

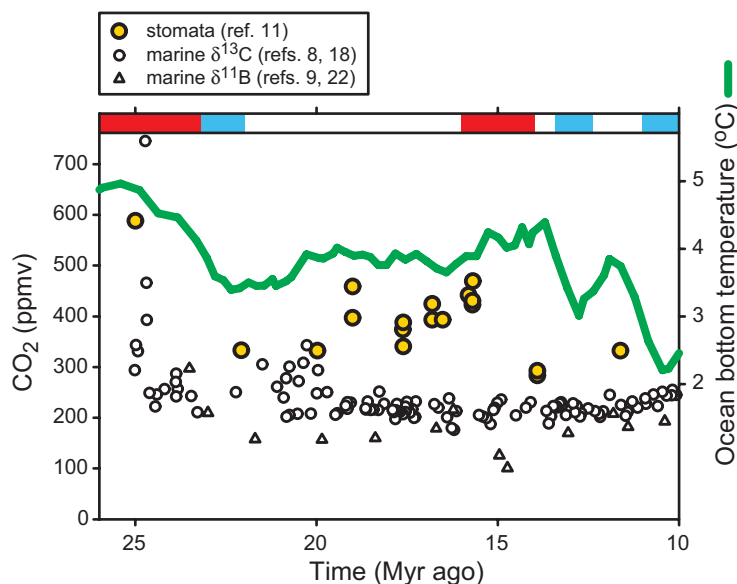
# Linkages between CO<sub>2</sub>, climate, and evolution in deep time

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The most recent assessment report from the Intergovernmental Panel of Climate Change (IPCC) clearly illustrates the links between atmospheric CO<sub>2</sub> 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<sub>2</sub> have been developed over the past two decades: these include the distribution of stomatal pores in fossil leaves, the δ<sup>13</sup>C of carbonate minerals from fossil soils, the δ<sup>13</sup>C of marine phytoplankton, and the δ<sup>11</sup>B of marine carbonate (3). Records of paleo-CO<sub>2</sub> from these methods as well as calculations of CO<sub>2</sub> from geochemical models (4) generally correlate well with independent records of temperature. Over the past 450 million years (Myr), CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> 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.

Kürschner *et al.* (11) use the stomatal method to reconstruct CO<sub>2</sub>; this method is based on the inverse relationship observed in many plants between stomatal numbers (specifically stomatal index, which is the percentage of stomatal den-



**Fig. 1.** Atmospheric CO<sub>2</sub> and temperature for the latest Oligocene to late Miocene. The ocean temperature record is based on paired δ<sup>18</sup>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).

sity relative to stomatal density plus epidermal cell density) and CO<sub>2</sub> (12, 13) (Fig. 2). In contrast to previous records (8–10), their record shows that CO<sub>2</sub> and temperature are coupled: the two major advances of the Antarctic ice sheet are marked by low CO<sub>2</sub> and the latest Oligocene and mid-Miocene warm periods, by comparatively high CO<sub>2</sub> (Fig. 1). Their study therefore reopens the possibility that CO<sub>2</sub> 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<sub>2</sub> 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<sub>2</sub> signal. This multiple-taxa approach offers an important way forward for improving stomatal-based CO<sub>2</sub> reconstructions.

Two other points about the climatic linkages are worth noting. First, global climate models (14) and geologic records (5) suggest that a CO<sub>2</sub> threshold of  $<500$  ppmv is important for trigger-

ing ice-sheet growth. While ice was present throughout the interval of the record of Kürschner *et al.* (11), CO<sub>2</sub> was more than ≈500 ppmv during the melting phases and  $<300$  ppmv during ice-sheet expansion (15) (Fig. 1). These patterns provide additional credence for a CO<sub>2</sub>–ice threshold of ≈500 ppmv.

Second, the calibration of Earth’s climate sensitivity to CO<sub>2</sub> is critical for understanding climate change; for today’s Earth, every doubling of CO<sub>2</sub> most likely results in a temperature increase [ $\Delta T(2\times)$ ] of ≈3°C (1). The CO<sub>2</sub> 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<sub>2</sub> 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];

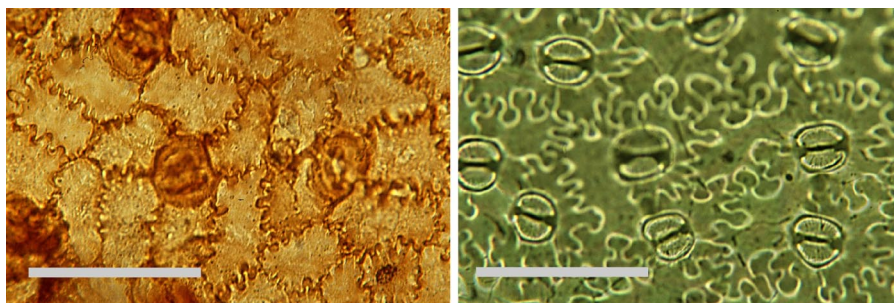
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**Fig. 2.** An illustration of the stomatal CO<sub>2</sub> proxy. (Left) Photomicrograph of fossil leaf cuticle of the fern aff. *Stenochlaena* from just after the Cretaceous/Tertiary (K/T) boundary. (Right) The fern's nearest living relative, *Stenochlaena palustris*. The stomatal index of the fossil cuticle is considerably lower than the extant cuticle, indicating that CO<sub>2</sub> 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  $\Delta T(2\times) = 2.8^\circ\text{C}$ ] (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<sub>3</sub> grasses (17). Both the CO<sub>2</sub> record of Kürschner *et al.* (11) and other records (18) indicate a marked drop in CO<sub>2</sub> 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<sub>2</sub> 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<sub>4</sub> plants. Physiological models predict that CO<sub>2</sub> starvation, warming, and drying should select against C<sub>3</sub> plants (20). Intriguingly, molecular evidence is consistent with a C<sub>4</sub> origin around the time of the large CO<sub>2</sub> drop at the beginning of the Miocene; however, fossil and geochemical data point to a somewhat younger origin (20). C<sub>4</sub> grasslands did not become common until ≈8 Myr ago, which postdates the final drop in CO<sub>2</sub> documented by Kürschner *et al.* by 6 Myr. Therefore, CO<sub>2</sub> was probably not a primary driver for the expansion of C<sub>4</sub> grasslands (20); however, the generation of more paleobotanical and CO<sub>2</sub> records is certainly warranted.

Kürschner *et al.* (11) provide a methodological framework for exploring quantitatively the linkages among CO<sub>2</sub>, climate, and evolution. Specifically, their study breathes new life into the possibility that CO<sub>2</sub> 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.

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