

Stable isotopes of fossil teeth corroborate key general circulation model predictions for the Last Glacial Maximum in North America

Matthew J. Kohn¹ and Moriah McKay²

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[1] Oxygen isotope data provide a key test of general circulation models (GCMs) for the Last Glacial Maximum (LGM) in North America, which have otherwise proved difficult to validate. High $\delta^{18}\text{O}$ pedogenic carbonates in central Wyoming have been interpreted to indicate increased summer precipitation sourced from the Gulf of Mexico. Here we show that tooth enamel $\delta^{18}\text{O}$ of large mammals, which is strongly correlated with local water and precipitation $\delta^{18}\text{O}$, is lower during the LGM in Wyoming, not higher. Similar data from Texas, California, Florida and Arizona indicate higher $\delta^{18}\text{O}$ values than in the Holocene, which is also predicted by GCMs. Tooth enamel data closely validate some recent models of atmospheric circulation and precipitation $\delta^{18}\text{O}$, including an increase in the proportion of winter precipitation for central North America, and summer precipitation in the southern US, but suggest aridity can bias pedogenic carbonate $\delta^{18}\text{O}$ values significantly. **Citation:** Kohn, M. J., and M. McKay (2010), Stable isotopes of fossil teeth corroborate key general circulation model predictions for the Last Glacial Maximum in North America, *Geophys. Res. Lett.*, 37, L22702, doi:10.1029/2010GL045404.

1. Introduction

[2] The geologic record provides crucial observations for testing climate models, and quantitative data for Pleistocene glacial periods provide one of the main datasets in testing general circulation models (GCMs). Somewhat surprisingly, geological observations in North America provide little direct support for GCM predictions during the Last Glacial Maximum (LGM). For example atmospheric GCMs (AGCMs) and coupled ocean-atmosphere GCMs (OAGCMs) predict a glacial anticyclone centered over Canada that produced easterlies over the midcontinent [e.g., *COHMAP Members*, 1988; *Shin et al.*, 2003; *Braconnot et al.*, 2007], generally decreased $\delta^{18}\text{O}$ values of annual precipitation at mid- and high-latitudes [e.g., *Hoffmann et al.*, 2000], and a strong winter vs. weak summer anticyclone [e.g., *Bromwich et al.*, 2004]. In contrast, loess deposits in the Great Plains and geomorphology of glacial Lake Bonneville in Utah indicate westerly winds [*Muhs and Bettis*, 2000; *Jewell*, 2010], groundwater stable isotopes are inconclusive [*Jouzel et al.*, 1994], and stable isotopes of mid-latitude paleosol carbo-

nates have been interpreted to indicate higher not lower $\delta^{18}\text{O}$ values of precipitation [*Amundson et al.*, 1996; *Takeuchi et al.*, 2009]. In particular, the high $\delta^{18}\text{O}$ values in Wind River glacial terraces (WRT) in Wyoming have been ascribed to an increase in summer precipitation, sourced from the Gulf of Mexico, and advected by a strong summer anticyclone [*Amundson et al.*, 1996]. Whereas much GCM research has focused on isotopic temperature calibrations in ice cores [*Jouzel et al.*, 1997, 2003; *Hoffmann et al.*, 2000], improved modeling rigor (e.g., OAGCMs vs. AGCMs [*Braconnot et al.*, 2007]) and changes to climate seasonality [*Bromwich et al.*, 2004], first order discrepancies between models and data in North America have not been addressed.

[3] Although we cannot resolve all model-data inconsistencies, we can provide further insights into $\delta^{18}\text{O}$ values of local water and precipitation, as well as changes to proportions of summer vs. winter precipitation, through a completely different precipitation $\delta^{18}\text{O}$ proxy—the $\delta^{18}\text{O}$ of tooth enamel of LGM large mammals. Isotope data from Florida, Texas, Arizona, and southern California have already been published [*Koch et al.*, 1998, 2004; *Higgins and MacFadden*, 2004; *Feranec et al.*, 2009], but were not interpreted within the context of GCMs. Key new data include specimens from a stratified cave deposit at Natural Trap Cave (NTC), located ~200 km NNE of the WRT; this area is well within the region of NCAR-CCSM OAGCM-predicted decreased precipitation and $\delta^{18}\text{O}$ (Figure 1), but sensitive to moisture source changes implied by the WRT data, i.e. it provides a crucial test of GCMs. The NTC and WRT areas have almost identical modern precipitation and temperature patterns (Western Regional Climate Center (WRCC), 2010, accessed 2010, <http://www.wrcc.dri.edu/>) (Table 1), so we presume that any increase in the proportion of high $\delta^{18}\text{O}$ summer precipitation in the WRT area would be matched by an increase in $\delta^{18}\text{O}$ at NTC. In this study, however, we show that $\delta^{18}\text{O}$ values during the LGM at NTC were *lower* than in the Holocene, in contrast to the conclusions of *Amundson et al.* [1996]. Our tooth enamel data, as well as published results elsewhere in North America, verify the accuracy of GCM models of atmospheric circulation and precipitation $\delta^{18}\text{O}$ values, and support the use of stable isotopes in fossil teeth for understanding past local water compositions and atmospheric circulation patterns.

2. Oxygen Isotopes of Teeth

[4] Teeth consist mineralogically of dahllite, or hydroxyapatite with major substitution of CO_3 for PO_4 and OH groups. For oxygen isotopes, either the PO_4 or CO_3 component may be analyzed for $\delta^{18}\text{O}$; in this study we analyzed the CO_3 component. Reviews of stable isotopes in teeth

¹Department of Geosciences, Boise State University, Boise, Idaho, USA.

²Department of Geological Sciences, University of South Carolina, Columbia, South Carolina, USA.

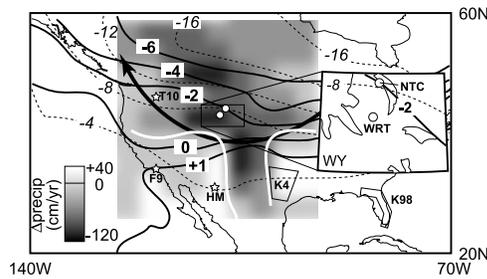


Figure 1. Sample localities, summer precipitation anomalies for the LGM vs. modern conditions [from *Shin et al.*, 2003] (white lines are zero contours), and contours of change to mean annual $\delta^{18}\text{O}$ of precipitation (solid lines; ECHAM model [Hoffmann et al., 2000]) and to JJA temperature (dashed lines [Shin et al., 2003]) for LGM vs. modern. Large arrow shows direction of LGM anticyclone predicted by GCM's [e.g., *COHMAP Members*, 1988]. Winter precipitation anomalies are negligible for the region considered, and winter and summer temperature anomalies are similar. Inset shows less distorted outline of Wyoming with relevant isotope and temperature contour. WRT = Wind River terraces studied by *Amundson et al.* [1996]; NTC = Natural Trap Cave. Both localities are within region of predicted drier summers, colder temperatures, and lower mean annual $\delta^{18}\text{O}$ of precipitation during LGM. Topographically high areas in Wyoming are outlined in inset. T10, F9, HM, K4, and K98 are areas studied by *Takeuchi et al.* [2009], *Feranec et al.* [2009], *Higgins and MacFadden* [2004], *Koch et al.* [2004], and *Koch et al.* [1998], respectively.

are provided by *Koch* [1998, 2007], *MacFadden* [2000], *Kohn and Cerling* [2002] and *Kohn and Dettman* [2007]. In general, oxygen isotopes in tooth enamel reflect local water compositions [Kohn, 1996], which in turn proxies for precipitation. Different species may exhibit second-order dependencies on relative humidity and different isotope offsets relative to other species, but in this study we focused on species whose modern representatives (same genus, subfamily, or family) are especially water dependent and exhibit mutually similar compositions in modern settings. Although different teeth mineralize at different times, there is as yet no evidence for ontogenetic differences in tooth $\delta^{18}\text{O}$ values in large herbivores [Kohn et al., 1998, 2002], implying that any tooth may be analyzed to infer local water $\delta^{18}\text{O}$.

3. Samples and Analysis

[5] Samples and methods are described in more detail in the auxiliary material.¹ In brief, ages were grouped into "LGM" (20–25 ka), "post-LGM" (13–20 ka), and Holocene (Holocene and historical specimens). We analyzed teeth from *Bootherium bombifrons* (woodland muskox), *Bison*

sp. (bison), *Equus* sp. (horse), and *Mammuthus* sp. (mammoth; Table 2) because (a) compositions of these groups are known to be particularly sensitive to local water compositions [Kohn and Cerling, 2002; Kohn and Dettman, 2007; Kohn and Fremd, 2007], (b) these teeth are common and many were made available for analysis, and (c) a large dataset already exists for modern representatives of the same genera, subfamilies and families. A single historical sample of *Bos taurus* from NTC was also analyzed. Sampling and analytical methods followed *Kohn et al.* [2005], which involves measuring isotope zoning along the length of a tooth, with chemical processing based on the work by *Koch et al.* [1997]. For converting tooth enamel compositions to water compositions (Table 2), we used the equations of *Kohn and Dettman* [2007] for the subfamily Bovinae (*Bootherium*, *Bison*, and *Bos*), *Kohn and Fremd* [2007] for *Equus*, and an average of these 2 equations for *Mammuthus*, noting that modern elephant compositions overlap those of Bovinae and Equidae [Kohn and Cerling, 2002]. Modern water compositions were inferred from regional trends in precipitation [Dutton et al., 2005], river water [Coplen and Kendall, 2000] or local water sources [Friedman, 2000].

4. Results and Discussion

[6] A plot of $\delta^{18}\text{O}$ vs. time for NTC (Figure 2a) shows a systematic increase in mean $\delta^{18}\text{O}$ from the LGM to the Holocene. Error bars in Figure 2 correspond to standard errors, and seasonal variation preserved as isotopic zoning contributes significantly to overall uncertainties. Standard errors are appropriate for comparing compositions from different times, although systematic errors in calibrations could cause compositions to be shifted systematically to higher or lower $\delta^{18}\text{O}$ values. Large shifts appear to be ruled out, however, by the good correspondence between inferred water compositions for modern measurements ($-15 \pm 2\text{‰}$) vs. inferences from *Bos* compositions (c. -14‰). All data imply lower $\delta^{18}\text{O}$ values for the LGM than for the Holocene: $-1.0 \pm 2.0\text{‰}$ for *Bison*, $-1.2 \pm 2.0\text{‰}$ for *Mammuthus*, $-2.3 \pm 1.1\text{‰}$ for *Bootherium*, and $-2.6 \pm 2.0\text{‰}$ for *Equus* (average of $-1.8 \pm 1.6\text{‰}$; all errors 2 s.e.). These data are most consistent with GCM model predictions that glacial age $\delta^{18}\text{O}$ values were lower by c. 2‰ than modern values [Hoffmann et al., 2000], and wholly different from interpretations of *Amundson et al.* [1996] that glacial-age $\delta^{18}\text{O}$ values were higher by c. 5‰. Geographic differences between NTC and WRT could not induce these differences, as modern and predicted LGM precipitation patterns are so similar (Table 1 and Figure 2). Our isotopic results have important implications for atmospheric circulation patterns

¹Auxiliary materials are available in the HTML. doi:10.1029/2010GL045404.

Table 1. Modern Climate Data for Sites Near NTC and WRT^a

Month	J	F	M	A	M	J	J	A	S	O	N	D	Ave.
NTC Precip	10.9	8.3	10.7	20.7	33.8	34.8	17.3	13.2	23.4	18.5	10.5	9.3	211.3
WRT Precip	4.7	5.2	10.3	26.9	44.2	34.1	19.5	14.1	21.4	17.2	8.9	5.5	212.1
NTC Temp	-7.8	-3.9	1.7	7.3	12.5	17.7	22.0	20.4	14.2	7.6	-0.1	-6.3	7.1
WRT Temp	-7.8	-4.3	1.1	6.6	12.5	17.2	21.5	20.0	14.5	8.0	-0.8	-6.4	6.8

^aPrecipitation is in mm/month, temperature is in °C. Stations used were Shell and Lovell (NTC), and Diversion, Morton 1, Pavillion, Riverton (downtown), and Shoshoni for WRT. The standard deviation for WRT mean annual averages is ~24 mm/yr (precipitation) and 0.5 °C (temperature).

Table 2. Means \pm 2 s.e. for Tooth Enamel $\delta^{18}\text{O}$ From Natural Trap Cave, Wyoming, and Calculated $\delta^{18}\text{O}$ of Local Water^a

Genus	Tooth LGM	Tooth Post-LGM	Tooth Holocene	Water LGM	Water Post-LGM	Water Holocene
<i>Bison</i>	17.8 \pm 1.6	17.7 \pm 1.1	18.7 \pm 0.9	-15.2 \pm 1.8	-15.2 \pm 1.2	-14.2 \pm 1.0
<i>Bootherium</i>	16.6 \pm 0.6	17.4 \pm 0.8	18.7 \pm 0.9	-16.4 \pm 0.6	-15.6 \pm 0.8	-14.2 \pm 1.0
<i>Equus</i>	16.9 \pm 0.3	18.2 \pm 0.5		-17.6 \pm 0.4	-16.0 \pm 0.6	-15.0 \pm 2.0
<i>Mammuthus</i>	17.4 \pm 0.4	18.6 \pm 0.4		-16.2 \pm 0.4	-14.9 \pm 0.5	-15.0 \pm 2.0

^aOxygen isotope compositions relative to V-SMOW. A complete tabulation of data is available in the supporting file.

during glacial periods, and the accuracy of recent GCM models overall.

[7] Modern precipitation patterns in central-western North America including Wyoming are dominated by moisture from the Pacific during the winter, with contributions from the Gulf of Mexico during the summer. Summer moisture from the Gulf of Mexico has higher $\delta^{18}\text{O}$ values, because of higher temperatures of precipitation and of the moisture source [e.g., *Vachon et al.*, 2010]. During glacial periods, the North American icecap should have induced anti-cyclonic circulation across central North America (large arrow in Figure 1 [*COHMAP Members*, 1988]). This circulation, in turn, should have drawn additional moisture from the Gulf of Mexico and Gulf of California/Pacific into the southern United States and northern Mexico. Presumably, this circulation induced higher $\delta^{18}\text{O}$ values and summer precipitation amounts over some region of the continent. Some GCM's do predict such increased precipitation and $\delta^{18}\text{O}$ values in the southern US and northern Mexico (Figure 1). Outside of Wyoming, fossils from central Texas are the best characterized isotopically and chronologically, and oxygen isotope data for the same mammal genera there in fact show higher LGM $\delta^{18}\text{O}$ values than post-LGM or modern compositions [*Koch et al.*, 2004; *Dutton et al.*, 2005] (Figure 2b), consistent with this prediction. Calculated Pleistocene water $\delta^{18}\text{O}$ values from Florida (-1.5‰ [*Koch et al.*, 1998]), Arizona (-5.5‰ [*Higgins and MacFadden*, 2004]) and southern California (-8‰ [*Feranec et al.*, 2009]) are also similar to or higher than modern estimates: -3.5, -8.0, and -7.5‰, respectively (data from *Coplen and Kendall* [2000] and *Friedman*

[2000]). The main question, however, is the degree to which such high $\delta^{18}\text{O}$ moisture penetrated northwards. Contra *Amundson et al.* [1996], our data demonstrate that enhanced transport of moisture from the Gulf of Mexico could not have advanced as far north as Wyoming. That is, our data strongly support the accuracy of some GCM models, including the occurrence of lower $\delta^{18}\text{O}$ values in Wyoming, and a decreased proportion of (high $\delta^{18}\text{O}$) summer precipitation [*Hoffmann et al.*, 2000; *Shin et al.*, 2003]. Recent OAGCMs now suggest an increase in proportion of summer precipitation [e.g., *Laine et al.*, 2009] and appear inconsistent with our data. A proper comparison, however, will require incorporating oxygen isotopes in several such models, especially because Wyoming is near the transition between zones of increased vs. decreased precipitation, and different models predict different locations for that transition [e.g., *Hoffmann et al.*, 2000; *Braconnot et al.*, 2007; *Laine et al.*, 2009]. In that regard, LGM precipitation and isotopic data from Wyoming provide particularly sensitive tests of GCM accuracy.

[8] Reinterpretation of the high $\delta^{18}\text{O}$ values of WRT pedogenic carbonates requires consideration of several factors. Such carbonate values depend principally on temperature of precipitation and on soil water $\delta^{18}\text{O}$ values. First, we note that pedogenic carbonate typically forms during the hottest and driest season. Maximum temperatures during the central Wyoming summer average ~ 20 °C today, so large decreases in temperature are theoretically permitted before reaching the freezing point of water. In fact, LGM temperatures in central Wyoming are predicted to have been at least ~ 8 °C cooler than today [*Shin et al.*, 2003], inducing

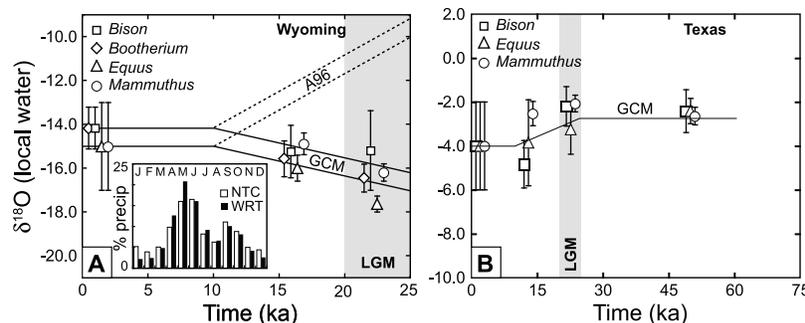


Figure 2. (a) Mean $\delta^{18}\text{O}$ of tooth enamel vs. time for faunas from NTC. Band labeled “GCM” assumes essentially linear change to precipitation $\delta^{18}\text{O}$ from LGM to 10 ka [*Bartlein et al.*, 1998; *Kutzbach et al.*, 1998], with limits defined by water compositions estimated from regional precipitation (-15‰) and from modern cow (-14‰). Model prediction labeled “A96” is expected composition based on pedogenic carbonate values from Wind River terraces [*Amundson et al.*, 1996], assuming these reflect precipitation $\delta^{18}\text{O}$ only. Gray shaded band is time of LGM. Observations show good correspondence with GCM, but not with A96, and imply decreased transport of summer moisture from the Gulf of Mexico. Inset shows proportion of precipitation that falls each month in the NTC vs. WRT areas (Table 2), and demonstrates comparable modern precipitation patterns. (b) Mean $\delta^{18}\text{O}$ of tooth enamel vs. time for faunas from central Texas [*Koch et al.*, 2004], showing good correspondence with GCM model.

a ~2‰ upward shift to pedogenic carbonate relative to modern values. This temperature effect would offset any LGM decrease in precipitation $\delta^{18}\text{O}$. Second, aridity in Wyoming can strongly influence local $\delta^{18}\text{O}$ values. For example, local water compositions in modern closed-basin lakes in Wyoming, including the Wind River Range, can be enriched relative to local precipitation and open lakes by as much as 10–15‰ [Henderson and Shuman, 2009]. Such an isotopic enrichment might be less during cooler glacial periods with less evaporation potential, but might well attain 5–10‰, as required to explain the pedogenic carbonate data. Tooth enamel $\delta^{18}\text{O}$ values are not expected to show such a strong aridity effect, however, because the mammals we analyzed obtain a substantial portion of their oxygen from drinking water, and there are no closed basin lakes in the NTC area. Similar arguments apply to paleosol carbonate data from eastern Washington [Takeuchi et al., 2009]. Pleistocene $\delta^{18}\text{O}$ values that are 2–3‰ higher than in the Holocene could readily reflect both decreased temperature (at least 8 °C [Shin et al., 2003]; Figure 1) and higher aridity (indicated by higher $\delta^{13}\text{C}$ values).

[9] In sum, we view the tooth enamel $\delta^{18}\text{O}$ data as more directly reflective of local surface water and precipitation compositions than pedogenic carbonates. These data strongly support some GCM models for the LGM that indicate a reduced proportion of summer precipitation and decreased $\delta^{18}\text{O}$ values in central North America, and increased $\delta^{18}\text{O}$ values and proportion of summer precipitation in the southern and southwestern United States (Figure 2a). Previously published high $\delta^{18}\text{O}$ values from glacial-age pedogenic carbonates [Amundson et al., 1996; Takeuchi et al., 2009] more likely result from both reduced temperature and evaporative enrichment of local soil waters. Important tests of LGM GCM's might include analysis of more sites from the Rocky Mountains, which should show especially depleted $\delta^{18}\text{O}$ values.

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References

- Amundson, R. G., O. A. Chadwick, C. Kendall, Y. Wang, and M. J. DeNiro (1996), Isotopic evidence for shifts in atmospheric circulation patterns during the late Quaternary in mid-North America, *Geology*, *24*, 23–26, doi:10.1130/0091-7613(1996)024<0023:IEFSIA>2.3.CO;2.
- Bartlein, P. J., K. H. Anderson, P. M. Anderson, M. E. Edwards, C. J. Mock, R. S. Thompson, R. S. Webb, T. Webb III, and C. Whitlock (1998), Paleoclimate simulations for North America over the past 21,000 years: Features of the simulated climate and comparisons with paleoenvironmental data, *Quat. Sci. Rev.*, *17*, 549–585, doi:10.1016/S0277-3791(98)00012-2.
- Braconnot, P., et al. (2007), Results of PMIP2 coupled simulations of the mid-Holocene and Last Glacial Maximum—Part 1: Experiments and large-scale features, *Clim. Past*, *3*, 261–277, doi:10.5194/cp-3-261-2007.
- Bromwich, D. H., E. R. Toracinta, H. Wei, R. J. Oglesby, J. L. Fastook, and T. J. Hughes (2004), Polar MM5 simulations of the winter climate of the Laurentide Ice Sheet at the LGM, *J. Clim.*, *17*, 3415–3433, doi:10.1175/1520-0442(2004)017<3415:PMSOTW>2.0.CO;2.
- COHMAP Members (1988), Climatic changes of the last 18,000 years: Observations and model simulations, *Science*, *241*, 1043–1052, doi:10.1126/science.241.4869.1043.
- Coplen, T. B., and C. Kendall (2000), Stable hydrogen and oxygen isotope ratios for selected sites of the U.S. Geological Survey's NASQAN and benchmark surface-water networks, *U.S. Geol. Surv. Open File Rep.*, 00-160.
- Dutton, A., B. H. Wilkinson, J. M. Welker, G. J. Bowen, and K. C. Lohmann (2005), Spatial distribution and seasonal variation in $^{18}\text{O}/^{16}\text{O}$ of modern precipitation and river water across the conterminous USA, *Hydrol. Processes*, *19*, 4121–4146, doi:10.1002/hyp.5876.
- Feranec, R. S., E. A. Hadly, and A. Paytan (2009), Stable isotopes reveal seasonal competition for resources between late Pleistocene bison (Bison) and horse (Equus) from Racho La Brea, southern California, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *271*, 153–160, doi:10.1016/j.palaeo.2008.10.005.
- Friedman, I. (2000), Database of surface and ground water samples analyzed for deuterium and oxygen-18 from the western states of Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, Oregon, Utah, Washington, and Wyoming., *U.S. Geol. Surv. Open File Rep.*, 00-388.
- Henderson, A. K., and B. N. Shuman (2009), Hydrogen and oxygen isotopic compositions of lake water in the western United States, *Geol. Soc. Am. Bull.*, *121*, 1179–1189, doi:10.1130/B26441.1.
- Higgins, P., and B. J. MacFadden (2004), "Amount effect" recorded in oxygen isotopes of Late Glacial horse (Equus) and bison (Bison) teeth from the Sonoran and Chihuahuan deserts, southwestern United States, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *206*, 337–353, doi:10.1016/j.palaeo.2004.01.011.
- Hoffmann, G., J. Jouzel, and V. Masson (2000), Stable water isotopes in atmospheric general circulation models, *Hydrol. Processes*, *14*, 1385–1406, doi:10.1002/1099-1085(20000615)14:8<1385::AID-HYP989>3.0.CO;2-1.
- Jewell, P. W. (2010), River incision, circulation, and wind regime of Pleistocene Lake Bonneville, USA, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *293*, 41–50, doi:10.1016/j.palaeo.2010.04.028.
- Jouzel, J., R. D. Koster, R. J. Suozzo, and G. L. Russell (1994), Stable water isotope behavior during the Last Glacial Maximum: A general circulation model analysis, *J. Geophys. Res.*, *99*(D12), 25,791–25,801, doi:10.1029/94JD01819.
- Jouzel, J., et al. (1997), Validity of the temperature reconstruction from water isotopes in ice cores, *J. Geophys. Res.*, *102*(C12), 26,471–26,487, doi:10.1029/97JC01283.
- Jouzel, J., F. Vimeux, N. Caillon, G. Delaygue, G. Hoffmann, V. Masson-Delmotte, and F. Parrenin (2003), Magnitude of isotope/temperature scaling for interpretation of central Antarctic ice cores, *J. Geophys. Res.*, *108*(D12), 4361, doi:10.1029/2002JD002677.
- Koch, P. L. (1998), Isotopic reconstruction of past continental environments, *Annu. Rev. Earth Planet. Sci.*, *26*, 573–613, doi:10.1146/annurev.earth.26.1.573.
- Koch, P. L. (2007), Isotopic study of the biology of modern and fossil vertebrates, in *Stable Isotopes in Ecology and Environmental Science*, edited by R. Michener and K. Lajtha, pp. 99–154, doi:10.1002/9780470691854.ch5, Blackwell, Boston, Mass.
- Koch, P. L., N. Tuross, and M. L. Fogel (1997), The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite, *J. Archaeol. Sci.*, *24*, 417–429, doi:10.1006/jasc.1996.0126.
- Koch, P. L., K. A. Hoppe, and S. D. Webb (1998), The isotopic ecology of late Pleistocene mammals in North America: Part 1. Florida, *Chem. Geol.*, *152*, 119–138, doi:10.1016/S0009-2541(98)00101-6.
- Koch, P. L., N. S. Diffenbaugh, and K. A. Hoppe (2004), The effects of late Quaternary climate and pCO₂ change on C₄ plant abundance in the south-central United States, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *207*, 331–357, doi:10.1016/S0031-0182(04)00046-X.
- Kohn, M. J. (1996), Predicting animal ^{18}O : Accounting for diet and physiological adaptation, *Geochim. Cosmochim. Acta*, *60*, 4811–4829, doi:10.1016/S0016-7037(96)00240-2.
- Kohn, M. (2004), Comment: Tooth enamel mineralization in ungulates: Implications for recovering a primary isotopic time-series by B. H. Passey and T. E. Cerling (2002), *Geochim. Cosmochim. Acta*, *68*, 403–405, doi:10.1016/S0016-7037(03)00443-5.
- Kohn, M. J., and T. E. Cerling (2002), Stable isotope compositions of biological apatite, *Rev. Mineral. Geochem.*, *48*, 455–488, doi:10.2138/rmg.2002.48.12.
- Kohn, M. J., and D. L. Dettman (2007), Paleoaltimetry from stable isotope compositions of fossils, *Rev. Mineral. Geochem.*, *66*, 119–154, doi:10.2138/rmg.2007.66.5.
- Kohn, M. J., and T. J. Fremd (2007), Tectonic controls on isotope compositions and species diversification, John Day Basin, central Oregon, *PaleoBios*, *27*, 48–61.
- Kohn, M. J., M. J. Schoeninger, and J. W. Valley (1998), Variability in herbivore tooth oxygen isotope compositions: Reflections of seasonality or developmental physiology?, *Chem. Geol.*, *152*, 97–112, doi:10.1016/S0009-2541(98)00099-0.

- Kohn, M. J., J. L. Miselis, and T. J. Fremd (2002), Oxygen isotope evidence for progressive uplift of the Cascade Range, Oregon, *Earth Planet. Sci. Lett.*, *204*, 151–165, doi:10.1016/S0012-821X(02)00961-5.
- Kohn, M., M. McKay, and J. Knight (2005), Dining in the Pleistocene—Who's on the menu?, *Geology*, *33*, 649–652, doi:10.1130/G21476.1.
- Kutzbach, J., R. Gallimore, S. Harrison, P. Behling, R. Selin, and F. Laarif (1998), Climate and biome simulations for the past 21,000 years, *Quat. Sci. Rev.*, *17*, 473–506, doi:10.1016/S0277-3791(98)00009-2.
- Laine, A., M. Kageyama, D. Salas-Melia, A. Voltaire, G. Riviere, G. Ramstein, S. Planton, S. Tyteca, and J.-Y. Peterchmitt (2009), Northern hemisphere storm tracks during the Last Glacial Maximum in the PMIP2 ocean-atmosphere coupled models: Energetic study, seasonal cycle, precipitation, *Clim. Dyn.*, *32*, 593–614, doi:10.1007/s00382-008-0391-9.
- MacFadden, B. J. (2000), Cenozoic mammalian herbivores from the Americas: Reconstructing ancient diets and terrestrial communities, *Annu. Rev. Ecol. Syst.*, *31*, 33–59, doi:10.1146/annurev.ecolsys.31.1.33.
- Muhs, D. R., and E. A. Bettis III (2000), Geochemical variations in Peoria Loess of western Iowa indicate paleowinds of midcontinental North America during last glaciation, *Quat. Res.*, *53*, 49–61, doi:10.1006/qres.1999.2090.
- Shin, S.-I., Z. Liu, B. Otto-Bliesner, E. C. Brady, J. E. Kutzbach, and S. P. Harrison (2003), A simulation of the Last Glacial Maximum climate using NCAR-CCSM, *Clim. Dyn.*, *20*, 127–151.
- Takeuchi, A., A. J. Goodwin, B. G. Moravec, P. B. Larson, and C. K. Keller (2009), Isotopic evidence for temporal variation in proportion of seasonal precipitation since the last glacial time in the inland Pacific Northwest of the USA, *Quat. Res.*, *72*, 198–206, doi:10.1016/j.yqres.2009.06.001.
- Vachon, R. W., J. M. Welker, J. W. C. White, and B. H. Vaughn (2010), Moisture source temperatures and precipitation $\delta^{18}\text{O}$ -temperature relationships across the United States, *Water Resour. Res.*, *46*, W07523, doi:10.1029/2009WR008558.

M. J. Kohn, Department of Geosciences, Boise State University, 1910 University Dr., Boise, ID 83725, USA. (mattkohn@boisestate.edu)

M. McKay, Department of Geological Sciences, University of South Carolina, 701 Sumter St., Columbia, SC 29208, USA.