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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

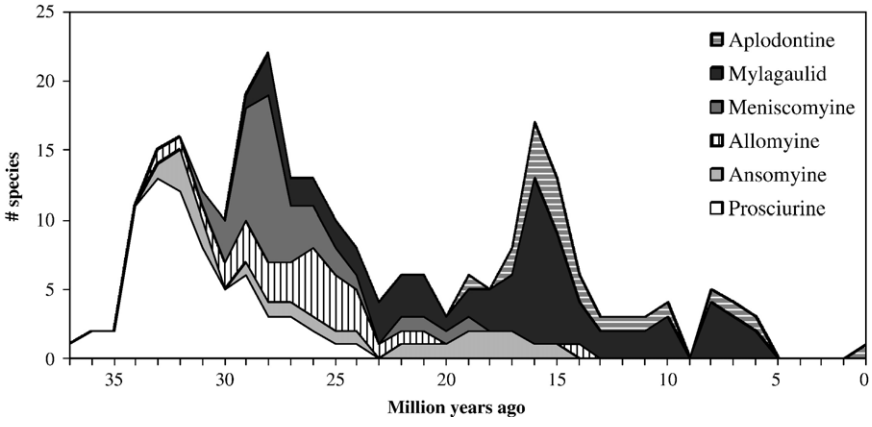

Fig. 1. Species diversity of aplodontids through the duration of the lineage. Total diversity is divided up among the six morphological groups considered in this study.