Because the Y chromosome is enriched with transcription-regulating genes, this means that it is far from being solely a male-determining switch that is flipped early in development. Instead, the Y chromosome has an impact on gene regulation across the genome in males, potentially influencing biological functions throughout life and in every tissue. It is fair to say that we are only beginning to understand the full extent of the differences in the molecular biology of males and females, and unanswered questions abound. For example, to what extent are male–female differences driven by specific interactions with Y-chromosomal factors?

In humans, the level of variation between individuals is considerably lower on the Y chromosome than on other chromosomes. However, Y-linked sequence changes can cause changes in gene expression across the genome, which could result in amplified differences among males. Despite the relative stability of the gene content on mature Y chromosomes, it is well known that DNA sequences evolve faster on the Y chromosome than on the X. Although this is generally perceived to be the result of the arrest of genetic recombination on the Y chromosome leading to reduced effectiveness of natural selection[8], it seems that the Y chromosome also has the potential to mediate remarkably rapid adaptive evolutionary change. ■

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CLIMATE SCIENCE

Sea levels from ancient seashells

The isotopic composition of oxygen in sea water correlates with changes in global mean sea level. Microfossils carrying oxygen-isotope signals have been used to extend sea-level records as far back as 5 million years ago. **SEE ARTICLE P.477**

RALPH SCHNEIDER

On page 477 of this issue, Rohling *et al.*[1] present a convincing approach for calculating sea-level fluctuations over the past 5 million years (Myr). Their method depends on variations in the oxygen-isotope composition of shells produced by unicellular organisms called planktonic foraminifera (Fig. 1). In this way, the authors provide much-needed information that should help to predict future rates of sea-level rise in the event of complete or partial melting of the ice caps over Greenland and Antarctica in response to global warming.

The most recent instances of ice-sheet growth and melting that generated sea-level variation of several metres took longer than hundreds of years, making it impossible to determine their effects directly from historical records. To infer how growing and melting continental ice sheets affect sea level, at least the past 500,000 years must be considered. During this time, there were five periods of sea-level rise of up to 100 m or more, corresponding to the terminations of recent glacial periods (the intervals of time within the current, ongoing ice age that, in general, correspond to colder temperatures and glacier advances).

One could argue, however, that these terminations do not adequately describe what would happen during complete melting of the Greenland ice cap and parts of the West Antarctic Ice Sheet. Hence, it is much more appropriate to consider past conditions when Northern Hemisphere glaciation was still young — that is, when small, juvenile continental ice caps controlled sea-level fluctuations on timescales of tens to hundreds of thousands of years (the timescales associated with variations in Earth's orbit, which dominate the timing of glacial–interglacial cycles and sea-level changes). But how can this be done? The shells of foraminifera offer a potential solution. Made of calcium carbonate, they contain a record of the ambient isotopic composition of seawater oxygen during the organisms' lifetime.

Since the pioneering work[2] of the geologist Cesare Emiliani in the 1950s, it has commonly been accepted that periodic variations in the ratios of oxygen-18 to oxygen-16 ($^{18}O/^{16}O$) in foraminifera preserved in deep-sea sediments follow a global pattern characteristic of orbitally forced climate change during the Late Pleistocene epoch (about 700,000 to 11,700 years ago). Cool temperatures and great ice volumes both resulted in high $^{18}O/^{16}O$ ratios, whereas high temperatures and low ice volumes had the opposite effect. So, if the temperature effect can be disentangled from this isotopic record, then the remaining signal represents relative changes in continental ice volume. And if this signal can then be scaled to the amplitude of sea-level rise between glacial and interglacial periods (as has been done for the most recent postglacial period by correlating sea-level rises to the oxygen-isotope composition of cores taken from coral terraces[3]), then fluctuations in global sea level over time can be calculated, as long as ocean sediments provide continuous, undisturbed $^{18}O/^{16}O$ records.

Going back even further in time, a 5-Myr-long composite record[4] of $^{18}O/^{16}O$ ratios from foraminifera that lived in deep-sea sediments was until now considered the best chronicle of ice-sheet volume as Earth shifted from a hot, 'greenhouse' climate (about 55 Myr ago) to colder, 'icehouse' conditions (approximately 2.6 Myr ago). However, there are two problems with this record. First, the proportions of the temperature and ice-volume effects in it are unclear, because deep-ocean temperatures may have changed substantially over this long period of climate transition. Second, it is difficult to scale deep-sea oxygen-isotope variations at orbital timescales into robust estimates (including error margins) for the amplitude of sea-level rise and fall over the past 5 Myr.

Rohling *et al.* overcome these problems by converting $^{18}O/^{16}O$ ratios of fossilized planktonic foraminifera that proliferated in the surface waters of the eastern Mediterranean Sea directly into sea-level variations — an approach previously developed for a study[5] of the Red Sea, and which does not require temperature and ice-volume effects to be disentangled first. Their method depends on a hydraulic model of water exchange through the Strait of Gibraltar, which connects the North Atlantic Ocean and the Mediterranean Sea. This exchange mechanism not only controls the balance of evaporation and water renewal in the Mediterranean, but also strongly affects the seawater oxygen-isotope ratios recorded in planktonic foraminifera.

Assuming that there have been no major tectonic movements in the Strait of Gibraltar during the past 5 Myr that affect its depth and width, the oxygen-isotope signal from these foraminifera is simply a function of global sea-level variations relative to the modern hydraulic state of the Mediterranean Sea. The authors find that estimates of ancient sea levels relative

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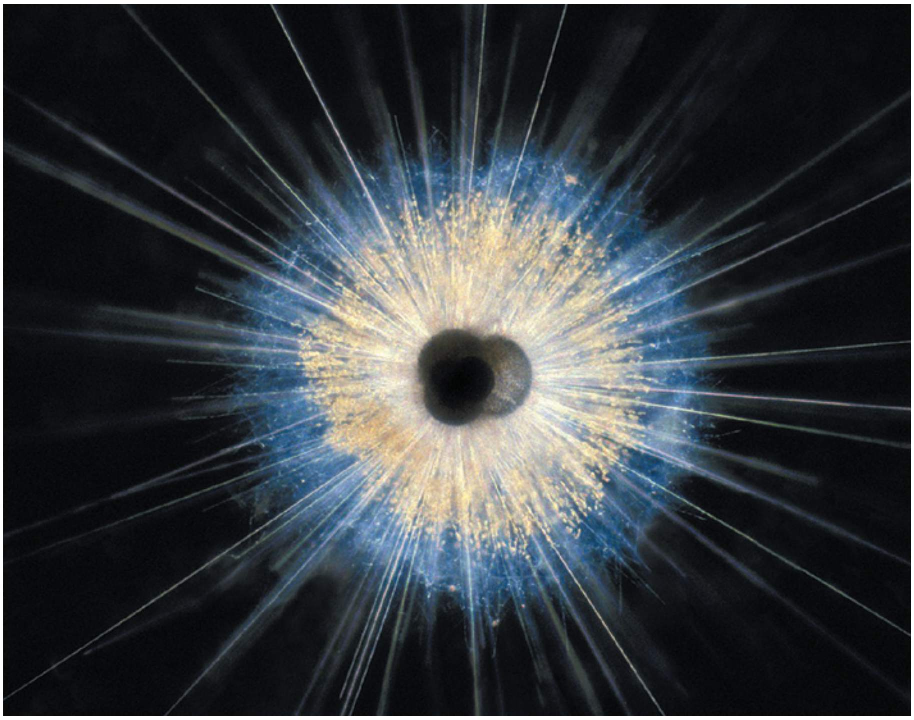

Figure 1 | Isotopic recorders. Planktonic foraminifera, such as *Globigerinoides ruber* (pictured), are unicellular organisms that live near the sea surface. Rohling *et al.*[1] have used oxygen-isotope data from microfossils of planktonic foraminifera from the Mediterranean Sea to deduce global sea levels during the past 5.3 million years.

to modern levels made using their approach are quantitatively similar to those obtained using other approaches, but have much better-defined error statistics. Accordingly, they confirm that sea level was about 10–30 m higher in the warm period that preceded the current ice age than it was when the ice sheets subsequently expanded.

As Rohling and co-workers acknowlege, their method has several limitations that require further study and improvement. Apparent mismatches exist between their results and those of hydraulic models applied to the Red Sea[5], particularly for periods corresponding to the maximum volume of ice, towards the end of three of the four most recent glacial periods. This could be because the researchers' model for converting planktonic oxygen-isotope data to sea levels might not fully account for freshwater input from rivers, or for perturbations in the oxygen-isotope signal of precipitation and rivers over time. Nonetheless, the striking similarity between Rohling and colleagues' results and those from two independent studies that used data from the Red Sea[5] and the southwest Pacific Ocean[6] to predict sea levels during the past 0.5 and 1.5 Myr, respectively, strongly suggest that the researchers' conclusions for older periods are correct.

As expected for any new approach, the findings leave several open questions. The conclusion that the first major sea-level fall took place more than 0.5 Myr after the onset of significant global cooling 2.75 Myr ago challenges commonly held assumptions (including some of my own[7]) inferred from the composite record[4] of $^{18}O/^{16}O$ ratios from foraminifera that lived in deep-sea sediments. But it receives a lot of support from other studies of regional palaeoclimatic trends for the period approaching the ice age in the Pleistocene epoch (roughly 2.6 million to 11,700 years ago; see Extended Data Table 2 of the paper[1]).

Rohling *et al.* also conclude that the ice volume during the Last Glacial Maximum — the peak of the most recent glacial period — was larger than that during previous glacial periods. This contradicts continental evidence for the extension of ice sheets over North America and Eurasia[8], but, if correct, will serve as a crucial benchmark for improved modelling of glacial ice-sheet volumes and heights. Finally, the authors' findings should also lead to improved forecasts for the fate of extant ice caps under global warming. ■

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This article was published online on 16 April 2014.

REPRODUCTIVE BIOLOGY

Sperm protein finds its mate

Knowledge of the sperm-specific protein that is required for the attachment of sperm to eggs during fertilization in mammals has led to the identification of the protein's receptor on the egg's plasma membrane. **SEE ARTICLE P.483**

PAUL M. WASSARMAN

Biology is full of surprises. Such is the case with the findings of Bianchi *et al.*[1] reported on page 483 of this issue. The authors report the end of a decade-long search for a partner for the sperm protein Izumo1, which is responsible for sperm–egg adhesion during fertilization. The elusive mate is a member of the folate-receptor protein family, and is located on the plasma membrane of unfertilized eggs. Because of its essential role in fertilization, the researchers propose that the folate receptor, currently known as Folr4, should be renamed Juno, after the Roman goddess of fertility and marriage.

Fertilization defines the process by which a sperm and an egg combine to form a single-celled zygote that, in time, gives rise to a new individual. In 2005, researchers reported[2] that a protein that spans the sperm's plasma membrane, called Izumo1 (named after a Japanese marriage shrine), is essential for fertilization in mammals. Male mice that lack Izumo1 are infertile — their sperm seem normal, but are unable to fuse with eggs. Subsequently, it was found that Izumo1 is part of a multiprotein family whose members form large complexes on sperm that may be essential for sperm–egg fusion[3]. However, the identity of the receptor