

Fish tooth $\delta^{18}\text{O}$ revising Late Cretaceous meridional upper ocean water temperature gradients

Emmanuelle Pucéat UMR CNRS, 5561 Biogéosciences, 6 Boulevard Gabriel, 21000 Dijon, France
Christophe Lécuyer UMR CNRS, 5125 PaléoEnvironnement et PaléobioSphère, Université Claude Bernard Lyon 1, Bât. Géode, 27-43 Boulevard du 11 Novembre 1918, 69622 Villeurbanne Cedex, France
Yannick Donnadié } UMR CEA/CNRS, 1572 Laboratoire des Sciences du Climat et de l'Environnement,
Philippe Naveau } CE Saclay, Orme des Merisiers, Bât. 701, 91191 Gif sur Yvette Cedex, France
Henri Cappetta UMR CNRS, 5554 Institut des Sciences de l'Evolution de Montpellier, Université de Montpellier II, Cc 064, Place Eugène Bataillon, 34095 Montpellier Cedex 5, France
Gilles Ramstein UMR CEA/CNRS, 1572 Laboratoire des Sciences du Climat et de l'Environnement, CE Saclay, Orme des Merisiers, Bat. 701, 91191 Gif sur Yvette Cedex, France
Brian T. Huber Department of Paleobiology, National Museum of Natural History, P.O. Box 37012 NHB MRC 121, Washington, D.C. 20013-7012, USA
Juergen Kriwet Museum of Natural History, Invalidenstrasse 43, 10115 Berlin, Germany

ABSTRACT

The oxygen isotope composition of fossil fish teeth, a paleo-upper ocean temperature proxy exceptionally resistant to diagenetic alteration, provides new insight on the evolution of the low- to middle-latitude thermal gradient between the middle Cretaceous climatic optimum and the cooler latest Cretaceous period. The new middle Cretaceous low to middle latitude thermal gradient agrees with that previously inferred from planktonic foraminifera $\delta^{18}\text{O}$ recovered from Deep Sea Drilling Project and Ocean Drilling Program drilling sites, although the isotopic temperatures derived from $\delta^{18}\text{O}$ of fish teeth are uniformly higher by $\sim 3\text{--}4^\circ\text{C}$. In contrast, our new latest Cretaceous thermal gradient is markedly steeper than those previously published for this period. Fish tooth $\delta^{18}\text{O}$ data demonstrate that low- to middle-latitude thermal gradients of the middle Cretaceous climatic optimum and of the cooler latest Cretaceous are similar to the modern one, despite a cooling of 7°C between the two periods. Our new results imply that no drastic changes in meridional heat transport are required to explain the Late Cretaceous climate. Based on climate models, such a cooling without any change in the low to middle latitude thermal gradient supports an atmospheric CO_2 decrease as the primary driver of the climatic evolution recorded during the Late Cretaceous.

Keywords: Cretaceous, climate, oxygen isotopes, apatite.

INTRODUCTION

The warm Cretaceous Period underwent a long-term climatic cooling from the middle (late Albian–Turonian) to latest Cretaceous (Campanian–Maastrichtian) (Huber et al., 1995; Pucéat et al., 2003). Climate models using different levels of atmospheric carbon dioxide predict that a global cooling should be associated either with an increase of the equator to pole thermal gradients or with conservation of this gradient, depending on the growth or absence of ice sheets at high latitudes (Huber and Sloan, 2001; Otto-Bliesner et al., 2002; Pierrehumbert, 2002). The Late Cretaceous interval therefore presents a peculiar situation, because the latitudinal sea surface temperature (SST) gradient is thought to have been steeper during the climatic optimum of the middle Cretaceous than during the cooler latest Cretaceous (D'Hondt and Arthur, 1996; Bice and Norris, 2002; Pucéat et al., 2003). If recent data indicate warmer low latitude SSTs for the middle Cretaceous (Bice and Norris, 2002; Norris et al., 2002), the latest Cretaceous still exhibits, with few exceptions, markedly cooler than

modern tropics, despite high latitude temperatures warmer than present (Spicer and Parrish, 1990; D'Hondt and Arthur, 1996). This evolution of the latitudinal thermal gradient has been taken to indicate a reorganization in ocean-atmosphere dynamics involving increased meridional heat transport rather than a direct response to a $p\text{CO}_2$ decrease (D'Hondt and Arthur, 1996; Huber and Sloan, 2001; Otto-Bliesner et al., 2002; Pierrehumbert, 2002).

Most quantitative determinations of seawater paleotemperatures were derived from $^{18}\text{O}/^{16}\text{O}$ ratios of planktonic foraminiferal tests recovered from marine Cretaceous sediments sampled during Ocean Drilling Program (ODP) cruises (Huber et al., 1995; D'Hondt and Arthur, 1996; Crowley and Zachos, 2000; Bice and Norris, 2002; Norris et al., 2002). The reliability of the recent middle Cretaceous data, recovered from pristine foraminifera in clay-hosted sediments, has not yet been questioned. By contrast, most available latest Cretaceous planktonic foraminiferal isotope data have been obtained from ooze and chalk-hosted foraminifera. Doubt has been cast on the reliability of these last SST estimates, because they may have been significantly modified by diagenetic alteration occurring in contact with cooler bottom water (Pearson et al., 2001; Bice and Norris, 2002; Norris et al. 2002). Pearson et al. (2001), using planktonic foraminifera shells from hemipelagic clays in southern coastal Tanzania, showed that latest Cretaceous tropical temperatures may have been at least as warm as today. However, whether a flat thermal gradient applies to the latest Cretaceous is debated (Zachos et al., 2002), primarily because of the rarity of clay-hosted pristine foraminifera from other locations. Therefore, there is clearly a need for new reliable $\delta^{18}\text{O}$ -derived sea surface paleotemperature estimates, particularly for the low and middle latitude regions.

The $\delta^{18}\text{O}$ signal preserved in apatite is considered less prone to diagenetic alteration than that in skeletal calcite. The oxygen in biogenic apatite is very tightly bound to phosphorus and is relatively insensitive to dissolution-reprecipitation processes (Kolodny et al., 1983; Lécuyer et al., 1999). In addition, a unique fractionation equation is applicable to all fish species and therefore can be used for extinct species (Kolodny et al., 1983; Vennemann et al., 2001), and fish remains can be collected over a large range of latitudes. Therefore, fish tooth $\delta^{18}\text{O}$ is especially valuable as an independent proxy to discuss the issue of the Late Cretaceous meridional thermal gradients. Here we combined 42 new fish tooth $\delta^{18}\text{O}$ analyses with existing fish tooth data from the literature to infer the Late Cretaceous low to middle latitude ($10^\circ\text{--}50^\circ$) thermal gradient evolution.

MATERIAL AND METHODS

The analyzed teeth belong to the order of Lamniforms (families Mitsukurinidae, Odontaspidae, Cretoxyrhinidae, and Anacoracidae) (see

*E-mail: Emmanuelle.Puceat@u-bourgogne.fr.

GSA Data Repository Table DR1¹). All the studied specimens come from faunal associations that were deposited in open-platform environments with a water column <200 m deep (Noubhani and Cappetta, 1997; Antunes and Cappetta, 2002). This ensures that the analyzed samples recorded the temperature and $\delta^{18}\text{O}$ of upper (0–200 m) ocean waters. However, the relevance of using temperatures from shelf environments to reconstruct a global latitudinal thermal gradient may be questioned. Comparison of available modern mean annual SSTs from coastal environments to those from the open ocean shows that the surface temperatures from both environments are similar (Fig. DR1; see footnote 1). This allows comparison of the temperature estimates obtained in this study to previously published SST estimates from open-ocean environments.

Substantial age differences can exist among the collection of samples used to reconstitute the middle (Cenomanian–Turonian) or latest Cretaceous (Campanian–Maastrichtian) gradient. However, focusing this study to more narrowly defined Cretaceous time intervals would result in a database too restricted to define ocean temperature gradients. Our compilation and analyzed samples recovered from various locations within the 10°–50° range of paleolatitude (Table DR1) ensure that data are widely distributed among ocean basins (Fig. 1).

Despite the very good resistance of biogenic apatite to diagenesis, a postmortem modification of the isotopic signal may occur, though still rarely, in the most porous and less mineralized parts of the teeth. For this reason, enamel was separated from the dentine except in the case of the smallest teeth, for which only bulk analyses are available (Table DR1). Phosphate from biogenic apatites was isolated as Ag_3PO_4 crystals following the procedure of Lécuyer et al. (1993). The CO_2 was extracted from silver phosphate using the graphite method (O’Neil et al., 1994), and analyzed with a GV Isoprime™ mass spectrometer at the PEPS laboratory in Lyon. Oxygen isotope compositions are reported in the delta notation relative to standard mean ocean water (SMOW). Repeated analyses of phosphorite NBS120c give an average $\delta^{18}\text{O}$ value of 21.7‰ and external reproducibility is better than $\pm 0.2\text{‰}$.

Calculation of paleotemperatures from phosphate $\delta^{18}\text{O}$ requires an assumption made on the oxygen isotope composition of the Cretaceous seawater. To account for changes in ice mass balance, a $\delta^{18}\text{O}_{\text{seawater}}$ of -1‰ SMOW is generally assumed for the Cretaceous Period (Shackleton and Kennett, 1975). We subtracted an additional 0.25‰ to this ice-free ocean value, to account for long-term ocean $\delta^{18}\text{O}$ changes resulting from interactions of seawater with the oceanic crust at low and high temperatures or from continental weathering (Wallmann, 2001). In addition, by analogy with the modern ocean (Zachos et al., 1994), an isotopic correction was performed that takes into account average latitudinal variations in the evaporation–precipitation balance, a process controlling the $\delta^{18}\text{O}$ of sea surface waters. Although the assumption of a $\delta^{18}\text{O}_{\text{seawater}}$ gradient similar to that of present day can be criticized, it allows taking into account first-order latitudinal variations in the salinity of the open ocean.

RESULTS AND DISCUSSION

The fish tooth $\delta^{18}\text{O}$ data present a large scatter (as high as 3.4‰; Table DR1 [see footnote 1]) for both periods. Because fish are swimming organisms and a fish tooth grows over several weeks to several months depending on species, part of this scatter arises from vertical (within the 0–200 m depth range) and horizontal migration of fish and from seasonal thermal variations. As a result, $\delta^{18}\text{O}$ values can typically differ from 0.6‰ to

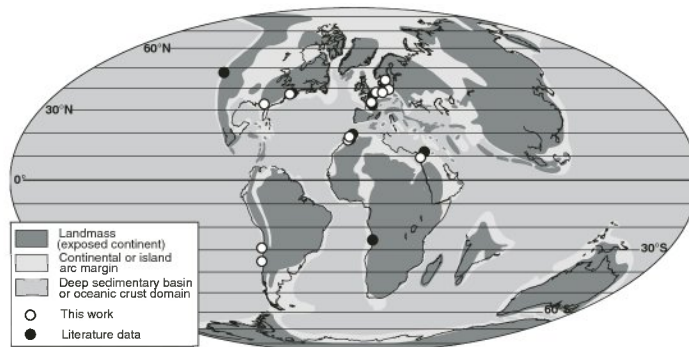


Figure 1. Locations of samples analyzed in this study and of data gathered from literature (Maastrichtian palaeogeographic map from Vrielynck and Bouysse, 2003).

1.1‰ between different teeth from a single modern shark (Vennemann et al., 2001). Rapid temperature variations within the time interval considered for the reconstruction of the gradient may also contribute to the observed scatter (Norris et al., 2002; Huber et al., 2002). The inferred temperature variability (up to $\sim 15\text{ °C}$; Fig. 2) is, however, congruent with the dispersion observed in the modern distribution of SSTs (Fig. 3). Because of this scatter, we assess the quality of the statistical fit by estimating the p-values for different linear models. The statistical model used in this work is detailed in Table DR2 along with its outputs. With respect to the p-value criterion,

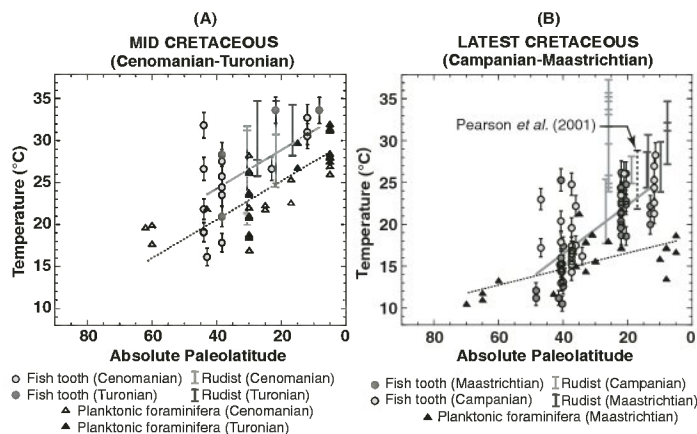


Figure 2. Comparison of low to middle latitude thermal gradient inferred from fish tooth $\delta^{18}\text{O}$ with that based on planktonic foraminifera $\delta^{18}\text{O}$ recovered from deep-sea sediment cores for middle Cretaceous (A) and latest Cretaceous (B). Fish tooth $\delta^{18}\text{O}$ data are from this work and from literature and are detailed in Table DR1 (see footnote 1). Middle Cretaceous foraminifera $\delta^{18}\text{O}$ data are from Bice and Norris (2002) and Huber et al. (2002) for Cenomanian and Turonian. Latest Cretaceous foraminifera $\delta^{18}\text{O}$ data are from compilation of Pucéat et al. (2003) for Maastrichtian. Fractionation equations from Kolodny et al. (1983) and Erez and Luz (1983) were used to calculate seawater temperatures from fish tooth $\delta^{18}\text{O}$ and planktonic foraminifera $\delta^{18}\text{O}$, respectively. To facilitate comparison of two proxies, $\delta^{18}\text{O}_{\text{seawater}}$ of -1‰ standard mean ocean water, constant with latitude, was used for calculation of paleotemperatures. Bold gray lines and dotted black lines represent best fit of fish tooth data and planktonic foraminifera data, respectively, simulated by statistical model used in this work (Table DR2; see footnote 1). Vertical lines represent range of isotopic temperatures inferred from exceptionally preserved rudists (gray; Wilson and Opdyke, 1996; Steuber et al., 2005) and Maastrichtian planktonic foraminifera (dotted black; Pearson et al., 2001). Error bars on fish tooth data include uncertainties arising from reproducibility of $\delta^{18}\text{O}$ measurements and from choice of fractionation equation (Table DR1; see footnote 1).

¹GSA Data Repository item 2007031, Figure DR1 (comparison of modern SSTs from the open ocean to that from coastal environments, and of surface air temperature from low altitude environments), Table DR1 (oxygen isotope compositions of fish teeth measured in this study and compiled from the literature), and Table DR2 (outputs of the statistical model), is available online at www.geosociety.org/pubs/ft2007.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

three points can be firmly supported (Table DR2): (1) the slope of the low to middle latitude thermal gradient inferred from fish tooth $\delta^{18}\text{O}$ is similar to that inferred from planktonic foraminifera $\delta^{18}\text{O}$ for the middle Cretaceous (p-value of $9.34\text{e-}11$); (2) these gradients have two different slopes for the latest Cretaceous (p-value $<2.2\text{e-}16$); and (3) the middle Cretaceous and latest Cretaceous low to middle latitude thermal gradients derived from fish tooth $\delta^{18}\text{O}$ have a similar slope with the latest Cretaceous temperatures $\sim 7^\circ\text{C}$ cooler than that of the middle Cretaceous (p-value $<2.2\text{e-}16$).

Although the slopes of the reconstructed middle Cretaceous gradients from both organisms resemble each other, the fish teeth tend to indicate higher temperature estimates than those of foraminifera ($3\text{--}4^\circ\text{C}$ warmer in average). Differences in neritic versus pelagic depositional environments and slight underestimation of SSTs by planktonic foraminifera (yielding isotopically derived temperatures that are $0\text{--}5^\circ\text{C}$ cooler than those of surface waters; Savin and Douglas, 1973) may account for this disparity between the temperatures inferred from fish teeth and foraminifera. By contrast, for the latest Cretaceous, if temperatures derived from foraminifera remain coherent with those derived from fish teeth for the middle latitudes, the low latitude temperatures inferred from the fish teeth are as much as $7\text{--}8^\circ\text{C}$ higher on average than those inferred from carbonates from ODP and Deep Sea Drilling Project sites. We argue that this is best explained by a partial recrystallization of the low latitude ($5\text{--}10^\circ$) foraminiferal tests from the latest Cretaceous at lower temperatures in deep waters, as suggested by Pearson et al. (2001). This is supported by the consistency of our estimates with those inferred from exceptionally well preserved planktonic foraminifera and rudists from low latitude locations (Wilson and Opdyke, 1996; Pearson et al., 2001; Steuber et al., 2005) (Fig. 2). The difference in reliability between the $\delta^{18}\text{O}$ values of middle Cretaceous and latest Cretaceous foraminifera may be explained by two factors. (1) It could result from a different preservation state (amount of recrystallization and diagenetic isotopic exchange) of the low latitude foraminifera calcite between the middle and latest Cretaceous. This hypothesis is supported by evidence for some shell recrystallization in all Campanian–Maastrichtian foraminiferal samples from low latitude deep-sea sites (Huber et al., 2002). By contrast, middle Cretaceous low latitude temperature estimates rely on more recently published data (e.g., Wilson et al., 2002; Norris et al., 2002), established after the work of Pearson et al. (2001), in which more attention has been paid to fine-scale recrystallization of planktonic foraminifera. (2) The $\delta^{18}\text{O}$ or temperature of pore waters at the seafloor may have changed between the middle and latest Cretaceous. A cooling of deep-water temperatures from 12 to 20°C in the middle Cretaceous to $9\text{--}12^\circ\text{C}$ in the latest Cretaceous has been inferred from benthic foraminifera (Huber et al., 2002). This deep-water cooling, however, does not necessarily involve an increase of the vertical temperature gradient, as this study suggests that low latitude upper ocean waters also cooled by a comparable amount (7°C ; Fig. 3).

Nevertheless, the similarity between reconstructed gradients based on fish teeth and planktonic foraminifera for the middle Cretaceous confirms that the $\delta^{18}\text{O}$ of planktonic foraminifera is trustworthy for paleoclimatic studies when carefully checked for microrecrystallization; however, the use of different and independent paleotemperature proxies, such as fish tooth, foraminiferal, and rudist $\delta^{18}\text{O}$, represents the best way to establish reliable ancient ocean water temperatures.

When an adjustment for latitudinal variation in the surface water $\delta^{18}\text{O}$ is considered, the middle and latest Cretaceous low to middle latitude thermal gradients are increased (Fig. 3). Maximum recorded middle Cretaceous temperatures are as high as 36°C , challenging the frequently assumed existence of a tropical “thermostat” (Ramanathan and Collins, 1991; Crowley and Zachos, 2000). By contrast, most of the latest Cretaceous temperatures are included in the envelope defined by the modern SSTs, which suggest that the latest Cretaceous latitudinal temperature distribution was not markedly different from that of the modern between

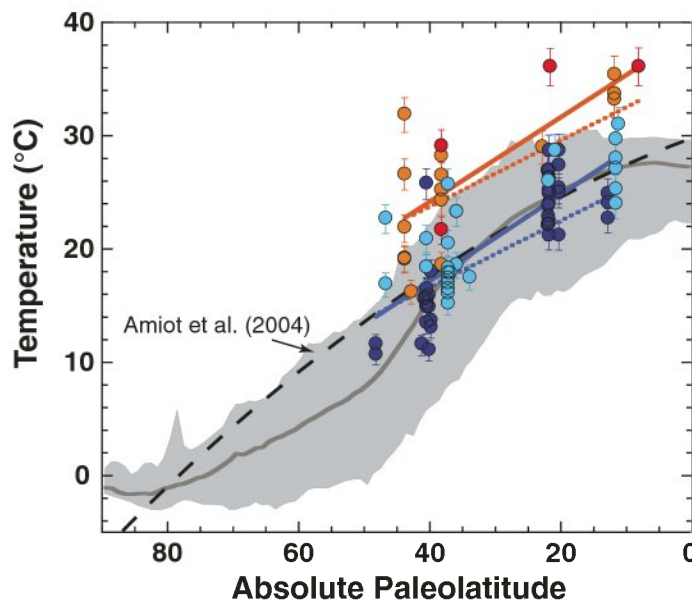


Figure 3. Evolution of meridional upper ocean temperature gradients between middle and latest Cretaceous. Paleotemperatures were calculated from fish tooth $\delta^{18}\text{O}$ using equation from Kolodny et al. (1983). Dotted lines represent middle Cretaceous (orange) and latest Cretaceous (blue) gradients estimated using $\delta^{18}\text{O}_{\text{seawater}}$ of -1‰ standard mean ocean water (SMOW) (for ice-free Earth; Shackleton and Kennett, 1975) constant with latitude. Dotted lines represent best fit of fish tooth data for middle Cretaceous and latest Cretaceous, respectively, simulated by statistical model used in this work (Table DR2; see footnote 1). Plotted data and gradients represented by solid lines (orange—middle Cretaceous; blue—latest Cretaceous) have been inferred using $\delta^{18}\text{O}_{\text{seawater}}$ of -1.25‰ SMOW and latitude-dependent adjustment. Modern sea surface temperature (SST) gradient (mean annual temperatures averaged over longitude and hemispheres) is represented by solid bold gray line. Gray envelope represents maximum range of modern seasonal SST when whole range of longitude is considered. Modern SSTs are from database LEVITUS94 (1994). Black dashed line—air temperatures inferred from $\delta^{18}\text{O}$ of late Campanian–middle Maastrichtian vertebrate phosphate recovered from coastal lowland environment (Amiot et al., 2004). Error bars as in Figure 2.

10° and 50° of latitude. When corrected for latitudinal variations of surface seawater $\delta^{18}\text{O}$, our latest Cretaceous low to middle latitude gradient is very similar to that of Amiot et al. (2004), inferred from $\delta^{18}\text{O}$ of phosphate measured in late Campanian–middle Maastrichtian terrestrial vertebrates recovered from coastal lowland environments (Fig. 3). Although the temperatures reconstructed by Amiot et al. (2004) are mean air temperatures, the similarity of modern shelf SSTs to air temperatures in coastal lowland environments allows comparison of the two proxies (Fig. DR1; see footnote 1). The similarity of the two gradients adds to the robustness of the Late Cretaceous climatic features we depict.

PALEOCLIMATIC IMPLICATIONS

The new documented middle Cretaceous and latest Cretaceous low to middle latitude upper ocean temperature gradients have implications for understanding the evolution of the Cretaceous greenhouse climate. First, previously published flat thermal gradients in greenhouse climates had been claimed to be a reflection of: (1) high latitude cloud feedback, which would help to warm the high latitudes without overheating the equator (Sloan and Pollard, 1998); (2) increased oceanic heat transport; and (3) increased atmospheric heat transport. These arguments were discussed in detail (Huber and Sloan, 2001; Pierrehumbert, 2002) and, except for 1, which remains highly

model dependent, no satisfactory physical mechanism has been provided to support 2 or 3. This calls into question both the validity of climate models to reproduce past warm climates and our understanding of these periods. Our new thermal gradients, which appear quite similar to that of the modern, allow reconciliation of the geologic proxy record with our current knowledge of the global climate system. Notably, our $\delta^{18}\text{O}$ records imply that the Cretaceous climate can be explained without resorting to extreme changes in meridional heat transport compared with the modern day, at least for low to middle latitudes. Second, comparison of the middle and latest Cretaceous thermal gradients indicates a latitudinal homogeneous $\sim 7^\circ\text{C}$ cooling of the marine surface waters. This feature is consistent with global circulation model experiments predicting a uniform cooling at low and middle latitudes with decreasing atmospheric CO_2 levels, while a larger cooling can occur at high latitudes due to the ice albedo feedback (e.g., Fig. 4 in Otto-Bliesner et al., 2002). Our results therefore support a decrease of atmospheric CO_2 level as the principal driver of the Late Cretaceous long-term cooling, and imply that no drastic change in the global heat transport is required between the middle and latest Cretaceous.

ACKNOWLEDGMENTS

We are deeply indebted to F. Atrops, G.R. Case, E. Collier, S.L. Cumbaa, D.C. Parris, I. Ploch, A. Radwański, M. Siverson, and M.E. Suárez, who provided part of the sample set. We also thank K.L. Bice, Y. Kolodny, and T. Steuber for constructive reviews. This study was funded by the French Centre National de la Recherche Scientifique program ECLIPSE.

REFERENCES CITED

- Amiot, R., Lécuyer, C., Buffetaut, E., Fluteau, F., Legendre, S., and Martineau, F., 2004, Latitudinal temperature gradient during the Cretaceous upper Campanian-middle Maastrichtian: $\delta^{18}\text{O}$ record of continental vertebrates: *Earth and Planetary Science Letters*, v. 226, p. 255–272, doi: 10.1016/j.epsl.2004.07.015.
- Antunes, M.T., and Cappetta, H., 2002, Sélaciens du Crétacé (Albien-Maastrichtien) d'Angola: *Palaeontographica, abteilung A*, v. 264, p. 85–146.
- Bice, K.L., and Norris, R.D., 2002, Possible atmospheric CO_2 extremes of the middle Cretaceous (late Albian-Turonian): *Paleoceanography*, v. 17, p. 22.1–22.17.
- Crowley, T.J., and Zachos, J.C., 2000, Comparison of zonal temperature profiles for past warm time periods, in Huber, B.T., et al., eds., *Warm climate in Earth history*: Cambridge, Cambridge University Press, p. 50–76.
- D'Hondt, S., and Arthur, M.A., 1996, Late Cretaceous oceans and the Cool Tropic Paradox: *Science*, v. 271, p. 1838–1841.
- Erez, J., and Luz, B., 1983, Experimental paleotemperature equation for planktonic foraminifera: *Geochimica et Cosmochimica Acta*, v. 47, p. 1025–1031, doi: 10.1016/0016-7037(83)90232-6.
- Huber, B.T., Hodell, D.A., and Hamilton, C.P., 1995, Middle-Late Cretaceous climate of the southern high latitudes: Stable isotopic evidence for minimal equator-to-pole thermal gradients: *Geological Society of America Bulletin*, v. 107, p. 1164–1191, doi: 10.1130/0016-7606(1995)107<1164:MLCCOT>2.3.CO;2.
- Huber, B.T., Norris, R.D., and MacLeod, K.G., 2002, Deep-sea paleotemperature record of extreme warmth during the Cretaceous: *Geology*, v. 30, p. 123–126, doi: 10.1130/0091-7613(2002)030<0123:DSPROE>2.0.CO;2.
- Huber, M., and Sloan, L.C., 2001, Heat transport, deep waters, and thermal gradients: Coupled simulation of an Eocene greenhouse climate: *Geophysical Research Letters*, v. 28, p. 3481–3484, doi: 10.1029/2001GL012943.
- Kolodny, Y., Luz, B., and Navon, O., 1983, Oxygen isotope variations in phosphate of biogenic apatites, I. Fish bone apatite—Rechecking the rules of the game: *Earth and Planetary Science Letters*, v. 64, p. 398–404, doi: 10.1016/0012-821X(83)90100-0.
- Lécuyer, C., Grandjean, P., O'Neil, J.R., Capetta, H., and Martineau, F., 1993, Thermal excursions in the ocean at the Cretaceous-Tertiary boundary (northern Morocco): $\delta^{18}\text{O}$ record of phosphatic fish debris: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 105, p. 235–243, doi: 10.1016/0031-0182(93)90085-W.
- Lécuyer, C., Grandjean, P., and Sheppard, S.M.F., 1999, Oxygen isotope exchange between dissolved phosphate and water at temperatures $\leq 135^\circ\text{C}$: Inorganic versus biological fractionations: *Geochimica et Cosmochimica Acta*, v. 63, p. 855–862, doi: 10.1016/S0016-7037(99)00096-4.
- LEVITUS94, World ocean atlas 1994: <http://ingrid.ideo.columbia.edu/SOURCES/LEVITUS94> (May 2006).
- Norris, R.D., Bice, K.L., Magno, E.A., and Wilson, P.A., 2002, Jiggling the tropical thermostat in the Cretaceous hothouse: *Geology*, v. 30, p. 299–302, doi: 10.1130/0091-7613(2002)030<0299:JTITIT>2.0.CO;2.
- Noubhani, A., and Cappetta, H., 1997, Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des bassins à phosphate du Maroc (Maastrichtien-Lutécien basal). *Systématique, biostratigraphie, évolution et dynamique des faunes: Paleo Ichthyologica*, v. 8, p. 1–327.
- O'Neil, J.R., Roe, L.J., Reinhard, E., and Blake, R.E., 1994, A rapid and precise method of oxygen isotope analysis of biogenic phosphates: *Israel Journal of Earth Sciences*, v. 43, p. 203–212.
- Otto-Bliesner, B.L., Brady, E.C., and Shields, C., 2002, Late Cretaceous ocean: Coupled simulations with the NCAR CSM: *Journal of Geophysical Research*, v. 107, doi: 10.1029/2001JD000821.
- Pearson, P.N., Ditchfield, P.W., Singano, J., Harcourt-Brown, K.G., Nicholas, C.J., Olsson, R.K., Shakleton, N.J., and Hall, M.A., 2001, Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs: *Nature*, v. 413, p. 481–487, doi: 10.1038/35097000.
- Pierrehumbert, R.T., 2002, The hydrologic cycle in deep-time climate problems: *Nature*, v. 419, p. 191–198, doi: 10.1038/nature01088.
- Pucéat, E., Lécuyer, C., Sheppard, S.M.F., Dromart, G., Reboulet, S., and Grandjean, P., 2003, Thermal evolution of Cretaceous Tethyan marine waters inferred from oxygen isotope composition of fish tooth enamels: *Paleoceanography*, v. 18, p. 7.1–7.12.
- Ramanathan, V., and Collins, W.D., 1991, Thermodynamic regulation of ocean warming by cirrus clouds deduced from observations of the 1987 El Niño: *Nature*, v. 351, p. 27–32, doi: 10.1038/351027a0.
- Savin, S.M., and Douglas, R.G., 1973, Stable isotope and magnesium geochemistry of recent planktonic foraminifera from the South Pacific: *Geological Society of America Bulletin*, v. 84, p. 2327–2342, doi: 10.1130/0016-7606(1973)84<2327:SIAMGO>2.0.CO;2.
- Shakleton, N.J., and Kennett, J.P., 1975, Paleotemperature history of the Cenozoic and the initiation of Antarctic glaciation: Oxygen and carbon isotope analyses in DSDP Sites 277, 279, and 281, in Kennett, J.P., et al., *Initial reports of the Deep Sea Drilling Project, Volume 29*: Washington, D.C., U.S. Government Printing Office, p. 743–756.
- Sloan, L.C., and Pollard, D., 1998, Polar stratospheric clouds: High latitude winter warming mechanism in an ancient greenhouse world: *Geophysical Research Letters*, v. 25, p. 3517–3520, doi: 10.1029/98GL02492.
- Spicer, R.A., and Parrish, J.T., 1990, Late Cretaceous-early Tertiary palaeoclimates of northern high latitudes: A quantitative view: *Geological Society [London] Journal*, v. 147, p. 329–341.
- Steuber, T., Rauch, M., Mase, J.-P., Graaf, J., and Malkoč, M., 2005, Low-latitude seasonality of Cretaceous temperatures in warm and cold episodes: *Nature*, v. 437, p. 1341–1344.
- Vennemann, T.W., Hegner, E., Cliff, G., and Benz, G.W., 2001, Isotopic composition of recent shark teeth as a proxy for environmental conditions: *Geochimica et Cosmochimica Acta*, v. 65, p. 1583–1599, doi: 10.1016/S0016-7037(00)00629-3.
- Vrielynck, B., and Bouysse P., 2003, The changing face of the earth: The break-up of Pangea and continental drift over the past 250 million years in ten steps: Paris, France, Commission de la Carte Géologique du Monde and Unesco, 32 p.
- Wallmann, K., 2001, The geological water cycle and the evolution of marine $\delta^{18}\text{O}$ values: *Geochimica et Cosmochimica Acta*, v. 65, p. 2469–2485, doi: 10.1016/S0016-7037(01)00603-2.
- Wilson, P.A., and Opdyke, B.N., 1996, Equatorial sea-surface temperatures during the Maastrichtian revealed through remarkable preservation of metastable carbonate: *Geology*, v. 24, p. 555–558, doi: 10.1130/0091-7613(1996)024<0555:ESSTFT>2.3.CO;2.
- Wilson, P.A., Norris, R.D., and Cooper, M.J., 2002, Testing the Cretaceous greenhouse hypothesis using glassy foraminiferal calcite from the core of Turonian tropics on Demerara Rise: *Geology*, v. 30, p. 607–610, doi: 10.1130/0091-7613(2002)030<0607:TTCGHU>2.0.CO;2.
- Zachos, J.C., Stott, L.D., and Lohmann, K.C., 1994, Evolution of early Cenozoic marine temperatures: *Paleoceanography*, v. 9, p. 353–387, doi: 10.1029/93PA03266.
- Zachos, J.C., Arthur, M.A., Bralower, T.J., and Spero, H.J., 2002, Tropical temperatures in greenhouse episodes: *Nature*, v. 419, p. 897–898, doi: 10.1038/419897b.

Manuscript received 16 June 2006

Revised manuscript received 8 September 2006

Manuscript accepted 15 September 2006

Printed in USA