

mobilized the reporter construct into new genomic locations. As demanded by selection for reporter-gene expression, these new sites were transcriptionally active, and each had 'trapped' the reporter-gene exon as part of a different chimaeric messenger RNA expressed in these cells.

As well as showing that L1 can transduce 3' flanking sequences into target genes, the new work illuminates aspects of L1 retrotransposition. For example, the authors estimate the frequency of L1 retrotransposition into actively transcribed genes to be at least 6%. The 3' transduction process also provides a convenient explanation for peculiarities of L1 structure, such as the dramatic variability in 3' untranslated sequences of different L1 subfamilies — they probably arise from different 3' transduction events, followed by internal deletions. Similarly, it is plausible that 5' transduction events could occur, explaining the great variability observed among 5' end sequences in different L1 subtypes. If a cellular promoter read into a full-length or partially truncated L1 element, the result would be a new 5' end for the element. Finally, 3' transduction explains the puzzling lack of target-site duplications for many L1 elements.

Moran and colleagues' results² indicate that read-through transcription of L1s is surprisingly efficient, even when the reporter gene's preferred polyadenylation signal is as much as two kilobases from the native L1 3' end. This L1 read-through transcription — terminated by a strong polyadenylation signal in 3' flanking DNA, subsequent processing, reverse transcription and incorporation into a new locus — provides a new mechanism for exon shuffling. Furthermore, this type of exon-shuffling mechanism allows fresh insights into the evolution of splicing, allowing us to tackle questions such as how alternative splicing arose, and why terminal exons are often unusually large¹¹ (Fig. 2). Until now, DNA recombination between introns was considered the best mechanism for exon shuffling. But this new mechanism implicates retrotransposons as being pivotal in large-scale modifications of gene structure.

Because most of the mammalian genome is made up of DNA that does not encode proteins, the consequences of L1 transporting such 'non-exonic' DNA are also notable. Although rearranging exons creates new proteins, L1-mediated shuffling of regulatory sequences may be equally crucial in evolution of the mammalian genome, concocting increasingly complex regulatory circuits. Changes in the timing and cell specificity of gene expression may facilitate fast morphological innovations, some of which could be enough to produce new variants or even species. The process of 3' transduction is the latest in the series of fanciful twists of logic that typify the retroelements — they have

found yet another way to mould not only their own fate, but also that of their host genome. □

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Holocene climate

Restless carbon pools

Philippe Ciais

The global carbon cycle is a significant object of study, because carbon dioxide (CO₂) is the most important greenhouse gas in the atmosphere, after water vapour. The CO₂ concentration in the atmosphere has risen by 80 parts per million by volume (ppmv) over the past two centuries¹, increasing the Earth's radiative forcing by 1.6 Watts m⁻², which causes a net reduction in outgoing infrared radiation, and it is expected to double from current levels during the next century. The concentration of atmospheric CO₂ increased by rough-

ly the same amount (80 ppmv) between the Last Glacial Maximum, 18,000 years ago, and the Early Holocene, 11,000 years ago². In-between, for the period of the Holocene spanning from 11,000 years ago to 1,000 years ago, reliable CO₂ data have not been available. This gap is now bridged in the article by Indermühle *et al.*³ on page 121 of this issue.

Previous measurements of air bubbles enclosed in polar ice sheets show that the atmospheric burden of CO₂ increased by 170 GtC (1GtC = 10¹⁵ grams of carbon),

Animal behaviour

Mothers of invention

What extra quality do animals that work out how to exploit new food sources have? If you're a guppy, it seems to help if you're small, hungry and female (*Anim. Behav.* 57, 331–340; 1999).

Kevin Laland and Simon Reader set up lab populations of the guppy *Poecilia reticulata* (below) consisting of males and females and hungry and well-fed fish. The fish were then put in a maze with food at the end of it. In three-quarters of the trials, a female was the first to discover the novel food source. Two-thirds of the time, it was a hungry fish that solved the problem. In a separate experiment the authors found that smaller fish were faster problem-solvers. There is some evidence that new behaviours can spread by imitation.



These results show that, rather than innovators being inherently creative, a fish's circumstances can drive it to experiment. Hungry fish are more active, better motivated to find food, and more likely to take risks than their better-fed counterparts. Small fish might do better to discover new food than fight with bigger fish for existing food sources.

Why, then, should females be smarter? Laland and Reader speculate that this is a consequence of motherhood. Guppies give birth to live young, so females, which are almost permanently pregnant, need extra food to nurture their brood. Males are probably better employed seeking out new mates than new food sources, so we might expect to see more innovative behaviour in this area of activity — something that could apply across the animal kingdom, as it is common for females to invest more in their offspring than males.

But it seems that innovators are born, as well as made. Fish that were 'past innovators' cracked new problems significantly quicker than 'past non-innovators'. So — starving artists take note — although perspiration helps, it's best to have a spark of inspiration too.

John Whitfield

between the Last Glacial Maximum and the Early Holocene². This is equivalent to a growth rate of 0.02 GtC per year during the period of deglaciation. In the more recent past, changes in atmospheric CO₂ have been observed during the last millennium, but at a rate which did not exceed 0.1 GtC per year⁴. To provide a continuous record of CO₂ over the entire Holocene, Indermühle and co-workers³ carefully analysed more than 400 precious pieces of ice from the Taylor Dome ice core in West Antarctica. The level of experimental precision in their measurements, on the order of 3 ppmv, is unprecedented.

In the new Holocene record, atmospheric CO₂ first decreased slightly during the Early Holocene, but has since increased by 25 ppmv. So, from 8,000 years ago to the eighteenth century, the atmospheric reservoir appears to have gained 50 GtC. Yet, the growth rate of CO₂ at that time is less than 0.01 GtC per year. In comparison, we now experience a build-up of CO₂ in the atmosphere at an average rate of 3 GtC per year, which clearly reflects an imbalance between sources and sinks that has absolutely no equivalent in the recent geological past.

The Holocene CO₂ record is fascinating because it reveals that small, but persistent, changes in the atmospheric CO₂ concentration can be sustained through several millennia, despite the fact that, overall, the global climate conditions have been rather stable. What are the carbon pools that have leaked carbon into the atmosphere since around 7,000 years ago? And what are the mechanisms that delivered CO₂ to the atmosphere?

Two principal active carbon pools, the oceans and the land biosphere, are connected to the atmosphere. To identify the respective role of these two reservoirs on the observed Holocene CO₂ variations, Indermühle *et al.*³ rely on measurements of the stable ¹³C isotope composition ($\delta^{13}\text{C}$) in atmospheric CO₂. The bottom line is that the $\delta^{13}\text{C}$ of atmospheric CO₂ provides a fingerprint of the terrestrial CO₂ fluxes. Photosynthesis incorporates preferentially the lighter ¹²C isotope into plant tissues. As a result, living biomass and soil organic matter are significantly depleted in ¹³C compared with the atmosphere. Therefore, if the land biosphere leaks CO₂ by respiration, it is expected to cause the global atmospheric $\delta^{13}\text{C}$ to decrease. In contrast, an ocean outgassing of CO₂ will not significantly alter the atmospheric isotopic composition.

Measuring $\delta^{13}\text{C}$ in addition to CO₂ concentration makes it possible, in principle, to infer separately the net ocean and land CO₂ fluxes. This technique is known as 'double deconvolution'⁵, but the use of ¹³C is not quite straightforward. First, it is difficult to accurately measure $\delta^{13}\text{C}$ in air enclosed in ice, and slight offsets in the calibration procedures⁶ may have a large effect on the results

of a double deconvolution. Another source of uncertainty is the fact that the air-sea gas exchange of CO₂ slightly modifies the isotopic composition of ¹³C as a function of temperature. In addition, the photosynthetic pathway common in tropical grasses (C4) fractionates much less ¹³C than the 'dominant' pathway found in trees (C3). Large-scale shifts between the C4 and C3 pathways in terrestrial ecosystems could therefore have independently caused $\delta^{13}\text{C}$ to vary during the Holocene.

Indermühle and co-workers² carefully address the above points and conclude that changes in the land biospheric carbon pool are predominantly responsible — although other processes must contribute — for the observed changes in atmospheric CO₂. The land biosphere appears to have gained carbon immediately after the deglaciation and up to 7,000 years ago, and then to have leaked about 10% of its carbon content, that is about 200 GtC. The ocean was the largest final recipient of this biospheric source, and gained 150 GtC, whereas the atmosphere retained 50 GtC. Further insights on the natural carbon cycle dynamics are expected to be gained from CO₂ and isotopic measurements in high resolution ice cores being drilled in Antarctica. A detailed CO₂ history of the last deglaciation is a high priority on research agendas.

It is worth noting that during the second half of the Holocene epoch, when the biosphere appears to have lost CO₂, the ice-core record also indicates an important change in the atmospheric concentration of methane⁷. This has been attributed to increasingly arid conditions in the tropics and peat development in the north. It appears that, even if the global average climate of the Holocene was rather stable, regional changes in the precipitation and temperature patterns over the past 11,000 years⁸ may have been sufficiently important to trigger some significant readjustments to the land carbon reservoir. Terrestrial and oceanic biogeochemical models of the carbon cycle, such as those used to predict future CO₂ levels, now face one more challenge: to reproduce the observed changes in the Holocene carbon pools. □

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Daedalus

Negative friction

Most lubricants are liquids. They keep the moving surfaces apart by hydrostatic pressure. But some, such as graphite and molybdenum disulphide, are solids. Their lamellar lattices have a very easy, low-friction slip-direction. Intriguingly, molybdenum disulphide works badly in moist air. At the contact-area of the moving surfaces, friction and compression heat the lubricant film; it reacts with water vapour to give molybdenum oxide and hydrogen sulphide. The reaction absorbs energy, which is drawn from the mechanism as added frictional loss.

Daedalus is now seeking the converse process. A lubricant which reacted under a roller to give out energy, would decrease the friction. Indeed, if the reaction were sufficiently energetic, the frictional loss would go negative. The lubricant would actually power the roller. DREADCO chemists are now developing this elegant and ultimately simple motor.

To generate propulsive power, the reaction must go with increase in volume. As the moving element rolls on a track lubricated with reagent, the rear of its contact-area would then be continuously 'jacked up' by reactive expansion, driving it along. Now metal oxidations run with vast expansion. Daedalus began to muse that a railway carriage ought to be propelled spontaneously by the thermally induced rusting of the track beneath its wheels — if rust were not such a bad lubricant. But graphite can also be expanded strongly, by the insertion of small molecules, including metal oxides, between its planes of carbon atoms. So DREADCO's 'active lubricant' will be a mixture of graphite and oxidizable metal dust. The transient heat of rolling contact will expand it strongly, thus accelerating the rolling.

Active lubrication will transform the design of small, low-powered mechanisms. They will run for ages on a modest supply of lubricant. Printers, cameras and innumerable office and domestic gadgets, will shed their motors, gear-trains and actuators, and be wonderfully quietened and simplified. More high-powered units will need special arrangements to replenish the lubricant and remove it when exhausted. Ultra-safe actively lubricated motors, free from heat and sparking, will colonize the fuel and chemical industries. An active road, pushing the cars along by reactive expansion beneath their tyres, is probably unfeasible. But an active skating rink should transform that energetic sport into a leisurely delight.

David Jones