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Micropaleontological Evidence for Increased Meridional Heat Transport in the North Atlantic Ocean During the Pliocene

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The Middle Pliocene (~3 million years ago) has been identified as the last time the Earth was significantly warmer than it was during the Last Interglacial and Holocene. A quantitative micropaleontological paleotemperature transect from equator to high latitudes in the North Atlantic indicates that Middle Pliocene warmth involved increased meridional oceanic heat transport.

Concern about the effects of anthropogenically increased atmospheric concentrations of greenhouse gasses has led to increased efforts to understand climates that were warmer than present conditions, such as those of the Late Cretaceous (*1*), Eocene (*2, 3*), Middle Pliocene (*4*), and Last Interglacial (*5*) (O isotope substage 5e). If a period of warm global climate can be accurately reconstructed from proxy paleoclimate data, then simulation experiments can be used to refine general circulation models and identify mechanisms responsible for the warming (*6*).

The Pliocene is an ideal interval to test such an approach. First, there is abundant evidence for global warmth. For example, the range of shallow marine and open-ocean faunas as well as terrestrial flora was displaced northward in the North Atlantic and surrounding regions (*7–9*). Geomorphological and stratigraphical evidence from the eastern United States (*10, 11*) indicates that sea level was at least 20 m higher than it is today. This height is also supported by deep-sea isotopic data (*12, 13*). Such a rise in sea level would require melting of part of the Antarctic ice cap. This potential for melting is confirmed by the occurrence of Pliocene marine diatoms in clasts within the Sirius Formation (Antarctica), which indicates marine conditions in the interior of East Antarctica (*14, 15*). Sea-surface temperatures of the North Atlantic 3 million years ago (Ma) in some regions are estimated to be more than 8°C higher than those of today (*8, 16*). In this report we use data from planktic foraminifers, ostracods, pollen, and plant macrofossils to characterize the Pliocene climate and evaluate the gradient of surface temperature in the North Atlantic region.

Many Pliocene marine, and increasing numbers of nonmarine, sites have reliable paleomagnetic and isotopic age control. Estimates of Pliocene environmental conditions are more reliable than those of pre-Pliocene periods because most Pliocene marine and nonmarine species are extant. Thus, Pliocene reconstructions generally have greater environmental and temporal resolution than paleoclimatic reconstructions of earlier times.

The boundary conditions we used for the Middle Pliocene reconstruction are like those of the present with a few notable exceptions. Although some workers have suggested that uplift of the Tibetan Plateau during the last 3 million years affected climate (*17*), recent work suggests that the Plateau reached its present elevation at 8 Ma (*18*) and, therefore, may not have been a primary factor in Pliocene climate change. The Central American Isthmus probably became a barrier to deep circulation during the latest Miocene or earliest Pliocene and a barrier to surface circulation near 3 Ma (*19*). The Bering Straits, which provide a shallow connection between the Pacific and Arctic oceans (*20*), opened at 3 Ma or earlier.

From analysis of planktic foraminifers and ostracods we produced a synoptic map of surface temperature for the North Atlantic ocean centered around 3 Ma (Fig. 1). We used factor-analytic transfer functions and dissimilarity coefficient matching techniques for planktic foraminifers (*21, 22*) and ostracods (*7, 23*) to estimate conditions of the sea surface and shallow sea bottom from Pliocene samples.

Our results, based on different quantitative methods (species-level factor analysis and dissimilarity coefficient mapping on the

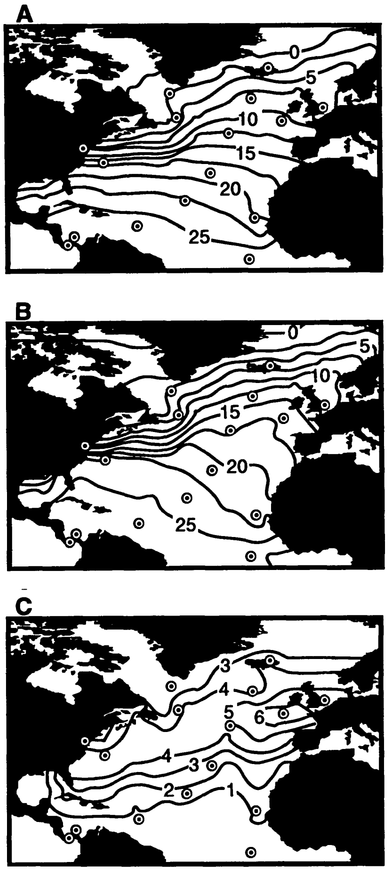

Fig. 1. Maps of (**A**) modern winter sea-surface temperatures, (**B**) Pliocene winter sea-surface temperatures, and (**C**) Pliocene winter sea-surface temperature anomalies (Pliocene minus modern), showing regional distribution of Middle Pliocene warming (in degrees Celsius). Circles show location of deep-sea cores and ocean margin sections used to constrain contours. See (*8*) for methodology.

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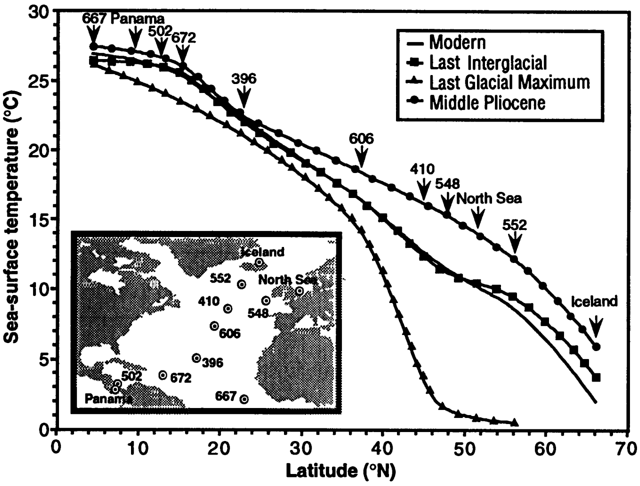

Fig. 2. Comparison of North Atlantic sea-surface temperature transects from four different climates: modern, Last Glacial Maximum (*38*), Last Interglacial (*5*), and Middle Pliocene. Circles on inset map show localities used to construct Middle Pliocene transect. Last Glacial Maximum shows consistently cooler than modern temperatures from equator to mid-latitudes and a sharply steeper than modern gradient between 35° and 45°N. Middle Pliocene transect shows that low-latitude marine temperatures were effectively similar to modern conditions (*41*). There is a general increase in temperature at mid- and high latitudes.

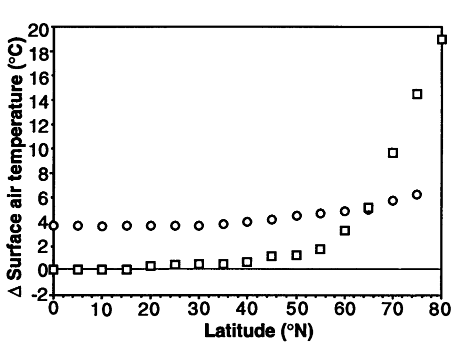

Fig. 3. Model results of contrasting surface air temperatures of a climate with twice the CO_2 level of today (circles) (*17*, *39*) against one with a 15% increase in ocean heat flux (squares) (*17*). Equatorial regions show little or no change in the increased heat-flux run while the high CO_2 model produced much warmer equatorial temperatures.

generic level), and independent modern calibrations show that analyses of two different fossil groups (planktic foraminifers and ostracods) give similar paleotemperatures in each of several climatic zones. These results are qualitatively supported by other fossil groups in Iceland (*24*) and England (*25*).

Inspection of Pliocene surface temperatures (Fig. 1) indicates that, despite the general anticyclonic nature of the North Atlantic gyre, the regions in higher latitudes were warmer than they are now. Terrestrial data around the North Atlantic region reflect a climatic pattern congruent with marine records. In low and temperate latitudes, temperatures were apparently no different from (*26*, *27*), or even cooler than, those of today (*28*–*30*). Mean annual precipitation during the Pliocene was greater than present rates in western North America, and in the western Mediterranean region summer rainfall was more abundant than it is today (*31*). Temperatures in northwestern Europe were warmer than they are now, and warmth-loving plants grew at least as far north as the Netherlands at 3 Ma (*32*, *33*). The increase in temperatures over modern values was substantially greater at more northerly latitudes. As a result, forests grew in Iceland (*24*) (which is now tundra), in the region surrounding the Labrador Sea and Baffin Bay (*34*, *35*), and even as far as ~80°N at Meighan Island (*9*, *36*, *37*) in the Canadian Arctic Archipelago.

The Pliocene and Last Glacial Maximum transects shown in Fig. 2 delineate the range of climate variability in the North Atlantic during the last few million years. Comparison of North Atlantic temperatures during winter for the Pliocene (3 Ma), Last Interglacial (*5*), Last Glacial (*38*), and today shows negligible differences at low latitudes and major differences at high latitudes. The Last Interglacial transect is indistinguishable from the modern transect, whereas the Last Glacial and Pliocene transects show substantial differences from the modern transect. The stability of low-latitude sea-surface temperature during the Pliocene warming is confirmed from reconstruction of a number of sites in the Caribbean and eastern tropical Atlantic (*8*). The positive temperature anomaly of 4° to 8°C at mid- to high-latitude Pliocene sites creates an equator-to-pole gradient less steep than that of the modern ocean. Studies of marine ostracods from the Coralline and Waltonian Red Crags of eastern England and correlative deposits in the southern North Sea area indicate that the Pliocene temperatures were 4° to 5°C higher than those of today in the shallow mixed zone of northern Europe. The wide geographical distribution of paleoclimatic data in the North Atlantic in Fig. 2 (about every 6° to 10° of latitude) indicates that our results are representative of the 3-Ma Pliocene ocean and are not an artifact of sampling.

Two mechanisms have been proposed to explain past warm periods: increased radiative forcing from trace gasses (that is, increased CO_2) and changes in meridional ocean heat flux. Modeling experiments (*17*, *39*) suggest that doubling the concentrations of atmospheric trace gasses over present values causes surface air temperature to increase ~3° to 6°C in both tropical and polar regions (Fig. 3). Amplification of warming at high latitudes is due primarily to the removal of sea ice. Conversely, small increases in oceanic heat transport would result in little or no warming at low latitudes (*17*, *40*) but substantial warming at high latitudes, driven by the decreased sea ice and planetary albedo feedback (*17*). Comparison of our Pliocene temperature reconstruction (Fig. 2) to temperature transects generated by a model (Fig. 3) suggests that an increased oceanic heat flux is the best explanation for the Pliocene gradient (*41*). Thus, oceanic heat transport and, by inference, thermohaline circulation were greater in the Pliocene than they are today, even though the equator-to-pole gradient of surface temperature was less than the modern gradient.

The cause of increased oceanic heat transport around 3 Ma is unknown. A number of studies have suggested that uplift of the Central American Isthmus resulted in intensification of the Gulf Stream, which led to warmer surface waters in the North Atlantic (*42*, *43*). However, the Central American Straits (*19*) began closing in the late Miocene. Furthermore, qualitative and quantitative studies indicate that considerable climate variability occurred before and after 3 Ma and that sea-surface temperature in some areas of the North Atlantic became as warm during the late Miocene, if not warmer, than at 3 Ma (*8*, *23*, *42*). Thus, the warm interval and poleward excursion of the isotherms at 3 Ma do not appear related in a simple linear way to the closing of Central America. Detailed documentation of the timing and magnitude of Pliocene climate variability in areas outside of the North Atlantic is needed to determine the causal mechanism for Pliocene warming.

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The Evolutionary Convergence of Hearing in a Parasitoid Fly and Its Cricket Host

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Parasitism is a widespread and diverse life strategy that connects species throughout the animal kingdom. Female parasitoid flies of the genus *Ormia* must find a specific cricket host on which to deposit their parasitic maggots. To reproduce, female flies must perform the same task as female crickets: find a singing male cricket. These flies have evolved a unique hearing organ that allows them to detect and locate singing male crickets. Through evolutionary convergence, these flies possess a hearing organ that much more resembles a cricket's ear than a typical fly's ear, allowing these parasitoids to take advantage of the sensory ecological niche of their host.

Throughout the evening from spring through fall, male field crickets of the genus *Gryllus* sing loud and persistent songs to attract females for mating. However, female crickets are not all that calling males may attract. Acoustically active female parasitoid flies of the genus *Ormia* (order Diptera, family Tachinidae, tribe Orminii) are also attracted to singing male crickets (*1*). The gravid female fly locates the calling male cricket and deposits maggots (length ~400 μm) on or near him. The larvae burrow into the host cricket, grow, feed, and kill him within 10 days; the fully grown larvae then emerge and pupate.

Female flies and female crickets must solve the same auditory problem: to detect and locate a male cricket by hearing his calling song over long distances. On the basis of physiological, anatomical, and behavioral studies, we report that ormiine flies have solved this problem by means of an ear that incorporates—in structure and function—the design principles common to all hearing organs in insects, including crickets, that must detect high-frequency sounds over great distances. This example of convergent evolution in a hearing organ demonstrates the constraints on morphological design that are imposed by behavioral function as well as by principles of physical acoustics.

Many flies produce acoustic signals. Mosquitoes use acoustic signals in courtship (*2*), and songs are prominent in the courtship of *Drosophila* (*3*). However, there is a major difference between the hearing organs in these flies and those in crickets that reflects the different acoustic demands made upon their hearing abilities (*4*). Most flies and mosquitoes emit low-frequency sounds (100 to 500 Hz) that operate over short distances (millimeters to centimeters). In contrast, crickets emit intense, higher frequency sounds (typically above 3 kHz) that attract female crickets over much longer distances (at least 15 m). The acoustic design features of the standard dipteran hearing organ—the Johnston's organ of mosquitoes and fruit flies—are based on a feathery antennal structure that senses local air movements in the near field of a sound source (*4*, *5*). In contrast, the structure and function of tympanal hearing organs in crickets (and other acoustically active insects such as katydids, grasshoppers, moths, cicadas, and mantises) permit detection in the pressure field (far-field) of sound (*4*). Key features of tympanal organs include a specialized thin, external cuticular membrane (tympanum) that is closely associated with internal tracheal air sacs, and a receptor organ consisting of a group of scolopale-type sensory cells (*4*, *6*). Tympanal organs, like the auditory organs of terrestrial vertebrates, are sensitive to minute changes in air pressure that are propagated from a distant sound source. In structure and in function the hearing organ of acoustically active parasitoid flies is tympanal, more like the ears of their hosts than like those of other flies.

The parasitoid ormiine flies that we used either were captured in the field, near Gainesville, Florida, or were first-generation stock reared from wild-caught flies (*7*). We characterized the morphology of the hearing organ of *Ormia ochracea* by embedding the whole thorax in plastic (JB-4, Polyscience Inc.) and sectioning and staining with toluidine blue and other conventional stains. To determine the auditory sensitivity of this novel dipteran ear, we recorded neural responses to acoustic stimuli by conventional extracellular recording techniques (*8*). The neural response was from higher order auditory cells, but in other species such activity reflects hearing sensitivity (*9*).

Our neurophysiological recordings confirm that the auditory system of parasitoid flies is tuned to the songs of their hosts. *Ormia ochracea* larviposits on or near the

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