sis of the receptor. Although they could not pinpoint the intracellular location of the cleavage event, an intense perinuclear accumulation of the DFrizzled2 extracellular domain is intriguing and raises the possibility that the cleavage and/or delivery of the intracellular fragment occurs at or near the nuclear membrane.

A correlation does not prove function, however, so the authors tested the requirement for receptor cleavage in Wingless signaling at the synapse. For multiple Wingless-mediated signaling events, DFrizzled2 activity is redundant with that of *Drosophila* Frizzled1 (*10*). However, synaptic maturation at the neuromuscular junction only requires DFrizzled2, and this allowed Mathew *et al.* to perform genetic studies and show that forms of DFrizzled2 that cannot be cleaved do not provide effective rescue of the *DFrizzled2* mutant phenotype.

These observations are surprising and raise several questions. In the past few years, cleavage of the intracellular domain of some cell surface receptors (e.g. Notch) has emerged as a way of modulating their activity (*11*, *12*). In all known cases, this is mediated by the γ-secretase complex and usually involves cleavage within the transmembrane domain. The observations of Mathew *et al*. (*5*) uncover a previously unknown mechanism that invites a closer examination of the activity and mode of action of the Frizzled receptor family. A second question concerns the exact role of the cleaved fragment. Although its presence in the nucleus in transcriptionally active areas suggests a role in gene expression, this remains to be shown. Mathew *et al*. have shown that cleavage is necessary for DFrizzled2 function at the neuromuscular junction—that is, to promote synapse maturation. However, they did not show that the intracellular domain itself provides that function, because expression of a soluble version of this domain has no activity. Perhaps the cleaved receptor is recycled to the cell surface or to some intracellular compartment where it acts in a functionally altered manner, and the carboxyl-terminal fragment is merely a byproduct of the process.

The observation that cleavage is triggered by Wingless echoes the unsolved question of how interactions between particular Wnt proteins and specific Frizzled receptors can elicit different molecular and mechanistic responses. Given the versatility of Frizzled-Wnt interactions in controlling signaling events and biological processes, it is not surprising that at the synapse, a highly specialized structure, these receptors and ligands exert their functional potential with an unexpected molecular twist.

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ATMOSPHERIC SCIENCE

Tiny Bubbles Tell All

Edward J. Brook

During the past 200 years, humans have caused a remarkable change in the levels of several atmospheric greenhouse gases. We know this from direct measurements that started in the latter half of the 20th century, but for earlier times we rely on tiny samples of the atmosphere trapped in polar ice. Coring the polar ice sheets provides access to these samples and allows us to place modern changes in the context of long-term natural cycles in greenhouse gases. Until recently, the longest of these ice core records (from Vostok Station in Antarctica) extended back 440,000 years (*1*). Now, reports by Siegenthaler *et al*. on page 1313 (*2*) and by Spahni *et al*. on page 1317 (*3*) extend our window into the past an additional 210,000 years.

The new ice core records come from the European Project for Ice Coring in Antarctica (EPICA) (see the figure). EPICA, an international collaboration of scientists, engineers, and drillers, made a major contribution to the study of past climates by recovering this deep ice core in East Antarctica where low snowfall rates allow the accumulation of an extremely old section of ice (*4*). One of the new findings from this project concerns the nature of long-term glacial-interglacial climate cycles. Ice core scientists use the ratio of deuterium to hydrogen in ice as a proxy for temperature. Records from EPICA Dome C show a strong 100,000-year periodicity for the past 740,000 years (*4*). The existence of this cycle is well known from ocean sediments and other types of climate records. Its origin is enigmatic, because external climate forcing caused by changes in Earth's orbit is weak on this time scale. In the Dome C record the oldest three cycles are of lower amplitude than their later cousins. The reason for the shift from low- to high-amplitude cycles is not clear, but an obvious question concerns the behavior of the major greenhouse gases during the older time period (*4*).

Siegenthaler *et al*. (*2*) and Spahni *et al*. (*3*) address this issue with new records of atmospheric carbon dioxide, methane, and nitrous oxide, created through the collaborative efforts of two European research groups. They combine their work on Dome C with previous work on Vostok and other ice cores to create records of these gases covering the past 650,000 years. These new records will no doubt become canonical figures in the global change literature, as did the Vostok records before them (*1*).

Two basic messages are apparent in this extended history of the atmosphere. First, even with this longer perspective, the modern atmosphere is still highly anomalous. At no time in the past 650,000 years is there evidence for levels of carbon dioxide or methane significantly higher than values just before the Industrial Revolution. Second, the covariation of carbon dioxide and methane with climate, strikingly evident in the Vostok record, follows essentially the same pattern in the earlier time period. The muted climate cycles (as indicated by the deuterium content of the ice) are accompanied by equally muted cycles of carbon dioxide and methane (see the figure). This relationship reinforces the view that the large-scale cycles in Antarctic temperature have global importance, and that climate and greenhouse gas cycles are intimately related.

For nitrous oxide, the picture is slightly less clear. The record is not complete, making it difficult to judge how or whether the amplitude of 100,000-year cycles changed with time, and anomalous levels of nitrous oxide appear to be related to high levels of dust in the ice. This had been observed before and was attributed to microbial activity in ice with high levels of terrigenous dust (*5*). Spahni *et al*. argue plausibly that the enrichment is significant only in very dusty ice, and use dust records to determine which samples they feel are reliable (*3*). This is probably the

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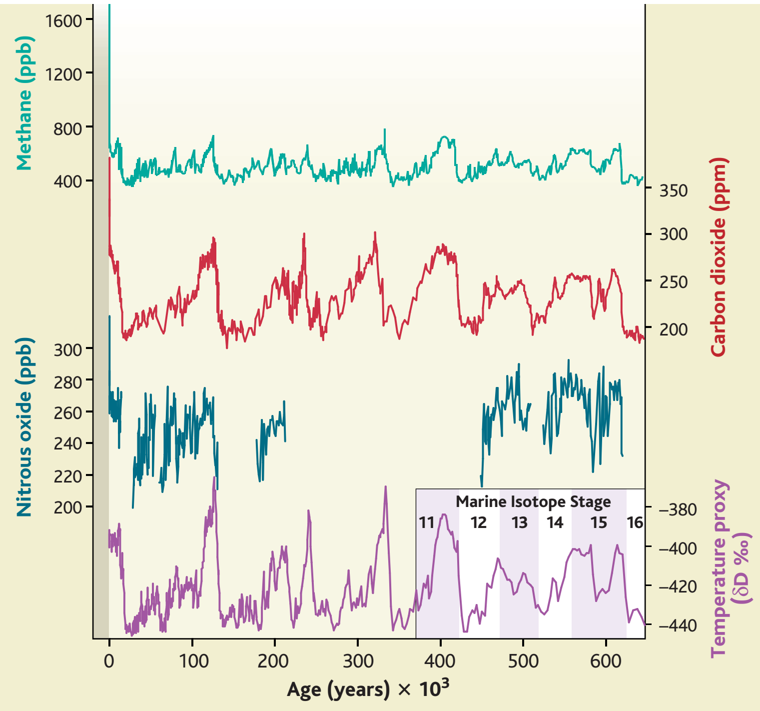

The long view. The greenhouse gas (CO_2, CH_4, and NO_2) and deuterium (δD) records for the past 650,000 years from EPICA Dome C and other ice cores, with marine isotope stage correlations (labeled at lower right) for stages 11 to 16 (*2*, *3*). δD, a proxy for air temperature, is the deuterium/hydrogen ratio of the ice, expressed as a per mil deviation from the value of an isotope standard (*4*). More positive values indicate warmer conditions. Data for the past 200 years from other ice core records (*20*–*22*) and direct atmospheric measurements at the South Pole (*23*, *24*) are also included.

best that can be done at this point, but it is less than satisfying, as one wonders about smaller levels of contamination at lower dust levels.

What causes the glacial-interglacial variations in these gases? For carbon dioxide, this question has been a grand challenge in geochemistry for decades. The answer most likely lies in the ocean, and the tight coupling with Antarctic climate suggests that high-latitude Southern Ocean processes are important. Dome C gives us more data to reinforce these thoughts, but convincing explanations are still elusive. Methane variations are widely believed to result from climate driven changes in emissions from tropical and boreal wetlands (*6*). The new methane data reinforce the climate-methane connection but leave on the table lingering questions about methane hydrates (*7*) and new ones about the atmospheric methane sink (*8*). For nitrous oxide, climate-driven variations in both marine and terrestrial sources are probably the dominant factors (*9*, *10*). Another challenge is to understand the feedbacks that control the rather uniform upper and lower limits of the natural concentration cycles. The Dome C record lengthens the target for biogeochemical modelers bold enough to accept these challenges. In fact, some have already risen to the bait, and the first evaluation of modeling skill will come when the results of the "EPICA Challenge," a contest of sorts to predict the Dome C greenhouse gas records (*11*), are evaluated.

The new results also provide a tantalizing view of greenhouse gas variations within the older climate cycles. These cycles have been correlated with marine isotope stages (MISs) of the oceanic oxygen isotope record, used by paleoceanographers. For both methane and carbon dioxide there are millennial-scale variations in cold stages that presage similar variability during the last ice age (*6*, *12*, *13*), known to be related to abrupt climate shifts recorded in Greenland ice cores and other archives. There are also interesting variations in warm stages. During MIS 11, an interglacial period between about 420,000 to 370,000 years ago, methane reached typical maximum levels, fell by about 100 parts per billion over 5000 years, then rose again toward the end of the interglacial period. This is similar to the pattern over the past 10,000 years (*14*), which has been the subject of an interesting argument over the impact of early human activities on the atmosphere (*15*, *16*). Apparently, natural variability can also result in relatively large oscillations in greenhouse gases during interglacial periods. MIS 11 has previously been identified as an exceptionally long interglacial (*17*), but the Dome C record now suggests that MISs 13 and 15 were similarly long, with surprisingly constant levels of carbon dioxide, methane, and nitrous oxide in MIS 15. Although this suggests that interglacial periods can last for quite a long time, and may assuage fears about the demise of the current one, there are complications. Isotopic records from benthic-dwelling foraminifera—which record a combined signal of temperature and continental ice volume change, and provide, to first order, a global record of climate change—don't support the long MIS 15, raising the possibility of some uncertainty in this part of the Dome C time scale.

Chronological uncertainties also may be apparent in MIS 14, where the temporal phasing of methane, nitrous oxide, and carbon dioxide are different than expected, and in MIS 13, where the Dome C temperature proxy appears to lag the benthic oxygen isotope signal (the reverse is expected because of the slow response of the ice sheets to climate change). The Dome C time scale is based on ties to the marine isotope record, but also on glaciological calculations of ice flow, thinning, and densification (*4*). (The latter is particularly important for estimating the age difference between gases and ice—and therefore the age difference between these gases and the temperature record—because of bubble close-off at depth in the snowpack.) These are in turn based on assumptions about ice thickness history, basal melting, and snow accumulation (derived from the temperature proxy). There are no ties to the marine record within MISs 13 to 15 (*4*), so inaccuracies in glaciological parameters, possibly anomalies in ice flow, may explain the chronological mismatches. It is worth pointing out that the entire pre-Vostok section of the Dome C core is in the bottom ~400 m of a 3200-m ice core (*4*). There is no evidence of large-scale irregularities in the stratigraphy of the record, but the risk of glaciological anomalies clearly increases as one approaches bedrock. Sorting out the chronological details related to these issues will take time, but these uncertainties in no way diminish the importance of the Dome C records, which set a new standard for ice core science.

What's next for old ice core gases? Further analysis of the Dome C and other cores, including stable isotopic composition of the three gases, will help establish the patterns and causes of variability more firmly. We also may go deeper and thus older. The Dome C ice record may ultimately extend to 900,000 years (*4*). Interpreting the bottom section of an ice core is a tricky business, however, because melting, folding, and other processes can distort the stratigraphic order and contaminate the record. Getting back this far is a tantalizing goal, though, because it is at about this time (the so called "mid-Pleistocene transition") when marine sediment records indicate a change in the period of Earth's major climate cycles, from a dominance of ~40,000-year cycles (the "40 k" world) to the 100,000-year cycles (the "100 k" world). This transition is not well understood. One commonly cited hypothesis involves long-term cooling and increasing ice volume due to a decrease in average atmospheric carbon dioxide levels over the past 2 million years (*18*). Many competing mechanisms have been invoked, however, and even the existence of a global long-term cooling trend is not clear (*19*).

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In reality, it is likely that an even older ice core record will be needed to adequately address this question, because even a 900,000-year record would probably end in the middle of the 40 k–100 k transition. Such a core is in the works. International Partnerships in Ice Coring Science, a diverse group of ice coring scientists and drillers, has been planning major drilling projects. An ice core record through the mid-Pleistocene transition and into the 40 k world was high on the agenda at the most recent meeting in Brussels, in October 2005. Careful survey work and logistics planning will be necessary, as the most probable locations for cores of this age are in the coldest and remotest parts of Antarctica. Nonetheless, as the new EPICA records show, the payoff of deep ice coring is a dramatically improved understanding of the coevolution of climate and greenhouse gases. Explaining the origins of these relationships remains a major goal of global Earth science.

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PLANETARY SCIENCE

Saturn's Strangest Ring Becomes Curiouser and Curiouser

Mark R. Showalter

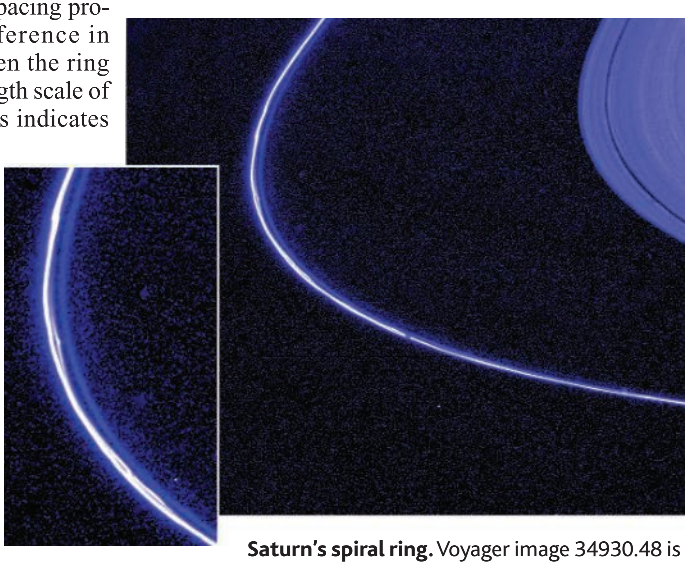
The Cassini spacecraft continues to send back astounding images of Saturn and its retinue of rings and moons. We have become so accustomed to new wonders that it is hard to remember the shock of seeing Saturn's F ring up close for the first time (see the figure). On 12 November 1980, Voyager 1 sent back its first closeup images of this faint and narrow ring orbiting just outside Saturn's main rings. The image revealed what were variously described as kinks, clumps, strands and, most famously, "braids" in the ring. On page 1300 of this issue, Charnoz *et al.* (*1*) offer a new and perhaps even more puzzling description of the F ring thanks to Cassini: It is a spiral.

The Voyager images showed features that deviated substantially from those of a simple ellipse, so concerns were initially raised that the F ring might violate Kepler's basic laws of orbital motion. Luckily, we have come to understand that Kepler's laws still apply: Each particle in the F ring follows its own elliptical orbit about Saturn. The kinks and so-called braids do not represent the paths of individual particles; they are instantaneous snapshots of a ring containing particle orbits that vary from place to place.

The ring's nearby "shepherding" moons, Prometheus and Pandora, have long been recognized as providing the gravitational tugs that continuously regenerate some of this ring's curious patterns. Because Keplerian orbits are closed, encounters between a moon and a ring recur each time the moon circles the planet. The effect on the ring is a pattern that roughly repeats, with a characteristic spacing proportional to the difference in orbital speeds between the ring and the moon. The length scale of most F-ring structures indicates that Prometheus, the larger and closer of the two moons, is the major "braid-maker."

However, perturbations by nearby moons are insufficient to explain many of the ring's other curiosities. The Voyager images showed that the brightest clumps are not periodic (*2*, *3*). Some of these, the so-called "bursts," appear suddenly and then spread out over time scales of days to weeks. Others evolve more slowly but still last no longer than months. What can cause such rapid changes? One hypothesis is that the most rapid "bursts" are dust clouds arising when a meteoroid hits the ring; the other is that all the clumps arise from mutual impacts among ring bodies (*4*). The debate hinges on whether mutual collisions can occur at high enough speeds to produce the bursts. In this regard, the discovery of the object designated S/2004 S6, which is either a small moon or a long-lived clump, is of particular interest. Its orbit can intersect the F ring at very high speeds, perhaps making mutual collisions a more viable explanation.

As far as F-ring structures go, the newly reported spiral is in a class by itself. It is clearly evolving according to the laws of Kepler, so that between November 2004 and May 2005 it has wound itself into a tighter spiral. By running the kinematics



Saturn's spiral ring. Voyager image 34930.48 is one of two that first revealed the kinks, clumps, and "braids" of Saturn's F ring. The faintest features have been enhanced in blue to make them more visible. The inset shows the ring's peculiar structures in finer detail. New Cassini data continue to challenge our understanding of how such surprising structures are able to form.

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