FORUM: BIOGEOCHEMISTRY

Ancient algae crossed a threshold

The finding that the shells of certain algae can contain a signature of low levels of atmospheric carbon dioxide has prompted the discovery of the emergence of this signature in the fossil record. Here, experts discuss the implications of this for climate science and ocean ecology. SEE LETTER P.558

THE PAPER IN BRIEF

- Coccolithophores are marine algae that use inorganic carbon for photosynthesis and for calcification — the precipitation of calcium carbonate to produce an exoskeleton made up of plates called coccoliths (Fig. 1).
- In this issue, Bolton and Stoll[1] report that coccolithophores allocate more inorganic carbon, in the form of bicarbonate from sea water, to photosynthesis than to calcification when atmospheric levels of carbon dioxide are low.
- This change in allocation causes a difference between the carbon-isotope signature of small and large coccoliths.
- The authors detect such a difference in the fossil record beginning about 7 million years ago.
- They conclude that a global decrease in the concentration of atmospheric CO_2 must have occurred at that time.

Climate lessons

RICHARD D. PANCOST & MARCUS P. S. BADGER

Bolton and Stoll have developed a tool to reconstruct ancient carbon dioxide concentrations on the basis of differences in the carbon isotopic composition of large and small coccoliths. Their method is not a direct CO_2 barometer, but is based on what seems to be a threshold response of coccolithophores, which undergo a change in physiology as CO_2 levels increase above about 375–575 parts per million (p.p.m.). The authors used their approach to test directly whether CO_2 concentration has slowly decreased from higher levels 10 million to 12 million years (Myr) ago. With CO_2 levels currently on the rise, the answer has implications for future climate. The authors' work goes beyond being just another (much needed) approach to reconstructing CO_2 concentrations, and has implications for our understanding of how phytoplankton adapt to the world around them.

Ancient CO_2 levels can be determined from bubbles in ice cores, but these records extend back by only about 1 Myr. For the rest of Earth's history, proxy approaches are necessary[2]. Such proxies can be based on the stomatal density of fossil leaves, the carbon-isotope discrimination of photosynthesis as recorded by alkenones (compounds produced exclusively by some marine coccolithophores) or the boron isotopic composition of marine plankton. Ideally, multiple methods are used to constrain uncertainties.

Unfortunately, the proxy data from 12 Myr to 5 Myr ago are largely limited to the alkenone approach[3], and even those data are restricted, originating largely from a single site in the southwest Pacific Ocean. That record suggests that, during this period, CO_2 levels were rather low (below 300 p.p.m.) and relatively stable, or increasing slightly. Combining that observation with alkenone data from other sites and from more recent time periods yields a record suggesting that CO_2 levels peaked at around 4–5 Myr ago[4]. By contrast, sea surface temperatures steadily dropped over the same period and continental ice sheets expanded, causing some researchers[5] to argue that climate was decoupled from CO_2 levels.

Using their approach, Bolton and Stoll have produced data that present a fundamentally different model for CO_2 evolution over the past 12 Myr from that derived from the combined alkenone record. Their data indicate that CO_2 levels were elevated 12–7 Myr ago and decreased 7–5 Myr ago. Crucially, this suggests that CO_2 levels were indeed coupled to ocean temperature during much of the past 12 million years.

One implication of the authors' work is for the aforementioned alkenone CO_2 barometer, because coccoliths and alkenones derive largely from the same organisms. The alkenone proxy is based on a theoretical framework[6] that does not include active uptake of CO_2 by coccolithophores, but Bolton and Stoll's work indicates that this framework is flawed. Although this does not necessarily mean that the empirical relationship on which the alkenone proxy is based is incorrect, the way in which the proxy is interpreted and extrapolated to ancient settings could be overly simplistic. This might help to explain the apparent disconnect between climate- and alkenone-based CO_2 proxies throughout the Miocene epoch (about 23–5 Myr ago).

It is useful to place the authors' conclusions in the context of the ongoing, human-caused increase in CO_2, which has risen from about 280 p.p.m. in pre-industrial times to almost 400 p.p.m. at some sites this summer[7], probably for the first time in millions of years[4]. Bolton and Stoll show that, during the past 12 Myr, periods of higher CO_2 levels were almost always characterized by markedly higher temperatures and smaller ice sheets than those of today.

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Sea changes

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It was recently reported[8] that at low concentrations of CO_2 coccolithophores seem to divert 'pumped' bicarbonate — sea water bicarbonate that has been actively transported into cells — away from calcification and towards photosynthetic production of organic carbon. Bolton and Stoll provide independent confirmation of this shift in carbon metabolism for a variety of coccolithophore species from the modern ocean and from the geological past, and they show that the expression of this shift depends on cell size. So what does this tell us about ocean ecology?

Most studies of the regulation of photosynthesis and calcification by CO_2 in coccolithophores have used various strains

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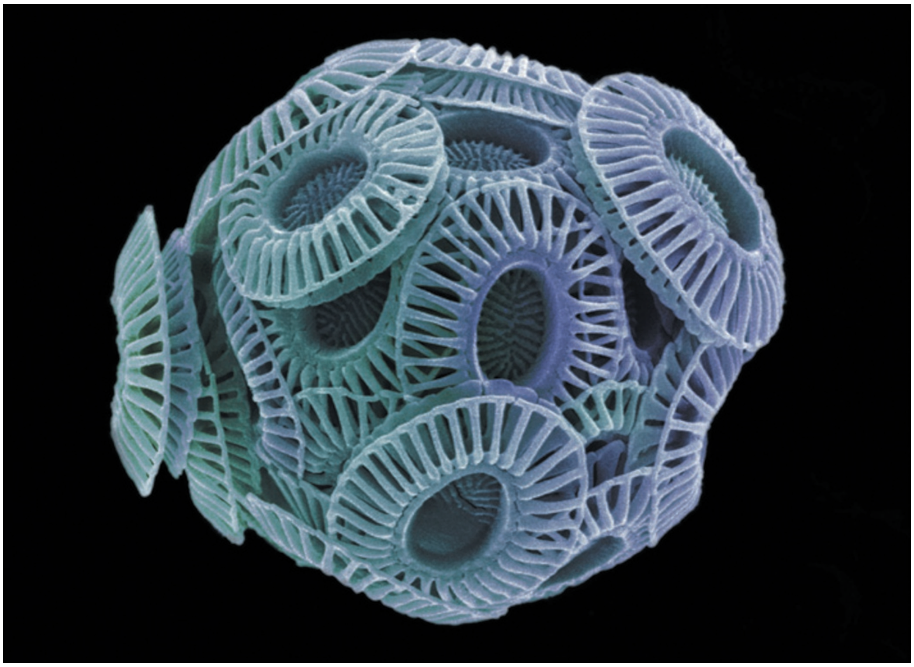

Figure 1 | A proxy for ancient carbon dioxide levels. Coccolithophores are marine algae characterized by an exoskeleton of overlapping plates (coccoliths) composed of calcium carbonate. Bolton and Stoll[1] report that differences in the carbon-isotope composition of large and small coccoliths preserved in the geological record provide information about atmospheric carbon dioxide levels in ancient times.

of the small-celled alga *Emiliania huxleyi*, but Bolton and Stoll's results highlight the need to examine species of a range of sizes. The greater CO_2 sensitivity of large coccolithophores reported by the authors might affect competition among different-sized species, causing small species to outcompete large species at low CO_2 concentrations, and large coccolithophores to proliferate as CO_2 levels rise. The size-dependent concentration of inorganic carbon in coccolithophores could also influence the vertical flux of particulate organic and inorganic carbon in the sea, because cells and coccoliths from large species sink faster than those from smaller species.

Central to Bolton and Stoll's results is the conclusion that, as the concentration of CO_2 in sea water declines, a larger proportion of calcification is supported by CO_2 that enters the cell by diffusion. This CO_2 is converted to bicarbonate inside the cell to compensate for the diversion of pumped bicarbonate to photosynthesis. Coccolithophores might therefore produce less acid during calcification as the concentration of CO_2 rises, because a larger proportion of calcification is fed by bicarbonate (which produces 1 mole of acid per mole of calcium carbonate precipitated) than by CO_2 (which produces 2 moles of acid per mole of calcium carbonate precipitated). As a result, and because coccolithophores account for a large fraction of total calcification in the ocean, the currently expected decrease in the surface ocean's pH may be partially offset as CO_2 levels rise.

Perhaps of greater consequence to the global carbon cycle is how rising CO_2 concentrations will affect calcium carbonate precipitation by coccolithophores overall. At low concentrations of 200–400 p.p.m., which occurred during past glacial periods and pertain today, calcification seems to decrease as atmospheric CO_2 levels rise[9]. Over a higher concentration range (400–750 p.p.m.), such as that expected during the next 100 years, the evidence relating to calcification trends is inconclusive[8–10].

If, as Bolton and Stoll's findings suggest, the proportion of pumped bicarbonate used for calcification increases at higher concentrations of CO_2, this may partially counteract any suppression of calcification associated with future ocean acidification.

As the concentration of CO_2 in the atmosphere increases over the next 50 to 100 years, the 3-million-year transition from high to low CO_2 levels that Bolton and Stoll conclude occurred some 7 Myr ago will play back in reverse, but 30,000 to 60,000 times faster. Although the effects of this rapid carbonation of Earth's oceans on marine ecology and on the ocean's ability to absorb atmospheric CO_2 are uncertain, Bolton and Stoll provide insight into how a crucial component of marine phytoplankton communities worldwide may respond. ■

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NEUROSCIENCE

Dopamine ramps up

We thought we had figured out dopamine, a neuromodulator involved in everything from learning to addiction. But the finding that dopamine levels ramp up as rats navigate to a reward may overthrow current theories. **SEE LETTER P.575**

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Scientific findings typically come in two flavours: explanations for things we already knew occurred but had no idea why, or new phenomena that are clearly important but still mysterious. Howe and colleagues' finding[1], on page 575 of this issue, is of the latter kind — even if we don't yet know what it means, it stands to alter the way we think about dopamine.

Dopamine is a molecule that is broadcast throughout the brain and is involved in processes ranging from decision-making to schizophrenia, as well as most forms of addiction. The authors measured levels of dopamine in the striatum of rats while the animals ran through mazes for food rewards. The striatum (Fig. 1a) is the area that contains the highest dopamine concentration in the brain. It is involved in action selection at all levels, from choosing which limb to move to selecting a goal to work towards. In a series of elegant experiments, Howe *et al.* established that dopamine concentration gradually ramps up as rats run towards a reward, and that the slope of the ramps relates to the amount of anticipated reward and the effort required to obtain it.

Why are these dopamine ramps so relevant? Dopamine-secreting (dopaminergic) neurons are special because they are thought to fire in unison, broadcasting a single all-important