

erties must differ before two neurons are assigned to distinct cell classes. Perhaps cell groups are more useful to neurobiologists than they are to the brains that they study.

Gupta *et al.* (2) provide a striking resolution of this apparent impasse. They group cortical interneurons in three different ways. First, according to their discharge pattern, which determines the temporal pattern of inhibitory synaptic events impinging simultaneously onto several hundred target neurons. A second classification based on the axonal tree of interneurons defines the number and spatial distribution of these target cells. The third, functional classification derives from an impressive number of simultaneous recordings from inhibitory cells and multiple postsynaptic targets. When inhibitory cells discharge repetitively, the efficacy of their synapses with pyramidal cells changes in one of three kinetic patterns (see the figure). Although the first two groupings fragment cortical interneurons into 14 different classes, the third sorting maps perfectly onto these classes

and reunites interneurons into three functional groups.

So where does the field go from here? Molecular approaches may resolve the question of inhibitory cell diversity. We will eventually be able to measure the entire complement of proteins that a single interneuron expresses and determine how this complement is regulated by cascades of transcription factors and by external signals. The use of gene targeting to kill subsets of interneurons may also help us understand their functions. An impressive study demonstrating motor deficits emerging after selective ablation of cerebellar Golgi cells (17) has shown the way, although the adaptive mechanisms initiated by the loss of these interneurons urge caution with this approach. Nonetheless, the current cooperation between anatomists, physiologists, and modelers is increasing our knowledge of inhibitory cell function at a fast pace. Maybe the next step should be to reunite yin and yang and examine how inhibitory and excitatory synaptic signals cooperate in the purposeful and harmonious brain.

## References and Notes

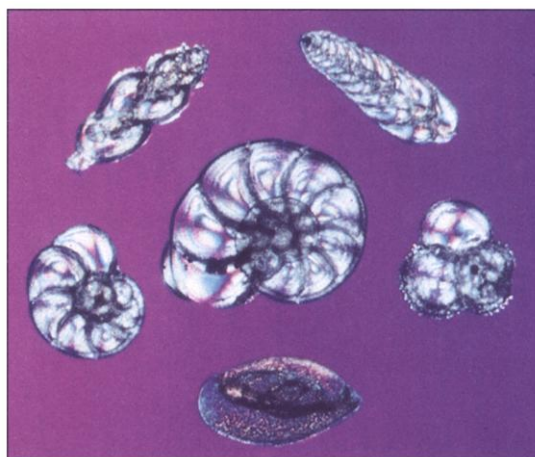
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## PERSPECTIVES: GEOSCIENCE

# Unraveling the Signals of Global Climate Change

Gary S. Dwyer

Over the past 50 million years, Earth's climate has been on a wobbly but persistent march toward cooler conditions. A telltale sign is the dramatic overall increase in global ice volume and decrease in deep-sea temperature. One of the best measures of this trend has been the oxygen isotopic composition ( $\delta^{18}\text{O}$ ) of shells of ocean-floor microfossils extracted from deep-sea sediment cores. These  $\delta^{18}\text{O}$  records, which simultaneously capture information regarding global ice volume and deep-sea temperature, are acquired in the vast majority of studies of past deep-sea conditions and have provided Earth scientists with critical paleoceanographic and paleoclimatic insight. Nevertheless, since the pioneering application of this technique in the 1950s and 1960s by Cesare Emiliani and Nicholas Shackleton (1), and regardless of the past period of interest, this basic and essential paleoclimatic tool has been plagued by the nagging ques-



**Paleothermometers.** A variety of shells of foraminifera, whose composition can provide insights into past climatic conditions.

tion of the relative influence of water temperature and ice volume. On page 269 of this issue, Lear *et al.* (2) make an important step toward solving this problem for the past 50 million years of Earth's history by combining a recently developed deep ocean paleotemperature

proxy—the ratio of magnesium to calcium concentrations in microfossil shells—with the  $\delta^{18}\text{O}$  record.

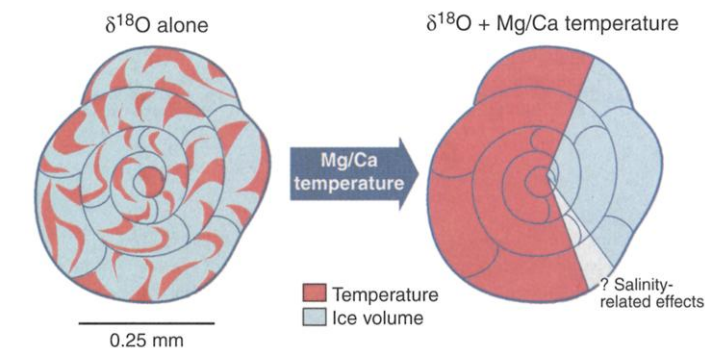
The Mg/Ca-based reconstruction of deep-sea temperature obtained by Lear *et al.* is remarkable in its similarity to the benthic  $\delta^{18}\text{O}$  record (3). This is critical independent confirmation that a substantial portion of the long-term increase in the benthic  $\delta^{18}\text{O}$  signal over the past 50 million years is indeed related to cooling of the deep ocean of around 12°C. In turn, it substantiates the hypothesis that this period is characterized by a shift to a global oceanic deep-water system much like the present one, which is driven by high-latitude sinking of cooled surface waters, and, further, that closing of tropical ocean gateways and opening of subpolar ocean gateways likely triggered the deep-water reorganization.

The residual benthic  $\delta^{18}\text{O}$  record, after removal of the temperature effect by means of the Mg/Ca data, thus provides a record of the  $\delta^{18}\text{O}$  of seawater for the past 50 million years, which is largely a function of global ice volume (see the figure on the following page). (With the major reorganization in deep-water production and circulation implied by the temperature record, the  $\delta^{18}\text{O}$  of seawater was likely af-

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affected by factors other than ice volume, such as those related to salinity changes. The extent of any non-ice volume contribution could be evaluated by comparing combined benthic  $\delta^{18}\text{O}$  and Mg/Ca records from additional sites in different ocean basins for the same time period). Assuming for now that the majority of the residual benthic  $\delta^{18}\text{O}$  signal is due to changes in ice volume, it is clear that there is a strong correspondence between ice volume and deep-sea temperature during cooling events. Although the detailed timing of cool event coupling requires further study [see figure 2 of Lear *et al.* (2)], the three periods of major ice sheet development generally coincide with times of most dramatic decrease in deep-sea temperature. Between the relatively rapid events of ice accumulation and deep-sea cooling are long periods of ice sheet decay, without a demonstrable equivalent recovery in deep-sea temperature. The possible mechanisms responsible for these observations and the implications, climatic and otherwise, of the Lear *et al.* reconstructions of deep-sea temperature and ice volume will be the subject of much discussion and debate among paleoclimatologists, although many will perhaps wait for validation. The most important immediate consequence of the Lear *et al.* work is its demonstration of the potential of this tool to separate ice-volume and deep-sea temperature signals.

It is imperative that we sort out these two vital signs of Earth's past climate. Serving not only as indicators of climate, ice volume and deep-sea temperature are also active players in shaping regional and global climatic conditions. The volume and distribution of glacial ice, for example, can play an important role in the amount of solar energy absorbed by Earth (surface albedo) and can alter surface air temperature gradients, atmospheric circulation patterns, and global sea level, which in turn each have potentially important impacts on a number of other climate variables. Deep-sea temperature is a fundamental factor controlling physical, biological, and chemical processes in the ocean. Changes in deep-sea temperature lead to changes in seawater density and sea level and, potentially, to reorganiza-



**Shell game.** Before the work of Lear *et al.*, long-term signals of global ice volume (blue) and deep-sea temperature (red) contained within the oxygen isotopic composition ( $\delta^{18}\text{O}$ ) of calcareous shells of deep-sea dwelling invertebrates were intertwined. This is represented schematically by a microfossil shell with mixed colors (left). By independently determining the deep-sea temperature at which the shells formed, the temperature effect on the  $\delta^{18}\text{O}$  of the shell can be removed. The residual  $\delta^{18}\text{O}$  of the shell thus provides a more direct estimate of the volume of ice stored in continental ice sheets, represented by the shell with clearly resolved shading (right). Water evaporated from oceans and stored in ice sheets is depleted in oxygen-18, thereby leaving ocean water enriched in this isotope, which in turn is recorded in the  $\delta^{18}\text{O}$  of shells that formed in the ocean. The extent of this enrichment is proportional to the amount of water stored in the ice sheets. Other factors may also affect the oxygen-18 enrichment of deep ocean waters. These are generally related to the salinity of the water and are likely substantially smaller than the ice-volume effect. Nevertheless, some portion of the residual  $\delta^{18}\text{O}$  of the shell is likely related to factors other than the extent of global ice volume (white). The shell depicted is benthic foraminifer genus *Oridorsalis*, the main deep-sea microfossil analyzed by Lear *et al.* (2).

tion of heat, salt, and biogeochemical inventories through changes in density-driven circulation of the global ocean. Deep-sea temperature also has strong linkages to greenhouse gases. Reflecting the sea surface temperature at the sites of deep-water formation, deep ocean temperature partially reflects the air-sea exchange of  $\text{CO}_2$ , with cooler temperatures perhaps signifying relatively enhanced oceanic storage of  $\text{CO}_2$  and concomitant decrease in atmospheric  $\text{CO}_2$ . Deep-sea temperature also plays a role in the stability of gas hydrates, solid complexes of greenhouse gases buried in ocean sediments whose breakdown and release have been linked to catastrophic warming events (4). Thus, ice volume and deep-sea temperature are indeed fundamental variables of Earth's climate system, and their accurate assessment for times past is critical to understanding the timing, extent, and mechanisms of climate change.

Although the Lear *et al.* findings are an exciting advance, seasoned paleoceanographers and paleoclimatologists may view these results with a fair amount of skepticism. Development of reliable proxy indicators of past environmental conditions is often a process of two steps forward, one step back. Lear *et al.* grapple with some of the complications related to the relatively

young method of Mg/Ca paleothermometry. These include factors other than temperature that may effect the amount of magnesium taken up during shell formation, such as enigmatic ontogenetic and interspecies variations ("vital effects"), and, over long time scales as here, changes in the Mg/Ca ratio of seawater. Post-mortem (diagenetic) effects, including partial dissolution and recrystallization of the shells, are also potentially important factors. Partial shell dissolution clearly alters the Mg/Ca ratios of some planktonic calcareous microfossils likely as a result of preferential removal of relatively soluble Mg-enriched zones. The effects of dissolution on benthic shell Mg/Ca ratios are less clear, although preliminary results suggest that dissolution effects are negligible perhaps because the relatively homogeneous intrashell distribution of magnesium.

Undoubtedly, our incomplete understanding of these factors contributes to the "scatter" in the Lear *et al.* Mg/Ca record. However, recent studies of modern (5) and ancient (6) ocean temperatures demonstrate the likelihood of rapid changes in deep-sea temperature driven by changes in deep-water production and circulation. Thus, an equally valid hypothesis is that some of the scatter represents real temperature variability of the past deep ocean.

Although it is clear that challenges lie ahead regarding the details of Mg/Ca paleothermometry, the results of Lear *et al.* reveal the potential of this new tool. The importance of understanding past ocean temperatures provides a strong impetus for the paleoclimatological community to pursue the continued development of this and other ocean paleothermometers.

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