length of Mmu 16. One 6-Mb region contains only 7 genes; another 1.1-Mb region contains 17 genes. In general, mouse genes tend to be smaller than their human counterparts. This is largely attributable to differences in the amount of SINE and LINE sequences in these two genomes. In human, these large repetitive-element families account for 46% of base pairs, whereas in mouse they account for only 36%.

In contrast to the high degree of conservation observed for single-copy genes, those located within tandem gene clusters differ extensively in their number, coding potential, and organization between the two species. A good example is the zinc finger (*ZNF*) genes located on Hsa 19. This human chromosome carries 262 C2H2 *ZNF* genes, dispersed among 11 different syntenic clusters. Most clusters contain closely related gene sequences that appear to have arisen by tandem duplication of ancestral copies. Many related mouse clusters, however, contain very different complements of *ZNF* genes, and gene analysis suggests that different founder genes were duplicated, lost, and selected independently in each conserved cluster. Most duplicated genes retain their coding capacity, suggesting that they have nonredundant adaptive functions that complement those of the ancestral parental genes. Because *ZNF* genes are important regulators of gene expression, these species-specific amplifications and deletions almost certainly helped to shape the evolution of these two species. Similar results were also reported for olfactory and putative pheromone receptors genes and could easily account for differences in the way humans and mice taste their food and attract sex partners.

The mosaic organization of mammalian genomes is likely to be due principally to lineage-specific rearrangements of these genomes over their evolutionary history. Evidence for these rearrangements can be seen in gene density changes—SINE + LINE density, and G + C content—in sequences located at the boundary of the rearranged syntenic segments. As pointed out by Mural and colleagues (*1*), these sequence differences could easily be explained by the breaking and joining of ancestral chromosomal regions with very disparate properties. Several syntenic breakpoints are located in clustered gene families, with the break splitting closely related family members. Mouse breakpoint clones also tend to be L1 sequence-rich, showing a twofold increase over the L1 repeat content of other mouse DNA. These repeated sequences might have been the driving force behind the genomic rearrangements; repeated sequences have been proposed to drive the genomic rearrangements documented in several human diseases.

As provocative and fascinating as these inferences are, they are only the harbinger of what is yet to come when the public sequencing project discloses a finished, more thoroughly curated, sequence of mouse and man. (Celera has deposited the Mmu 16 sequence at GenBank, but the remaining mouse sequence is proprietary, requiring hefty fees for inspection and analysis.) The prospect of whole-genome sequencing for other mammals (rat, chimpanzee, macaque, cattle, pig, dog, and cat are likely candidates) offers an unprecedented opportunity to address a variety of genomic mysteries, hitherto restricted to speculation and learned guesswork. What is the nature of and the selective pressure responsible for the high incidence of conserved syntenic anchors outside coding gene limits, estimated here as 44%? What are the evolutionary forces that drive and maintain the chromosomal exchanges, translocations, and internal inversions that punctuate the genomes of modern mammals? In lineages with highly reshuffled chromosomes (rodents, bears, chimps, owl monkeys, squirrel monkeys muntjaks, and others) (*6*, *8*), which events favor the burst of these rare genomic reorganizations? How do new genes arise and others disappear in species genomes? Do these events actually matter in species adaptation and survival? As whole genome sequences become interpreted against the mammalian evolutionary background and dynamic genome tinkering is revealed, we shall be able to view what has happened in our evolutionary past, what matters to our future, how modern genomes and developmental adaptations were sculpted. Our genomes hold the gene-script for specifying modern species, including ourselves, and are now beginning to reveal a rich new perspective of how they came to be.

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PERSPECTIVES: CLIMATE CHANGE

Carbonate Mysteries

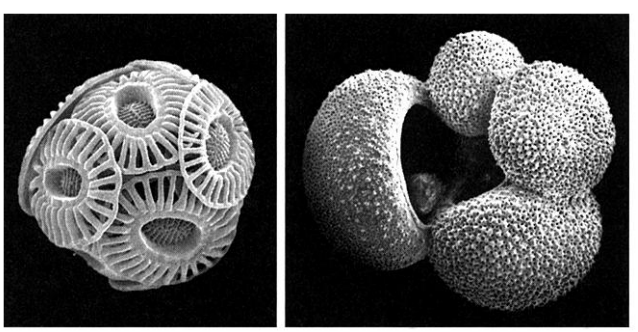
Henry Elderfield

The pH of seawater is controlled by dissolved calcium carbonate, which provides a buffer against pH perturbations—natural or manmade—that strive to change it. One such perturbation is atmospheric carbon dioxide (CO_2), an acidic gas that is exchanged between atmosphere and ocean.

During glacial cycles, concentrations of CO_2 in the atmosphere vary widely, putting the carbonate buffer through a tough test. A recent study suggests that it coped more efficiently than previously thought (*1*). A second study reaches the opposite conclusion (*2*). Other work, on the short time scale of a laboratory experiment, suggests that changes in buffer strength may be balanced by changes in biological precipitation of calcium carbonate from seawater (*3*).

Who is right? The answer has considerable implications for the ability of the oceans to sequester anthropogenic CO_2 from the atmosphere.

The seawater carbonate system works just like a buffer used in a chemistry laboratory. It counters changes in pH by altering the proportions of the abundant weak acids bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}). The oceans are currently buffered to a slightly alkaline pH of 7.6 to 8.2. The buffer works well as long as relatively small amounts of acid or base are added. However, all chemical buffers are only effi-



Scanning electron microscope images of marine calcifying organisms. (Left) The coccolithophore *Emiliani huxleyi* (diameter 5 μm) and **(right)** the foraminifer *Globigerina bulloides* (diameter 400 μm).

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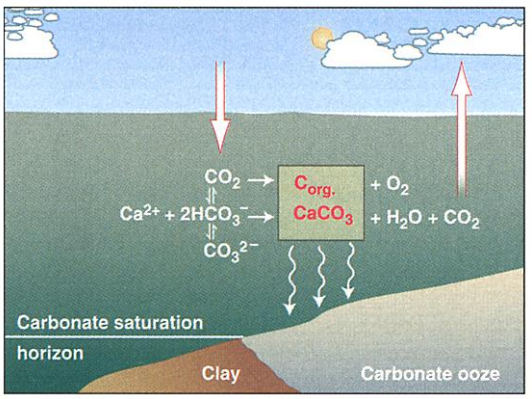
cient over a limited pH range. The capacity of the ocean carbonate system to absorb additional acid (such as CO_2 from the atmosphere) can eventually break down. Even today, the buildup of CO_2 in the atmosphere is decreasing the buffer capacity, making the oceans more acidic.

It has been predicted that the pH of the surface oceans will drop by 0.35 by 2100 in response to the "business as usual" scenario of anthropogenic emissions (*4*). This scenario assumes atmospheric CO_2 concentrations of 700 parts per million (ppm) by 2100 (*5*) (compared with 280 ppm before the industrial revolution and ~370 ppm today). The deep oceans respond more slowly to atmospheric CO_2 changes than the surface oceans, on time scales of thousands of years, because it takes about 1000 years to mix surface and deep waters.

At the last glacial maximum, CO_2 concentrations were much lower (~190 ppm) than they are today. Sanyal *et al.* have estimated that the pH of the glacial ocean as a whole was 0.3 units higher than it is today (*6*). They based their estimate on the pH sensitivity of boron isotopes, measured in the calcium carbonate shells of marine microfossils called foraminifera (see the first figure). A new estimate by Anderson and Archer suggests, however, that there was no such whole-ocean pH change (*1*). The authors measured the proportions of different surface-dwelling (planktonic) species of foraminifera preserved in glacial-age sediments. Apart from the temperature of the surface seawater in which the species calcified, preservation is the next important factor controlling their distribution. The authors found that there was little overall difference between glacial times and today.

We know from the modern oceans that some foraminiferal species are more affected by dissolution on the sea floor than others. Therefore, the proportions of different species present in the sediments provides a measure of the corrosiveness of bottom waters to calcium carbonate shells. The solubility of calcium carbonate depends on the concentrations of calcium and carbonate ions in seawater. Calcium does not vary much in seawater and so solubility is controlled by the CO_3^{2-} concentration (as well as temperature and pressure).

The link between CO_3^{2-} and pH comes from the thermodynamics of seawater. The CO_3^{2-} concentration is proportional to pH and inversely proportional to the CO_2 concentration. This is intuitively obvious: A lower CO_2 concentration makes seawater less acidic, which in turn reduces $CaCO_3$ dissolution. Thus, the dissolution susceptibility of assemblages of surface-dwelling foraminifera is a measure of the pH of the seawater above the deep-sea floor on which the shells settle after death of the calcifying organisms. This approach yields evidence of only a small rearrangement in the present day contrast of CO_3^{2-} between ocean basins and no whole-ocean change; hence, there is no overall change in pH.



Aspects of the ocean's carbon pump. Carbon exists inorganically dissolved in seawater as aqueous CO_2, bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}). The organic pump is a sink for atmospheric CO_2, whereas the carbonate pump is a source of CO_2 on short time scales. Therefore, depending on the ratio of organic to calcite carbon sequestered by the organism, calcifying organisms sequester less carbon than noncalcifying organisms and may provide a potential source of CO_2 to the atmosphere. Upon death of the organisms, the carbonate skeletons fall to the seabed, where they are generally preserved if the overlying water is saturated with respect to calcium carbonate solubility, although dissolution susceptibility varies between species.

There are two problems in reconciling this result with what we already know. The first is that the lower glacial CO_2 concentration must be accompanied by higher CO_3^{2-} concentrations, at least in surface waters, which then sink to ventilate the deep ocean. Yet Anderson and Archer found no evidence for the higher CO_3^{2-} concentrations. To explain the second problem, we have to consider how the interplay of ocean chemistry with ocean physics and biology affects the distribution of CO_3^{2-}. I will digress a little to explain this point.

The ocean's organic carbon pump (see the second figure) fixes CO_2 through the combined activities of phytoplankton and bacteria, which provide carbon for the marine food chain. Sinking of organic matter out of surface waters acts as a biological pump that draws down atmospheric CO_2 (there is a second component to the biological pump that I shall mention later). A proportion of this carbon becomes oxidized in intermediate and deep waters, increasing CO_2 (called "respired CO_2") and thereby decreasing CO_3^{2-} concentrations. This overall process, coupled with the sinking and upwelling of ocean waters, transports CO_2 into and out of ocean depths. Today's deep Atlantic Ocean is high in CO_3^{2-} because it is ventilated by waters sinking from the surface to form North Atlantic Deep Water (NADW), whereas the Pacific is low in CO_3^{2-} because its deep waters accumulate respired CO_2 on the journey from the Atlantic.

We know from paleochemical proxies that a glacial equivalent of NADW existed but that it ventilated the Atlantic at intermediate depths only, down to around 2 km. The dissolution data of Anderson and Archer, over sea-floor depths of 1 to 5 km, show no such feature, whereas another recent study of the ocean's carbonate system does show the existence of CO_3^{2-}—enriched glacial intermediate waters (*2*). This second method is also based on foraminiferal dissolution.

Broecker and Clark (*7*) use foraminiferal shell weight as a measure of CO_3^{2-} concentration. Focusing on single species of foraminifera in a narrow size range, they calibrated the shell weight of samples in modern core tops against bottom-water CO_3^{2-} concentration, normalized to account for depth (pressure) effects. The first application of the method (*7*) showed large depth gradients of CO_3^{2-} in the glacial Atlantic, but it was difficult to pin this down to the influence of glacial NADW. In their latest work, the authors use cores from the Caribbean to show that this water mass had higher CO_3^{2-} during glacial times than today, in agreement with paleochemical proxies (*2*).

Why are such different results reached by two approaches that are both based on foraminiferal dissolution? One complication is that carbonate dissolution occurs mainly in the pore waters of sediments and not on the sea floor. Both approaches assume that the difference between bottom-water and pore-water CO_3^{2-} remains the same for both glacial times and today. However, if this assumption is not correct, it should affect both approaches. Other possibilities are that the dissolution susceptibility of carbonate was different in glacial times, or that the initial shell weight is affected by environmental factors (*8*).

The factors influencing marine calcification and the mechanisms by which carbonate dissolution occurs in sea sediments remain poorly understood. Yet, they are crucial for understanding the role of the oceans in the regulation of atmospheric CO_2 on short and long time scales. A recent investigation of regulation on short time scales focuses on another type of sur-

face-dwelling marine calcifying organism: the coccolithophores (see the first figure), perhaps the largest contributors to global marine calcium carbonate precipitation. In laboratory experiments, Zondervan *et al.* have shown that the ratio of calcium carbonate to organic matter decreased with increasing CO_2 (*3*). This is logical: Increased CO_2 is accompanied by decreased CO_3^{2-}. But the implications of this observation are potentially very important, because of the second component of the biological carbon pump in the oceans.

As discussed earlier, the ocean's organic carbon pump provides a sink for CO_2. The calcium carbonate pump transports inorganic carbon from the surface ocean to the deep-sea floor, but calcification uses carbon dissolved in seawater as HCO_3^- ions. Two moles of HCO_3^- react with 1 mole of Ca^{2+} to precipitate 1 mole of calcium carbonate, releasing the extra mole of carbon as CO_2. Thus, biogenic calcification is a potential source of CO_2 to the atmosphere, rather than a carbon sink.

This seemingly counterintuitive observation is important for marine calcification. We imagine that the carbonate accumulations that drape the deep-sea floor or form the White Cliffs of Dover provide a sink for CO_2, which they do—but only on long time scales. The HCO_3^- used in calcification is indeed originally from the atmosphere. But it is delivered to the ocean from the weathering of continents and is buried as carbonates on long time scales, relative to the surface-ocean process that exchanges CO_2 with the atmospheric reservoir on time scales shorter than 1000 years.

The most interesting part of the work by Zondervan *et al.* is that the decrease in calcification associated with increased CO_2 exerts a negative feedback on rising atmospheric CO_2. Higher CO_2 leads to less calcification and hence less CO_2 release, counteracting the decreased buffer capacity of the anthropogenic carbon world. However, this should not lead to complacency. Decreased calcification might have major effects on ecosystems [calculations (*9*) and biosphere experiments (*10*) suggest that corals will be affected]. It may inhibit sinking of organic carbon from surface waters and lower the ocean's ability to take up CO_2.

To counteract the rising levels of atmospheric CO_2, the strategy of carbon sequestration, or carbon fixation, is receiving increased attention. The goal is to capture the CO_2 produced by fossil fuel burning and put it out of harm's way. Some are looking at ways to help the oceans sequester more carbon. It is clear that we have a lot to learn about how this process works, even without human enhancement. Certainly, the influence of manmade or glacial-interglacial shifts in atmospheric CO_2 on oceanic carbon sequestration remains unclear.

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PERSPECTIVES: PALEOCLIMATE

Toward Solving the UV Puzzle

Jelte Rozema, Bas van Geel, Lars Olof Björn, Judith Lean, Sasha Madronich

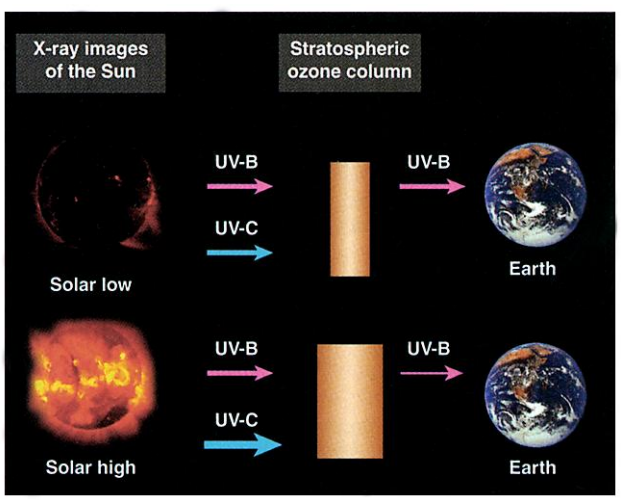
Springtime depletion of the ozone layer above the Antarctic was first observed by ground-based measurements from Halley Bay from 1979 to 1984 (*1*). Ever since, there has been great concern about ozone depletion and its consequences for the biosphere, because lower ozone concentrations lead to increased exposure to harmful solar ultraviolet radiation from 280 to 315 nm (called UV-B).

Today's ozone depletion and increased UV-B levels are mainly caused by human-made chemicals, especially chlorofluorocarbons (CFCs). But both ozone and UV-B also vary naturally. Knowledge of past stratospheric ozone concentrations and surface UV-B radiation is rudimentary, but recent research is beginning to shed light on how they have varied on time scales of tens to hundreds of years.

At wavelengths shorter than 242 nm, UV light dissociates molecular oxygen to form oxygen atoms, which combine with additional O_2 to produce ozone. The ozone absorbs solar radiation at UV wavelengths of 200 to 340 nm and in the visible spectrum. This absorption of UV light by ozone is the primary energy input to the stratosphere.

Variations in ozone concentration modulate the stratospheric temperature, leading to changes in atmospheric circulation that may propagate to Earth's surface and influence atmospheric circulation patterns worldwide (*2–4*). Ozone changes directly alter UV-B received at the surface. However, relating surface UV-B levels to the overhead ozone concentration has proven difficult because ozone variability has multiple causes, the ground-based database is generally poor, and changes in cloud cover and other climate parameters can further alter the surface UV-B.

Systematic instrumental measurements of stratospheric ozone over the Antarctic started only in 1957. Solar UV-B measurements began even later, and systematic ground-



Solar activity, stratospheric ozone, and surface UV-B. At a solar high, solar UV-C is enhanced, leading to a thicker ozone layer and reduced surface UV-B fluxes. Surface UV-B is thus anticorrelated with changes in solar activity (see the second figure). The changing thickness of the stratospheric ozone layer may amplify the changes in solar activity (*2*) because more ozone means extra absorption of heat, with effects on the stratospheric and atmospheric circulation patterns.

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