

climate changes. The glacial-interglacial fluctuations explored by Tudhope *et al.* document ENSO's sensitivity to more severe climate change. At their site, modern (late 19th century to today) corals show the highest amplitude of interannual ENSO variance of all samples over the past 130,000 years—even in the late 19th century when anthropogenic greenhouse forcing was minimal.

The coral records preserve a mixed signal of rainfall and ocean temperatures, and changes in interannual variability may relate to either or both of these. Tudhope *et al.* use multidecadal sequences (18 to 235 years) obtained from several well-dated intervals over the past 130,000 years to argue that in the past, ENSO intensity has been damped relative to modern by two factors. First, the 22,000-year precessional cycle of Earth's orbit changes the seasonal insolation and alters the strength of Pacific trade winds during seasons that are critical for the growth of interannual anomalies. Second, a suppression of ENSO fluctuations during glacial intervals is implied by the glacial-age samples in their record.

The first mechanism for damping ENSO has been studied in climate models of varying complexity. In a simple model of the equatorial Pacific Ocean and atmosphere, the seasonal insolation changes associated with the precession of Earth's equinoxes alter the seasonal strength of the trade winds. When perihelion (the point in Earth's orbit where Earth is closest to the sun) falls in the boreal summer or autumn, the trade winds in that season are strengthened, inhibiting the development of warm El Niño anomalies (13). Moreover, the Asian monsoon intensifies when perihelion falls in the boreal summer, and this well-known response has been shown to enhance Pacific summertime trade winds in a global coupled ocean-atmosphere model (4). These seasonally forced responses should act together to weaken ENSO variability in the mid-to-late Holocene and to enhance it when perihelion falls in boreal winter, as it does today.

The mechanisms for glacial ENSO weakening are not nearly as well understood. Tudhope *et al.* suggest several possibilities, including weaker ocean-atmosphere interactions in a cooler Pacific and intensified trade winds resulting from a stronger average temperature gradient across the Pacific. A lower sea level that exposes shallow continental shelves in the western Pacific may also anchor the Indonesian Low atmospheric convection system, whose mobility during ENSO is critical for propagating ENSO's impacts to the extratropics.

However, one can also imagine mechanisms that may strengthen ENSO in a glacial world. For example, a shallower, steeper thermocline in the eastern Pacific could lead to greater interannual variability. In initial results from the National Cen-

ter for Atmospheric Research (NCAR) coupled climate model, more intense ENSO variability is simulated during the Last Glacial Maximum, although precise mechanisms have not yet been identified (14). The inference of weaker glacial ENSO from the coral data does not necessarily conflict with this simulation, however. The "glacial" intervals in the Tudhope study [at 40,000, 85,000, 112,000, and 130,000 years before present (15)] are less extreme than the Last Glacial Maximum (LGM), and their precessional forcings are not uniformly the same as those at the LGM. Competing mechanisms could push the ENSO system in either direction during glacial times; additional data are required to determine which ones win out when.

Records such as those preserved in Tudhope *et al.*'s New Guinea corals are rare and offer only tantalizingly brief glimpses of past variability. Short records risk misrepresenting the full range of interannual variability. Nonetheless, Tudhope *et al.* identify a pattern in the amplitude of ENSO that is consistent with a response to changing seasonal insolation and background climate state. Their hypothesis essentially predicts the amplitude of ENSO variance as these boundary conditions change—a proposition clearly testable with additional samples. As more information about ENSO's slow dance to orbital rhythms is uncovered,

we will better understand its sensitivity to ongoing climate change and its potential role as a feedback or amplifier in the global climate system.

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PERSPECTIVES: PALEOCLIMATE

Was the Medieval Warm Period Global?

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The reconstruction of global temperatures during the last millennium can provide important clues for how climate may change in the future. A recent, widely cited reconstruction (1) leaves the impression that the 20th century warming was unique during the last millennium. It shows no hint of the Medieval Warm Period (from around 800 to 1200 A.D.) during which the Vikings colonized Greenland (2), suggesting that this warm event was regional rather than global. It also remains unclear why just at the dawn of the Industrial Revolution and before the emission of substantial amounts of anthropogenic greenhouse gases, Earth's temperature began to rise steeply.

Was it a coincidence? I do not think so. Rather, I suspect that the post-1860 natural

warming was the most recent in a series of similar warmings spaced at roughly 1500-year intervals throughout the present interglacial, the Holocene. Bond *et al.* have argued, on the basis of the ratio of iron-stained to clean grains in ice-rafted debris in North Atlantic sediments, that climatic conditions have oscillated steadily over the past 100,000 years (3), with an average period close to 1500 years. They also find evidence for the Little Ice Age (from about 1350 to 1860) (3). I agree with the authors that the swing from the Medieval Warm Period to the Little Ice Age was the penultimate of these oscillations and will try to make the case that the Medieval Warm Period was global rather than regional.

One difficulty encountered when trying to reconstruct Holocene temperature fluctuations is that they were probably less than 1°C. In my estimation, at least for time scales greater than a century or two, only

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two proxies can yield temperatures that are accurate to 0.5°C: the reconstruction of temperatures from the elevation of mountain snowlines and borehole thermometry. Tree ring records are useful for measuring temperature fluctuations over short time periods but cannot pick up long-term trends because there is no way to establish the long-term evolution in ring thickness were temperatures to have remained constant. Corals also are not accurate enough, especially because few records extend back a thousand years. The accuracy of the temperature estimates based on floral or faunal remains from lake and bog sediments is likely no better than $\pm 1.3^\circ\text{C}$ (4) and hence not sufficiently sensitive for Holocene thermometry.

The Mountain Glaciation Record

At the Last Glacial Maximum, mountain snowlines throughout the world were on average about 900 m lower than today (5). On the basis of today's rates of temperature change with elevation, this required an air temperature cooling at the elevation of the glacier of about 5°C (and a corresponding tropical sea surface temperature cooling of about 3°C). During the Younger Dryas—a cold “spell” of about 1200 years during the last deglaciation—snowlines in the Swiss and New Zealand Alps dropped to about 300 m below the lowest levels reached in the subsequent Holocene.

Since their 1860 maximum at the end of the Little Ice Age, the retreat of Swiss glaciers represents a rise in snowline of about 90 m (6). If this rise could be attributed entirely to air temperature, the required warming would be between 0.5° and 0.6°C. However, simple considerations suggest that precipitation changes result in a negative feedback of about 20% (7). The warming required to account for the post-1860 retreat of Alpine snowlines would then be between 0.6° and 0.7°C.

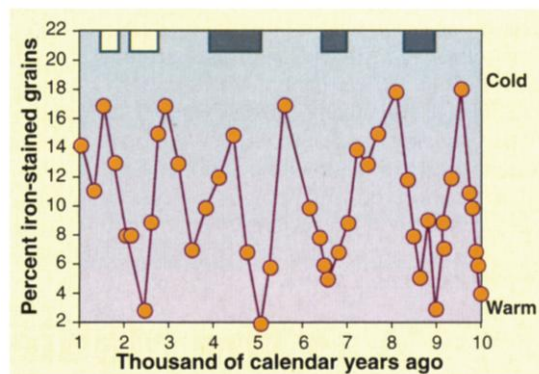
The post-1860 glacier retreat is not confined to Switzerland. With the exception of Antarctica, it has been well documented everywhere on Earth where ice-covered mountains are present (2). There is no doubt that the Little Ice Age was global in extent and that the post-1860 warming was also global. In this regard, the Mann *et al.* (1) reconstruction is consistent with the mountain snowline record.

The Medieval Warm Period has also left its traces in the Swiss Alps. Holzhauser has reconstructed the history of a larchwood aqueduct constructed by medieval farmers (8). It ran from a small mountain lake along the valley occupied by the Grosser Aletsch Glacier, supplying water to an Alpine vil-

lage. The aqueduct was first constructed around 1200 A.D. (toward the end of the Medieval Warm Period). It was partially destroyed when the glacier advanced in 1240 A.D. and had to be totally rerouted after a further advance in 1370 A.D.

Swiss geologists and geomorphologists agree that the large moraines marking the maximum glacier extent during the Little Ice Age are a composite of debris left behind by a series of Holocene advances (9). For example, soils separating individual advance episodes have been found within the moraines. Precise dating has proven difficult, however, and the chronology of these prior advances remains uncertain.

Two recent studies of Holocene climate cycles in the Swiss Alps have greatly improved this situation. Both focus on establishing the times of glacial retreats rather than advances. Holzhauser (8), on the basis of radiocarbon dating of larchwood stumps exposed by the ongoing retreat of the Grosser Aletsch Glacier, finds warm episodes 2400 ± 300 and



Climatic oscillations during the Holocene. Circles show the ratios of iron-stained to total grains (for grains with diameters $>63 \mu\text{m}$) in a North Atlantic core (3). The chronology is taken from (22). The green (10–12) and yellow (8) boxes are based on radiocarbon dating on wood and peat formed when the glaciers had retreated to positions similar to or up-valley from those at present (see text).

1500 ± 200 calendar years ago. Hormes and Schlüchter (10–12) have dated wood and peat fragments that are being disgorged from beneath a number of Swiss glaciers. Radiocarbon dates of a large number of these samples cluster in three major groups centered at 8700, 6600, and 4300 calendar years before present. The correlation between these Alpine warm phases and the warm phases of Bond's North Atlantic ice-rafting record, although imperfect, is encouraging (see the figure).

Borehole Thermometry

Geothermal heat is produced deep inside Earth, and the shape of the vertical temperature profile measured in a borehole from any point on Earth's surface thus reflects the depth dependence of the thermal conductivity of the crustal material. The temperature at the sur-

face does not remain constant, however, and the thermal profiles therefore have kinks that reflect past air temperature fluctuations. Mathematical deconvolutions are used to reconstruct these fluctuations from the temperature profile, but because of smoothing due to diffusive spreading of past thermal anomalies, many different time histories fit the observed downhole temperature record. The modeler selects from these possibilities the temperature history with the least complicated shape. The details are thus lost, and only the broad features of the time history are captured.

Deconvolutions of thermal records from holes drilled through the polar ice caps reveal broad maxima that reflect the colder temperatures during glacial times. In Greenland boreholes, this broad glacial feature is preceded by a narrower one, which requires a temperature oscillation to have occurred in the late Holocene. The timing of this swing broadly matches that of the Medieval Warm Period to Little Ice Age oscillation. Its magnitude is about 2°C (13). The borehole temperature record for Greenland thus appears to reflect the climate changes thought to have led to the establishment and eventual abandonment of the Viking colonies in southern Greenland (2). It is also consistent with records in the Swiss Alps.

Far Field Evidence

Evidence for the Medieval Warm Period from other parts of the world exists but is spotty and/or circumstantial. From an analysis of 6000 continental borehole thermal records from around the world (14), Huang *et al.* conclude that 500 to 1000 years ago, temperatures were warmer than today, but that about 200 years ago, they cooled to a minimum some 0.2° to 0.7°C below present. However, as is the case for the thermal profiles in ice, those for continental boreholes are highly smoothed. Although suggestive, the fluctuation postulated by Huang *et al.* does not prove that the Medieval Warm Period was global in extent.

Evidence that climate during the latter part of the Medieval Warm Period was much different from today's comes from moisture records for the western United States. Stine has studied lodgepole pine trees rooted at 8 to 19 m depth in Lake Tenaya in the high Sierra Nevada (15). For the trees to have grown, the lake must have been nearly dry. In contrast, only once during the past 50 years has the lake not overflowed during snowmelt. Using radiocarbon dating and ring counting, Stine has shown that for 70 years before 1093 A.D., the lake stood at least 13 m below its outflow spillway, and for 141 years before 1333 A.D., it stood at least 11 m below its spillway (16). Stine has documented similar events at Mono Lake and the Walker River (17). He concludes that late in the Medieval Warm Period, California experienced sever-

al decade-long periods of profound drought.

If, as Bond *et al.* (3) suggest, the cyclic changes in ice-rafted debris composition reflect oscillations in the strength of the Atlantic's conveyor circulation, one might expect temperature changes in Antarctica to have been opposite in phase to those in the North Atlantic, as was the case during the last deglaciation (18). Clow has carried out a deconvolution of the temperature record at the Antarctic Taylor Dome site (19). His reconstruction shows that the air temperature was 3°C colder during the time of the Medieval Warm Period than during that of the Little Ice Age. This record suggests that conditions in Antarctica underwent an antiphased oscillation during the Medieval Warm Period–Little Ice Age period.

The Case for a Global Event

The case for a global Medieval Warm Period admittedly remains inconclusive. But keeping in mind that most proxies do not have adequate sensitivity, it is interesting that those capable of resolving temperature changes of less than 1°C yield results consistent with a global Medieval Warm Period. To test whether this is indeed the case, we require Holocene snowline fluctuation records for tropical and Southern Hemisphere sites and continued studies of wood and peat exposed by the continuing retreat of Northern Hemisphere glaciers. As the world's mountain glaciers continue to retreat, ever more evidence for past Holocene warm episodes will be exposed.

One might ask why the strength of the Atlantic's conveyor circulation oscillates on a time scale of one cycle per 1000 to 2000 years. I suspect that it has to do with the ex-

port through the atmosphere of water vapor from the Atlantic to the Pacific Ocean. The magnitude of this export has been estimated to be $(0.25 \pm 0.10) \times 10^6 \text{ m}^3/\text{s}$ (20). If this freshwater loss were not balanced by the export of salt from the Atlantic, the latter's salt content would rise at the rate of about one gram per liter each 1500 years. Such an increase in salt content would densify cold surface water by an amount equivalent to a 4 to 5 K cooling, thereby strongly altering the buoyancy of surface waters in the North Atlantic and hence their ability to sink to the abyss.

I believe that this salt export is not continuous but episodic. The salt content of the Atlantic periodically builds up until a strong conveyor circulation mode is turned on, causing the salt content to drain down. Eventually, a weak circulation mode kicks in, allowing the salt content to build up again. I have suggested previously (21) that an apparent mismatch between radiocarbon and chlorofluorocarbon-based estimates of the rate of deep-water formation in the Southern Ocean may reflect a change in circulation after the Little Ice Age.

The geographic pattern of Holocene climate fluctuations remains murky, but several things are clear. The Little Ice Age and the subsequent warming were global in extent. Several Holocene fluctuations in snowline, comparable in magnitude to that of the post–Little Ice Age warming, occurred in the Swiss Alps. Borehole records both in polar ice and in wells from all continents suggest the existence of a Medieval Warm Period. Finally, two multidecade-duration droughts plagued the western United States during the latter part of the Medieval Warm

Period. I consider this evidence sufficiently convincing to merit an intensification of studies aimed at elucidating Holocene climate fluctuations, upon which the warming due to greenhouse gases is superimposed.

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PERSPECTIVES: CELL CYCLE

Centrioles at the Checkpoint

Andrew W. Murray

The cellular organelle called the centriole has been an enigma to biologists for more than a century. Centrioles were first seen as a pair of dots at the center of the cell surrounded by a granular mass (the centrosome) from which radiated arrays of fibers. Subsequent work revealed that these fibers are composed of microtubules assembled from monomers of α - and β -tubulin. The centrosome contains a special form of tubulin (γ -tubulin) that initiates microtubule assembly (a process called nucleation), and the centrioles are composed of highly ordered arrays of

short, specialized microtubules. Like DNA, centrioles replicate once during the cell division cycle, but they do so conservatively by forming a completely new centriole (1), rather than by distributing the original material between daughter molecules, as DNA does (see the figure). Applying to the centriole the maxim of baseball sage Yogi Berra—"You can observe a lot by watching"—Hinchcliffe, Piel, and their colleagues (2, 3) report on pages 1547 and 1550 of this issue that the centriole regulates key steps in the cell division cycle.

Centrosomes control cell organization and polarity by initiating formation of microtubules, but what is the role of the centrioles that lie within them? Centrioles are

not absolutely essential for progression through the cell cycle because some animal oocytes divide successfully despite having destroyed their centrioles early in the meiotic cell cycle, and early embryos can replicate their DNA and pass through mitosis without either centrioles or centrosomes (4). Previous (although indirect) attempts to investigate centrosomes in postembryonic cells concluded that centrioles were needed for cells to enter mitosis, the final phase of the cell cycle (5).

Hinchcliffe *et al.* (2) examined the problem directly. They delicately cut cultured cells in half to separate the centriole from the nucleus and then watched the halved cells for several days with a video microscope. In contrast to earlier results, the abused cells entered mitosis normally and assembled the typical bipolar mitotic spindle. Beyond this point, however, their behavior became increasingly abnormal. There were long delays before the initiation of chromosome segregation, many of

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