Article

Cenozoic Mammals and Climate Change: The Contrast between Coarse-Scale *versus* High-Resolution Studies Explained by Species Sorting

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Abstract: Many paleontologists have noticed the broadly similar patterns between the changes in Cenozoic mammalian diversity and taxonomic dominance and climate changes. Yet detailed studies of fossil population samples with fine-scale temporal resolution during episodes of climate change like the Eocene-Oligocene transition in the White River Group, and the late Pleistocene at Rancho La Brea tar pits, demonstrates that most fossil mammal species are static and show no significant microevolutionary response to major climate changes. This mismatch between patterns seems best explained by species sorting. As the punctuated equilibrium model demonstrated, over long time spans most fossil species are stable and do not respond to climate change. Instead, change occurs at the next hierarchical level, with species sorting adding and subtracting to the total diversity pattern revealed by coarse-scale taxon counting, apparently responding to longer-term changes in climate as revealed by proxies like the oxygen isotope record.

1. Introduction

For decades, it has been asserted that the record of Cenozoic mammals is strongly affected by climate change. Such ideas go back to the early twentieth century with the work of Osborn [1], Stirton [2], and Simpson [3], when they attributed the changes in horse tooth hypsodonty and limb proportions to the expansion of open grasslands over the Miocene, which have long been attributed to drier and cooler temperatures as climate changed. When detailed climatic records for the global oceans

(especially the early oxygen isotope curves) became available as a proxy for North American climates, the claim that there was a strong association between climate and mammalian diversity appeared in papers such as those by Webb [4,5] and especially in papers by Janis [6–8] and Vrba [9,10]. In recent years, the number of studies asserting the climatic causes of Cenozoic mammalian diversity is increasing [11–18]. But Alroy [19–21], using similar methods of analysis but different statistical methods, concluded that there was no statistical relationship between North American mammalian diversity and Cenozoic climate proxies, such as the oxygen isotope curve.

Nearly all these studies are based on counting the presence or absence of taxa in specific faunas, or in databases (such as the Paleobiology DataBase [22]) that are aggregates of many faunas. This practice is often known as "taxon counting", and serves as an indirect proxy for detailed records of individual specimens from each species at a finer-scale faunal analysis. For most fossil mammal localities, the specimens are so fragmentary and rare, and the temporal sequence of faunas is so sparse, that no other approach is possible. Using this approach allows a scientist to generalize over all the instances of poor data quality and look at broad-scale patterns that would otherwise be unobtainable. But generalization of so much data into a handful of time intervals spanning millions of years or arbitrary taxonomic units, such as taxon-counting does, carries risks as well.

There are places where the fossil record of mammals is very "dense and continuous" and allows for finer-scale examination of faunal response during episodes of climate change. These make it possible to look directly at the changes in the fossils through time, and ask whether they show obvious response to climate change (as measured by independent external variables) or not. Such analysis is common in the studies of many other groups of marine invertebrates and microfossils, where the fossil record consists of large samples of specimens at many different levels over a significant span of geologic time. But despite the large number of studies of change through time in fossil vertebrates, few places provide such an opportunity in fossil mammals.

Prothero and Heaton [23] and Prothero [24] published a contrasting point of view to the studies discussed above. These reports looked at the detailed fine-scale evolutionary records of thousands of specimens in dozens of taxa over an interval of climate change. In particular, Prothero [24] looked at four of the largest climatic events of the past 50 million years and concluded that there was no significant faunal response in the North American mammalian record associated with these climatic events. In that paper, two of the climatic events were examined using the taxon-counting method (the only data available for these intervals), but the other two studies were based on fine-scale records of individual specimens over a densely fossiliferous time interval, not coarse-scale taxon-counting. Since that time, the record for all these studies has improved, and one of them (the record of the late Pleistocene) has been the subject of much additional research. In this paper, I will examine these two key faunal records of climate change in greater detail, and see if the original conclusions hold over a decade later.

2. Results

2.1. The Eocene-Oligocene Transition

The Eocene-Oligocene transition is considered one of the most important climatic changes of the Phanerozoic, when the "greenhouse" world of the Mesozoic through Eocene was replaced by our

modern "icehouse" planet [25–28]. One of the best, most complete records of the North American Eocene-Oligocene transition occurs in the White River Group of the High Plains, best known from its richly fossiliferous exposures in the legendary Big Badlands of South Dakota. The fossil collecting in this region goes back to 1846, and the fossil collections are enormous and dense at nearly every level in some collections.

Retallack [29] studied the color bands visible in the Badlands sections, and found that they were paleosols, or ancient soil horizons. Those from the upper Eocene Chadron Formation were formed under forests with closed canopies of large trees (the big root casts are particularly conspicuous) with between 500–900 mm of rainfall per year. In the overlying lower Oligocene (Orellan) Brule Formation, the paleosols indicate more open, dry scrubland with only 500 mm of rainfall per year. In eastern Wyoming, Evanoff *et al.* [30] found that the moist Chadronian floodplain deposits abruptly shifted to drier, wind-blown deposits by the Orellan. Zanazzi *et al.* [31] examined the oxygen isotopes of the teeth of the oreodont *Merycoidodon*, the deerlike *Leptomeryx*, the rhinocerotid *Subhyracodon*, and the horse *Mesohippus* spanning the Chadronian-Orellan in western Nebraska. They found that mean annual temperatures dropped 8.2 °C and seasonality increased. However, their study was based on a truncated, condensed section, and did not include the much better record of the earliest Oligocene *Hypertragulus calcaratus* Interval Zone of Prothero and Whittlesey [32] and Prothero and Emry [33] in eastern Wyoming (Lusk and Douglas areas), which is missing from the Nebraska sections.

According to Evanoff *et al.* [30], Chadronian land snails are large-shelled taxa similar to those found in wet subtropical regions, like modern Central America. Based on modern analogues, these snail fossils indicate a mean annual temperature of 16.5 °C (63 °F), and a mean annual precipitation of about 450 mm, very similar to the results obtained by Retallack [29] for neighboring South Dakota. By contrast, Orellan land snails are drought-tolerant small-shelled taxa indicative of warm-temperate open woodlands with a pronounced dry season. Their living analogues are found today in Baja California.

The amphibians and reptiles suggest similar trends of cooling and drying in the early Oligocene [34,35]. The Eocene is dominated by aquatic species (especially salamanders, pond turtles, and crocodilians) that had been steadily declining in the middle and late Eocene. Crocodiles were gone by the Chadronian, but there are a few fossil alligators recovered from the Chadron Formation. By the Oligocene, only land tortoises are common, indicating a pronounced drying trend. In fact, these tortoises (*Stylemys nebraskensis*) are so common in the Orellan that these beds were originally called the "turtle-oreodon beds" after their two most common vertebrate fossils.

Land plants are not well preserved in the highly oxidized beds of the Big Badlands (except for the durable hackberry seeds, which are calcified while they are alive), so we must look to other regions to understand the floral change. But the rest of North American floras show a clear trend. Based on leaf-margin analysis, Wolfe [36–38] suggested that mean annual temperatures in North America cooled about 8–12 °C (13–23 °F) in less than a million years. This is by far the most dramatic cooling event of the entire North American floral record, and as noted above, was the original basis for the phrase "Terminal Eocene Event" (even though revised dating now places it in the early Oligocene). Although recent redating and re-assessment of the floras has modified the temperature change in the early Oligocene to be less extreme [39,40], nonetheless the change was still significant.

All of these White River deposits now have excellent chronostratigraphic control, thanks to recent ^{40}Ar/^{39}Ar dates [41,42] and magnetic stratigraphy [33]. In addition, the biostratigraphic control on the

Frick Collection specimens in the American Museum of Natural History in New York is excellent (zoned to the nearest foot from marker ashes), allowing detailed biostratigraphic zonations for the first time [32,33]. The fine-scale chronostratigraphic control through dated ashes and magnetic stratigraphy extends to many of the key plant localities as well [39,40].

Despite these dramatic changes in the soils, land plants, land snails, and reptiles and amphibians, the change in the mammalian fauna was insignificant [23,24,26]. Most of the archaic Eocene taxa (especially the forest dwellers and arboreal forms) were already gone by the late Eocene, with only a few multituberculates straggling on to the middle Chadronian. A few groups, such as the brontotheres, oromerycids, epoicotheres, and two groups of rodents (cylindrodonts and yoderimyines) did die out near the end of the Chadronian, but none was around to witness the early Oligocene climatic deterioration. Most of the taxa that were present before the climatic crash showed no change whatsoever, except for a slight size reduction in one lineage of the oreodont *Miniochoerus* (Figure 1); this dwarfing begins in the late Chadronian, at least 500,000 years before the climatic change. Most of the other mammals with large sample sizes (e.g., *Merycoidodon* in Figure 2) show no measurable changes across this time interval, with stable mean body size documented by huge samples with good stratigraphic control.

Figure 1. Gradual size change (as measured by the length of the M1-3 molar row) in the small oreodont *Miniochoerus* across the Eocene-Oligocene transition in the White River Group, near Lusk, Converse County, Wyoming. The dwarfing begins in the late Eocene (lower 60 feet of section), long before the big climatic event, which occurs about 100 feet above the base of the section. The Eocene-Oligocene boundary (as determined by magnetic stratigraphy) occurs at about 40 feet above the base of the section, but the boundary in not a climatic event. This lineage is the only example of gradualism in the entire fauna, and it begins dwarfing over a million years before the climate change.
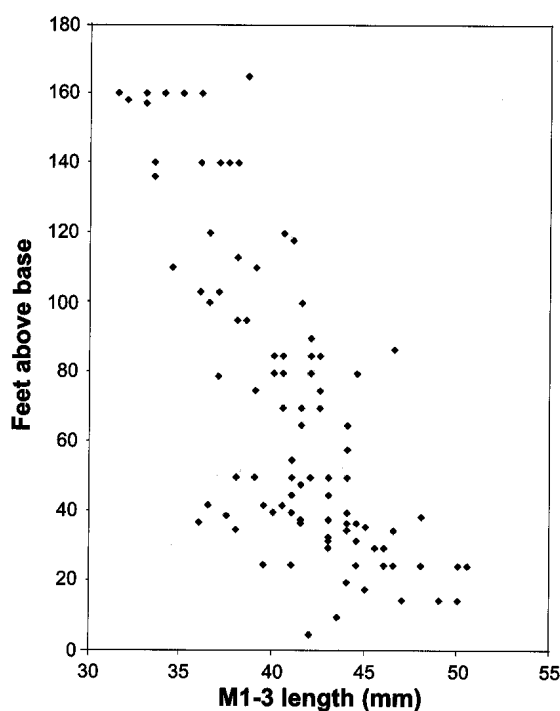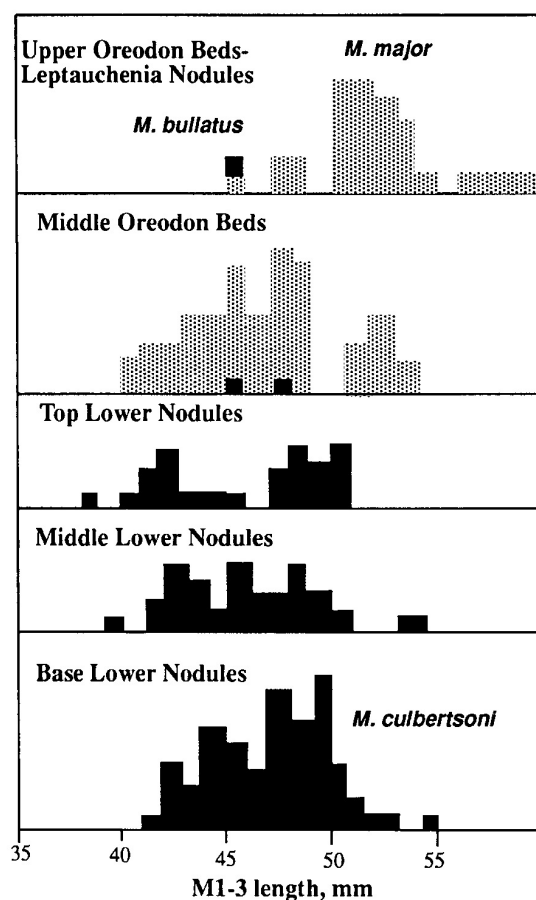
Figure 2. Histograms of size distribution (as measured by the length of the M1-3 upper molar row) in the common large oreodont *Merycoidodon*, in the Brule Formation, White River Group, Big Badlands, South Dakota. The early Oligocene climatic event occurs between the base lower and middle lower nodules in this section; the Eocene-Oligocene boundary (which is not a climatic event) occurs below these samples. The commonest of all Badlands species is *M. culbertsoni* (black squares). It shows no change through the entire early Oligocene, until it is suddenly replaced in the Middle Oreodon beds by *M. bullatus* (smaller stippled specimens) with inflated auditory bullae, and also speciates into the larger *M. major* (larger stippled specimens) with small bullae (after [23], Figure 1).

Thanks to updated taxonomy of these groups (mostly published in [33] and summarized in [23]), over 170 different species are reported from this time interval, and this is not a sample, but the entire fauna; no taxa are left out (Figures 3,4). Of the 70 lineages of mammals known in the latest Eocene, nearly all (62 out of 70) pass through the climate change with no discernable change in size or morphology of their skeletons or teeth. A few other lineages went extinct, and a few more speciated, but this is a remarkably weak response for the largest climatic change of the past 50 million years (Figure 4).

If there is no change in the morphology of these fossils across such a large environmental change, are there any other responses? Dewar [43] reported that the teeth of many of the herbivorous taxa show a greater incidence of wear and scratches, apparently due to a grittier diet by the middle Oligocene, but there is no expected increase in hypsodonty at this interval. In addition, there were two groups of

animals with relatively high-crowned teeth (leptauchenine oreodonts, eumyine cricetid rodents) that appeared in the Orellan, but there are extremely rare at that time and do not become abundant until much later in the Oligocene (Whitneyan).

Figure 3. Temporal durations of all of the valid species of artiodactyls from the Eocene-Oligocene transition as represented by fossils from the White River Group. The Eocene-Oligocene boundary occurs in magnetic Chron C13r, and is roughly equivalent to the Chadronian-Orellan boundary. The climatic event occurs about 500,000 years later in early Oligocene Chron C13n. Most have long temporal ranges, and almost none are affected by the dramatic climate change in the early Orellan (stippled vertical line). Prothero and Heaton [23] provided similar plots of all the other valid White River mammals, showing the same pattern throughout the entire fauna. (after [23], Figure 3).
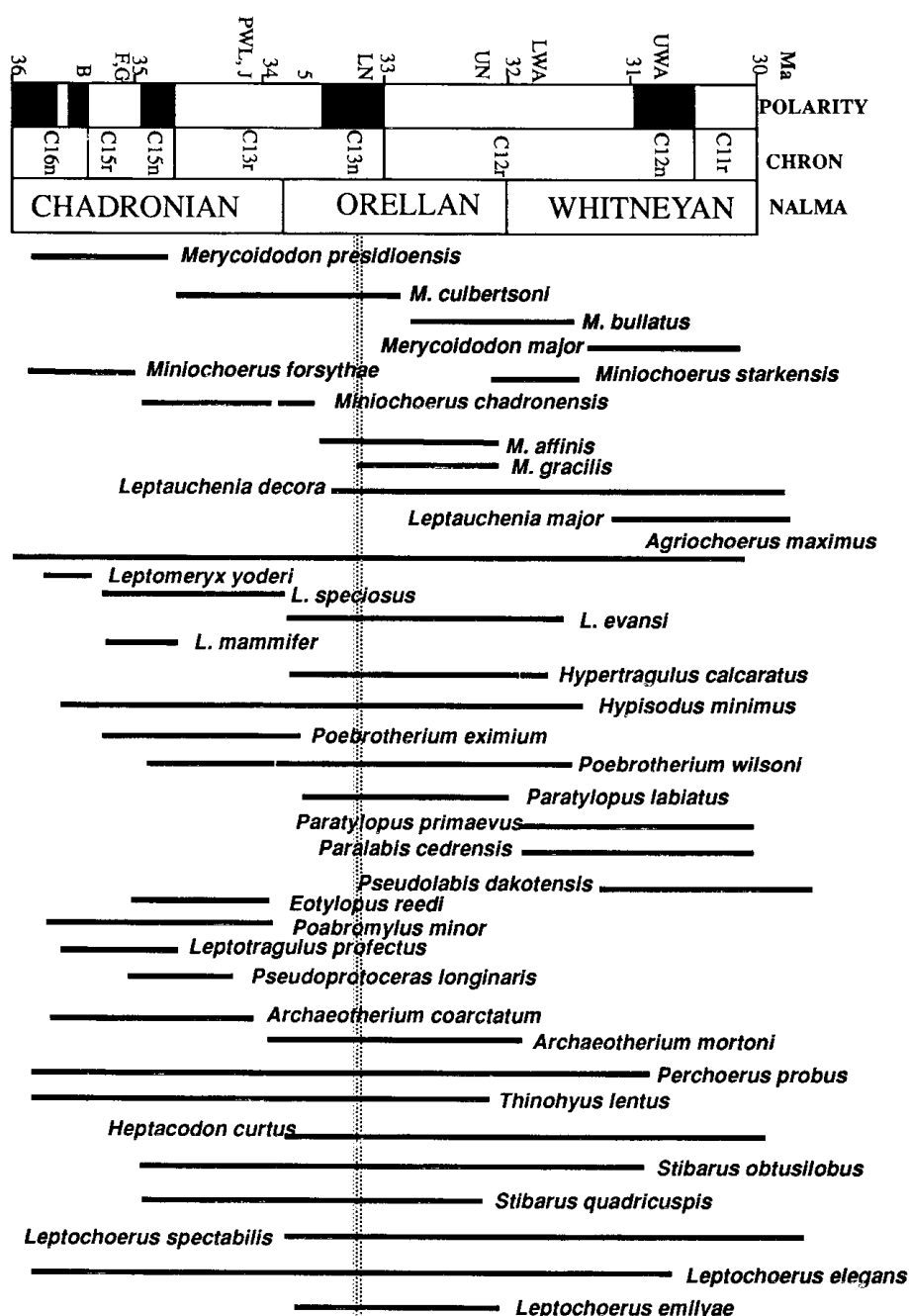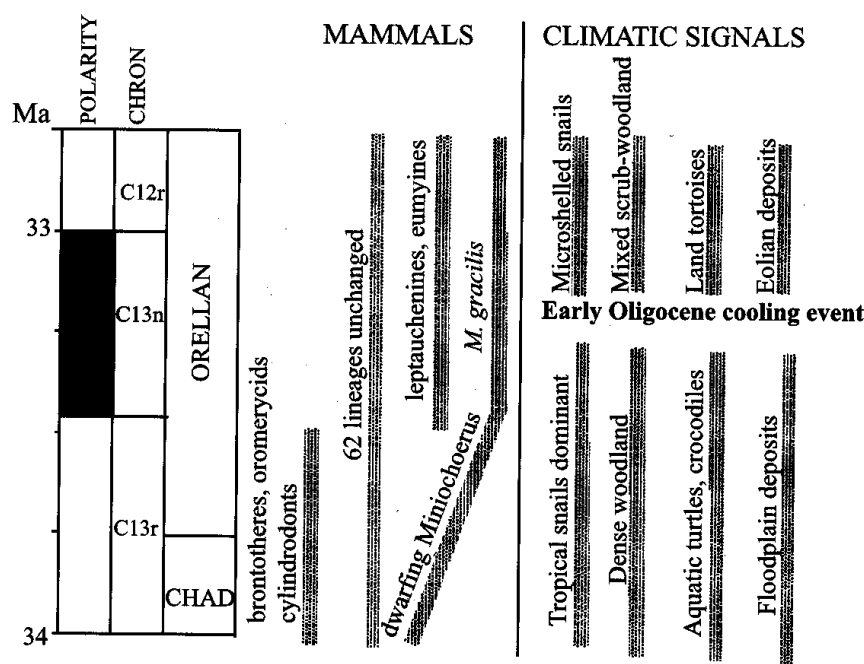
Figure 4. Summary of the climatic indicators (right side of diagram) and the mammalian faunal response (left side of diagram) during the Eocene-Oligocene transition in the White River Group.

Nor can we dismiss the overwhelming stasis of this fauna and its individual lineages as they passed through the big climate change as some sort of "generalized feeder" response. Some of the mammals, such as the tapirs, are obligate leaf-eating browsers, yet they persist unchanged into the Orellan, while the paleosol evidence suggests that most of the trees and shrubs on which they depended had vanished.

Thus, the large-scale "diversity curves" of fossil mammals changing taxonomic composition over the span of the Eocene through Miocene do not capture the non-response to climate that can be seen in the actual mammalian fossils of the White River Group. With its coarse resolution and large time bins, taxon-counting does not reflect the detailed record that a direct and detailed sampling of the fossils can demonstrate. The former gives the impression of a response to climate change, while the latter gives the opposite picture.

2.2. The Late Pleistocene

The second interval of time discussed by Prothero [24] was the glacial-interglacial climate cycles of the Pleistocene, which dramatically shifted the vegetational belts across all the temperate continents. Yet since Hugh Falconer [44] first pointed to the stasis of mammoths in 1863, Pleistocene paleontologists had known that most glacial–interglacial climatic changes do not stimulate speciation, nor do they result in gradual changes in body shape or size ([45–50], and many other papers). Barnosky [47] wrote, "climatic oscillations on the multi-millennial scale may not stimulate speciation much." Barnosky [48] commented that "despite the increased potential for isolation of populations that should occur with multiple advances and retreats of glaciers and rearrangement of climatic zones, empirical data suggest that speciation rates were neither appreciably elevated for Quaternary mammals, nor strongly correlated with glacial-interglacial transitions." Barnosky [48] also wrote,

"research that has focused on tracing the morphological characters that had taxonomic significance in these taxa revealed no direct correlation between climate changes and morphologic changes." Bennett [45,46] suggested that Quaternary climate change did not stimulate speciation in plants, a conclusion that has since been well supported [51–53]. Likewise, studies of Pleistocene birds show very little evolutionary effect of climate change [54–56]. Nor do fish [54], reptiles and amphibians [54,57] or insects [58] seem to show major morphological change or speciation in response to Quaternary climate cycles. McGill *et al.* [59] argued that even Quaternary small mammal communities showed remarkable inertia and resistance to change, despite dramatic climatic changes of the glacial-interglacial cycles.

To test this hypothesis, Prothero *et al.* [60] looked at all the common birds and mammals from the tar pits at Rancho La Brea, which record the last 35,000 years of climate change from the last glacial to the current interglacial cycle. These fossils also come from an area with a well-dated climatic record [61–63]. A study by Heusser [64] on pollen recovered from well-dated deep-sea cores just offshore showed that southern California went through intervals of extreme climatic and environmental changes over the past 59 ka. These transitions suggest a climate and landscape much different from the one today. The most detailed and well-calibrated record comes not from Rancho la Brea itself, but from deep-sea cores drilled just offshore in the California borderland. According to Heusser [64], the region changed from oak and chaparral vegetation around 59 ka to pine-juniper-cypress woodlands by 24 ka, then to a closed-cone juniper-ponderosa forest with abundant winter snow during the last glacial maximum (24–14 ka). During the glacial-interglacial transition from 14 to 10 ka, the landscape returned to dominant oak-chaparral and coastal sagebrush with pulses of alder, and in the past 10,000 years, the region has been vegetated by the modern assemblage of oak-chaparral-herbaceous vegetation. Coltrain *et al.* [62] performed stable isotope analysis and found evidence of increased seasonal aridity during the last interglacial and previous glacial.

Prothero *et al.* [60] summarized the work of Madan *et al.* [65], Linden [66], Raymond and Prothero [67], Prothero and Raymond [68], and DeSantis *et al.* [69]. These studies performed a detailed analysis of all the suitably abundant bones of all the common mammal species from each pit with good radiocarbon dates [70,71]. These included the following mammals: dire wolves (*Canis dirus*), saber-toothed cats (*Smilodon fatalis*), giant lions (*Panthera atrox*), Harlan's ground sloth (*Paramylodon harlani*), horses (*Equus "occidentalis"*), bison (*Bison antiquus*), and camels (*Camelops hesternus*). Although there are other mammals (mammoths, mastodonts, pronghorns, peccaries, bears, rodents, *etc.*), they are not common enough in most of the well-dated pits to be suitable for this type of analysis.

Prothero *et al.* [60] also summarized the studies of Syverson and Prothero [72], Molina and Prothero [73], and Fragomeni and Prothero [74] on five of the most common birds at Rancho La Brea: the golden eagles (*Aquila chrysaetos*) and bald eagles (*Haliaeetus leucocephalus*), the condor (*Gymnogyps amplus*), the caracara (*Caracara plancus prelutosus*), and the California turkey (*Meleagris californica*).

The analysis was performed by ANOVA on all the well-dated pit samples to see if any of the samples stood out as significantly different in size or robustness, especially during the peak glacial at 20 ka, when the chaparral vegetation gave way to snowy pine forests. For samples that were non-parametric, the significance testing was done with a Kruskal-Wallis test. In nearly every case of hundreds of different analyses, ANOVA or Kruskal-Wallis tests revealed no samples that were

significantly different from the rest of the pit samples (Figure 5). The only exception was the Pit 13 sample of dire wolves (about 16 ka), which is significantly smaller, as O'Keefe [75,76] also noted with their stunted skull development. The reason for this size reduction is not understood, but it clearly it is not tracking the climate events during the glacial maximum at 20 ka. The sequence of samples from well-dated pits was also subjected to time series analysis using R software. In every case, the sequence of pits either displayed stasis or a random walk, but there were no cases of directional change. There is some time averaging of samples in each pit, but not as much as in the pits (like pit 4 and pit 16) with large scatter in their dates. More importantly, there is no overlap in the error bars of the radiocarbon dates between the oldest pits (35 ka) and the next youngest pits (23 and 21 ka), or between the pits between 18–16 ka and the youngest pits (11 ka and 9 ka), so it is still possible to recover a temporal sequence in these data.

Thus, late Pleistocene mammals and birds show no response to dramatic climatic changes, as Pleistocene paleontologists have known for more than a century. This goes against the idea that these mammals and birds are delicately sensitive to changes in their environment and respond to climate change by adapting in size (Bergmann's rule) or shape (Allen's rule). Instead, fossil species are largely indifferent to climate change, and respond instead by changing geographic ranges or by going extinct (most of them) or speciating (e.g., the condors, which gave rise to the smaller Holocene species *G. californicus*, the California condor).

Figure 5. Representative plots of dimensions of mammal and bird specimens from Rancho La Brea over time (from left to right on the horizontal axis). Small solid symbols represent individual specimens; large open symbols are the means for each pit. These plots are but a small but typical sample of hundreds of unpublished graphs, and the dozens of published diagrams, all of which show complete stasis through the last 35,000 years of glacial-interglacial cycles [60,65,67–69,72–74]. (**A**). *Smilodon fatalis* MC3 length. (after [65]); (**B**). MC3 (cannon bone) length of *Equus "occidentalis"* (after [69]); (**C**). Astragalus length of *Paramylodon harlani* (after [67]); (**D**). Femur length of *Gymnogyps amplus* (after [72]).
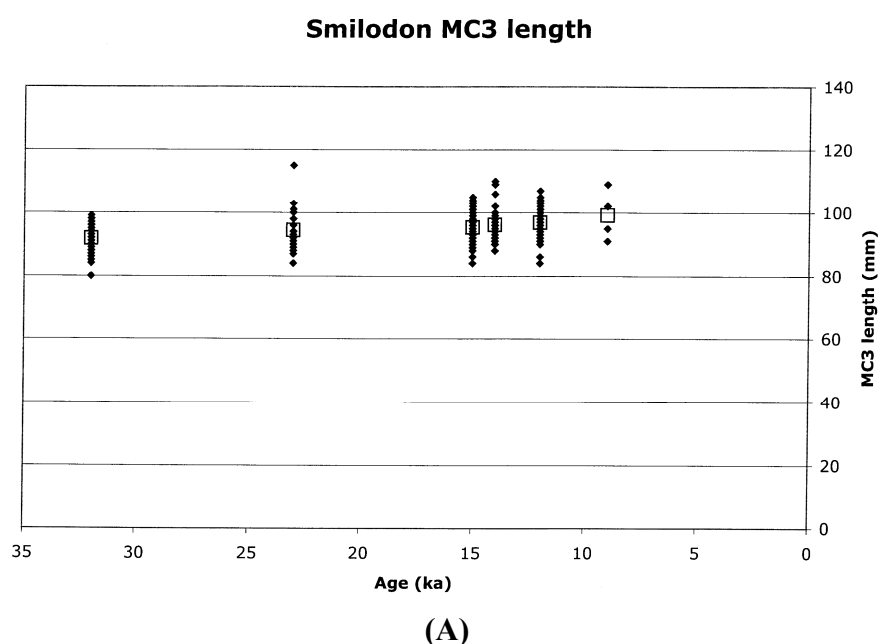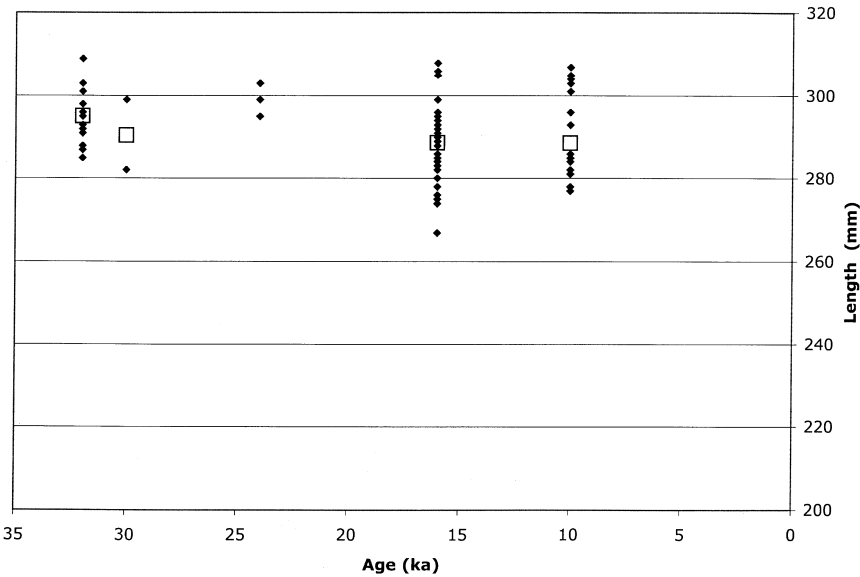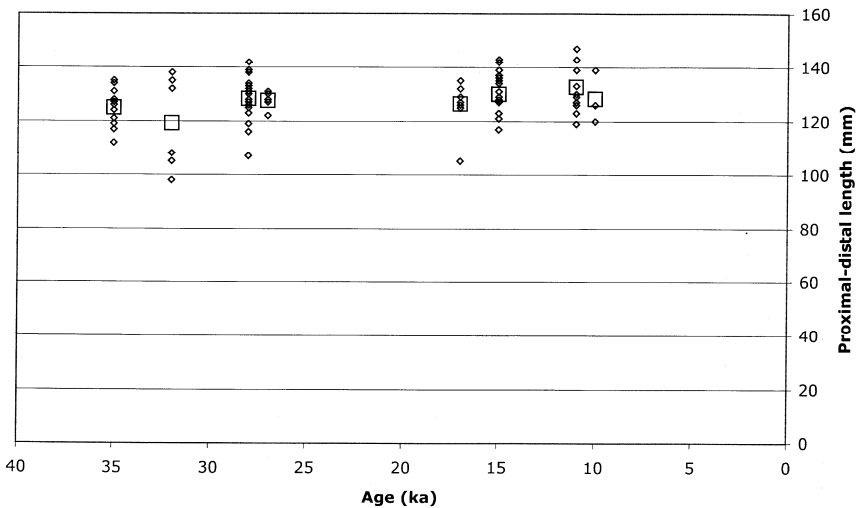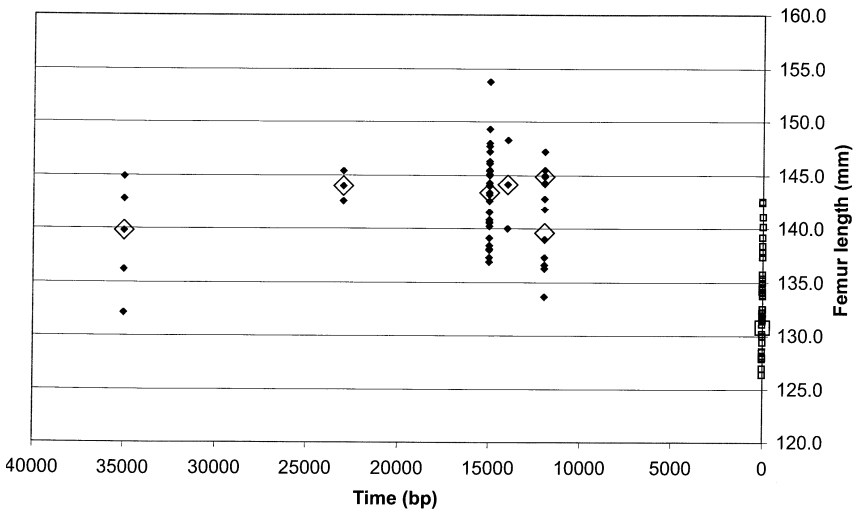

Smilodon MC3 length

(A)

Figure 5. *Cont.*

(B)

(C)

(D)

3. Discussion

As Prothero [24] pointed out, when we look at the fine-scale data of faunal response during these two episodes of climate change (large samples of many taxa in a well-dated sequence of fossils), we find no evidence of the predicted responses to climate that neo-Darwinian theory has long preached. Instead, we find overwhelming evidence of stasis as climate goes from one state to another, with animals adapting by changing their geographic ranges or going extinct, not by changes in size or morphology. This is exactly the prediction made over 40 years ago by Eldredge and Gould [77] in their landmark paper about the punctuated equilibrium model of evolution. In the four decades since that paper, the evidence is overwhelmingly in support of the idea that most metazoan species are static through millions of years and show no evidence of gradual change in response to climate or anything else [78–85]. The evidence of Oligocene mammals from the White River Group and late Pleistocene mammals and birds from Rancho la Brea strongly support the notion that species are stable and resistant to small-scale adaptations to climate, even when there are climate changes and other environmental pressures.

If this is true, then how do we account then for the apparent correlation between large-scale taxonomic data bases and climate proxies? This may be a previously unrecognized case of species sorting [81,82,86,87] where the hierarchically higher units of analysis (species) behave differently than their components (individual populations through time). If climate is causing change in mammalian faunas, it is through sorting discrete species over long periods of time, not by making population-level changes within species over shorter intervals of time. Such sorting has only rarely been noted in previous studies of fossil mammals [15,88–91], but clearly its importance must receive more emphasis. For example, some authors [15,88,89] have commented on sorting and tracking of favorable environments, or about environmental-mammal interactions [90], or about tolerance and resilience [91].

Thus, the repeated conclusion that mammalian diversity curves seem to reflect climate variables is not necessarily false (although Alroy and coauthors [19–21] claim that there is no correlation). Instead, the process that might cause mammalian species to track climate is the sorting of many different species, each of which is static and unchanged after it forms by speciation. As such, when paleontologists talk about "mammals responding to climate change", they should be cautious about thinking at the population level (as most neontologists do). Instead, they should think of the correlation as "mammalian species units are being sorted by climate" if they wish to be consistent with the data.

4. Conclusions

For decades, paleontologists have pointed to the apparent correlation between climate proxies and mammalian diversity as a simple case of climate causing the evolution of mammalian faunas. But detailed analyses of mammalian fauna samples in closely spaced well-dated intervals of climate change show that mammals and birds are unresponsive to climate forcing, but instead are static through time. The resolution of this paradox is to recognize that taxonomic databases are built upon static species compiled over long intervals of time. Any response to apparent climate change is not local adaptation on the short term, but species sorting of static species through long intervals of time.

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