Linkages between CO_2, climate, and evolution in deep time

Dana L. Royer*
Department of Earth and Environmental Sciences, Wesleyan University, Middletown, CT 06459

The most recent assessment report from the Intergovernmental Panel of Climate Change (IPCC) clearly illustrates the links between atmospheric CO_2 and climate (1) and the impacts of climate change on life (2). The geologic record contains a treasure trove of "alternative Earths" that allow scientists to study how the various components of the Earth system respond to a range of climatic forcings. These past examples illustrate how ecosystems function, and often they provide constraints for predicting the magnitude and impact of future climate change. Multiple independent methods for reconstructing ancient levels of atmospheric CO_2 have been developed over the past two decades: these include the distribution of stomatal pores in fossil leaves, the $\delta^{13}C$ of carbonate minerals from fossil soils, the $\delta^{13}C$ of marine phytoplankton, and the $\delta^{11}B$ of marine carbonate (3). Records of paleo-CO_2 from these methods as well as calculations of CO_2 from geochemical models (4) generally correlate well with independent records of temperature. Over the past 450 million years (Myr), CO_2 was low when extensive, long-lived ice sheets were present (≈330–290 Myr ago and 35 Myr ago to the present day) and moderately high to high at other times (5, 6). However, some intervals in Earth's past fail to show any consistent relationship. One conspicuous example is the Miocene (23.0–5.3 Myr ago), an Epoch where multiple advances of the Antarctic ice sheet are juxtaposed with a period of global warmth ≈15 Myr ago (7). Most CO_2 records during this period are low [<300 ppm by volume (ppmv)] and do not covary with temperature (8–10) (Fig. 1). These records imply that other radiative forcings such as changes in paleogeography or meridional heat transport were disproportionately more important than CO_2 at this time. In this issue of PNAS, Kürschner *et al.* (11) present new data that overturn this notion and provide important insights into the climatic linkages during this Epoch.

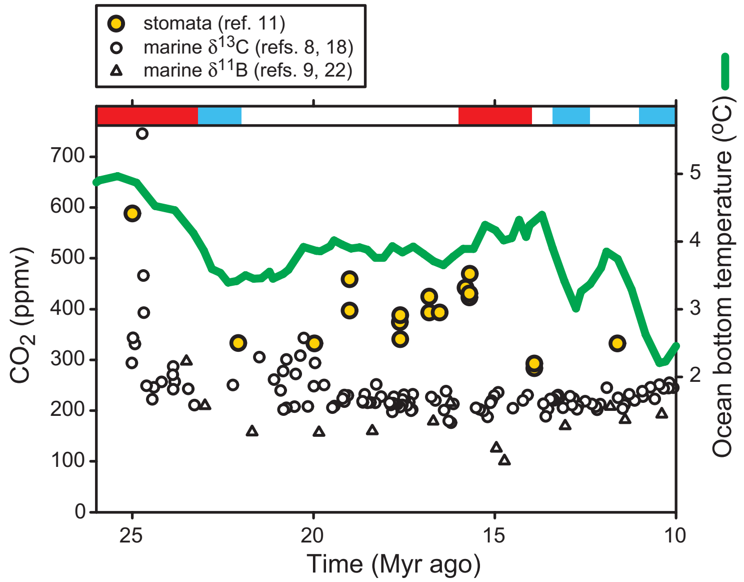

Fig. 1. Atmospheric CO_2 and temperature for the latest Oligocene to late Miocene. The ocean temperature record is based on paired $\delta^{18}O$ and Mg/Ca measurements of benthic foraminifera (15); a five-point running mean of the raw data is plotted. The red and blue bands mark intervals of significant warming and cooling, respectively (7).

Kürschner *et al.* (11) use the stomatal method to reconstruct CO_2; this method is based on the inverse relationship observed in many plants between stomatal numbers (specifically stomatal index, which is the percentage of stomatal density relative to stomatal density plus epidermal cell density) and CO_2 (12, 13) (Fig. 2). In contrast to previous records (8–10), their record shows that CO_2 and temperature are coupled: the two major advances of the Antarctic ice sheet are marked by low CO_2 and the latest Oligocene and mid-Miocene warm periods, by comparatively high CO_2 (Fig. 1). Their study therefore reopens the possibility that CO_2 was a prominent force in controlling climate during the Miocene.

A major strength of the Kürschner *et al.* (11) study is their use of three independently calibrated taxa; in contrast, most stomatal-based reconstructions use only one taxon. The similarity in the CO_2 estimates across distantly related taxa greatly reduces the likelihood that an additional factor such as water availability or light intensity (12) compromised the stomatal indices and therefore the fidelity of the CO_2 signal. This multiple-taxa approach offers an important way forward for improving stomatal-based CO_2 reconstructions.

Two other points about the climatic linkages are worth noting. First, global climate models (14) and geologic records (5) suggest that a CO_2 threshold of <500 ppmv is important for triggering ice-sheet growth. While ice was present throughout the interval of the record of Kürschner *et al.* (11), CO_2 was more than ≈500 ppmv during the melting phases and <300 ppmv during ice-sheet expansion (red and blue bands in Fig. 1). These patterns provide additional credence for a CO_2–ice threshold of ≈500 ppmv.

Second, the calibration of Earth's climate sensitivity to CO_2 is critical for understanding climate change; for today's Earth, every doubling of CO_2 most likely results in a temperature increase [$\Delta T(2\times)$] of ≈3°C (1). The CO_2 record of Kürschner *et al.* (11) provides an opportunity to calculate climate sensitivity for the Miocene world. For the cooling event ≈25–22 Myr ago $T(2\times) = 1.9$–2.7°C if CO_2 is compared with deep-sea paleotemperatures (15) [the range in $\Delta T(2\times)$ arises from using a five-point running mean vs. the individual data points of the paleotemperature record];

Author contributions: D.L.R. wrote the paper.

The author declares no conflict of interest.

See companion article on page 449.

*E-mail: droyer@wesleyan.edu.

www.pnas.org/cgi/doi/10.1073/pnas.0710915105

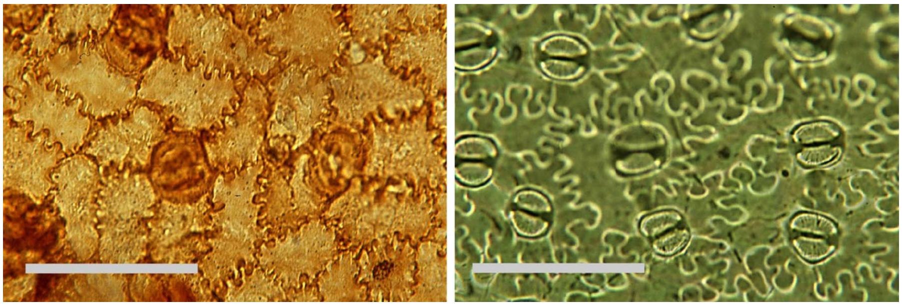

Fig. 2. An illustration of the stomatal CO_2 proxy. (*Left*) Photomicrograph of fossil leaf cuticle of the fern aff. *Stenochlaena* from just after the Cretaceous/Tertiary (K/T) boundary. (*Right*) The fern's nearest living relative, *Stenochlaena palustris*. The stomatal index of the fossil cuticle is considerably lower than the extant cuticle, indicating that CO_2 was higher directly after the K/T boundary than today (21). Photos courtesy of Barry Lomax (University of Sheffield, Sheffield, U.K.). (Scale bars, 10 μm.)

because the deep sea is an excellent indicator of the total heat budget of the ocean–atmosphere system, over short time periods the deep sea is a good proxy for changes in global surface temperatures. These calculated values of $\Delta T(2\times)$ are similar to an independently derived estimate of mean climate sensitivity for the last 420 Myr [most likely $\Delta T(2\times) = 2.8°C$] (16).

The Miocene is marked by the evolution of modern biomes, including the expansion of grass-dominated ecosystems. In particular, the late Oligocene to early Miocene may be an important transition in terrestrial settings from ecosystems dominated by closed forests to more open systems dominated by C_3 grasses (17). Both the CO_2 record of Kürschner *et al.* (11) and other records (18) indicate a marked drop in CO_2 across this transition from >600 ppmv to ≈ 300 ppmv (Fig. 1). Crucially, coupled climate–vegetation models are consistent with a mechanistic link between a CO_2 drop of this order and the replacement of forest systems with grasslands (19). Another important change in terrestrial ecosystems is the origin and geographic expansion of C_4 plants. Physiological models predict that CO_2 starvation, warming, and drying should select against C_3 plants (20). Intriguingly, molecular evidence is consistent with a C_4 origin around the time of the large CO_2 drop at the beginning of the Miocene; however, fossil and geochemical data point to a somewhat younger origin (20). C_4 grasslands did not become common until ≈ 8 Myr ago, which postdates the final drop in CO_2 documented by Kürschner *et al.* by 6 Myr. Therefore, CO_2 was probably not a primary driver for the expansion of C_4 grasslands (20); however, the generation of more paleobotanical and CO_2 records is certainly warranted.

Kürschner *et al.* (11) provide a methodological framework for exploring quantitatively the linkages among CO_2, climate, and evolution. Specifically, their study breathes new life into the possibility that CO_2 and global temperatures were strongly coupled during the Miocene, a time when the climate oscillated between icy and less icy states. As we continue on a path to a less icy future, it would be wise to continue studying the Miocene for clues about our ancient past.

1. Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averty KB, Tignor M, Miller HL (2007) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Solomon S, Qin D, Manning M (Cambridge Univ Press, Cambridge, UK), Available at www.ipcc.ch.
2. IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE (Cambridge Univ Press, Cambridge, UK), Available at www.ipcc.ch.
3. Royer DL, Berner RA, Beerling DJ (2001) *Earth-Sci Rev* 54:349–392.
4. Berner RA (2004) *The Phanerozoic Carbon Cycle: CO_2 and O_2* (Oxford Univ Press, New York).
5. Royer DL (2006) *Geochim Cosmochim Acta* 70:5665–5675.
6. Royer DL, Berner RA, Montañez IP, Tabor NJ, Beerling DJ (2004) *GSA Today* 14(3):4–10.
7. Zachos J, Pagani M, Sloan L, Thomas E, Billups K (2001) *Science* 292:686–693.
8. Pagani M, Freeman KH, Arthur MA (1999) *Science* 285:876–879.
9. Pearson PN, Palmer MR (2000) *Nature* 406:695–699.
10. Royer DL, Wing SL, Beerling DJ, Jolley DW, Koch PL, Hickey LJ, Berner RA (2001) *Science* 292:2310–2313.
11. Kürschner WM, Kvaček Z, Dilcher DL (2008) *Proc Natl Acad Sci USA* 105:449–453.
12. Royer DL (2001) *Rev Palaeobot Palynol* 114:1–28.
13. Woodward FI (1987) *Nature* 327:617–618.
14. DeConto RM, Pollard D (2003) *Nature* 421:245–249.
15. Billups K, Schrag DP (2002) *Paleoceanography* 17(1), 10.1029/2000PA000567.
16. Royer DL, Berner RA, Park J (2007) *Nature* 446:530–532.
17. Stromberg CAE (2004) *Palaeogeogr Palaeoclimatol Palaeoecol* 207:239–275.
18. Pagani M, Zachos JC, Freeman KH, Tipple B, Bohaty S (2005) *Science* 309:600–603.
19. François L, Ghislain M, Otto D, Micheels A (2006) *Palaeogeogr Palaeoclimatol Palaeoecol* 238:302–320.
20. Sage RF (2005) in *A History of Atmospheric CO_2 and Its Effects on Plants, Animals, and Ecosystems*, eds Ehleringer JR, Cerling TE, Dearing MD (Springer, New York), pp 185–213.
21. Beerling DJ, Lomax BH, Royer DL, Upchurch GR, Kump LR (2002) *Proc Natl Acad Sci USA* 99:7836–7840.
22. Demicco RV, Lowenstein TK, Hardie LA (2003) *Geology* 31:793–796.