

to haploid individuals. In this way, we may discover why haploidy has arisen in some, but not other, groups of predominantly diploid organisms.

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PERSPECTIVES: PALEOCLIMATE

Extending the Calibrated Radiocarbon Record

Edouard Bard

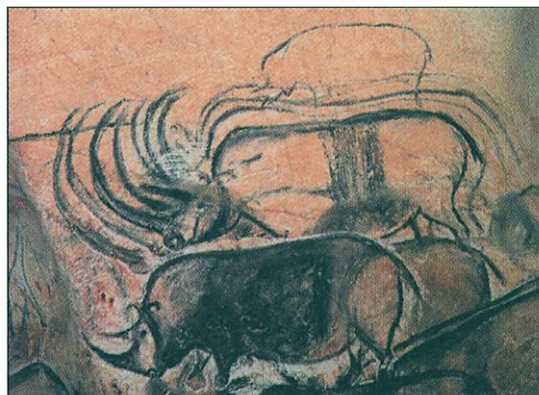
Since the 1950s, radiocarbon measurements have been used to obtain accurate dates for archaeological artifacts, climatic records, and other records of past events. While alive, organisms equilibrate with the atmospheric $^{14}\text{C}/^{12}\text{C}$ ratio, but when they die, the ratio starts to decrease as ^{14}C decays. The $^{14}\text{C}/^{12}\text{C}$ ratio of biological remains therefore correlates with their age.

It was originally assumed that the atmospheric $^{14}\text{C}/^{12}\text{C}$ ratio stays constant, but we now recognize that it varies with time. To calculate accurate ages, atmospheric ^{14}C fluctuations must be corrected for with a calibration curve obtained by comparing raw ^{14}C data with true calendar ages derived from independent dating methods. In principle, the radiocarbon record can be extended to ~50,000 years before present (yr B.P.), in the middle of the last Ice Age, but current calibrations only reach 24,000 yr B.P.

On page 2453 of this issue, Beck et al. (1) report a much needed radiocarbon record for 25,000 to 45,000 yr B.P. (2). During this period, large climatic swings occurred abruptly over periods of decades to centuries and sometimes lasted just a few millennia (3, 4). Serious problems arise when we try to compare the timing of climatic changes observed in different types of paleoclimatic records from different parts of the world. For example, there is still no real constraint on the relative timing of major glacial surges (Heinrich events) into the North Atlantic and global sea-level variations between 25,000 and

45,000 yr B.P. Accurate ^{14}C dating is also crucial for evaluating the correlation between climatic events and variations in Earth's orbit around the Sun.

An accurate clock for 25,000 to 45,000 yr B.P. is also important in prehistoric archaeology (5). For example, some workers are convinced that Neanderthals overlapped chronologically with modern humans (6), raising the possibility of cultural and even genetic transfers. Other specialists claim (7) that the last technological and artistic devel-



A rhinoceros herd from the Chauvet Cave. Prehistoric paintings in this cave have been dated at ~31,000 ^{14}C yr B.P. This corresponds to ~38,000 calendar yr B.P. according to Beck et al.'s record (1), but only ~33,000 calendar yr B.P. using the Suigetsu record (21).

opment of the Neanderthals, the Chatelperronian culture, predated by several millennia the Aurignacian culture of the Cro-Magnon people, the first modern humans in Western Europe. Accurate chronological studies will help resolve this controversy and advance our knowledge about this major technological and social revolution.

Several approaches have been used to construct the ^{14}C calibration curve. For the Holocene (the past ~11,000 years),

fossil trees are abundant, allowing a high-resolution atmospheric $^{14}\text{C}/^{12}\text{C}$ curve to be produced by comparing ^{14}C concentrations and tree-ring counts from the same tree sections (8). Unfortunately, this "dendrocalibration" cannot be extended much beyond the Holocene because trees are scarce during the preceding Late Pleistocene, a period characterized by an extreme glacial climate. Therefore, other types of records are used to extend the calibration, such as annually laminated (varved) sediments (9, 10) and shallow-water tropical corals that can be cross dated by ^{14}C and uranium-thorium (U-Th) dating (11–14).

This international scientific effort has led to the periodic release of an "official" calibration curve, which represents a state-of-the-art consensus on this issue.

The last of these updates, INTCAL98 (15, 16), extends back to 24,000 yr B.P. with a relatively dense sample coverage (16). However, extending the record to older periods is difficult because residual ^{14}C concentrations in samples become extremely low, just a few percent of those in modern samples. Furthermore, old samples have often been altered by geochemical and diagenetic processes.

To extend the record, Beck et al. (1) measured and compared ^{14}C and U-Th ages obtained from a well-preserved stalagmite of the Bahamas. The backbone of their high-resolution record is a series of U-Th ages measured by thermal ionization mass spectrometry (TIMS) (17). The data reveal extremely large increases in ^{14}C concentrations beyond 30,000 yr B.P. (more than double the modern atmospheric $^{14}\text{C}/^{12}\text{C}$ ratio). These variations imply extreme, concomitant changes in the overall production of ^{14}C by cosmic rays and in its distribution among different reservoirs of the global carbon cycle.

High values of the atmospheric $^{14}\text{C}/^{12}\text{C}$ ratio between 30,000 and 40,000 yr B.P.

The author is at Centre Européen de Recherche et d'Enseignement en Géosciences de l'Environnement, CNRS-Université d'Aix-Marseille III, UMR-6635, Europe de l'Arbois, 13545 Aix-en-Provence cedex 4, France. E-mail: bard@cerege.fr

are not completely unexpected. Some previous studies have suggested high ratios based on TIMS U-Th dating of carbonate samples (13, 18, 19) and the apparent correlation between ^{14}C -dated marine sediments and the Greenland ice record (20). However, these studies lacked precision and often yielded noisy data. The unprecedented resolution and accuracy of U-Th ages in the new record strengthen the case for elevated $^{14}\text{C}/^{12}\text{C}$ between 30,000 and 40,000 years ago, although one previous study based on the annually laminated sediments of Lake Suigetsu in Japan (21) contradicts the results. It suggests atmospheric $^{14}\text{C}/^{12}\text{C}$ ratios close to the modern value between 30,000 and 40,000 years ago (22).

To illustrate the implications of Beck *et al.*'s extended calibration, consider the age of the prehistoric paintings recently discovered in the Chauvet Cave in southern France. Among the wild animals painted by Cro-Magnon people in this cave, we find numerous woolly rhinoceroses (see the figure). Charcoals used for these prehistoric paintings have been dated by ^{14}C

accelerator mass spectrometry (23). The four available ^{14}C ages are indistinguishable within error and give a weighted average of $\sim 31,000$ ^{14}C yr B.P. The calibrated age of the Chauvet paintings would thus be $\sim 38,000$ calendar yr B.P. according to the new record, but only $\sim 33,000$ calendar yr B.P. using the Suigetsu record.

The broad agreement of the new Bahamian record with previous results suggests that the "old chronology" is probably correct, but some problems must be resolved before we can update and extend the INTCAL98 curve. Future work on varved sediments beyond 30,000 yr B.P. should indicate whether the Suigetsu varves are accurately dated or whether these annual counts provide only lower bounds on absolute ages (22).

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PERSPECTIVES: ECOLOGY

Marine Bugs and Carbon Flow

Tom Fenchel

Oceans are thought to act as carbon sinks: Atmospheric CO_2 is assimilated during photosynthesis by plankton in the ocean and is converted to organic carbon, which then enters the food chain. Twenty-five years ago the flow of carbon through organisms in the open ocean appeared simple: Algae "fix" CO_2 during photosynthesis and are eaten by zooplankton, which in turn serve as food for fish (1). Since then, however, the simple diagrams of plankton food chains in ecology textbooks have had to be redrawn many times as new findings have added extra layers of complexity. For example, ubiquitous unicellular cyanobacteria are important producers of organic carbon (2, 3). Carbon and other organic compounds dissolved in the ocean are metabolized by heterotrophic bacteria, and these bacteria are eaten by protozoa (4, 5). To complicate matters further, viruses regulate bacterial populations (6), and photosynthetic protozoa can also be predators (see the figure) (7). With the report by Kolber *et al.* (8) on page 2492 of this issue, the diagrams in ecology textbooks will have to be redrawn

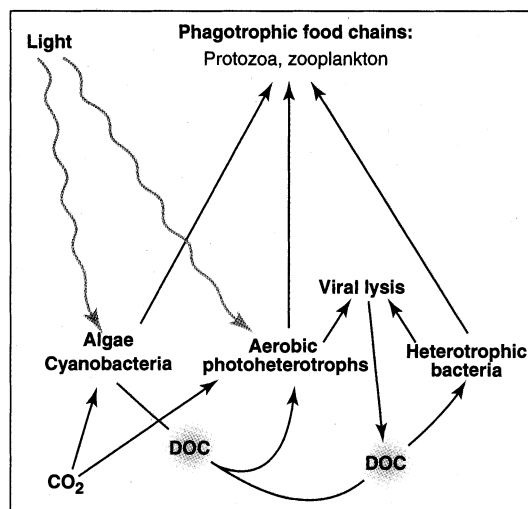
again. These investigators provide evidence that a long-ignored group of bacteria could be a key determinant of carbon flow in oceans. This group is composed of aerobic anoxygenic photoheterotrophs that

metabolize carbon when it is abundant or trap light and CO_2 for energy by photosynthesis when it is not.

Photosynthetic bacteria belong to one of five unrelated eubacterial lineages. Of these, only the cyanobacteria (like their green eukaryotic cousins that contain chloroplasts) carry out oxygenic photosynthesis: They use H_2O as a hydrogen donor to reduce CO_2 to organic matter with the production of O_2 as a metabolite.

All other photosynthetic bacteria engage in anoxygenic photosynthesis that depends on reductants other than water (usually reduced sulfur compounds, H_2 , and ferrous iron), without the production of O_2 . These anoxygenic phototrophs—purple sulfur bacteria, purple nonsulfur bacteria, green sulfur bacteria, green nonsulfur bacteria, and *Heliobacter*—are usually anaerobes (they have oxygen-independent respiration) but some are oxygen-tolerant and may even use O_2 respiration in the dark, although photosynthesis is confined to anoxic conditions.

Photosynthetic bacteria have special chlorophylls—bacteriochlorophylls—characterized by absorption peaks in the near-infrared part of the spectrum; they also possess accessory photosynthetic pigments (carotenoids) that enable them to absorb blue light. These bacteria are



Tangled webs and carbon flow. The flow of carbon through microorganisms in the water column of the open ocean. Components include protozoa, zooplankton, algae, cyanobacteria, viruses, heterotrophic bacteria, and aerobic (anoxygenic) photoheterotrophic bacteria. Dissolved organic carbon (DOC) is derived from the photosynthetic activities of cyanobacteria, algae, and other sources.

The author is at the Marine Biological Laboratory, University of Copenhagen, DK-3000 Helsingør, Denmark. E-mail: tfenchel@zi.ku.dk