A Paleoclimatic Enigma?

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tion of gene promoter regions is observed in most species. It is correlated to gene expression in plants and animals, which suggests that the role of promoter methylation in gene regulation may be derived. In mammals and flowering plants, this process has been developed into the imprinting system that generates parent of origin–dependent methylation marks on a small subset of genes and leads to their monoallelic expression (*11*, *12*).

On the other hand, several species underwent loss of DNA methylation to a large degree, such as the nematode *C. elegans*, the insect *D. melanogaster*, and the yeasts *S. pombe* and *S. cerevisiae*; hence, DNA methylation is not essential under all conditions of life, and its loss may even be beneficial. This could be connected to the resources allocated to global DNA methylation or to the fact that 5-methylcytosine is mutagenic, because its deamination is repaired less efficiently than deamination of unmethylated cytosine.

Human DNA methylation patterns vary with cell type and developmental stage (*3*, *10*, *13–18*), with disease (*10*, *15*, *16*), between alleles (*11*, *19–22*), and among individuals (*14*, *15*). Future methylome studies may reveal similar features in the other model organisms as well. Functional investigations of the properties of Dnmts and their interaction with chromatin and additional factors will clarify the mechanisms by which methylation patterns are set and maintained. Other questions yet to be resolved surround the means by which repeats and transposable elements are identified, the processes that target DNA methylation to gene bodies in an expression-dependent manner, the biological function of gene body methylation that led to its high stability in evolution, and the mechanisms to generate and modify tissue-specific patterns of promoter methylation in mammals.

References

1. M. M. Suzuki, A. Bird, *Nat. Rev. Genet.* **9**, 465 (2008).
2. J. A. Law, S. E. Jacobsen, *Nat. Rev. Genet.* **11**, 204 (2010).
3. R. Lister *et al.*, *Nature* **462**, 315 (2009).
4. S. J. Cokus *et al.*, *Nature* **452**, 215 (2008).
5. R. Lister *et al.*, *Cell* **133**, 523 (2008).
6. S. Feng *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* 10.1073/pnas.1002720107 (2010).
7. A. Zemach *et al.*, *Science* **328**, 916 (2010); published online 15 April 2010 (10.1126/science.1186366).
8. M. P. Ball *et al.*, *Nat. Biotechnol.* **27**, 361 (2009).
9. X. Zhang, *Science* **320**, 489 (2008).
10. E. Hodges *et al.*, *Genome Res.* **19**, 1593 (2009).
11. W. Reik, J. Walter, *Nat. Genet.* **27**, 255 (2001).
12. P. E. Jullien, F. Berger, *Curr. Opin. Plant Biol.* **12**, 637 (2009).
13. A. Meissner *et al.*, *Nature* **454**, 766 (2008).
14. Y. Zhang *et al.*, *PLoS Genet.* **5**, e1000438 (2009).
15. S. Maegawa *et al.*, *Genome Res.* **20**, 332 (2010).
16. R. A. Irizarry *et al.*, *Nat. Genet.* **41**, 178 (2009).
17. R. Straussman *et al.*, *Nat. Struct. Mol. Biol.* **16**, 564 (2009).
18. C. Popp *et al.*, *Nature* **463**, 1101 (2010).
19. K. Kerkel *et al.*, *Nat. Genet.* **40**, 904 (2008).
20. B. Panning, *J. Biol.* **7**, 30 (2008).
21. Y. Zhang *et al.* *Genome Biol.* **10**, R138 (2009).
22. L. C. Schalkwyk *et al.*, *Am. J. Hum. Genet.* **86**, 196 (2010).
23. K. A. Borkovich *et al.*, *Microbiol. Mol. Biol. Rev.* **68**, 1 (2004).
24. C. Goyon, T. I. Nogueira, G. Faugeron, *J. Mol. Biol.* **240**, 42 (1994).

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CLIMATE

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What caused the onset of major Northern Hemisphere glaciation about 2.75 million years ago?

Major glaciations began in the Northern Hemisphere around 2.75 million years ago, after a long prior interval of climatic cooling. Numerous observations reveal how climate cooled before glacial onset, but our understanding of the driving forces behind the cooling remains incomplete.

Climate had been cooling from pole to pole for 50 million years before northern glacial onset (see the figure). Arctic forests changed from frost-intolerant evergreens to temperate deciduous trees to cold-adapted spruce and larch and eventually to tundra near the time of glacial onset (*1*). Antarctica was mostly ice-free until 34 million years ago; glaciers of varying size then existed on the continent until 14 million years ago, after which a large and relatively stable ice sheet formed. The gradual shift toward heavier $\delta^{18}O$ values in $CaCO_3$ shells of sea-floor foraminifera since 50 million years ago documents a combined deep-ocean cooling and increase in Antarctic ice (*2*, *3*).

Until a decade ago, most paleoclimate modelers attributed this ongoing bipolar cooling to a gradual reduction in the CO_2 concentration in the atmosphere. This inferred CO_2 decrease was ascribed to a combination of reduced volcanic CO_2 input to the ocean and atmosphere because of a slowing rate of sea-floor spreading (*4*) and increased CO_2 removal by enhanced chemical weathering in tectonically uplifting regions like Tibet (*5*).

Methods devised to reconstruct the CO_2 concentration of the atmosphere on longer time scales later tested this conclusion. One method relied on the ^{13}C composition of marine organic molecules called alkenones (*6*), another on boron-isotopic values in marine carbonate sediments (*7*). Results from both methods suggested estimated CO_2 concentrations of around 1000 parts per million (ppm) or more during much warmer climates tens of millions of years ago, compared with ice-core values of just 180 to 300 ppm during the glacial cycles of the past 800,000 years.

In a broad sense, this long-term CO_2 decrease provided some support for the idea that CO_2 has been the long-term driver of global cooling, but a closer look revealed major problems. By 22 million years ago, the alkenone and boron isotope data both showed that estimated CO_2 concentrations were already within the range typical of the glacial cycles of the past 800,000 years. If CO_2 concentrations of 180 to 300 ppm have played an integral role in allowing glacial cycles in the past 800,000 years, why did comparably low CO_2 values 22 million years ago not initiate glacial cycles? And if the average CO_2 trend has not fallen in the past 22 million years, what caused the substantial bipolar cooling during that time?

Other proposed causes seem insufficient to explain large-scale cooling. Gradual plate motions and falling sea level have extended the northern margins of circum-Arctic continents into cooler near-polar latitudes (*8*), but models suggested that these factors were not enough to explain the major cooling observed. Closing of the Isthmus of Panama, about two million years before the onset of northern glaciations, has been proposed as a causal factor in glacial inception. Results from coupled ocean-atmosphere models indicate, however, that isthmus closure would have sent greater amounts of sensible heat northward in the Atlantic and melted more snow and ice, rather than promoting ice growth by delivering more moisture (*9*).

In the past 15 million years, broad-scale uplift of plateaus and mountains has occurred in the northern and eastern Tibetan Plateau, the east-central Andes and Altiplano, the east African rift valley, and the northern Canadian Rockies. Elevation of these rock surfaces to cooler levels in the atmosphere would have cooled the uplifted terrain and nearby regions,

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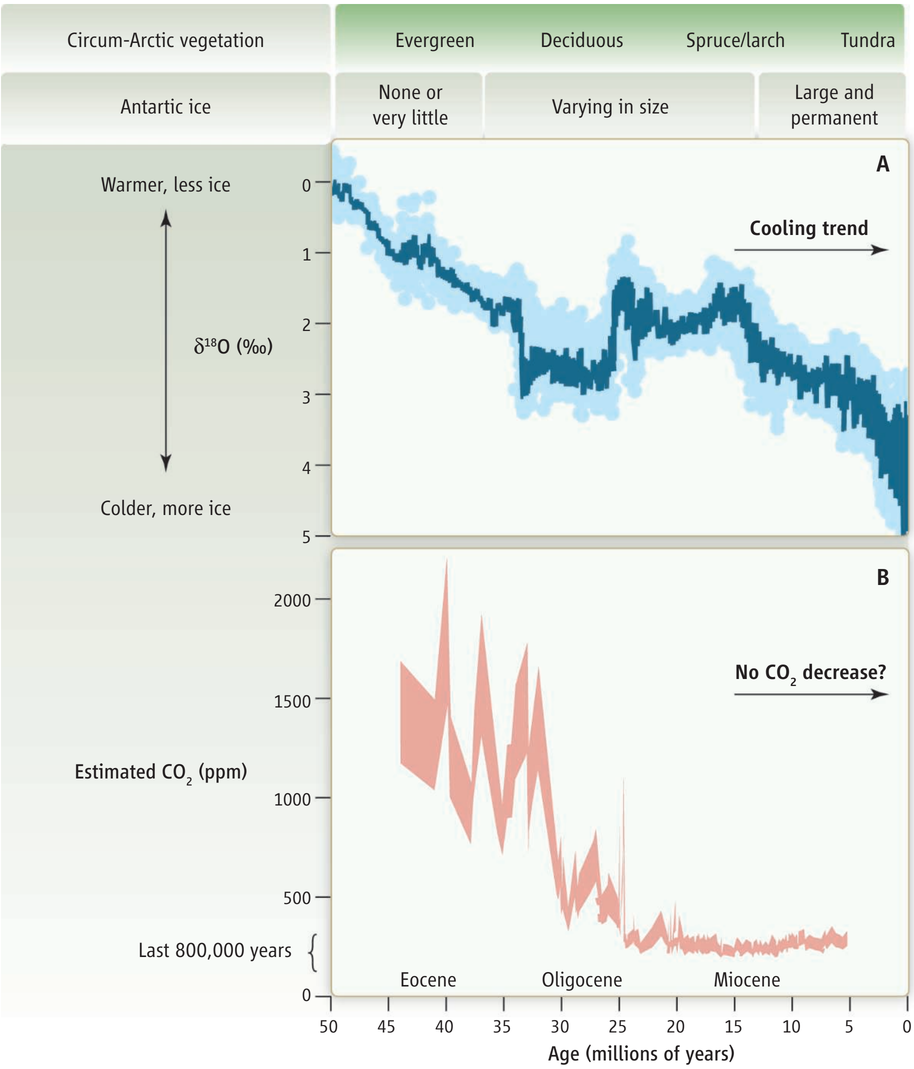

Indices of climate change in the past 50 million years. (**A**) Changes in circum-Arctic vegetation (*1*). (**B**) Changes in Antarctic ice sheet size. (**C**) Oxygen isotopic ($\delta^{18}O$) index of deep-ocean temperature and ice volume (*2*, *3*). (**D**) Estimates of past CO_2 concentrations from alkenones (*6*). Paleoclimatic data from both poles indicate a progressive cooling from 50 million years ago until the onset of Northern Hemisphere glaciation 2.75 million years ago, but reconstructions of atmospheric CO_2 concentrations from two prominent proxy methods show very low values by 25 million years ago and no subsequent decrease. If the CO_2 trend did not fall after 25 million years ago, the cooling trend would be difficult to explain.

but apparently without causing a large cooling in far-off polar regions (*10*). Chemical weathering of eroded debris in these uplifted regions is a plausible means of reducing atmospheric CO_2 concentrations (*5*), but this explanation brings us back to the problem of the persistently low CO_2 concentrations estimated for the past 22 million years (see the figure).

Paleoclimatologists were left with three possibilities. First, we might have overlooked something crucial. This option seems unlikely for a science that has been growing toward maturity for decades.

Second, one or more of the physical mechanisms previously proposed to account for global cooling could have had a much stronger effect than thought. Slow northward plate motions (*8*) and gradual plateau and mountain uplift (*10*) seem like good candidates to drive a gradual cooling, and in recent years, many interactive feedback processes added to general circulation climate models have boosted the size of climatic responses to these imposed forcings. Still, these feedbacks seem unlikely to have provided the amplification required.

Third, the proxy methods used to reconstruct CO_2 concentrations prior to ice-core records could be invalid. CO_2 concentrations estimated from the two proxies disagree by large amounts between 45 and 25 million years ago, with boron-isotope estimates having fallen to very low values but alkenone estimates still at high concentrations. Another problem is a disagreement with climate model simulations, which indicate that CO_2 concentrations below ~750 ppm should cause a large ice sheet to form on Antarctica (*11*). By this measure, the CO_2 estimates from boron isotope data predict the appearance of a large ice sheet by 55 to 50 million years ago, some 20 million years before the onset of substantial Antarctic ice (see the figure). The CO_2 trend from the alkenone proxy predicts that a large ice sheet would have formed by 30 million years ago, a few million years after the time that ice masses of varying sizes first formed, but long before the appearance of a large and stable ice mass.

Recent data have now raised further questions about the older CO_2 proxy estimates. The new boron/calcium (B/Ca) ratio predicts CO_2 concentrations of 350 to 450 ppm between 20 and 10 million years ago, a time when the other two techniques indicated values of 200 to 300 ppm (*12*). It also predicts somewhat higher concentrations between 1.4 and 0.9 million years ago than recent results from the boron isotope method (*13*). And a recent alkenone-based study shows a substantial CO_2 decrease from 5 to 2 million years ago (*14*). In general, these newer results suggest that a gradual CO_2 decline did play a role in northern glacial inception, contrary to previous proxy estimates.

From a paleoclimatic perspective, the simplest way to explain the large and ongoing bipolar cooling during the past 50 million years remains what it was a decade or more ago: a progressive decrease in atmospheric CO_2 levels that began at high levels 50 million years ago and continued to fall until the past few million years, rather than "bottoming out" as a forcing factor about 22 million years ago. If this view is correct, geochemists still have work to do in refining the CO_2 proxies.

References

1. J. A. Wolfe, *Am. Sci.* **66**, 994 (1978).
2. K. G. Miller, R. G. Fairbanks, *G. S. Paleoceanography* **2**, 1 (1987).
3. J. Zachos *et al.*, *Science* **292**, 686 (2001).
4. R. A. Berner *et al.*, *Am. J. Sci.* **283**, 641 (1983).
5. M. E. Raymo et al., *Geology* **16**, 649 (1988).
6. M. Pagani *et al.*, *Science* **309**, 600 (2005).
7. P. N. Pearson, M. R. Palmer, *Nature* **406**, 695 (2000).
8. E. J. Barron, W. M. Washington, in *The Carbon Cycle and Atmospheric CO_2: Natural Variations, Archaean to Present*, E. T. Sundquist, W. S. Broecker, Eds. (*Geophys. Monogr*. **32**, American Geophysical Union, Washington, DC, 1985), pp. 504–529.
9. U. Mikolajewicz *et al.*, *Paleoceanography* **8**, 409 (1993).
10. W. F. Ruddiman, J. E. Kutzbach, *Sci. Am.* **264**, 66 (1991).
11. R. M. DeConto, D. Pollard, *Nature* **421**, 245 (2003).
12. A. K. Tripati *et al.*, *Science* **326**, 1394 (2009).
13. B. Hönisch *et al.*, *Science* **324**, 1551 (2009).
14. M. Pagani *et al.*, *Nat. Geosci.* **3**, 27 (2010).

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