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Did impacts, volcanic eruptions, or climate change affect mammalian evolution?

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Abstract

In recent years, it has become popular to attribute faunal change and mass extinction to impacts, volcanic eruptions, or climatic change. How well do these supposed causes compare to the excellent record of Cenozoic life, especially that of fossil mammals? Two different Cenozoic mammal diversity curves were compared, and important climatic, volcanic, and impact horizons were examined in detail. In no case is there a strong correlation between impacts, eruptions, or climatic events and any episode of mammalian turnover. On the contrary, most of the known impact, eruption, and climatic events of the Cenozoic occurred during intervals of faunal stability. Conversely, episodes of high turnover and faunal change among Cenozoic mammals correlate with no known extrinsic causes. Apparently, extrinsic environmental factors such as impacts, eruptions, and climate change have a minimal effect, and intrinsic biological factors must be more important.

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1. Introduction

Conventional Neo-Darwinian theory has long argued that species are well adapted to their environment and should respond with adaptation and evolutionary change when their habitat changes (Gould, 2002). The advent of the impact hypothesis in 1980 (Alvarez et al., 1980) has led to many attempts to attribute mass extinction and faunal changes to impact

events. Specifically, the impacts of the late Eocene were originally blamed for the Eocene–Oligocene extinctions (Alvarez et al., 1982; Asaro et al., 1982), although later work has not substantiated this (Prothero, 1994). The discovery of the large late Eocene Chesapeake and Popigai impact craters (Poag, 1999) has prompted an intense search for correlated extinctions or other faunal change (Poag et al., 2003; Fawcett and Boslough, 2002), with results discussed below. Finally, the volcanist school has long advocated that massive flood basalt eruptions are important drivers of faunal turnover and extinction (Rampino and Stothers, 1988; Courtillot, 1999).

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The excellent record of the Cenozoic is a good place to test such hypotheses. Because the events are much more recent and better preserved, we can examine them in greater detail, and test our hypotheses against multiple sources of paleontological, paleoclimatic, and isotopic data. The fossil record of marine plankton is extraordinarily well known for most of the Cenozoic, and the land plant and land mammal records are also excellent for most of the era. In addition, the Cenozoic was a very active time of climatic change, with the greenhouse climates of the late Mesozoic gradually changing to the icehouse conditions of the late Cenozoic, and with numerous plate tectonic events, many major volcanic eruptions, and several large impacts. Thus, if there is any validity to the idea that impacts, volcanoes, or climatic change is important in evolution, the Cenozoic should be a good place to test such hypotheses.

The Cenozoic record of North American mammals has additional advantages as well. The systematics of most important mammalian groups has been redone over the past two decades (e.g., Janis et al., 1998), so that most of the published species records can be considered valid and monophyletic, and their phylogenetic relationships are well known. In the past decade, detailed databases have been compiled which allow us to track every known genus of North American mammal through its entire range. The database of Stucky (1990, 1992) had resolution of better than 1–2 million years for most of the interval sampled, and shorter than that for some intervals. In recent years, our chronostratigraphic control on North American Cenozoic sections has improved tremendously with the advent of magnetic stratigraphy and $^{40}\text{Ar}/^{39}\text{Ar}$ dating. Hence, the evolution of most mammalian lineages in North America can now be dated to the nearest 100,000 years in many cases, allowing very precise estimates of evolution and extinction rates. In some cases (such as the Paleocene–Eocene Fort Union–Willwood formations of the Bighorn Basin of Wyoming, or the Eocene–Oligocene White River Group of the High Plains), the density and completeness of the mammalian record is extraordinary. In the case of the White River Group, the common mammalian lineages (and there are several hundred species known, summarized in Prothero and Emry, 1996) are known from dozens or hundreds of specimens (Fig. 1) in each interval of a few meters

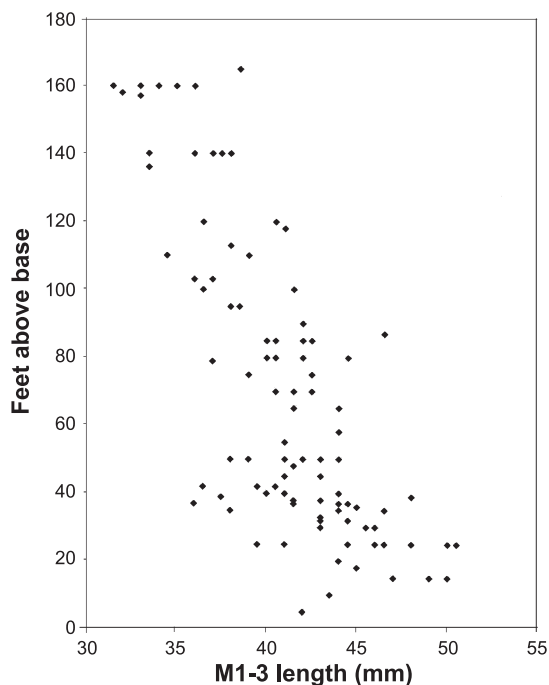


Fig. 1. Typical sample density of the smaller oreodont *Minochoerus* through one of the classic White River sections north of Lusk, WY. Each cross represents the upper molar row length of a single skull or maxilla, and each is plotted to the nearest foot from a marker ash (the “Persistent White Layer” or PWL). The early Oligocene climatic crash occurs at about 90 ft above the base on this section, and there is almost no response in this oreodont, which had already begun this gradual size reduction trend almost a million years earlier. Such data density is typical for the better-sampled White River mammals in the Frick Collection (see Prothero and Heaton, 1996).

(Prothero and Heaton, 1996). This kind of stratigraphic resolution and sample density is the best known anywhere in the vertebrate record, allowing the mammalian record to be compared to global climatic signals in great detail.

Using different methods, Alroy (1998; Alroy et al., 2000) has recompiled the entire record of Cenozoic mammals in North America and resolves the diversity curve at less than 1 myr intervals. Because of his methods, Alroy is able to subject the data to statistical analyses that were not possible on earlier data sets.

2. Impacts and extinction

Ever since the discovery of the iridium anomaly at the Cretaceous–Tertiary boundary (Alvarez et al.,

1980), many scientists have searched for evidence of impacts and have attributed extinctions and other terrestrial events to impacts. As the evidence for the K/T impact improved, there were many premature announcements that most other mass extinctions had been correlated to impacts as well. At one time or another, the Eocene–Oligocene, Triassic–Jurassic, Permian–Triassic, and Late Devonian extinctions were all attributed to impacts, although the evidence for these has diminished as it was more critically examined (Prothero, 2003). In 1989, Digby McLaren told an audience at the International Geological Congress in Washington, D.C., that all mass extinctions were caused by impacts, whether or not there was evidence of an impact in the fossil record. Raup (1991) wrote that all extinctions might be caused by impacts. With untestable statements such as this, why bother gathering data at all? Impacts occurred, and extinctions occurred—therefore impacts caused the extinctions—end of discussion. Ironically, in the past 24 years since the Alvarez hypothesis, the K/T impact now stands as the only well documented association of impacts with extinctions. Judging from the presentations at the 2003 Geological Society of America annual meeting in Seattle, the support for impacts at the Permo-Triassic, Triassic–Jurassic, and Late Devonian extinctions has greatly diminished as new evidence pointing to other causes emerges.

In 1982, several groups of scientists reported slightly elevated concentrations of iridium in late Eocene limestones (Alvarez et al., 1982; Asaro et al., 1982; Ganapathy, 1982; Glass et al., 1982), followed by the discovery of tektites and microtektites from the same layers (discussed in Prothero, 1994, p. 137). In 1992, the first good candidate for the source of this impact debris was discovered in the Chesapeake Bay area (Poag et al., 1992; Poag, 1999). As the evidence accumulated for the size of the Chesapeake Bay and Tom’s River craters, a third crater was identified at Popigai in Siberia (Masaitis et al., 1975; Bottomley et al., 1997). As soon as the first iridium was reported in 1982, some scientists concluded that impacts explained the Eocene–Oligocene extinctions. However, a more detailed examination showed that only five species of radiolaria (out of dozens known) die out at the level of the impacts (Maurrasse and Glass, 1976). Furthermore, there are no other extinctions in any other group of organisms, including the foramin-

ifera (Hut et al., 1987), or any other group of marine or terrestrial organisms (Prothero, 1994; Prothero and Berggren, 1992; Prothero et al., 2003). Such an insignificant extinction event is below the background “noise” level and clearly suggests that the impacts at Chesapeake Bay, Tom’s River, and Popigai had little or no extinction effect on the global biota (Poag, 1997).

Even more striking is the implications of the non-extinction during the late Eocene impacts. Poag (1997) points out that the diameters of the Chesapeake Bay and Popigai impact craters are about 100 km, about the same order of magnitude as the 180 km diameter of the K/T impact crater at Chicxulub. Raup (1991) originally fit a “kill curve” (Fig. 2) to the Chicxulub crater that suggested as much as 20% species extinction occurred with only a 40-km-diameter crater, and 50% extinction resulted from the impact that produced a 100-km crater. As Poag shows, the non-extinction resulting from impacts which produced 100-km craters forces the kill curve into a completely different shape (Fig. 2), predicting that only an impact which generated a crater much greater than 100 km in diameter is capable of producing a mass extinction. Effectively, the curve shown in Fig. 2 is constrained by only two points, the non-extinction at 100 km diameter, and the 65% extinction for the 180-km crater at Chicxulub. The other two larger craters, Vredefort and Sudbury, were

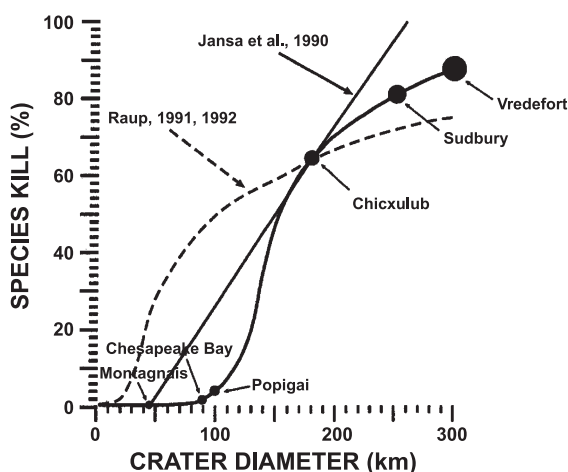


Fig. 2. Poag’s (1997) modifications of the Raup (1991) “kill curve”, showing that only impacts producing craters much greater than 100 km in diameter are capable of producing mass extinction (from Poag, 1997).

formed in the Precambrian, so we do not know whether they caused any significant extinction or not. What the curve in Fig. 2 really shows is that only the very largest impacts have any potential to produce a mass extinction, and anything less than an impact generating a crater of approximately 130 km in diameter causes no extinction in the earth's biota. Given the uncertainty as to whether any impacts—let alone large ones—occurred at the other major mass extinctions (Permo-Triassic, Triassic–Jurassic, Late Devonian), this fact alone casts serious doubts on whether impacts can be blamed for those events. Only the K/T event is solidly associated with mass extinction, although whether it is a sufficient cause for the extinctions is also still controversial (Archibald, 1996).

Nonetheless, the impact advocates have not been daunted. Because of the overwhelming evidence that the late Eocene impacts had little or no biotic effect, they have instead argued that impacts might have caused some of the late Eocene climatic perturbations that preceded the extinctions in the earliest Oligocene (Poag, 1999; Vonhof et al., 2000; Coccioni et al., 2000; Poag et al., 2003; Fawcett and Boslough, 2002). What is problematic about these explanations is that they predict opposite effects. The direct effect of an impact should (based on the models of the K/T impact) produce a debris ring and global cooling (Vonhof et al., 2000; Fawcett and Boslough, 2002), yet the isotopic and paleoclimatic records of the late Eocene show that the exact opposite, a short-term warming event, actually occurred (Poag, 1999; Poag et al., 2003). Clearly, impacts cannot cause global warming and cooling simultaneously. Even if they could do so, there is no clear explanation for how either climatic change might have caused extinctions in the early Oligocene, almost 2 million years later, given that the effects of such impact events diminish in years or decades, not millions of years.

But this is just a single episode of the last 65 million years of the Phanerozoic. Is there any other evidence of impacts causing mass extinctions during this time? Fig. 3 shows two diversity curves for North American mammals (modified from Alroy, 1998), the most well-sampled and finely resolved record of terrestrial organisms that we have for the entire Cenozoic. There are also multiple impacts during the Cenozoic (summarized in the Impact Database, <http://www.unb.ca/passc/ImpactDatabase>). As can be

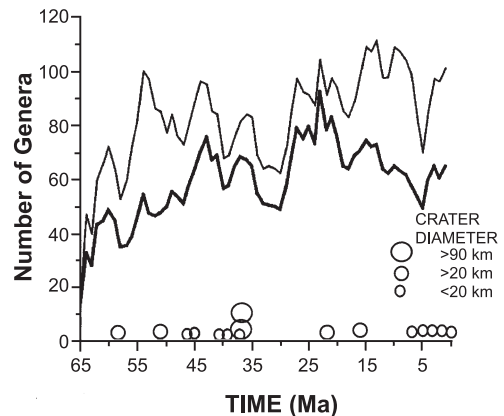


Fig. 3. Comparison of the Cenozoic mammalian diversity curve of Alroy (1998) with the record of Cenozoic impact craters (see text). Upper thin curve indicates the raw data; bold curve is sampling-standardized data (Alroy, 1998). Circles indicate approximate diameter of crater, and their position on the time scale.

seen from Fig. 3, there is no association between any of the impacts and any peak of extinction in land mammals. Two of the largest (other than Chesapeake and Popigai) and best known Cenozoic impacts are the Ries impact in Germany (24 km in diameter, 15.1 ± 0.4 Ma in age) and the Montagnais impact off the coast of Nova Scotia (45 km in diameter, 50.5 ± 0.76 Ma in age). In both cases, there are no significant extinctions associated with either the Montagnais impact (Bottomley and York, 1988; Aubry et al., 1990) or the Ries impact (Heissig, 1986). As Poag's (1997) kill curve (Fig. 2) shows, clearly if the two 100-km-diameter late Eocene impacts had no effect, it is not surprising that the smaller ones had no effect, either.

Independent of this research, Alroy (2002) presented a paper that corroborated these conclusions. He subjected his mammalian diversity database to every possible statistical manipulation, but in the end could find no statistical association between impacts and extinctions of Cenozoic mammals.

3. What about volcanic eruptions?

Another popular explanation for mass extinctions has been volcanic eruptions. Rampino and Stothers

(1988) and Courtillot (1999) have pointed out that two of the largest known flood basalt eruptions, the Siberian traps of the Late Permian, and the Deccan traps of the Late Cretaceous, coincide with the Permo-Triassic and K/T extinction events. Courtillot (1999) fit a curve of the major flood basalt eruptions to the timing of major extinction events, and there did seem to be some correspondence between the two.

This correlation breaks down, however, when examining the Cenozoic. Courtillot and Renne (2003) summarized the latest dates on major flood basalt eruptions. The eruptions of the North Atlantic Tertiary volcanic provinces at 61 and 56 Ma are found in the middle and end of the Paleocene, and do not correspond to significant extinctions in either mammals or any other group of organisms. (The Late Paleocene Thermal Maximum at 55 Ma affected primarily benthic foraminifera and is clearly associated with changes in bottom-water conditions, possibly due to a release of methane hydrates). The Ethiopian and Yemen traps, originally blamed for the Eocene–Oligocene extinctions (Rampino and Stothers, 1988), are now dated between 29.5 and 31 Ma, or the middle of the late Oligocene, when there were no extinctions of consequence in land mammals or any other group of organisms (Stucky, 1990; Alroy et al., 2000). In fact, North American mammalian diversity in the late Oligocene was already at a low level, but a new diversification occurred around 30 Ma, not further extinction (Fig. 3). This is the exact opposite of the prediction that volcanic eruptions trigger extinctions. Likewise, the massive Columbia River basalt eruptions, dated between 15.3 and 16.6 Ma, do not match any extinction events in land mammals or other organisms—indeed, this is the peak of late Cenozoic mammal diversity (Fig. 3), and the beginning of the permanent Antarctic ice cap.

Thus, the contention that volcanic eruptions might have caused pre-Cenozoic mass extinctions (Courtillot, 1999) is still plausible, but there is no evidence that they had any effect in the Cenozoic.

4. What about climatic change?

The long-favored cause for the changes in the Cenozoic faunas is climatic change. Certainly, the major transitions from greenhouse to icehouse cli-

mate, and the concomitant changes in vegetation, have long been linked to changes in mammal communities. Since the time of Cuvier, Lyell, and especially Matthew's (1915) classic paper, it has been *de rigueur* to attribute changes in mammalian faunas to extrinsic causes, such as climate change. More recently, studies by Webb (1977, 1984), Barnosky (1989), Janis (1989, 1997, 1993) explicitly tied mammalian diversity to global climatic change and host of related factors. However, most of these studies were done before the advent of the high-resolution magnetostratigraphic and $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the past decade, and so they represented very broad-brush comparisons between faunal change in North America and the generalized picture of global climatic change. In many cases (such as the redating of the formerly "early Oligocene" Chadronian as late Eocene; Swisher and Prothero, 1990), the old correlations were so far off that the comparisons between North American land mammals and global climate were completely invalid.

At the coarse scale of such previous studies, it might seem plausible to claim that climate drives mammalian evolution. However, the recent improvement in our resolution and dating of Cenozoic deposits and their mammalian faunas has allowed us to re-examine these long-accepted hypotheses. In two independent analyses, Prothero (1999) and Alroy et al. (2000) concluded that there was no link between climatic and faunal change in North American mammals. Prothero (1999) examined the four largest climatic events of the past 50 million years (the 37-Ma cooling event at the end of the middle Eocene; the early Oligocene refrigeration at 33 Ma; the expansion of C4 grasslands at 7 Ma; and the glacial–interglacial cycles of the Pleistocene) and found no association between the detailed records of these well-documented climatic changes and any significant extinctions. Instead, mammalian faunas showed almost no change through all four of these intervals and showed much more faunal turnover at times when there was no evidence of climatic change.

The most impressive demonstration of this phenomenon occurs for the first two events, at 37 and 33 Ma. In this interval, the sampling density of fossil mammals (Fig. 1) is very high (Prothero and Heaton, 1996), the systematics of most of the groups is very well known (papers in Prothero and Emry, 1996), and the stratigraphic resolution and dating is excellent

(summary in Prothero and Emry, 1996). We can plot total diversity, extinctions and originations into relatively short intervals (mostly 0.5–1 myr in duration), calibrated by precise magnetic stratigraphy and $^{40}\text{Ar}/^{39}\text{Ar}$ dates. Thanks to the improved correlations to the global Eocene–Oligocene climatic record, we can also locate the level at which major global events occurred and compare them directly to the mammal record.

What emerged was a surprise to many of us. The late middle Eocene cooling (Fig. 4) can now be dated at 37 Ma. Globally, it was marked by a 4–5°C drop in marine temperatures (Miller et al., 1987) and major cooling in the ocean bottom waters (Boersma et al., 1987). There was a major extinction in the warm-water foraminifera (Boersma et al., 1987), tropical nannoplankton (Aubry, 1992), and 84% of the species of bivalves and 89% of the species of gastropod

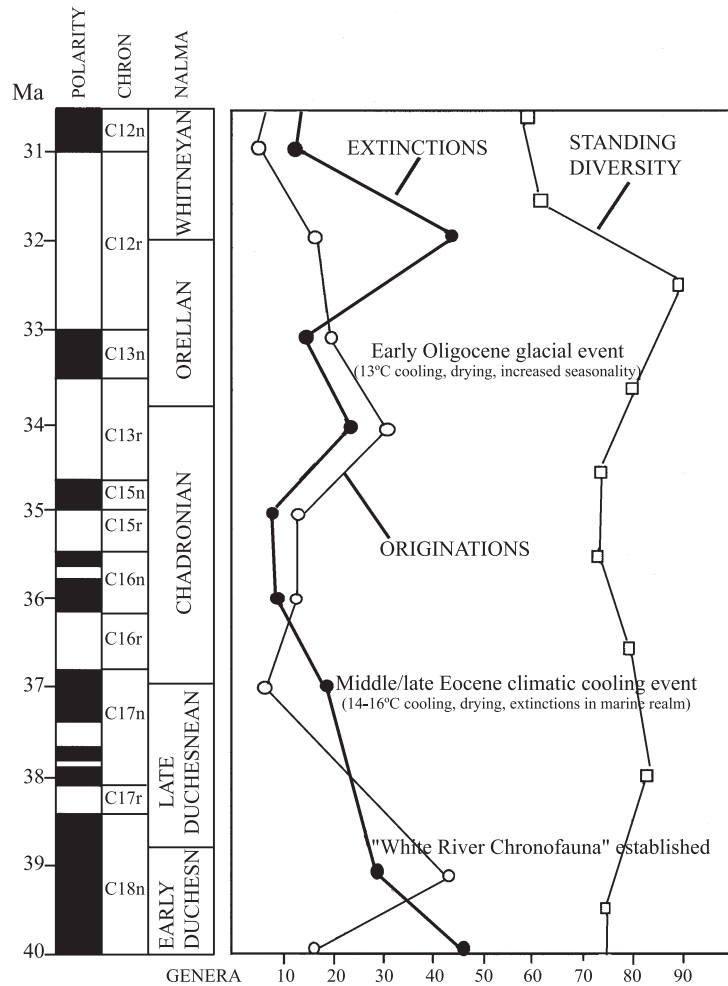


Fig. 4. Mammalian diversity and turnover through the late middle Eocene (Duchesnean), late Eocene (Chadronian), and early Oligocene (Orellan and Whitneyan). Note that the Chesapeake and Popigai impacts occurred between 35 and 36 Ma, in the middle of the late Eocene, when both originations and extinctions were at an all-time low. Diversity data modified from Stucky (1990, 1992) for the Duchesnean, and Prothero and Heaton (1996) for the Chadronian through Whitneyan. Total generic diversity (open squares) shown in the middle of 1 my increments; originations (open circles) shown at the beginning of each 1 my interval, and extinctions (solid circles) shown at the end of each 1 my interval. NALMA=North American land mammal "ages". Time scale after Berggren et al. (1995) and Prothero and Emry (1996).

molluscs in the Gulf Coast (Hansen, 1987, 1992). Similar levels of extinction are seen in the molluscs of the Pacific Coast (Squires, 2003; Hickman, 2003). In North America, it was marked by a drop in terrestrial mean annual temperature of 14–16 °C (Wolfe, 1978, 1994), with dense tropical forests experiencing over 1 m of rainfall being replaced with less dense forests experiencing less than half that amount of rainfall (Retallack, 1983).

Yet the mammalian record shows no response to this event (Fig. 4). Diversity, extinction, and origination curves are constant through the interval, with a stable value of between 72 and 84 genera between the late Duchesnean and early Chadronian, and turnover rates no greater than average for the Paleogene. In fact, Emry (1981) and Wilson (1984, 1986) argued that the Duchesnean should be considered a subage of the Chadronian because the differences were so slight. Much greater faunal change occurred between the early and late Duchesnean (Fig. 4) at 39 Ma, when there is no record of significant climatic change.

The data for the 33 Ma early Oligocene event are even better than the previous example. It is well known for the global climatic changes that occurred when glaciation returned to Antarctica, the circum-Antarctic current and the psychrosphere developed, and the oceans cooled 5–6 °C (summarized in Prothero, 1994). There were major extinctions in the calcareous nannoplankton (Aubry, 1992), diatoms (Baldauf, 1992), and benthic foraminifera (Gaskell, 1991). Gulf Coast molluscs suffered another decimation (Hansen, 1987, 1992), as did those of the Pacific Rim (Squires, 2003; Hickman, 2003). Echinoids were also affected, both in the Gulf Coast (Carter, 2003), where they suffered about 50% extinction, and also in the Pacific (Burns and Mooi, 2003). Planktonic foraminifera suffered a lesser extinction, so that most of the surviving Oligocene species were small, low in diversity and cold-water adapted (Boersma et al., 1987).

In North America, we have excellent climatic records across this time interval (Fig. 5). Land plants from the Gulf Coast to Alaska show about a 13°C decrease in mean annual temperature (Wolfe, 1978, 1994), and a great increase in seasonality as well. The floras of North America changed from paratropical rain forests (like those of modern Central America) to broad-leaved deciduous forests (like those of modern

New England) in less than 0.5 million years. Paleosols from the Big Badlands of South Dakota show that the dense late Eocene forests, which received almost a meter of annual rainfall, were replaced by scrublands that received less than half a meter of precipitation (Retallack, 1983). In some places, floodplain deposits were replaced by sand dunes (Evanoff et al., 1992), indicating greater aridity. Late Chadronian land snails are large forms adapted to wet tropical climates (like those of modern Central America); these were replaced in the Orellan by land snails with smaller shells and restricted apertures, typical of seasonally dry regions such as modern Baja California (Evanoff et al., 1992). Finally, late Chadronian reptiles and amphibians were predominantly aquatic taxa, such as crocodylians, pond turtles, and salamanders, but in the Orellan they were replaced by dry-land tortoises (Hutchison, 1982, 1992).

What was the mammalian response to this dramatic climatic change? We have the enormous samples of mammal fossils from the White River Group of the High Plains, with dozens to hundreds of specimens of some lineages known from nearly every meter of section in some places (such as eastern Wyoming). Prothero and Heaton (1996) compiled the records of over 177 species lineages known from the interval. Standing diversity was again nearly constant and turnover (origination and extinction) was actually below average Paleogene levels (Fig. 4). Of 70 species known from the earliest Orellan, 62 persisted unchanged into the late Orellan with no appreciable changes (Fig. 5). The oreodont *Miniochoerus* underwent dwarfing (Fig. 1), but there were no gradual changes in any other lineages (Prothero and Heaton, 1996). A few extinctions of archaic groups, such as brontotheres, cylindrodont rodents, oromerycid artiodactyls, occurred in the late Eocene, at least 0.5 myr before the early Oligocene climatic crash of the early Orellan. In short, the most dramatic climatic change of the entire Cenozoic (the transition from the “greenhouse” to “icehouse” world) produced almost no changes in the mammalian faunas during the two critical intervals of climatic change (37 and 33 Ma).

Critics of an earlier draft of this paper suggested that extinction and turnover rates are not the only metric of change. Community changes which maintained the same level of diversity would not show up in these calculations. However, during both the

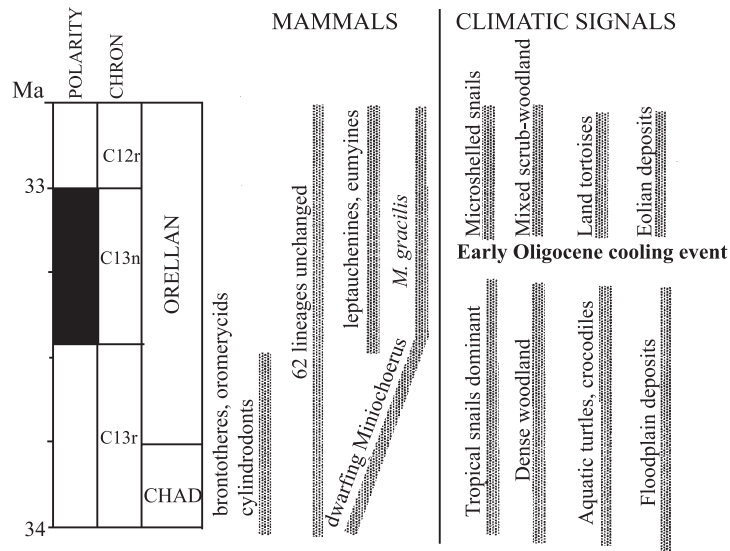


Fig. 5. Summary of detailed record of climate and mammalian faunas through the Eocene–Oligocene boundary in the Whiter River Group of the High Plains of North America. Note that the few family-level extinctions (brontotheres, camel-like oromerycids, and cylindrodont rodents) take place at least 0.5 my before the climatic changes. This is no artifact of sampling or of compiling different records, since the record is very dense and continuous, and all the data drawn from the same sections (primarily Douglas, WY—see [Evanoff et al., 1992](#)). Other than those three extinctions, and a few originations and dwarfing in one lineage of oreodonts, there are no changes in the 62 other lineages recorded from this interval. Climatic signals after [Evanoff et al. \(1992\)](#), [Hutchison \(1982, 1992\)](#) and [Retallack \(1983\)](#). Details of the mammalian record can be seen in [Prothero and Heaton \(1996\)](#), but are not reproduced here for space reasons.

Duchesnean–Chadronian and mid-Orellan climatic events, there were no significant changes in the community composition. As mentioned above, authors such as Wilson and Emry were so unimpressed with the differences between the Duchesnean and Chadronian that they wanted to make the Duchesnean a subage of the Chadronian, so clearly neither the community composition nor the overall diversity and turnover changed very much. As for the mid-Orellan event, 62 lineages ([Figs. 4 and 5](#)) persisted without change through the entire climatic event, so virtually the entire mammalian community remained unchanged, with constant relative abundances, through the entire early Oligocene climatic crash (see further documentation in [Prothero and Heaton, 1996](#), where the ranges of individual species are plotted in detail).

In addition to the Duchesnean–Chadronian (middle–late Eocene) and mid-Orellan (earliest Oligocene) events, there were other important climatic events in

the Cenozoic that might have caused faunal change in mammals. For example, the expansion of C4 grasslands at 7.5 Ma at almost all middle latitudes produces a dramatic isotopic signal in both tooth enamel and in soil carbonates everywhere we have a late Miocene terrestrial record: North America, Pakistan, South America, and East Africa. Yet as [Prothero \(1999\)](#) showed, there is almost no faunal response to this great expansion of C4 grasslands. Most of the hypsodont mammals with high-crowned teeth for eating grasses had appeared 9 million years earlier, and at the 7.5 Ma isotopic event itself, there is almost no turnover in the fauna, nor change in faunal composition, either. One would expect browsers to decline and grazing taxa to increase, but in North America, there are actually fewer grazers with the expansion of the C4 grasslands ([Prothero, 1999](#)). There is turnover in the late Miocene in both North America and Pakistan, but it happens at 9 Ma and at 4.5 Ma, nowhere near the dramatic expansion of C4 grasslands.

Elsewhere in the Neogene, the middle Miocene is well known for the climatic optimum that preceded the growth of the Antarctic ice sheets (Zachos et al., 2001). Barnosky and Carrasco (2002) examined the diversity changes in North American land mammals during this interval and found that there was no faunal change in response to this global climatic signal; indeed, the trends are the opposite of those one might predict from the climatic indicators.

Finally, the most dramatic and best known climatic changes of the entire Cenozoic are the glacial–interglacial cycles of the Pliocene and Pleistocene, when ice sheets repeatedly advanced and retreated across North America and Eurasia every 120,000 years or so. The classic Neo-Darwinian model predicts that we should see morphological changes in response to subtle climatic changes (the Galapagos finch model), as well as extinctions and speciation events at periods of maximum climatic change. Yet Agusti and Anton (2002, p. 231) commented that the beginning of the Pliocene–Pleistocene glaciation at 2.6 Ma had almost no effect on the mammalian community. Barnosky (1987, 1994) and Barnosky et al. (1996) have shown that Pleistocene mammals do not respond to climatic change by evolving new adaptations or producing new species. Instead, communities change composition, usually as they migrate north and south in response to the changing climatic and vegetational belts. Most Pleistocene mammalian species are well known for their long-term stasis and lack of change through several climatic cycles. As Barnosky (1994) put it, “climatic oscillations on the multi-millennial scale may not stimulate speciation much.” The same evolutionary stability has been documented for Pleistocene reptiles and amphibians (Holman, 1995).

Alroy et al. (2000) used different methods, comparing the diversity curve of Alroy (1998) with global climatic proxies, such as the oxygen isotope curve. They also concluded that there was no statistically significant association between any major diversity change in North American mammals and any episode of climatic change.

This is not to say that no Cenozoic organisms responded to climatic change. Certainly, the relationship between changes in climate and such organisms as planktonic and benthic microfossils, benthic molluscs and echinoids, land plants, land snails, and reptiles and amphibians, is well established (Prothero

and Berggren, 1992; Prothero et al., 2003). Although they respond to climate, none of these groups shows any significant extinction during the impact events and flood basalt eruptions discussed above. What Prothero (1999) and Alroy et al. (2000) did show, however, is that the long-assumed sensitivity of land mammals to tiny changes in their environment is not supported by a rigorous analysis of the data. Despite our biases, land mammals are much less sensitive to environmental change than previously thought.

5. Conclusion

Where does this leave us? If the three most popular extrinsic environmental factors (impacts, volcanic eruptions, and climate change) have no appreciable effect on land mammals, then why do these faunas change so much during the Cenozoic? The answer is not yet clear, but if extrinsic factors (the “Court Jester” hypothesis of Barnosky, 2001) can be ruled out, then the answer must lie with intrinsic biological factors (the “Red Queen” hypothesis of Barnosky, 2001), such as community dynamics and evolutionary trends within lineages (Prothero, 1999; Alroy et al., 2000). Clearly, we have a lot to learn about what forces control the evolution of life, and we need to be cautious when assuming that some apparent cause (such as an impact or volcanic eruption or climatic change) MUST have an effect. As we improve our data bases and reach higher and higher levels of stratigraphic and taxonomic resolution, it is incumbent upon us to critically re-evaluate previously tested or tacitly assumed hypotheses of the past and see if they continue to hold up to scrutiny.

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