

fine-scale approaches, such experimental systems hold great promise for helping us to achieve a better understanding of the patterns we see in nature. ■

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1. Fisher, R. A. *Ann. Eugen.* **11**, 53–63 (1941).
2. Lively, C. M. & Lloyd, D. G. *Am. Nat.* **135**, 489–500 (1990).
3. Goodwillie, C., Kalisz, S. & Eckert, C. G. *Annu. Rev. Ecol. Syst.*

- 36, 47–79 (2005).
4. Jarne, P. & Auld, J. R. *Evolution* **60**, 1816–1824 (2006).
5. Morran, L. T., Parmenter, M. D. & Phillips, P. C. *Nature* **462**, 350–352 (2009).
6. Lande, R. & Schemske, D. W. *Evolution* **39**, 24–40 (1985).
7. Charlesworth, D., Morgan, M. T. & Charlesworth, B. *Evolution* **44**, 1469–1489 (1990).
8. Haldane, J. B. S. *The Causes of Evolution* (Harper, 1932; reprinted with introduction and afterword by E. G. Leigh, Princeton Univ. Press, 1990).
9. Peck, J. *Genetics* **137**, 597–606 (1994).
10. Colegrave, N. *Nature* **420**, 664–666 (2002).
11. Goddard, M. R., Godfray, H. C. J. & Burt, A. *Nature* **434**, 636–640 (2005).
12. Agrawal, A. F. *Curr. Biol.* **16**, R696–R704 (2006).

PALAEOCLIMATE

Kink in the thermometer

David Noone

Temperature estimates derived from isotopes in polar ice cores reveal much about Earth's past climate. According to the latest analysis, interglacial periods were rather warmer than previously thought.

For the past million years or so, the transition between glaciations and warm interglacials has been dominated by a cycle of about 100,000 years. The last warm period, the Eemian, occurred around 128,000 years ago, and from various proxy measurements it is widely accepted that temperatures then were higher than those during modern pre-industrial times. The Eemian therefore offers a window on the consequences of contemporary global warming. For instance, the warmer climate was associated with significant changes in the volume of the Greenland ice sheet, and as a result sea level could have been about 4–6 metres higher than it is today¹.

In this issue, Sime and collaborators² (page 342) describe how they have used climate-model simulations to re-examine the temperature history recorded by the isotopic composition of three long ice cores from Antarctica. The authors conclude that previous estimates of southern-polar warmth during the Eemian and other interglacials have in fact been underestimates. They suggest that temperatures peaked at some 6 kelvin higher than at present, about double the usually accepted figure.

Climate records from polar ice cores provide arguably the best indication of global environmental change on timescales from centuries to many millennia. Like tree rings that mark each year by a season of growing, the continuous accumulation of snow on the ice sheets provides a chronology. The isotopic chemistry of the ice then provides a measure of climate at the time the snow fell. This use of the stable hydrogen- and oxygen-isotope composition of polar snow as an indicator of past temperature comes from pioneering work performed almost half a century ago^{3,4}. At sites outside the tropics, a strong relationship exists between annual mean temperature and the annual mean

isotopic composition of precipitation⁵, which hints at the possibility of using the isotopes from a single site as a palaeothermometer. However, the question remains as to what degree this spatial information can be used to interpret the temporal variability captured in polar ice cores^{6,7}.

The mechanism leading to the temperature–isotope relationship at high latitudes is the preferential removal of the heavy nuclides oxygen-18 and deuterium (¹⁸O and ²H) during precipitation. During transport to the cold polar atmosphere, continual precipitation from an air mass originating at a lower latitude will deplete that air mass in the heavy nuclides. The isotopic composition will depend on the fraction of the original water mass remaining, which depends exponentially on temperature via the Clausius–Clapeyron relation. This gives an approximately linear relationship between the isotopic composition of precipitation and temperature, with a slope of about 8‰ per kelvin for ²H (Fig. 1). Knowing this slope, one can in principle convert measured changes in isotopic composition to a temperature scale.

There are, however, various confounding factors⁸. The isotopic composition of vapour at the source region is unlikely to remain constant; and changes in the distribution of the moisture source will change the isotope–temperature slope, because less-distant sources are less depleted and lead to a reduction of the slope⁹. Further, different cloud microphysical processes dictate a different efficiency in isotopic fractionation. Also, the average isotopic composition of annual layers of snow will be biased towards that of the season in which most of the precipitation falls, so changes in the time of year when snow falls could distort the reconstruction of annual mean temperature. Such factors mean that the spatial relationship



50 YEARS AGO

It has often been suggested that the dark areas of Mars consist partly of vegetation, particularly in view of the seasonal variation of the intensity of the dark regions. Tests for the high near-infrared reflectivity characteristic of many plants have all given negative results. A few terrestrial plants, such as some lichens, do not show this characteristic, and possibly such plants are present on Mars. W. M. Sinton ... has suggested and twice carried out a new test for the presence of vegetation. All organic molecules possess strong absorption bands at wave-lengths near 3.4μ ... The radiation received from Mars was analysed theoretically into thermal radiation and reflected solar radiation. The latter shows three absorption bands at 3.43μ, 3.56μ and 3.67μ ... Although one cannot be certain that no inorganic molecule can explain these absorption bands, the observed spectrum does fit very closely that of organic compounds and plants ... Sinton's results are the best evidence yet produced for the existence of vegetation on Mars.

From *Nature* 21 November 1959.

100 YEARS AGO

With reference to the recent paper by Dr. Pocklington before the Royal Society, on the functions of the Martian canals ... I should like to suggest that these canals may perhaps be used for power-storage purposes. In Mars, possibly, there are seasons of winds or monsoons during which the upper reaches of the canals would be pumped full by innumerable windmills, and the power thus stored utilised during calm seasons, and transmitted electrically for lighting, heating, and general power purposes. For a population which had exhausted all its mineral fuel, which possessed no extensive ocean, and whose soil and climate were unsuitable for the growth of fuel, this would indeed appear to be the only means of obtaining heat and power.

From *Nature* 18 November 1909.

50 & 100 YEARS AGO

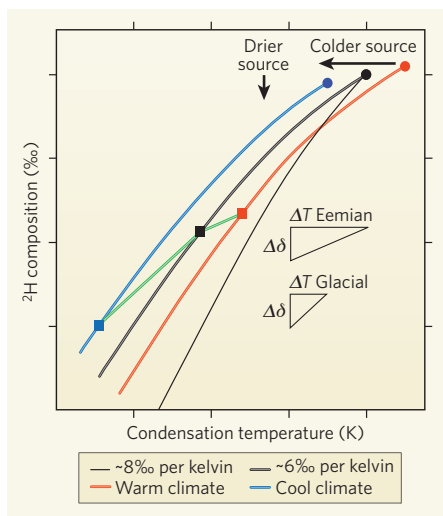


Figure 1 | Temperature-isotope relationships. As a moist air mass moves polewards from a lower-latitude source, and experiences continuous precipitation, the preferential loss of the heavy, ^2H , isotope gives an approximately linear dependence of ^2H composition on temperature. The result that emerges in spatial data⁶ is shown by the thin black line (slope $\sim 8\text{‰}$ per kelvin). Additional mixing during transport to the pole reduces the slope (thick black line, $\sim 6\text{‰}$ per kelvin). Change in the mean temperature and humidity of the source region (dots) will change the position of the curve but not the slope (blue and red lines). Change in the isotopic composition for a fixed ice-core site (squares) combines the spatial slope with any changes in the air-mass origin and mixing, and in cloud microphysics. The green lines depict Sime and colleagues' conclusion²: a reduced slope for warmer climates such as the Eemian implies a larger temperature change (ΔT) for a given isotopic difference ($\Delta\delta$) compared with the slope for glacial climates.

between the isotopic composition and temperature is more typically about 6‰ per kelvin. For reliable reconstructions, the extent to which these atmospheric processes influence the temporal slope must come into question — in fact, the slope itself can perhaps be seen as a measure of the processes.

In their re-evaluation of the evidence, Sime *et al.*² used isotope records from three Antarctic ice cores extending back to 340,000 years ago. These data show that the relevant temporal isotope slope differs from location to location, and that the slope is generally smaller during times when the climate is warmer. In their model simulations, the authors tested whether the isotope changes were attributable to local temperature change or to changes in the isotope-temperature slope. Their results show that the latter dominates. While challenging a tenet of temperature reconstructions from isotopes, their findings imply that the processes that control regional hydrology need not directly control the local annual mean temperature. During cold climates, the relatively small changes in the slope are consistent with temperatures inferred from earlier studies^{6,10}. But the lower slope during warmer, interglacial

climates leads Sime *et al.*² to conclude that temperatures were higher than those derived using the usual slope (Fig. 1).

The idea that interglacial climates were warmer than previously thought raises questions about the strength of climate feedbacks and regional amplification of warming at high latitudes. It is also relevant to the question of the stability of the existing Greenland and West Antarctic ice sheets — at what level of warming will large-scale melting occur?

The principle that the relationship between isotope composition and temperature is non-linear represents a coming-of-age for reconstructions of this kind: it is clear that a simple relationship is not adequate to capture the influence of atmospheric processes underlying the ultimate isotopic composition. A full appreciation of the meteorological underpinnings of this more complicated relationship remains

elusive, but such knowledge will provide insight into how changes in high-latitude storminess may change during warmer climates. ■

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1. Overpeck, J. T. *et al.* *Science* **311**, 1747–1750 (2006).
2. Sime, L. C., Wolff, E. W., Oliver, K. I. C. & Tindall, J. C. *Nature* **462**, 342–345 (2009).
3. Epstein, S., Sharp, R. P. & Goddard, I. J. *Geol.* **71**, 698–720 (1963).
4. Dansgaard, W. *et al.* *Science* **218**, 1273–1277 (1982).
5. Dansgaard, W. *Tellus* **16**, 436–468 (1964).
6. Jouzel, J. *et al.* *J. Geophys. Res.* **102**, 26471–26487 (1997).
7. Masson-Delmotte, V. *et al.* *J. Clim.* **21**, 3359–3387 (2008).
8. Worden, J. *et al.* *Nature* **445**, 528–532 (2007).
9. Noone, D. J. *J. Geophys. Res.* **113**, D04102 (2008).
10. Lee, J.-E., Fung, I., DePaolo, D. J. & Otto-Bliesner, B. *J. Geophys. Res.* **113**, D19109 (2008).

EPIGENOMICS

Methylation matters

Dirk Schübeler

Genome-wide maps of methylated cytosine bases at single-base-pair resolution in human cells reveal distinct differences between cell types. These maps provide a starting point to decode the function of this enigmatic mark.

Methylated cytosine, often referred to as DNA's fifth base, makes up a subset of nucleotides in the mammalian genome. As cytosine methylation does not affect base pairing, deposition of this mark can regulate processes, such as transcription, without affecting the genetic blueprint. Once established, the methylated cytosine modification can be faithfully copied to newly synthesized DNA, and so can be passed on to daughter cells, making it a true epigenetic mark. Many groups have studied the genomic distribution of DNA cytosine methylation and other chemical modifications of histone proteins to describe what has been dubbed the epigenome. On page 315 of this issue, a team headed by Joseph Ecker — Lister *et al.*¹ — provide the first complete DNA-methylation map of the human genome at single-base-pair resolution. Their accomplishment reveals intriguing features of the methylcytosine mark that were not identified in previous, less-comprehensive maps^{2,3}.

Many eukaryotes (plants and animals) use DNA cytosine methylation to silence parasitic elements that have invaded their genome, such as transposons and retroviruses. However, the mark can also be used to regulate the expression of naturally occurring genes, allowing an expanded repertoire of tissue-specific gene transcription. Because DNA cytosine methylation patterns change with age and in certain diseases (particularly in cancer), the distribution, function and regulation of this modification

are of great interest as a diagnostic marker and potential therapeutic target.

To achieve such a high-resolution genomic map of DNA methylation, Lister *et al.*¹ treated genomic DNA from human cells with sodium bisulphite, which converts non-methylated cytosines to uracil, but leaves methylated cytosines untouched⁴. The authors then sequenced the whole genome multiple times — a tour de force that was made possible through the recent development of high-throughput sequencing technologies. In total, 178 gigabases of sequence were generated, the equivalent of sequencing the entire genome 57 times. Sequencing at this unprecedented scale was crucial to these studies, as it is inherently difficult to map bisulphite-converted sequences back to the genome. Furthermore, only multiple sequence reads allow for confidence in base allocation — here, an astounding 94% of all cytosines in the genome were identified.

Such sequence coverage not only provides an outstanding information resource, but detailed analysis of these data also reveals several surprises, particularly in the differences in cytosine methylation patterns between certain cell types. The authors chose the cells they compared wisely: a human stem cell, which is pluripotent and so can develop into any other cell type; and a fibroblast, which is fully differentiated. Although the observed methylation patterns are comparable between both cell types, there are remarkable