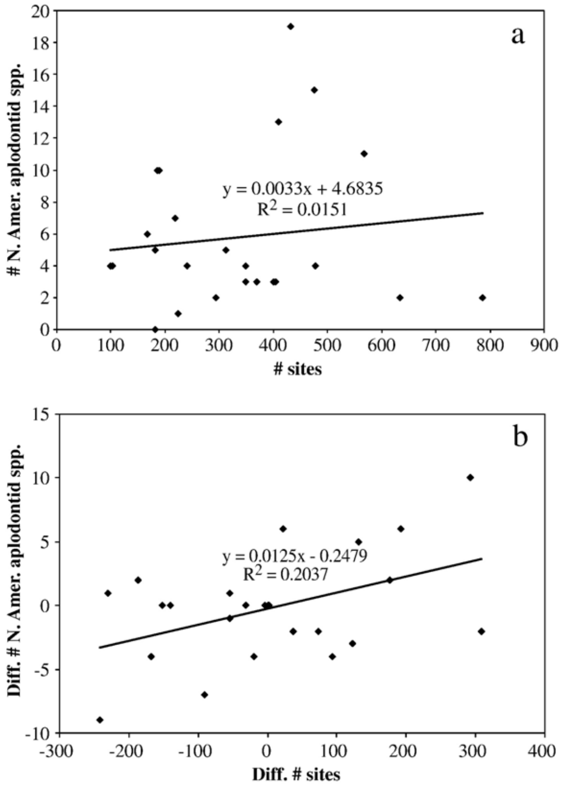

Fig. 5. Test for sampling bias in aplodontid species richness. The number of sites is from the MIOMAP database of mammal localities in western North America, for each of the one-million year intervals from 30 Ma to 5 Ma, using the locality age ranges recorded in MIOMAP. Species richness is for North American species of aplodontids only. $p=0.55$, $R^2=0.02$.

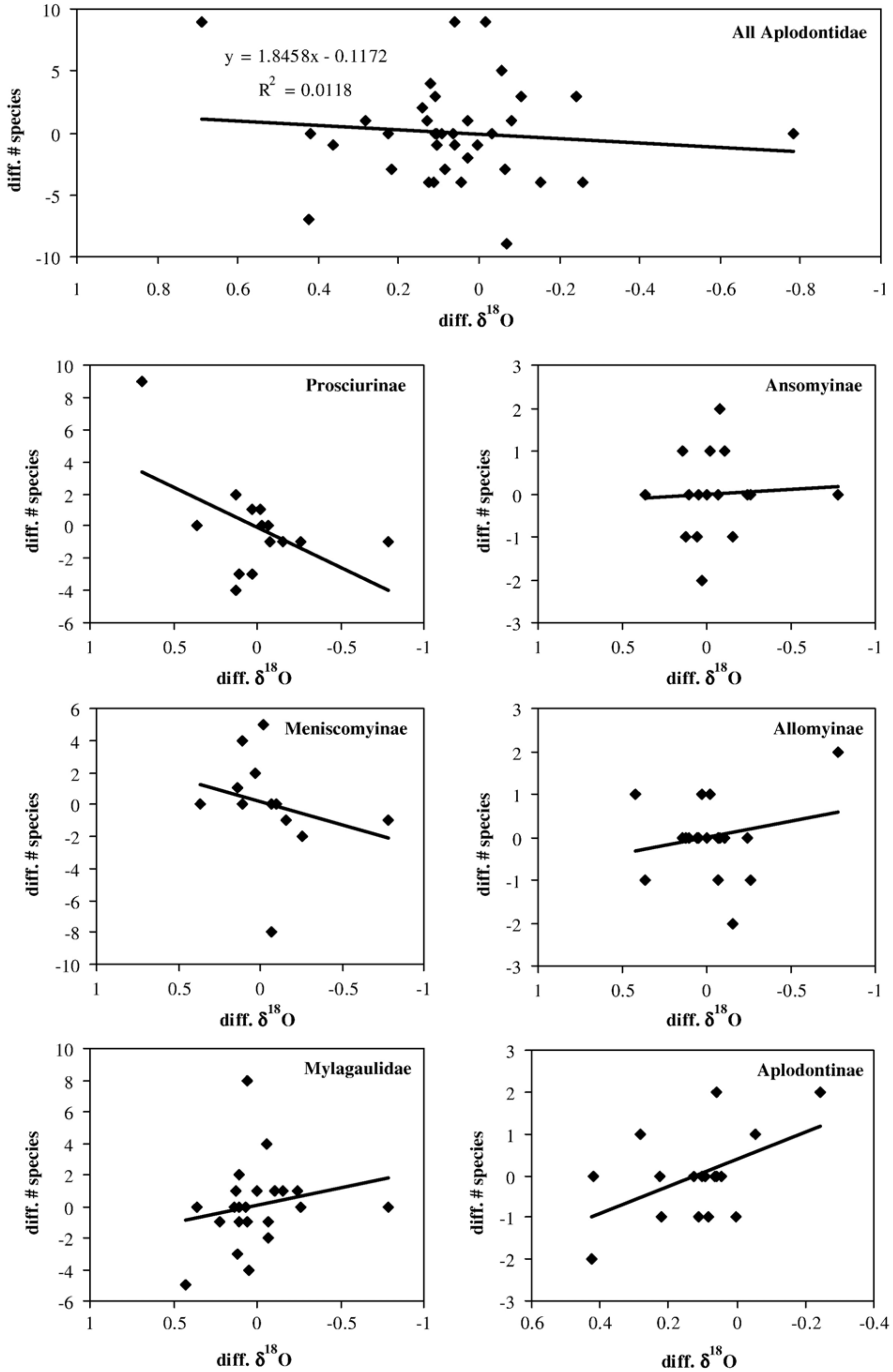

Fig. 6. Relationship between first-order differences of species richness and climate in aplodontids. Cooler temperatures are to the left, with higher δ^{18}O values. The aplodontines have the only significant relationship, which is not significant when corrected for the number of regressions run. *p* values for the slopes of the differenced regressions are as follows: All Aplodontidae = 0.53, Prosciurinae = 0.07, Ansomyinae = 0.80, Allomyinae = 0.38, Meniscomyinae = 0.43, Aplodontinae = 0.03, Mylagaulidae = 0.36. All have an R^2 of 0.26 or less.

Within the six groups of aplodontids examined here, there is no significant sampling effect on either differenced or undifferenced diversity values except in meniscomyines. In meniscomyines the significant ($p = 0.008$ for differenced data, 0.01 for simple richness) relationship between sampling and number of species is almost entirely a function of the same well sampled interval from 28 to 29 Ma, which is followed by poor sampling in the 27 to 28 Ma bin. Therefore, I take this potential sampling bias into account in drawing conclusions about relative abundances of meniscomyines during that time period.

Within the constraints noted above, in general these results indicate that the raw counts of species reasonably reflect relative changes in standing diversity of aplodontids in each time interval, and that the fluctuations have biological significance rather than reflecting only sample biases. Even sampling biases that are too small to meet standards of statistical significance should not affect the comparisons between aplodontids and their purported competitors, because the same biases affect all of the fossils.

3.2. Climate and aplodontid diversity

Simple linear relationships are not evident between aplodontid diversity and climate (as represented by $\delta^{18}O$ ratio). This holds if all aplodontids are treated as a single group, or if they are broken up into subclades (Fig. 6). Only one of the regressions shows a correlation between climate and diversity that is significant at $\alpha=0.05$, and that one (Aplodontinae) is not significant when a Bonferroni correction is applied for the number of regressions run. Furthermore, the Hildreth-Lu procedure finds no significant correlations at all, nor even any that are close to significant (Table 2).

Some studies of diversity through time have looked for diversity response to climate with a time lag (i.e. Alroy et al., 2000); in this case, I have looked for significant relationships with climate on a lag of either 1 or 2 million years in addition to no lag. The median mammalian species duration is only 2.6 million years (Alroy, 2000). Because this analysis is concerned exclusively with small mammals, which generally have a shorter life span and a shorter generation time than mammals as a whole, considering a lag of more than 2 million years in response to climate on a million year time scale seems unwarranted. None of the lagged correlations were significant. Neither is there a significant relationship in the comparison of average body size in aplodontid groups with climate (Fig. 7), except in the Allomyinae. This group, however, had a strong serial correlation, and when this effect was removed, the correlation was no longer significant ($p=0.41$ for first order differencing, $p=0.79$ for Hildreth-Lu). Regressions were also performed on data with lags of 1 and 2 million years; none of them showed significant results.

3.3. Floral change and aplodontid diversity

Both soil carbonate $\delta^{13}C$ and proportion of grass phytoliths were significantly related to aplodontid diversity (Fig. 8). Both correlations are significant ($p=0.027$ for grass phytolith %, $p=0.0282$ for soil carbonate $\delta^{13}C$). Independently each one would not be significant if a Bonferroni correction were applied; however, the fact that both come up significant is very important, especially because there is so little temporal overlap between the data, and they both describe different types of vegetative change and are not simply two proxies for the same change in vegetation. Both proxies suggest that species richness of aplodontids in the Great Plains was negatively related to the spread of grasslands. The R^2 values of these correlations are relatively low (0.3669 for the correlation with grass phytoliths, 0.5852 for soil carbonates), indicating that there is clearly more to the decline of aplodontids than the simple percentages of grass; however, these are vastly oversimplified proxies for the sort of habitat change that would be expected to drive changes in species diversity of aplodontids. Not only are these proxies not absolute measures of the actual percentage of grass in the ecosystem, but it would be excessively simplistic to expect that the number of species of

Table 2
Results of Hildreth-Lu procedure on serially correlated values of species richness and $\delta^{18}O$. Terms r, a, and b are fit parameters from the equation presented in the Methods section

	n	r	std err r	a	std err a	b	std err b	t	p	R^2
All aplodontids	37	0.749	0.117	10.04	7.056	−1.138	2.494	−0.075	0.941	0.013
Aplodontines	19	0.494	0.243	4.482	1.637	−1.196	0.554	−0.495	0.627	0.358
Allomyines	20	0.860	0.132	2.838	2.334	−0.649	0.894	−0.162	0.873	0.067
Meniscomyines	13	0.102	0.278	−12.10	4.655	6.951	2.109	0.914	0.380	1.448
Ansomyines	19	0.231	0.251	1.160	1.245	0.029	0.577	0.012	0.991	0.001
Prosciurines	14	0.701	0.249	−6.632	7.326	5.082	2.948	0.461	0.653	0.498
Mylagaulids	24	0.374	0.207	7.613	3.452	−1.984	1.486	−0.273	0.788	0.243

Their standard errors are presented, along with t values, probabilities, and R^2 values for the slope of the regression.

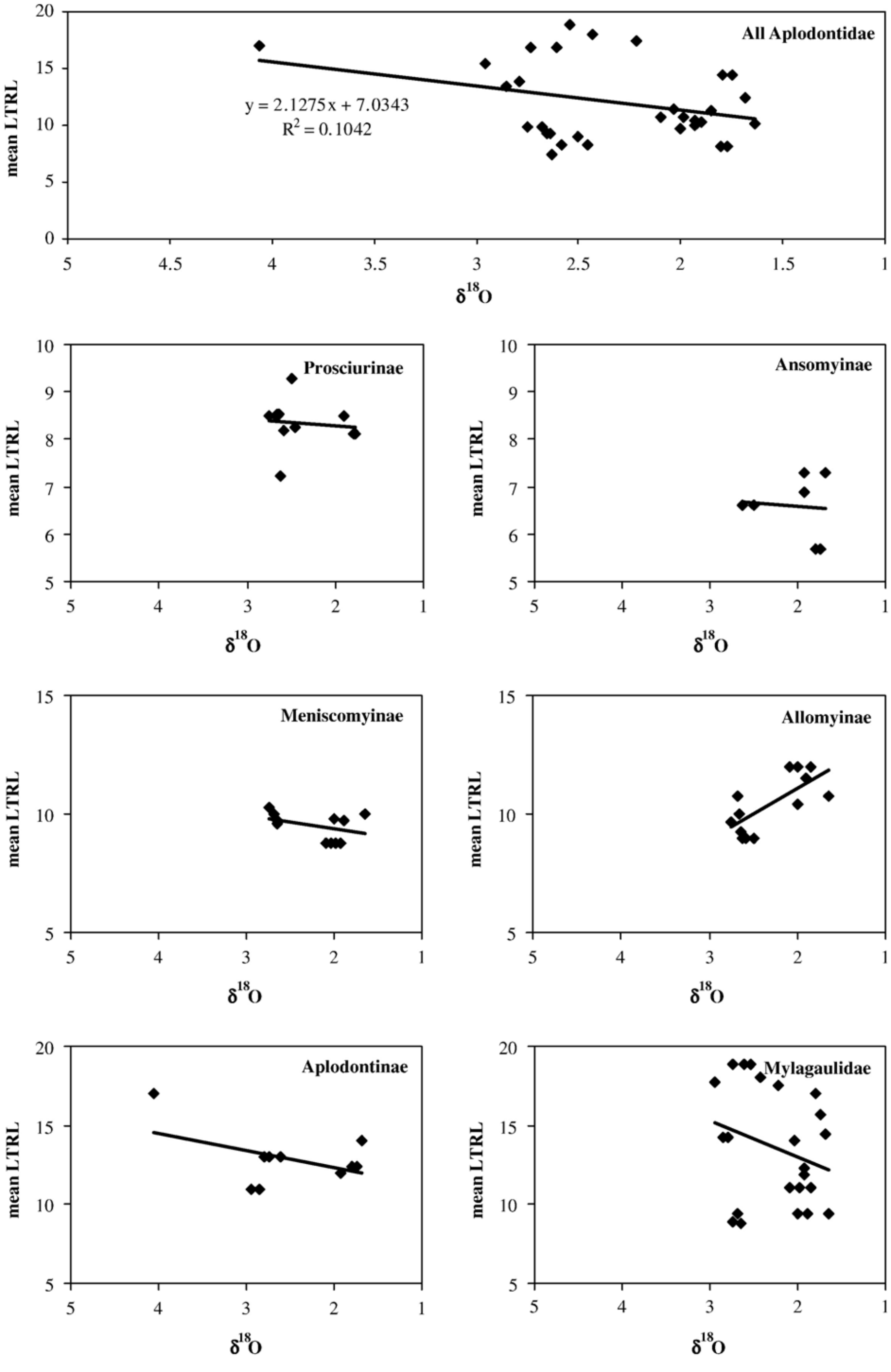

Fig. 7. Relationship between body size and climate in aplodontids. Cooler temperatures are to the left, with higher $\delta^{18}O$ values. Mean LTRL = mean lower tooth row length, used as a proxy for body size. *p* values for body mass-climate regressions are as follows: All Aplodontidae = 0.72, Prosciurinae = 0.72, Ansomyinae = 0.86, Allomyinae = 0.005 (but see above), Meniscomyinae = 0.22, Aplodontinae = 0.18, Mylagaulidae = 0.22. None of the relationships are significant, and all have a fairly low R^2.

aplodontids in the system would be directly and linearly related to the percentage of grass in the system; rather, one would expect an influence of random effects such as the presence or absence of specific plant species, predator species, and simple stochastic effects on the number of species. Ecological evolution is driven by

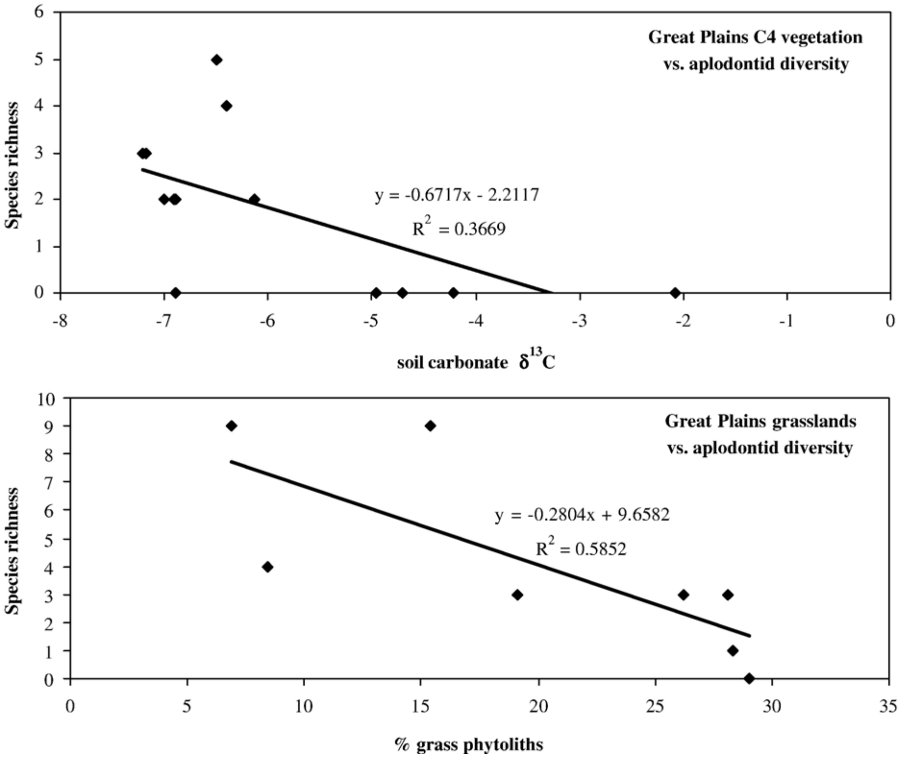

Fig. 8. Influence of the spread of grasslands on aplodontid species in the Great Plains. The upper graph shows the relationship between aplodontid species richness and the proportion of C_4 grasses. More positive values for $\delta^{13}C$ indicate more C_4 grasses. The lower graph shows the influence of the increasing proportion of grass in Great Plains vegetation on species richness of aplodontids.

complex causes, so the relatively low explanatory power of these regressions should not be seen as an indication that they are not evolutionarily meaningful. It is very likely, however, that habitat change is not the sole factor driving the decline in aplodontid species richness.

The vegetation data are available only for the Great Plains. However, this geographic scale is in fact the appropriate one for a vegetational analysis, because vegetation differs from one biotic region to the next. Substantial differences exist in climatic characteristics from one region to the next, and faunas of different bioregions frequently also have discrete evolutionary histories. The Great Plains are, furthermore, the best region to examine the influence of vegetation on aplodontids, because that region has the most continuous record of these rodents, and the publication history is uniform throughout the studied time period.

3.4. Competitive replacement

3.4.1. Patterns of diversity

The diversity patterns of putative competitors are shown in Fig. 9. Prosciurines and meniscomyines show a pattern suggestive of competitive replacement by ground squirrels, but not by tree squirrels (Fig. 9a). Prosciurines peak in diversity in the early Oligocene, 33 million years ago; afterward they decline, coincident with the diversification of meniscomyines and ground squirrels from 31 to 28 million years ago. Meniscomyines decline rapidly after 28 Ma, as ground squirrels continue to diversify. While this pattern would also be consistent with meniscomyines competitively replacing prosciurines, it also reflects evolution within a clade, because meniscomyines are nested within the monophyletic group defined by the “prosciurines.” It is unlikely that the offset between the meniscomyine peak and the ground squirrel peak results from the sampling bias noted above, because the same sampling biases should be affecting both groups.

Ansomyines and allomyines show a pattern possibly consistent with competitive replacement of ansomyines by allomyines and of allomyines by flying squirrels, but not with competitive replacement by tree squirrels or ground squirrels (Fig. 9b). Ansomyines peak in diversity (at only 3 species, not an exceptionally large peak) 32 million years ago; this diversity declines

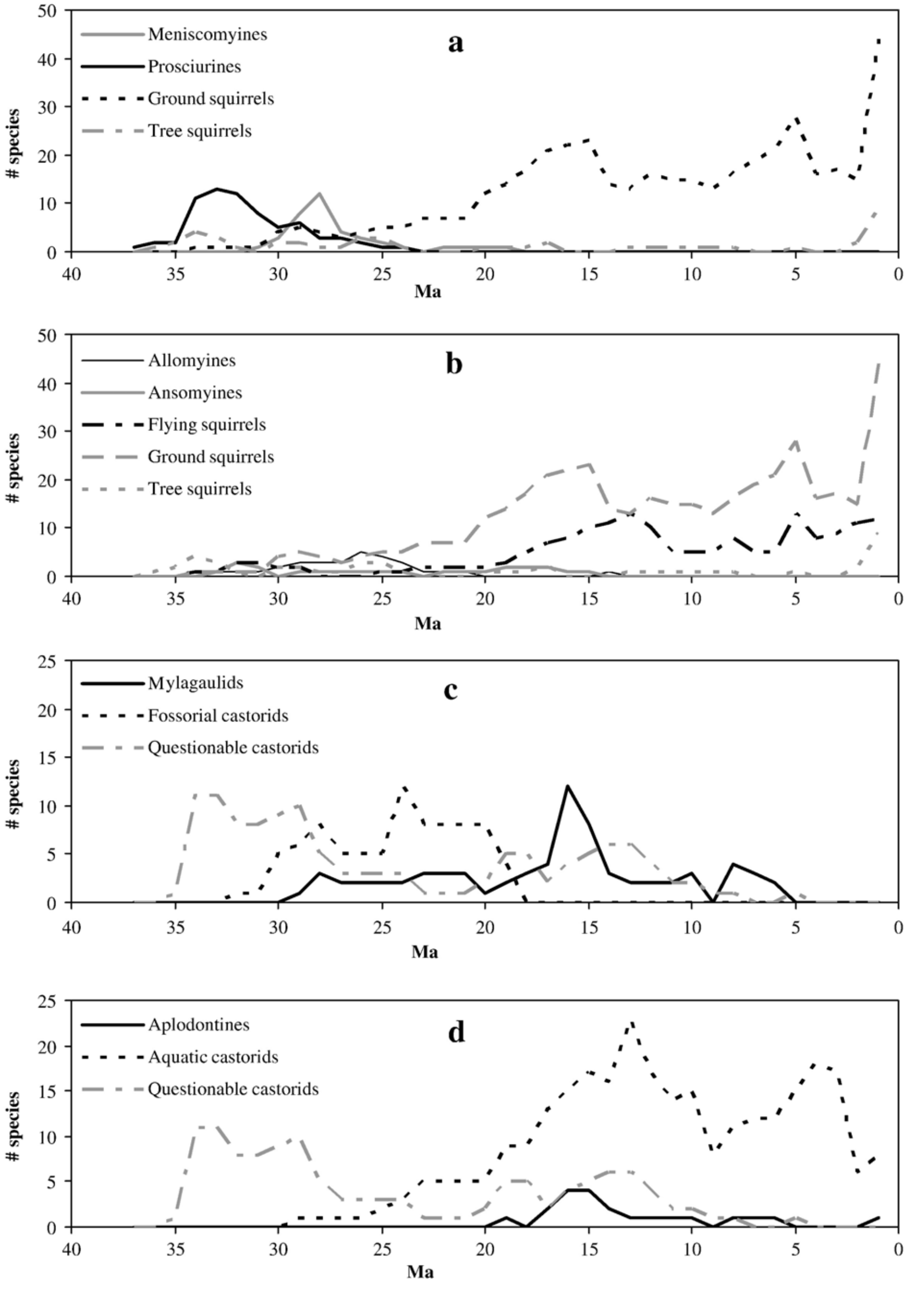

Fig. 9. Patterns of diversity between putative competitors through time. Solid lines represent aplodontids; dashed lines are putative competitors. a. prosciurines and meniscomyines versus ground and tree squirrels. b. allomyines and ansomyines versus ground, tree, and flying squirrels. c. mylagaulids versus fossorial castorids and castorids of unknown ecology. d. aplodontines versus aquatic castorids and castorids of unknown ecology.

thereafter and remains very low through the mid-Miocene. The decline in ansomyines coincides with the rise in diversity of allomyines. Allomyines remain diverse through much of the Late Oligocene, peaking at a diversity of 5 species 26 million years ago. They decline to only 1 species by 23 Ma, and remain at low diversity through the middle Miocene as well. Flying squirrels increase in richness roughly 20 million years ago, and continue to increase in diversity through the rest of the Neogene. The sequential peaks of ansomyines

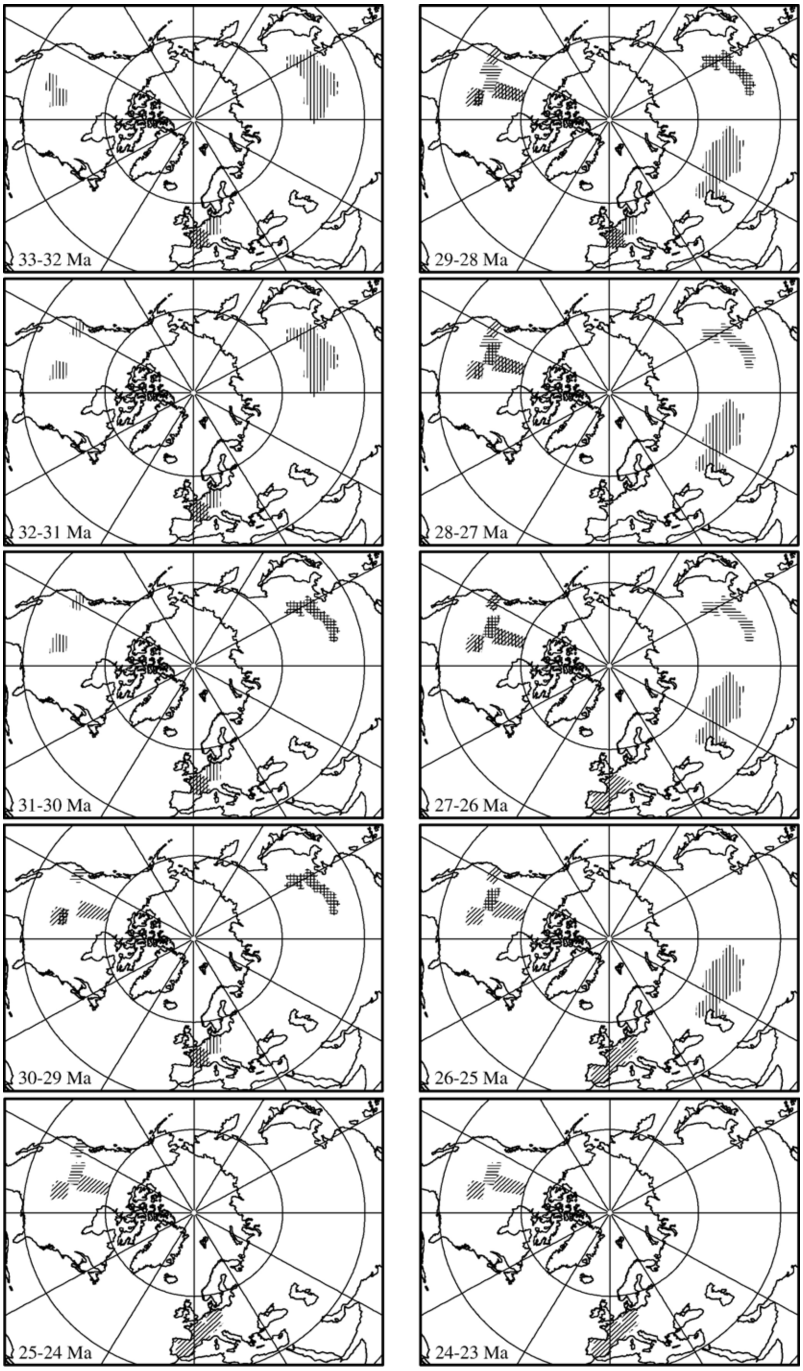

Fig. 10. Geographic distributions of prosciurines (vertical bars), meniscomyines (horizontal bars) and ground squirrels (diagonal bars) from 33 to 24 Ma. Each map is for the million year bin indicated in the lower left hand corner. Where taxa overlap, cross-hatching is created, indicating co-occurrence. The three taxa co-occur extensively in North America, especially between 30 and 26 Ma.

and allomyines are suggestive of competitive replacement. The decline of allomyines precedes the diversification of flying squirrels by several million years; however, given the potential role of sampling or taphonomy in shifting the timing of diversity changes, I have erred on the side of further testing cases, such as this one, which are even weakly consistent with competition.

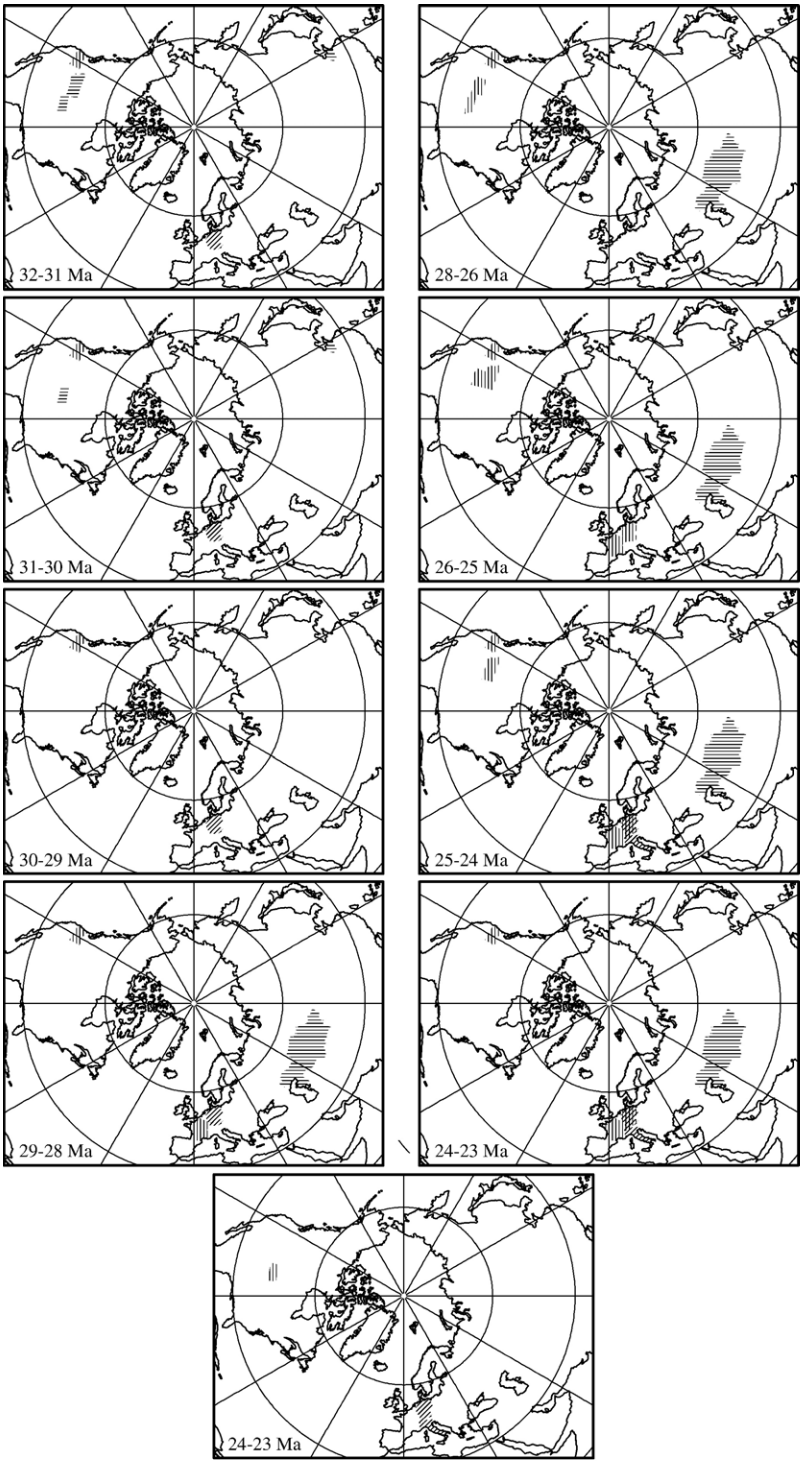

Fig. 11. Geographic distribution of allomyines (vertical bars), ansomyines (horizontal bars), and flying squirrels (right diagonal bars) from 32 to 24 Ma. Each map is for the million year bin indicated in the lower left hand corner. Where taxa overlap, cross-hatching is created, indicating co-occurrence. The distributions of taxa are identical for the two million year bins from 28–26 Ma, so a single map is given for these two intervals. These three taxa are essentially allopatric throughout most of their history, except that allomyines overlap with flying squirrels in Germany from 25–23 Ma; this overlap is between *Parallomys ernii* and *Blackia miocaenica*.

Mylagaulids show a pattern consistent with competitive replacement, but not in a direction that could explain their decline (Fig. 9c). Rather, the pattern suggests competitive replacement of fossorial castorids by mylagaulids; the decline of fossorial castorids is coincident with the diversification of mylagaulids between 20 and 17 million years ago. Further testing of this possibility is beyond the scope of this paper; it is sufficient to say that the decline of mylagaulids cannot be explained by competition, no matter the ecological role of the castorids for which ecology is uncertain. Similarly, the diversity of aplodontines does not relate in any way to that of aquatic castorids (Fig. 9d), a fact which is unsurprising given the ecological differences between the modern representatives of these clades.

3.4.2. Geographic distributions

The taxa exhibiting a pattern of Holarctic diversity dynamics suggestive of competitive replacement are plotted geographically through time to determine whether their spatiotemporal overlap also is consistent with competitive replacement. Distributions are mapped for potential competitors from the time of peak diversity of the first-diversifying taxon to the time when its diversity decline has leveled off, or when it has gone extinct. The critical intervals, from the diversity plots, are 33 to 24 Ma for prosciurines and meniscomyines (Fig. 10) and 32 to 23 Ma for allomyines and ansomyines versus flying squirrels (Fig. 11).

Prosciurines overlap extensively with ground squirrels geographically; the two groups coexist in France through much of the critical interval, from 33 to 28 Ma, as well as in Saskatchewan from 29 to 27 Ma and South Dakota from 30 to 27 Ma. Meniscomyines overlap with ground squirrels as well, but only in South Dakota, where all three taxa co-occur from 30 to 28 Ma. There is proximity between the three groups in North America; hence, the potential exists there for competitive replacement of prosciurines and meniscomyines by ground squirrels. Allomyines, ansomyines, and flying squirrels are completely allopatric until 25 Ma, at which time *Parallomys ernii* co-occurs with *Blackia miocaenica* in Germany. This co-occurrence of a single pair of allomyine-squirrel species occurs after allomyines begin to decline in diversity, so it provides little geographic evidence for competition.

3.4.3. Morphological overlap

The patterns of body size overlap between the two remaining pairs of potential competitors are shown in Fig. 12. In both cases, the pattern of morphological change is inconsistent with competitive replacement. Morphological overlap is extensive between prosciurines and ground squirrels (Fig. 12a). Similarly, meniscomyines overlap extensively with the size distribution of ground squirrels extant during the time of their greatest diversity, from 30 to 24 Ma (Fig. 12b). *Ameniscomys selenoides*, an unusual meniscomyine from Wintershof-West in Germany, is somewhat larger than

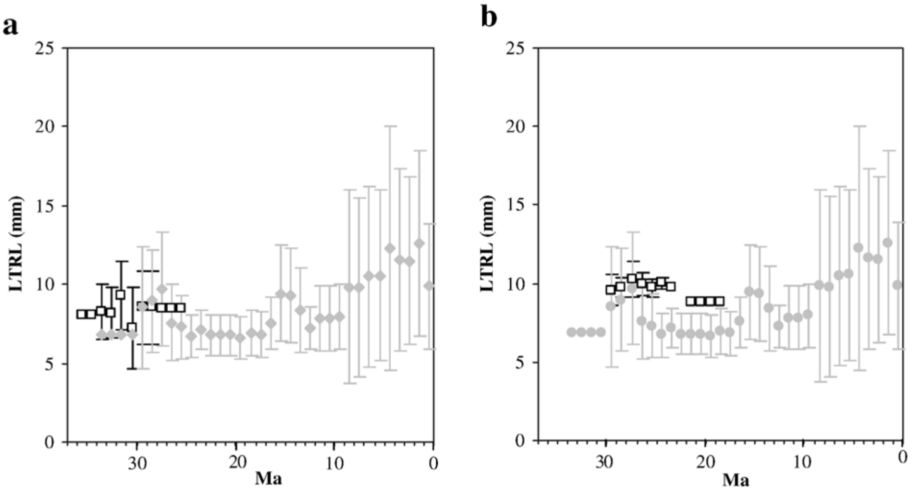

Fig. 12. Patterns of morphological overlap between potential competitors through time. Points are mean lower tooth row length, error bars indicate one standard deviation above and below the mean. Open squares are always aplodontid groups, while closed circles are always sciurids and castorids. a. Prosciurines (black boxes) vs. ground squirrels (light gray dots). b. Meniscomyines (black boxes) vs. ground squirrels (light gray dots).

most ground squirrels present in the early Miocene; otherwise, meniscomyines and ground squirrels overlap almost perfectly. Ground squirrels even seem to shift their mean to overlap more precisely with meniscomyines during the 6 million year period when meniscomyines were diverse in North America. Given that ground squirrels predate meniscomyines by several million years, there is no evidence for competitive interactions driving the morphological dynamics in these two groups.

4. Discussion

4.1. Climate and aplodontid diversity

The analyses presented here find essentially no support for the possibility that the diversity of aplodontids is tied to global climatic conditions. This is hardly surprising, as studies of mammalian diversity dynamics have frequently failed to find a simple relationship between global temperature and taxonomic richness (Prothero, 1999; Alroy et al., 2000; Barnosky and Carrasco, 2002). The test applied here is not very powerful in detecting a correlation; using the procedure for the determination of power in a regression analysis from Zar (1999, p. 385), the power of the regression for all aplodontids against climate is only 0.516 ($n=36$, $r=0.323$, $r_{\mathrm{crit}}=0.329$), so that a significant relationship between these variables would only be detected about half the time, and the power of the subclade analyses is even smaller. However, improving the power of the test would require either data with finer time resolution or a group with a larger number of species; neither of which is practicable for this study. I find, furthermore, that there is no indication that body size among aplodontids responds linearly to climate. Given that many aplodontid species are hypothesized to be fossorial, this result is also consistent with *a priori* expectations, as the subterranean environment provides some buffer against changes in ambient temperature. This is not to say that there is no response to climate among these rodents. The large geographic and taxonomic scale of analysis used here obscures any within-species geographic range changes that may take place to adjust to changing temperatures, a common response found among Pleistocene mammals during glacial-interglacial cycles (Graham et al., 1996). Changes in the areas occupied by aplodontids would be essentially impossible to detect given the sparse nature of their fossil record. Likewise, the scale and methods of this analysis would not identify ecophenotypic body-size changes that have been demonstrated to take place in response to climate changes that take place on decadal, millennial, and Quaternary time scales (Guilday et al., 1964; Smith and Patton, 1988; Barnosky, 1993; Hadly, 1997). The results of the comparison with floral change, however, suggest a mechanism by which climate change may be driving change in the fauna. Changes in habitat (the spread of grasslands) are likely to be, at least in part, a response to changing climates. As these habitat changes seem to be related to the decline in aplodontid diversity, this may provide an indirect mechanism by which climate could be a driver in aplodontid diversity decline. As the climate proxy used here is global in scale, and the interaction between climate and habitat change is on a much smaller scale, as well as being likely a non-linear effect, such an effect of climate on diversity would not be detected by this analysis, although it is suggested by the combined results of this study.

4.2. Floral change and aplodontid diversity

The finding that changes in vegetation are correlated to dynamics in aplodontid species richness is particularly interesting, especially as the correlation is a negative one. Small herbivores such as these might be expected to be positively correlated with the spread of grasslands. The hypsodont dentitions of the majority of Miocene aplodontids would be interpreted by some authors to indicate that grass is a likely food source for these animals. Furthermore, the evolution of increasing fossoriality in the lineage suggests adaptation to open environments. It has been suggested in the past that increasing diversity of subterranean rodents through the Neogene may be a result of the spread of grasslands (Nevo, 1999); while aplodontids are not subterranean, burrowing in general provides an escape from predation when vegetative cover is sparse. Notwithstanding this adaptive speculation, it appears that the aplodontid lineage as a whole is negatively impacted by the spread of grasslands. Several explanations can be offered for the negative relationship found here. First, the correlation may be simply a spurious one. The R^2 value is not exceptionally high for either relationship, so it may be that the aplodontids were simply declining from the late Oligocene to the recent for an unrelated reason, and their decline happens to coincide with the rise of grasslands in the Great Plains through the Miocene. This possibility seems unlikely, both because the correlation is present for two independent proxies for predominance of grasslands and because the trend in aplodontids as a whole does not give a significant relationship with these two vegetation proxies, so the trend in the whole clade is not driving the correlation. Another possible explanation is that aplodontids as a group have features which make them more successful in more closed environments, and the taxa that adapt to life in the open, grassland habitats can compensate only so far for their physiological, anatomical, or ecological deficiencies before being driven finally extinct by the dominance of widespread prairie grasslands in the Pliocene and Pleistocene. For example, the increasing fossoriality among aplodontids through the late Oligocene and early Miocene made them well-suited to the open woodland habitats of the early Miocene, and the evolution of head-lift digging in mylagaulids may have been extremely effective in the early Miocene, with sandy, volcanic ash-rich soils predominant (Retallack, 1997). However, this digging mode exerts huge forces on the dorsal neck muscles, especially in well-consolidated soils. The mature, mollic grassland soils of the later Miocene may have made poor substrate for these specialized animals. An effective test of this hypothesis requires data on the mechanical properties of Miocene soils, currently unavailable, and perhaps unobtainable.

4.3. Competitive replacement

The three tests applied here show that it is extremely unlikely that competitive replacement was responsible for the decline of aplodontid groups. Consideration of the only groups (sciurids and castorids) that could reasonably be suggested to be responsible for competitively replacing certain groups of aplodontids shows that the patterns of diversity, biogeography, and morphology in these clades are inconsistent with the expectations of competitive replacement. The evidence presented here does not eliminate the possibility of competition between mylagaulids and fossorial castorids; however, if this is the case, the mylagaulids were the winners, not the losers. In all other comparisons, the expectations of competition are violated by the data at hand. While this does not definitively demonstrate that competition did not occur, it does indicate that, with the data available, there is no support for a hypothesis of competitive replacement driving the decline of aplodontids. Much more difficult to demonstrate, however, is the hypothesis that competition with sciurids and castorids contributed to the decline of aplodontids. The fact that some of the comparisons show size overlap over longer time periods than would be predicted by competitive replacement is not inconsistent with a hypothesis of simple competition. Changes in climate and habitat coincident with overlap in ecomorphology could lead to groups coming into competition that had not previously interacted strongly. Such interactions, however, would be near-impossible to test in the fossil record, and, indeed, would be extremely difficult to test even in extant organisms; however, when considering the big picture of diversity decline, such possibilities must be acknowledged.

5. Conclusions

Changes in climate, changing habitats, and biotic interactions are three of the most commonly-cited explanations for the decline and extinction of fossil taxa. For this study, I have examined aspects of each of these three hypotheses as they apply to the diversification and decline of aplodontid rodents. There is no evidence from the data examined here to support the hypothesis that global climate change directly drove the diversity dynamics in aplodontids, either for the group as a whole, or for the different aplodontid ecomorphs individually. However, the test applied here for an influence of habitat change (specifically change in broad floral patterns) on aplodontid diversity found some evidence for an effect of vegetation change, in that the spread of Great Plains grasslands is negatively correlated with aplodontid diversity in that region. If such habitat change was driven by changes in climate, then this result may show a regional climate effect on aplodontid diversity, mediated through the flora. Competitive replacement alone fails to explain the declines in aplodontid species richness in the early and late Miocene, although some features of the changes in diversity and body size in the putative competitors suggest a degree of interaction between the taxa compared here, or perhaps simply differential responses to the changes in climate and habitat.

The early Miocene decline is largely a result of the lack of continued diversification among the allomyine and meniscomyine groups; both speciate dramatically in the Oligocene, but do not continue to diversify in the early Miocene. The vegetation analyses discussed above suggest that decline may have been the result of the early Miocene spread of grasslands. The diversity of aplodontids is largely regained, however, by speciation in mid-Miocene mylagaulids, which in turn decline in the late Miocene. The reason for the decline of mylagaulids remains unclear, because there is no evidence for climate or competition driving them out; there is only an inverse correlation of species richness with spreading grasslands. Some of this decline could be an artifact of publication, as there are known undescribed species of mylagaulids from the middle and late Miocene of the Santa Fe Group and the southern Great Plains (Korth, 2000), and from the Great Basin of Nevada and Oregon (Korth, 1999). The addition of these new species will add to the known diversity of mylagaulids, but the fact remains that mylagaulids go extinct at the end of the Miocene, leaving only the aplodontine lineage of the former aplodontid diversity. Because mylagaulids are head-lift diggers (Hopkins, 2005a), one possible explanation is the change in soil character in North America through the Neogene. Retallack (1997) found that paleosols in the Great Plains and Oregon suggested an increase in the predominance of organic-rich, mature grassland soils through the late Miocene. Changes in the character of the soil from the sandy, volcanic ash-rich soils predominant in the late Oligocene and early Miocene to thicker, more consolidated grassland soils may have driven these fossorial animals to extinction.

These results have important implications for understanding larger-scale patterns in mammalian diversity. The absence of a correlation between diversity and climate on even this narrow scale suggests, when taken in concert with the similar results of studies looking at mammalian diversity as a whole (Alroy et al., 2000; Barnosky and Carrasco, 2002), that the diversity of mammals does not respond linearly to climate change. This is not to say that climate does not influence diversity of mammals; rather, the diversity does not respond in a linear manner that could be detected by simple regression. Diversity response to climate is more likely to be contingent on a variety of factors unique to a climate change event, such as patterns of physical geography and biogeography of other organisms. This supposition is bolstered by the findings of the FAUNMAP project (Graham et al., 1996), which indicate that species respond individualistically to climate changes by shifting their geographic ranges. The results of this study are not consistent with the idea of climate-driven diversity change in individual clades "averaging out" into a broad picture of apparently random diversity change, as even within ecologically consistent groups, there is no evidence for an influence of climate on diversity among aplodontids. Considering the results of studies on diverse taxonomic scales, it seems that the best scale on which to see the influence of climate on mammals is that which considers the responses of individual species (Graham et al., 1996) or populations within a species (Barnosky, 1993; Guilday et al., 1964; Hadly, 1997). Smaller, regional geographic scales may also be more appropriate for looking at the influence of the environment on diversity, as suggested by the relationship between diversity and habitat change.

The finding that vegetation change may have played a role in the decline of the aplodontid lineage is consistent with the suggestion of Alroy et al. (2000) that biotic interactions may be more important in driving actual diversity trends. In this case, when the problem is considered on the geographic scale at which mammals are expected to interact with the flora, a potential cause for declining diversity can be found. A significant relationship between floral change and aplodontid diversity would not be apparent if considered on a larger scale. This significant result emphasizes the importance of looking at diversity change within individual clades, as well as on the larger scale of mammals as a whole, in order to understand the dynamics of diversity through time.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2006.10.006.

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