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genetics and biochemistry, focused on single genes and testable hypotheses. But functional genomics should make traditional approaches more efficient and productive, and will provide a new perspective on the behaviour of biological systems as a whole. *Philip Hieter is at the Centre for Molecular Medicine and Therapeutics, University of British Columbia, 950 West 28th Avenue, Vancouver, British Columbia, Canada V5Z 4H4. e-mail: hieter@cmmt.ubc.ca* 

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### Ocean biogeochemistry

# Sulphur in the mix

Ronald P. Kiene

he ocean surface layer influences climate not only through exchange of greenhouse gases such as carbon dioxide and methane with the atmosphere, but also gases like dimethylsulphide (DMS) which is thought to exert a cooling influence on the climate system. Climatic factors in turn influence the biogeochemical cycles of these trace gases, and there may then be feedbacks to the global climate system through the biota in the surface ocean. In 1987, Charlson *et al.*<sup>1</sup> proposed a phytoplankton– climate link that could operate through emission of DMS. Little was known about how climatic factors affect DMS production in surface waters, but Simó and Pedrós-Alió (page 396 of this issue<sup>2</sup>) now present evidence that the depth of sea-surface mixing, which largely depends on factors such as wind and temperature, may control DMS production and concentration.

Oceanic emissions of DMS are the largest biogenic source of sulphur to the atmosphere<sup>3</sup>, and are thought to have a cooling influence on global climate through formation of sunlight-scattering sulphur aerosols and cloud-condensation nuclei<sup>4</sup>. According to the feedback hypothesis of Charlson et al.1, a global warming trend could be mitigated to some degree by an increase in DMS emission stimulated by the warming. Whether such a homeostatic feedback truly exists and how it might work has been difficult to ascertain, partly because both DMS and its phytoplankton-derived precursor, dimethylsulphoniopropionate (DMSP), have complex biogeochemical cycles in the surface ocean<sup>3,5</sup>.

Simó and Pedrós-Alió<sup>2</sup> provide evidence that the short- and long-term response of the upper-ocean biogeochemistry to very shallow mixing conditions leads to increases in DMS concentration. Warmer climate conditions, leading to more intense or longerlasting stratification (and hence shallower mixing), could therefore lead to more DMS emissions and a cooling influence on climate — as called for in Charlson and colleagues' hypothesis<sup>1</sup>. The strength of any cooling effect by increased DMS emission is still highly uncertain<sup>4</sup>, however, so the overall significance of the biogeochemical response to mixing remains to be determined. Moreover, any such feedback acting through the sulphur cycle must be considered together with other climatic effects of enhanced stratification. These effects could include lower uptake of carbon dioxide by the ocean<sup>6</sup>, leading to its accumulation in the atmosphere, which would act in opposition to DMSinduced cooling.

How might mixing depth control DMS accumulation in surface waters? An essential consideration here is that only a fraction of the phytoplankton DMSP undergoing degradation in sea water is converted to DMS. Based on their own data from the North Atlantic, and on data from the literature, Simó and Pedrós-Alió suggest that mixing-layer depth (driven by wind and temperature variations) controls the conversion efficiency of DMSP into DMS (hereafter the DMS yield) and ultimately the concentration of DMS in surface waters. They conclude that an unusual relationship exists whereby the DMS yield is highest (nearly 100%) in waters with a very shallow mixed layer, whereas it is lowest (about 10%) when mixing occurs to 10-20 m, and then higher again with deeper mixing to 30-65 m. At shallower mixing depths, plankton become more isolated from the rich nutrient reservoir below and are subject to more intense bombardment by solar radiation, including harmful ultraviolet-B.

The explanation given by Simó and Pedrós-Alió for the DMS yield pattern centres on the probable differential photoinhibition of the phytoplankton (DMSPproducing) and bacterial (DMSP-consuming) populations that would be strongest, for the surface layer, under shallow mixing conditions. With few data available, there is still considerable uncertainty in the observed relationship, but the authors point out that



#### **100 YEARS AGO**

The scientific lessons of the war are crowding upon us. We have already referred to the blunder made by our military authorities in not sending Marconi apparatus to South Africa amongst the first equipments. We now learn indeed, after the investment of Ladysmith is drawing to a close, that Marconi apparatus is being sent out. The silence of Ladysmith during the last eventful weeks will point the moral, which is not likely to be forgotten in the future ... Some time ago the importance of a locomotive search-light in operations of war was strongly represented to the military authorities; but they would have none of it. Fortunately, however, the naval force in Natal has now provided the army with one.

As a proof of his cordial sympathy with the cause of bird protection, the Poet Laureate, Mr Alfred Austin, has written a special poem for the Christmas card which the Society for the Protection of Birds is issuing this year. It is entitled "Peace and Goodwill to the Birds," and is illustrated by a coloured picture of that much persecuted bird the tern, designed for the purpose by Mr. A. Thorburn. From *Nature* 23 November 1899.

#### **50 YEARS AGO**

Prof. H. Yukawa, who has been awarded the Nobel Prize for Physics for 1949, is best known for his theory of nuclear forces which. in 1935, first postulated the existence of a particle a few hundred times heavier than the electron. The nuclear forces would then bear the same relation to the possible emission and absorption of such a particle as the electromagnetic forces in an atom bear to the emission and absorption of light. The discovery of the meson in cosmic rays appeared to be a confirmation of Yukawa's prediction, but the study of its properties gradually led to the conviction that it could not be identical with the particle required for Yukawa's theory. It was not until 1947 that Powell and his collaborators demonstrated the existence of a second short-lived particle, the  $\pi$ -meson, which is known to be the parent of the cosmic-ray meson, and which is strongly linked to protons and neutrons. This provided a brilliant vindication of Yukawa's idea. The detailed theory of the relation between this particle and the nuclear forces is still in its infancy; but, whatever the outcome, all thought about nuclear forces ... is entirely dominated by the ideas of Yukawa. From Nature 26 November 1949.

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the unusual pattern is similar to the effect of mixing depth on water-column-integrated photosynthesis in the Antarctic<sup>7</sup>. One key to interpreting the mixing-depth pattern might be that ultraviolet radiation or other factors such as nutrient limitation or grazing could diminish the assimilatory metabolism of DMSP<sup>5</sup>, thereby allowing more DMSP to be converted to DMS.

Regardless of the actual cause, the relationship between higher DMS production and shallow mixing observed by Simó and Pedrós-Alió is consistent with the oceanwide build-up of surface DMS in summer, when stratification is greatest and mixing depths shallowest (see their Fig. 2 on page 397). What is especially intriguing about the 'summer DMS paradox' is that maximum DMS concentrations in surface waters are found at a time of year when phytoplankton biomass (as judged by levels of chlorophyll *a*) and DMSP concentration are well below their annual maxima.

The clear illustration of this discordance is a notable contribution because most researchers are still looking for close ties between DMS and algal biomass or DMSP. The data synthesis by Simó and Pedrós-Alió suggests that the crucial ties may lie elsewhere, perhaps in the food-web structure (for instance a shift to DMSP-rich picophytoplankton) or in the photophysical effects on DMS biogeochemistry. Processes such as photooxidation of DMS and the influence of algal-derived photosensitizers are probably important<sup>8,9</sup>. Inhibition of DMSconsuming bacteria by increased ultraviolet exposure in shallow mixing layers could also contribute to DMS build-up. Further research on what controls net production of DMS is necessary, and the mixing regime needs to be considered in any such work.

The studies of Simó and Pedrós-Alió and of others<sup>7,10</sup> show that mixing of the upper ocean can have significant effects on biological and biogeochemical processes. These investigations indicate that the responses of the upper-ocean biogeochemical system to variations in climate-driven mixing are both complex and surprising. Clearly, we need a better understanding of how the upper ocean will respond in the context of events such as El Niño and future global warming. *Ronald P. Kiene is in the Department of Marine Sciences, University of South Alabama, LSCB-25, Mobile, Alabama 36688, USA.* 

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### **Phylogenomics**

# Ancestral primate viewed

Stephen J. O'Brien and Roscoe Stanyon

ow did the genomes of modern mammals come to be organized the way they are? Improvements in genome sequencing, gene mapping and chromosome recognition mean that, by comparing the order and sequence of genes in different genomes, we may be able to trace the evolutionary pathways that our ancestors took. The potential of such an approach is illustrated by three new studies<sup>1-3</sup>, which compare the genome maps and chromosomes of 15 species of primate, using four non-primate orders - carnivores, rodents, artiodactyls (hoofed mammals) and tree shrews — as a reference standard for the organization of ancestral mammalian genomes. Although the approach itself is not new, the chance to explore entire vertebrate genomes with such a high level of precision is.

Comparative cytogenetics (the study of differences in chromosome structure and appearance) dates back three decades. Then, factors such as the position of the centromere, a chromosomal structure involved in nuclear division, alerted researchers to differences between distantly related species<sup>4</sup>. Later, specific banding patterns (obtained by staining chromosomes) were used to infer sub-chromosomal homologies, and many of these have turned out to be correct<sup>5</sup>. Today, comparative gene maps have been started for over 40 mammalian species<sup>6</sup>. Chromosome painting (where flow-sorted individual chromosomes of one species are labelled with fluorescent dyes and hybridized in situ to chromosomes of another species) has allowed long stretches of conserved gene segments to be identified among very distantly related species.

Such comparisons have given us a glimpse of the genome rearrangements that punctuate adaptation and species formation<sup>7</sup>. Because exchanges between genomes are rare, and the junctions between gene segments can be easily identified, such rearrangements are powerful evolutionary characters that proscribe the

history of species that retain them. Comparative 'phylogenomic' approaches therefore combine what we know about segment homology with the strategies of evolutionary cladistics (a method of classification based on those shared characteristics that are assumed to indicate a common ancestry). In the first of the new papers<sup>1</sup>, Haig restates an idea often heard from palaeontologists working with a tooth or cranial fragment, when he writes that describing the process of reconstructing ancestral chromosome structures "can be likened to the difficulty of writing an entertaining account of the piece-by-piece assembly of a jigsaw puzzle". The process is indeed tedious and treacherous, but the goal of reconstructing genomic history is a lofty one.

So how is it done? First, work out how many chromosomes or segments are conserved between the genomes of two species. Second, from this count, estimate how many chromosome exchanges (translocations, transpositions, fusions, fissions or inversions) it takes to rearrange one genome to the other — that is, how many scissor cuts would allow a human genome arrangement to be turned into that of a tree shrew, and vice versa? Next align additional species to the first two and identify the conserved homology blocks. The ancestral forms can be regarded as those shared between several species. (By contrast, derived segments or connections are unique to one or more closely related species, and serve as evolutionary signatures of particular lineages.) Finally, assemble the hypothetical ancestral genome - for example, for all primates - by comparison with the genomes of 'outgroup' species. In the new studies these included tree shrews; carnivores (cats, mink and seals); perissodactyls (horses); artiodactyls (cows, sheep and goats); or rodents (rats and mice). The ancestral chromosomal traits were defined as those shared between primates and the outgroups.

This process allows the minimum-sized fragments of chromosome exchange to be identified (termed the smallest conserved evolutionary unit segment; SCEUS<sup>8</sup>). The SCEUS is then treated as an evolutionary character. Haig<sup>1</sup> introduces a 'Cambridge grid', which tabulates the chromosomes of one species along the horizontal axis and those of a second species vertically. He then assigns individual Greek letters in the matrix to ancestral SCEUS associations. Once the ancestral genome is designed, the genomic exchanges that have occurred in lineages leading to the living species can be recapitulated.

The new studies<sup>1–3</sup> interpret available data to reconstruct chromosomal characteristics from the ancestor of all primates (Fig. 1, overleaf). This creature last lived at least 65 million years ago, so it seems remarkable that, compared to the ancestral types, 18–20 human chromosomes remain unchanged and the rest have but a single exchange. Different exchanges have occurred in the lineages lead-