

Large temperature drop across the Eocene–Oligocene transition in central North America

Alessandro Zanazzi¹, Matthew J. Kohn¹, Bruce J. MacFadden² & Dennis O. Terry³

The Eocene–Oligocene transition towards a cool climate (~33.5 million years ago) was one of the most pronounced climate events during the Cenozoic era¹. The marine record of this transition has been extensively studied. However, significantly less research has focused on continental climate change at the time, yielding partly inconsistent results on the magnitude and timing of the changes^{2–8}. Here we use a combination of *in vivo* stable isotope compositions of fossil tooth enamel with diagenetic stable isotope compositions of fossil bone to derive a high-resolution (about 40,000 years) continental temperature record for the Eocene–Oligocene transition. We find a large drop in mean annual temperature of 8.2 ± 3.1 °C over about 400,000 years, the possibility of a small increase in temperature seasonality, and no resolvable change in aridity across the transition. The large change in mean annual temperature, exceeding changes in sea surface temperatures at comparable latitudes^{9,10} and possibly delayed in time with respect to marine changes by up to 400,000 years, explains the faunal turnover for gastropods, amphibians and reptiles, whereas most mammals in the region were unaffected. Our results are in agreement with modelling studies that attribute the climate cooling at the Eocene–Oligocene transition to a significant drop in atmospheric carbon dioxide concentrations.

During the Eocene–Oligocene transition (EOT), at ~33.5 Myr ago, climate rapidly changed, marking a dramatic move from a 'greenhouse' to an 'icehouse' world¹. Likely causes for this shift include opening of marine gateways¹¹, and/or reduction of atmospheric CO₂ concentrations¹². The marine record of the EOT has been extensively studied, and shows major faunal turnovers that affected numerous organisms on a global scale^{13–15}. In addition, oxygen isotope records of benthic foraminifera show a rapid increase in $\delta^{18}\text{O}$ near the EOT, due to combined ice sheet growth on Antarctica and deep-water cooling¹. The increase in $\delta^{18}\text{O}$ of the EOT was accomplished in two 40-kyr-long steps separated by a 200-kyr-long intermediate plateau¹⁶.

In contrast to the marine record of the EOT, significantly less research has focused on the continental climate change during this time. Terrestrial faunal records in North America indicate major extinctions for gastropods, amphibians and reptiles^{2,8}, but little change to mammals, except for brontotheres³. Unfortunately, North American continental climate data are ambiguous, implying changes in mean annual temperature (MAT) ranging from 0 to 8 °C (refs 2, 4, 5). The timing relationship between the continental and oceanic climate change of the EOT also remains unclear, with either climatic synchrony^{7,8} or a possible continental time lag of 200–800 kyr (refs 3, 6). These inconsistencies, along with the coarse time resolution of these studies (~1–2 Myr time slices), preclude accurate understanding of links between continental and oceanic climate during major episodes of global change.

In this study, we analysed the stable isotope composition of fossil bones and teeth collected from the late Eocene–early Oligocene rocks in northwestern Nebraska, southwestern South Dakota, and eastern Wyoming (Fig. 1). The northern Great Plains of the US represents an ideal study site by virtue of its unparalleled fossil record and chronological controls. Tephrochronologic, single crystal ⁴⁰Ar/³⁹Ar dates on volcanic ashes¹⁷, and biostratigraphic¹⁸ and magnetostratigraphic¹⁹ studies indicate sufficiently high sedimentation rates to allow high-resolution relative chronologic control (\pm a few tens of kyr) comparable to marine studies.

Bones and teeth in living animals are composed of calcium phosphate with significant substitutions of CO₃²⁻. Stable isotope systematics in biogenic phosphates have been reviewed in ref. 20. Tooth enamel is resistant to isotopic exchange, so after burial and fossilization it retains an *in vivo* signal, largely reflecting dietary ($\delta^{13}\text{C}$) and, in obligate drinkers, local water ($\delta^{18}\text{O}$) compositions. Seasonal climate changes are preserved in $\delta^{18}\text{O}$ zoning along the length of each tooth. Mammals are homeotherms, so there is no temperature dependence to these isotope compositions. In contrast, the CO₃²⁻ component of bone is altered on timescales of 20–50 kyr, resetting with an important temperature-dependence to diagenetic compositions comparable to palaeosols²¹. $\delta^{18}\text{O}$ values of CO₃²⁻ in fossil bone are conceptually similar to foraminiferal CO₃²⁻ in that they reflect both local water composition and temperature. $\delta^{13}\text{C}$ values in bone reflect $\delta^{13}\text{C}$ of soil CO₂, which depends on plant organic matter composition and penetration of atmospheric CO₂ (ref. 22). Because C₄ plants were not yet abundant in the late Eocene and early Oligocene²³, $\delta^{13}\text{C}$ values principally reflect C₃ water stress, plant productivity, and canopy structure, increasing with increasing aridity. In this study, we use $\delta^{13}\text{C}$

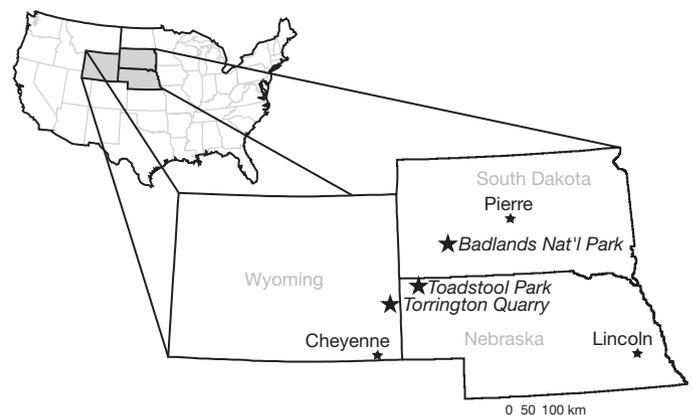


Figure 1 | Location map showing the sampling sites. Toadstool Park (northwestern Nebraska), Badlands National Park (southwestern South Dakota), and Torrington Quarry (eastern Wyoming).

¹Department of Geological Sciences, University of South Carolina, Columbia, South Carolina 29208, USA. ²Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA. ³Department of Geology, Temple University, Philadelphia, Pennsylvania 19122, USA.

values of bone to monitor changes in aridity, and combined $\delta^{18}\text{O}$ values of tooth enamel and bone to distinguish changes in water composition from changes in temperature.

The analysed samples include 231 bone fragments from various (usually unknown) mammalian taxa and turtles, and third molars (M3) of four of the most abundant White River mammals: *Mesohippus* (an ancestral horse), *Merycoiododon* (a sheep-sized artiodactyl), *Leptomeryx* (a small artiodactyl) and *Subhyracodon* (an ancestral rhino), which were all present before and after the transition. We also analysed middle molars (M2) and premolars for *Mesohippus* and premolars for *Subhyracodon* to ensure that we sampled all seasons. Oxygen isotope analyses were performed on the CO_3^{2-} component of tooth enamel and, for a few selected samples, also on the PO_4^{3-} component to test for diagenetic alteration. The *in vivo* relationship between $\delta^{18}\text{O}_{\text{CO}_3}$ and $\delta^{18}\text{O}_{\text{PO}_4}$ obtained for these samples indicates no significant diagenetic isotopic alteration of tooth enamel (see Supplementary Information). Isotope zoning in *Subhyracodon* and *Mesohippus* suggests that all seasons are sampled.

For tooth enamel $\delta^{18}\text{O}$ (Fig. 2), statistical tests (two-tailed *t*-tests unless mentioned below) indicate that mean values of Eocene versus Oligocene teeth cannot be distinguished for the following four mammals (*n* values are shown in the order Eocene then Oligocene): *Mesohippus* ($P = 0.436$; $n = 29, 91$), *Merycoiododon* ($P = 0.664$; $n = 19, 11$), *Leptomeryx* ($P = 0.605$; $n = 15, 7$) and *Subhyracodon* ($P = 0.607$, two-tailed Mann–Whitney test; $n = 89, 30$). Statistical tests also indicate that mean $\delta^{18}\text{O}$ values among the taxa are not statistically different, except *Merycoiododon*, which has a lower $\delta^{18}\text{O}$ ($P < 0.001$, single factor analysis of variance and Tukey test), and that $\delta^{18}\text{O}$ variances for Eocene versus Oligocene teeth cannot be distinguished (by *F*-test) for *Mesohippus* ($P = 0.200$), *Merycoiododon* ($P = 0.479$), *Leptomeryx* ($P = 0.856$) and *Subhyracodon* ($P = 0.672$).

Bone carbonate $\delta^{13}\text{C}$ values (Fig. 3) show no resolvable change across the EOT: $-7.77 \pm 0.14\text{‰}$ (± 2 standard errors, s.e.) versus

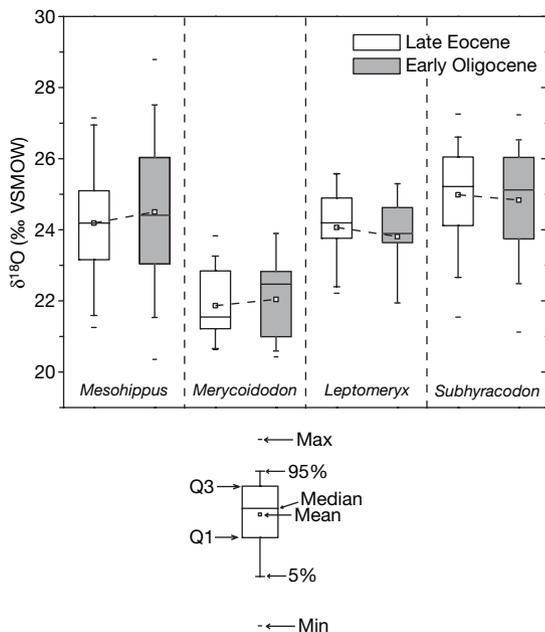


Figure 2 | 'Box and whiskers' plots for enamel $\delta^{18}\text{O}$. Lower and upper sides of boxes indicate lower and upper quartiles, respectively. Inside boxes, solid lines indicate median and squares indicate mean. Length of whiskers indicates 5th to 95th percentile range. Outside boxes, small tick-marks indicate minimum and maximum values. All taxa show insignificant changes in mean and median enamel $\delta^{18}\text{O}$ across the EOT, suggesting no change in rainwater composition. *Mesohippus*, *Merycoiododon* and *Subhyracodon* show a slightly higher Oligocene versus Eocene range in $\delta^{18}\text{O}$, suggesting a slightly higher Oligocene versus Eocene MART.

$-7.62 \pm 0.13\text{‰}$ (± 2 s.e.). In contrast, $\delta^{18}\text{O}$ values show a $\sim 1.7\text{‰}$ positive shift: $22.98 \pm 0.18\text{‰}$ (± 2 s.e.) versus $24.63 \pm 0.22\text{‰}$ (± 2 s.e.). Linear regressions of $\delta^{18}\text{O}$ versus time resolve no statistically significant trends at 95% confidence for either the Eocene or Oligocene data subsets. The isotope shift in our continental record appears to lag the marine transition by ~ 400 kyr, but this may simply reflect sparse data in the time range 33.7–33.3 Myr ago. Similarly, our data do not sample the largest shift to marine $\delta^{13}\text{C}$ values at 33.4–33.6 Myr ago.

For the bone $\delta^{13}\text{C}$ data, the lack of a resolvable change across the EOT implies that major changes in water stress or canopy structure did not occur, although minor changes might have occurred without affecting $\delta^{13}\text{C}$. For the enamel $\delta^{18}\text{O}$ data, it is important that modern horses and rhinos are quite water-dependent because of their digestive physiology²⁴, which is thought to have developed by the early Eocene²⁵. Therefore, the similar or lower mean $\delta^{18}\text{O}$ for all taxa imply that they were all water-dependent, even the artiodactyls. As a consequence, the lack of a resolvable change to mean enamel $\delta^{18}\text{O}$ across the EOT implies that water composition remained unchanged. In addition, the indistinguishable variance of Eocene versus Oligocene enamel $\delta^{18}\text{O}$ suggests no major change in temperature seasonality (mean annual range of temperature, MART) across the transition, although the small increase in the range of *Mesohippus*, *Merycoiododon* and *Subhyracodon* enamel $\delta^{18}\text{O}$ may reflect a slightly higher Oligocene versus Eocene MART.

Assuming that digestive physiology conferred similar dependencies of oxygen isotopes on climate variables for fossil equids and rhinos as observed in modern horses, we used the oxygen isotope data from *Mesohippus* to calculate MAT, changes in MAT (ΔMAT), and a minimum estimate of MART: $\text{MAT}(\text{Eocene}) = 21.0 \pm 10.1\text{ °C}$, $\text{MAT}(\text{Oligocene}) = 13.1 \pm 9.5\text{ °C}$; $\Delta\text{MAT}(\text{EOT}) = -8.2 \pm 3.1\text{ °C}$; and $\text{MART}(\text{Eocene}) \geq 21.9 \pm 7.5\text{ °C}$, $\text{MART}(\text{Oligocene}) \geq 25.8 \pm 8.8\text{ °C}$ (all errors ± 2 s.e.; see Supplementary Information). Our MAT estimates are broadly compatible with those from faunal change ($\sim 20\text{ °C}$ and $\sim 15\text{ °C}$ for the Eocene and Oligocene²), and leaf morphology ($\sim 19\text{ °C}$ and $\sim 12\text{ °C}$; ref. 26) studies. The decrease in MAT of $\sim 8\text{ °C}$ is far larger than found in marine records, which support at most 2–3 °C of cooling at low to mid-latitudes^{9,10}. Oligocene MART estimates agree with those from leaf morphology ($\sim 22\text{ °C}$ and 20–30 °C ; refs 5, 26). However, our Eocene MART estimates are larger than those from these previous investigations ($\sim 10\text{ °C}$ and $\sim 15\text{ °C}$; refs 5, 26). We find no evidence for a systematic shift in cold-month mean temperatures, as observed in fish otoliths from the Gulf of Mexico²⁷. Within uncertainty, the $\sim 8\text{ °C}$ temperature drop could have caused cold-month mean temperatures in the Oligocene to approach freezing, probably accounting for the demise of many terrestrial heterotherms^{2,8}, while almost all large mammals survived³.

Because ocean water $\delta^{18}\text{O}$ probably increased by $\sim 0.75\text{‰}$ (ref. 16), constant meteoric water compositions imply a compensating, about -0.75‰ , temperature-induced decrease in $\delta^{18}\text{O}$. That is, the temperature coefficient for meteoric water $\delta^{18}\text{O}$ associated with the approximately -8 °C change in MAT is $\sim 0.1\text{‰ per °C}$, consistent with theoretical models (albeit for coastal areas) that suggest minimal temperature coefficients at mid-latitudes²⁸.

The large temperature drop in the North American mid-continent during the EOT supports the results of recent simulations that attribute the climatic deterioration during this time to a major decrease in the atmospheric partial pressure of CO_2 (ref. 12). The opening of Southern Ocean gateways probably had a minor role in driving the transition because the Antarctic Circumpolar Current is expected to produce warming of middle and high latitudes of the Northern Hemisphere²⁹, directly contrary to our results.

In sum, enamel and bone isotope compositions indicate a large MAT decrease, a possible small MART increase, and no resolvable change in aridity across the transition. Therefore, in contrast to previous studies^{2,8,27}, our results indicate that a decrease in MAT, rather than an increase in seasonality or aridity, is the primary cause of the

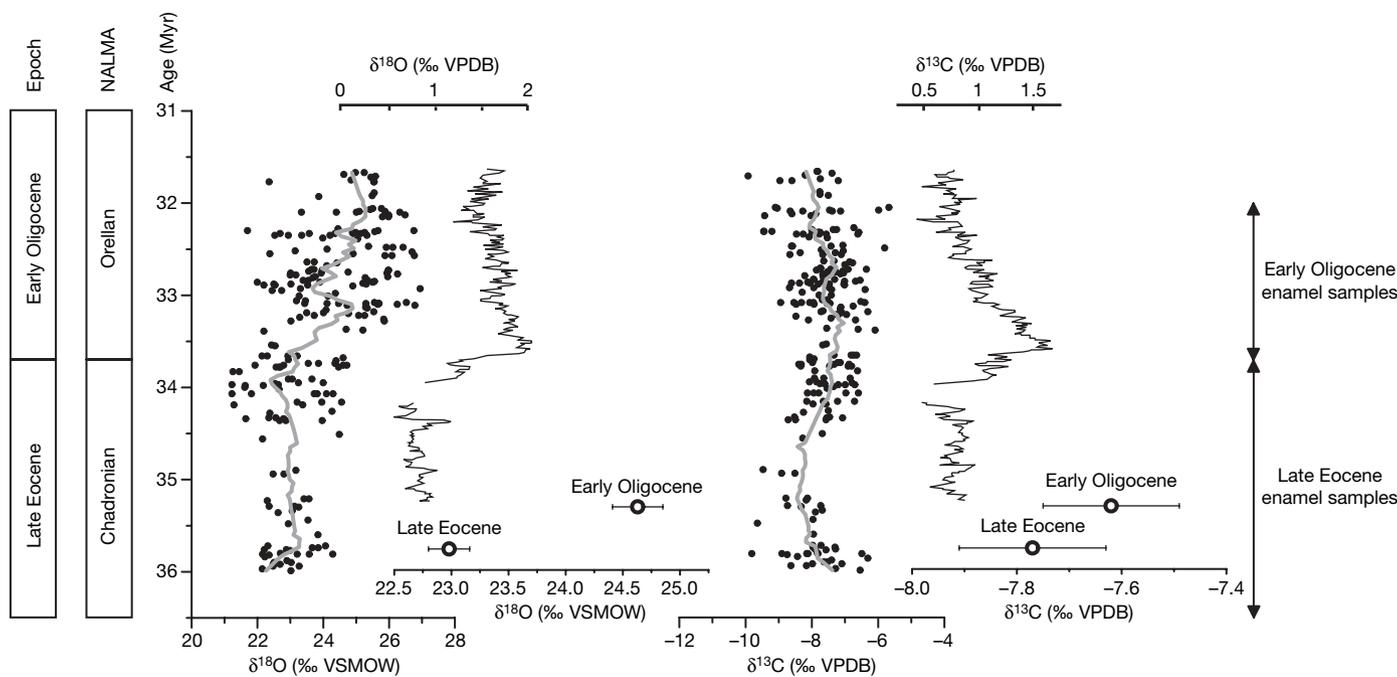


Figure 3 | High-resolution bone carbonate $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ plotted versus time for the time interval 36–32 Myr ago. The grey curves are obtained by exponential smoothing of the raw data. The open circles show the average Eocene and Oligocene $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (on the axes directly below) with the error bars corresponding to ± 2 s.e. The new high-resolution marine curve from ref. 16 is plotted (solid line) along with our continental data (filled circles). The time interval covered by the tooth enamel samples is also

shown. Bone $\delta^{13}\text{C}$ values show no consistent trend, suggesting no major change in water stress and canopy structure across the EOT. In contrast, bone $\delta^{18}\text{O}$ values show an abrupt, $\sim 1.7\text{‰}$, statistically significant increase across the transition. This increase translates into a $\sim 8^\circ\text{C}$ decrease in MAT. The continental isotopic shift may lag the marine transition by as much as 400 kyr. NALMA, North America Land-Mammal Ages.

turnovers or extinctions of gastropods, amphibians and reptiles associated with the EOT. Relative to the oceanic record, the continental transition is of higher magnitude and may lag the marine transition by as much as 400 kyr, possibly indicating a decoupling of the terrestrial and oceanic components of the climate system during major episodes of climate change.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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