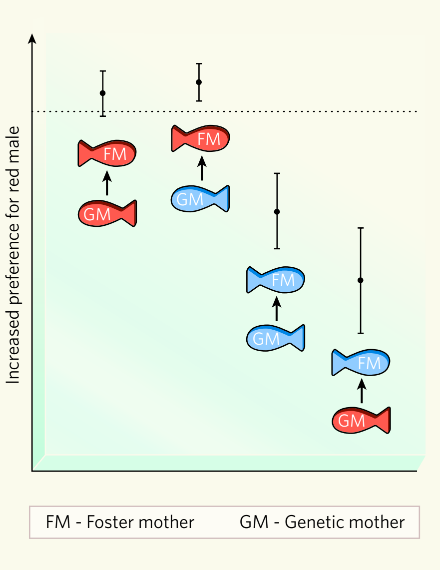

Figure 2 | The mother who raised you determines with whom you mate. In choice tests[7] with mouth-brooding cichlids, female fish raised by foster mothers belonging to different species from their genetic mothers preferred males of that different species. The stylized pictures are of males; females are dull and generally similarly coloured. The preference was measured by the difference in the number of approaches per male display when female fish are given a pair-wise choice (with standard errors; dashed line indicates random choice). This evidence suggests that learning at a young age contributes to reproductive isolation in cichlids, in addition to other mechanisms such as the action of natural selection on vision described by Seehausen and colleagues[1]. (Modified from ref. 7.)

contributes to speciation above and beyond its effects on mate choice.

But is even this enough? Other findings point to an additional mechanism that complements reproductive isolation via vision. The females of these remarkable fish brood their eggs in their mouths, then guard the young fry after they hatch. In experiments reported last year, Verzijden and ten Cate[7] swapped eggs between the mouths of red morph and blue morph mothers. Females raised from the experimental broods strongly preferred males from their foster morph over those of their own morph (Fig. 2). As females of the two species look very similar, it is unclear whether the offspring preference is based on colour or some other correlated cue such as odour. Regardless of that, learning at a young age (sexual imprinting) apparently contributes to reproductive isolation in these cichlids, as it does in other groups such as birds[8]. The implication is that assortative mating — the tendency of like to mate with like — can arise whenever male characteristics diverge in response to differences in the environment, which might happen even without divergence in the opsin pigments. It remains to be seen if imprinting, vision and perhaps other mechanisms have been sufficient to generate new species without geographical isolation.

An intriguing observation mentioned by Seehausen *et al.*[1] is that the red- and blue-biased opsin alleles are evolutionarily much older than the species studied here. Red and blue colour morphs are found in other species of cichlid[9], suggesting that the colour polymorphism may also be ancient. Perhaps one key to the spectacular species radiation of African cichlids is that they inherited from distant ancestors a trove of genetic variation for sensory systems and male signals, possibly contributed during the inferred episode of interbreeding 20,000 years ago. This variation is entrained again and again in speciation events. To systematists, these events represent independent nodes on the evolutionary tree. From the fish's point of view, however, they are perhaps more like an evolutionary play that is re-enacted, night after night, with the same genetic cast. ■

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CLIMATE CHANGE

When did the icehouse cometh?

Stephen F. Pekar

The concentration of atmospheric carbon dioxide decreased between 45 million and 25 million years ago, a trend accompanied by glaciation at the poles. Modelling results suggest when and where the ice closed in.

As atmospheric carbon dioxide is predicted to rise to concentrations not seen in perhaps 25 million years (Myr)[1], scientists are working to understand the impact on Earth's climate and ice sheets. This requires a shift in perspective: geologists typically use the present as a key to the past, but in this case the past might well be the key to predicting how climate will change in the future.

The concentration of CO_2 in the atmosphere is predicted to increase to between 500 and 900 parts per million (p.p.m.) by the end of this century. Geochemical proxies indicate that the last time CO_2 levels were that high was about 45 to 25 Myr ago[1]. This was when Earth changed from a generally ice-free 'greenhouse world' to a more heavily glaciated 'icehouse world'[2,3], with atmospheric CO_2 gradually decreasing from more than 1,000 p.p.m. to near pre-industrial levels (280 p.p.m.)[1]. So how did the falling atmospheric CO_2 concentrations affect ice-sheet development during this period? On page 652 of this issue, DeConto *et al.*[4] use numerical modelling to constrain the timing of the initiation of glaciation in relation to decreasing levels of CO_2. Their results not only address a long-standing geological debate, but are also relevant to today's discussion about climate change.

Given the current interest in the effects of CO_2 on climate, it may be surprising to learn that there is a great deal of uncertainty about the extent of ice sheets, and the causal factors in their development, during the last period when atmospheric CO_2 concentrations reached levels as high as those predicted for the end of this century. Some information can be gleaned by studying the remains of shells from foraminifers — single-celled marine organisms — of that period. The ratio of oxygen isotopes in the shells depends on both the temperature and the isotopic composition of the water in which the foraminifers lived. The isotopic composition, in turn, was controlled by the ice volume at the poles, and by the evaporation–precipitation history of the water when it was near the ocean's surface. By contrast, the ratio of magnesium to calcium in the shells is controlled mainly by the seawater temperature alone. By measuring the two ratios, the isotopic composition of sea water can be calculated and used to constrain the polar ice volume for the period in which the foraminifers were alive.

The data suggest[5,6] that the ice volume was much larger than could be reasonably placed on the Antarctic continent. These high ice-volume estimates, combined with evidence of ice-rafted debris off the coast of Greenland, raise the possibility that glaciation in the Northern Hemisphere might have developed about 40 Myr earlier than was previously thought (that is, up to 44 Myr ago, rather than 3 Myr ago).

DeConto *et al.*[4] cast fresh light on this issue. They developed a model of global climate and of ice-sheet formation that incorporates the decreasing levels of atmospheric CO_2 found

45 to 25 Myr ago, the oxygen-isotope composition of ancient glacial ice, and the expected effects of these parameters on deep-sea records from foraminifers. Their results show that continental-scale Antarctic glaciation would not have developed until CO_2 concentrations reached about 750 p.p.m. — which occurred in the early Oligocene period, 34 to 32 Myr before present (Fig. 1). However, they also predict that the threshold for significant ice-sheet development in the Northern Hemisphere is much lower (280 p.p.m.), and would have occurred about 25 Myr ago.

The authors' results show that, for glaciation to have occurred in the Northern Hemisphere, the drop in CO_2 at the start of the Oligocene must have resulted in CO_2 concentrations far below those estimated by geochemical proxies. They conclude that a unipolar glacial world developed for the first time about 34 Myr ago, coeval with a decrease in water temperature at the sea bottom that was not registered in previously recorded proxy data. These findings are supported by new data from pristinely preserved foraminiferal shells of that period, which show that significant bottom-water cooling must have occurred at the same time that Antarctic ice sheets grew to near modern-day volumes[7]. The new foraminiferal data are also in good agreement with stratigraphic records of sea-level change from sediments that were deposited on mid- to low-latitude continental margins[8,9].

DeConto and colleagues[4] also show that, at the CO_2 concentrations that occurred during the middle to late Eocene epoch (45 to 34 Myr ago), small, ephemeral ice sheets could have existed on the highlands of Antarctica — even though CO_2 concentrations were up to six times those of pre-industrial levels. Their conclusions are consistent with ice-volume estimates from stratigraphic records from non-polar continental margins[9,10]. Similarly, the authors demonstrate that small, isolated sheets of glacial ice could have formed in the Northern Hemisphere during the cooler intervals of the Eocene and Oligocene, especially during periods when variations in Earth's orbit produced relatively cold northern summers. This could explain why ice-rafted debris existed off the coast of Greenland during the late–middle Eocene (about 44 Myr ago)[6] without having to invoke the presence of massive continental ice sheets. The transient glacial ice in the Northern Hemisphere might have left a sedimentary record, but would have had insufficient volume to be detectable in oxygen-isotope records.

One of DeConto and colleagues' more intriguing conclusions is that, once CO_2 reached near present-day concentrations (about 25 Myr ago), large ice sheets could develop in the Northern Hemisphere during favourable orbits of the Earth. Given that the East Antarctic Ice Sheet is believed to have responded little to changes in climate once it reached near-continental size[11,12], the large variations in ice-volume indicated in isotopic and stratigraphic records[8] younger than 25 Myr old could therefore be explained in part by episodic ice-sheet growth in the Northern Hemisphere. This suggests that substantial ice growth in the Northern Hemisphere might have started up to 20 Myr earlier than previously believed — up to 25 Myr ago, rather than in the Miocene to the Pleiocene epochs 7 to 3 Myr ago. But there is currently scant evidence to suggest that large amounts of glacial ice existed in the Northern Hemisphere before the late Miocene. In addition, the large changes in ice volume suggested by proxy data for the period in which CO_2 reached near-present-day concentrations (less than 25 Myr ago) do not bode well for long-term sea-level changes in the future, as they suggest that small variations in CO_2 might have large effects on ice volume.

With such a paucity of information about the timing of Earth's ice development (especially in the Northern Hemisphere), there is a clear need for data from high-latitude sites in the Northern Hemisphere and around Antarctica to test DeConto and colleagues' conclusions. Fortunately, help is on its way, as several upcoming projects[13–15] will target strata from the greenhouse–icehouse transition in Antarctica, and are expected to provide additional insight into ice-sheet development in the region during this critical time interval. ■

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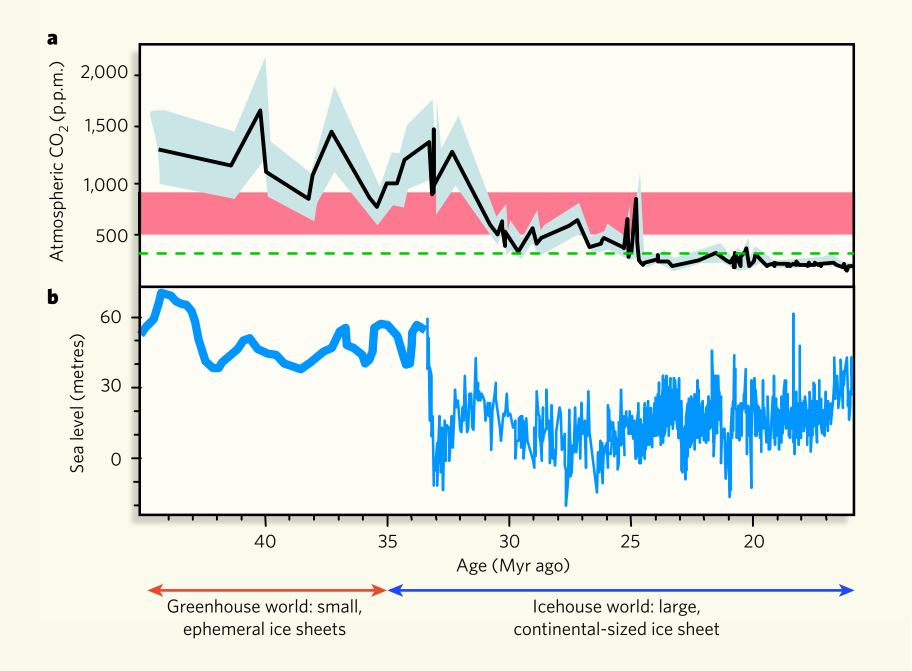

Figure 1 | Atmospheric carbon dioxide at the start of large-scale glaciation. About 34 million years (Myr) ago, Earth changed from a greenhouse world (which was generally ice-free) to an icehouse world (which was heavily glaciated). **a**, The concentration of atmospheric CO_2 during this period declined drastically, reaching pre-industrial levels (280 p.p.m., dashed line) about 25 Myr ago. Grey shaded areas represent the uncertainty in the estimates; the red shading shows the range of CO_2 values predicted for the latter part of this century[16]. Estimates of CO_2 concentrations are taken from ref. 1. **b**, Global sea level shows a downward trend. Zero represents sea level when Antarctica is fully glaciated, and increasing values indicate higher sea level (that is, lower ice volume). DeConto and colleagues' model[4] of global climate and ice-sheet formation suggests that, when Earth was a greenhouse world, short-lived glacial formation could occur at a small scale. But when Earth entered its icehouse phase, a large, continental-sized ice sheet formed, with a correlated lowering of the sea level. Apparent sea-level (ASL) estimates from 45 to 34 Myr ago are modified from ref. 9; ASL estimates from 34 to 16 Myr ago are modified from ref. 8.

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