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Neogene Ice Age in the North Atlantic Region: Climatic Changes, Biotic Effects, and Forcing Factors

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ABSTRACT

Long-term climatic trends culminated in the recent ice age of the Northern Hemisphere. As late as mid-Pliocene time, however, many sectors of the North Atlantic region remained substantially warmer than today. Oxygen isotope ratios for marine microfossils indicate that a pulse of cooling occurred relatively suddenly at high and middle latitudes at ~3.2 to 3.1 million years ago (Ma) and that large ice sheets formed ~2.5 Ma, when more severe cooling and regional drying of climates occurred. Cycles of glacial expansion and contraction reflected orbital forcing at periodicities of ~41,000 yr until about 0.9 Ma and ~100,000 yr thereafter. Aridification in Africa at ~2.5 Ma resulted in the extinction of many forest-dwelling species of mammals and, soon thereafter, in the origins of numerous species adapted to savannas. Mammalian extinction intensified closer to 2 Ma in North America and was weaker in Europe, where forests changed in floral composition but remained widespread. Beginning at ~2.5 Ma and continuing into mid-Pleistocene time, life occupying shallow seafloors in the North Atlantic region suffered heavy extinction from climatic cooling, leaving an impoverished, eurythermal Recent fauna. Long-term climatic trends in the North Atlantic region during Neogene time probably resulted primarily from tectonic events, notably closure of the Straits of Panama and uplift of the Tibetan Plateau and other regions. A decrease in atmospheric CO_2 and consequent weakening of a greenhouse effect also appears to be required, perhaps due to increased weathering that accompanied the uplifting of plateaus.

INTRODUCTION

In this chapter, we discuss climatic events that marked the onset of the recent ice age, their impact on biotas, and their likely causes. Our focus is on the North Atlantic region because this part of the world, which became bordered in the north by major ice caps, was the scene of more severe environmental and biotic changes than occurred in other areas of the globe.

The detailed chronology for major glacial events of the past 3 million years (m.y.) or so has come primarily from deep-sea deposits. Many deep-sea cores provide relatively continuous records, for which magnetic reversals and biostratigraphic data yield key dates. Also especially useful are changes in the isotopic composition of microfossils; the proportion of ^{18}O increased in these forms at times of glacial maxima, both because isotopic partitioning during skeletal secretion varies with temperature and because ^{16}O is preferentially evaporated from the oceans, transported in water vapor, and sequestered in glacial ice.

Fossils in shallow marine and terrestrial sequences also record climatic changes of the recent ice age. Some biotic changes represent clear evidence of climatic transitions, but others, which will be discussed separately, can only be interpreted a posteriori as reflecting these environmental changes.

Historically, a great variety of hypotheses have been invoked to explain the onset of Plio-Pleistocene glaciation in the Northern Hemisphere. Although the issue is complex, forcing factors resulting from tectonic events were probably responsible. We also review ways in which ice sheets have been influenced by periodicity in the Earth's orbital motion and have themselves behaved as climatic forcing factors in a complex feedback system.

CLIMATIC EVENTS

The climatic changes that have occurred in the North Atlantic region since the ice age began about 2.5 Ma can be understood only in the context of events that were under way millions of years earlier. The climatic changes of the past 2.5 m.y. have been cyclical, relatively rapid, and associated with orbital-scale variations in ice volume in the Northern Hemisphere. In contrast, the major changes prior to 2.5 Ma represented net trends that were relatively gradual. For the most part, they resulted from tectonic events that are discussed in the final section of this chapter.

In the present section, we first evaluate climatic events prior to the Late Pliocene, which began at 3.4 Ma; next, events at 3.2-3.1 Ma that preceded the start of the ice age; and finally, events that marked the development of vast ice sheets close to 2.5 Ma.

Responses Prior to the Late Pliocene

Climatic responses to tectonic events of Miocene and Early Pliocene time were regionally complex. Although in general these climatic trends developed gradually over many millions of years, they were at times interrupted by more dramatic "steps," or brief intervals when critical thresholds in the system were exceeded and large-amplitude responses were triggered. Both the slow climatic drift and the steps altered the distributions of plants and animals, and may also have affected their evolution. Some marine records appear to be relatively continuous, but the discontinuous nature of most continental sedimentation precludes fully adequate resolution of many long-term climatic trends. The basic patterns that can be detected involve widespread cooling, especially at high and middle latitudes, and a mosaic of more regional trends toward wetter and drier climates.

The cooling trend is particularly evident at higher latitudes and elevations. Thick ice appeared on Antarctica early in the Cenozoic (Barron et al., 1989). Deposits from small mountain glaciers are first recorded between 10 and 5 Ma in the Coast Range of Alaska (Denton and Armstrong, 1969) and the Andes of South America (Mercer, 1983). Pollen data from high-altitude sites in Iceland indicate significant cooling by 10 Ma (Mudie and Helgason, 1983). Traces of ice-rafted sand in Norwegian Sea sediments by 4 Ma (Henrich et al., 1989) suggest at least the sporadic presence of mountain glaciers along the east coast of Greenland or the west coast of Scandinavia at this time.

Another major late Cenozoic trend was a progression toward more highly differentiated regional extremes of wet and dry climate. During the past 15 m.y., deserts have formed or expanded into new terrain in Asia (Wolfe, 1979), North Africa (Tiedemann et al., 1989), and North America (Axelrod, 1950), while monsoonal climates have persisted or intensified in the Indo-Asian subtropics and South American tropics.

Several regions of west-central North America became markedly drier during the late Cenozoic. On the Northern Plains, prairie savanna gave way to grasses and herbs after 15 Ma (Thomasson, 1979). During the same interval, vegetation adapted to summer drought gradually came to dominate the California coast (Axelrod, 1966).

The Pliocene Prior to 2.5 Ma

Most of the profound climatic changes in the Northern Hemisphere during the Pliocene Epoch prior to about 3.1 Ma were regional in scale. Forest yielded to scrub vegetation in the rain shadow of the Cascades around 4 Ma, for example (Leopold and Denton, 1987), and desert vegetation expanded in the Great Basin near 4 to 3 Ma (Axelrod,

1950). Saharan dust fluxes also increased abruptly near 4.2 Ma (Tiedemann *et al.,* 1989). In general, climates of the Northern Hemisphere prior to about 3.2 Ma were warmer than those of the past 2.5 m.y., including climates during glacial minima. To set the scene for discussion of the ice age, we review climatic indicators of the widespread warmth that preceded it.

The terrestrial floras that have thus far been used most effectively to document continent-wide climatic changes during the Pliocene Epoch are those of Europe (Figure 7.1). Early in Pliocene time, dense coastal forests fringed the northwestern coast of the Mediterranean Sea. Dominance here of species belonging to the cypress family indicates that moist and relatively warm conditions persisted throughout the year (Suc and Zagwin, 1983).

The Mediterranean Sea itself was characterized by a marginally tropical, or at least warm subtropical, thermal regime during Early Pliocene time. This is indicated, for example, by fossil occurrences of numerous species of the generally tropical gastropod genus *Conus* (Marasti and Raffi, 1979). Furthermore, 5% of the polysyringian bivalve mollusks of the Mediterranean that survive from the Early Pliocene are restricted to tropical seas along the west coast of Africa today, apparently being unable to tolerate subtropical conditions (Raffi *et al.,* 1985). Quantitative assessment of the history of extant lineages of planktonic foraminifera reveals that surface waters of the Early Pliocene Mediterranean were characterized by equable thermal conditions, with winter temperatures usually higher than those of the present (Thunell, 1979).

The North Sea was also warmer than today: 20% of the extant polysyringian bivalve species from the lower Pliocene of the North Sea region today live only south of the North Sea, and 10% occur only in waters at least as warm as subtropical. The reproductive requirements of the warm-adapted survivors suggest that for 3 or 4 months, mean temperatures reached 20° C or more (Raffi *et al.,* 1985).

Marine biotas reveal that in the Western Atlantic region, as well, climates prior to about 3 Ma were warmer than today. Fossiliferous strata representing a highstand of sea-level between about 3.5 and 3.0 Ma are exposed along the Atlantic Coastal Plain from Virginia to Florida. They were deposited seaward of the Orangeburg scarp, a conspicuous topographic feature from North Carolina to Florida cut by wave erosion during a stillstand coinciding with the maximum advance of the shoreline, when sea-level stood 35 ±18 m above its present level (Dowsett and Cronin, 1990). At the border between North and South Carolina, the scarp lies about 150 km inland from the present shoreline. Fossil ostracods and microplankton from the Duplin Formation, which extends eastward from the scarp in this region, indicate an age of about 3.5 to 3.0 Ma, and the thermal tolerances of surviving ostracods suggest that nearshore bottom-water temperatures ranged from 26°C in August to 18°C in February (Dowsett and Cronin, 1990). By way of comparison, bottom temperatures along the continental shelf of this region today at a depth of 30 m drop to about 12°C in February. Rich fossil molluscan faunas represent themid-Pliocene highstand from Virginia to southern Florida. In southern Florida they are associated with coral reefs at latitudes about 150 km north of the limit of reef growth today (Meeder, 1979).

Although climates in the southeastern United States were generally warmer than today throughout the 3.5 to 3.0 Ma interval, they became especially warm toward the end of the interval. Ostracod occurrences also suggest a rise of temperatures during the mid-Pliocene transgression. In Virginia, changing ostracod and molluscan faunas indicate a shift from warm temperate to subtropical conditions during deposition of the uppermost Yorktown For

Figure 7.1 Examples of warm-adapted genera of plants that disappeared from northwestern Europe at about 2.3 Ma. Left: *Pseudilarix* (golden larch); center: *Liquidambar* (sweet gum); right: *Zelkova* (Caucasian elm).

mation (Hazel, 1971; Stanley and Campbell, 1981). This pulse of warming has been taken to reflect a strengthening of the Gulf Stream with the closure of the Isthmus of Panama. The temporary disappearance of the planktonic foraminiferan *Pulleniatina* from the Caribbean at 3.1 Ma suggests that this was the time of complete closure (Keigwin, 1978), as does evidence of strongly increased winnowing along the Yucatan Channel (Brunner, 1984). The interval of warming in the southeastern United States was short-lived. As discussed below, ice age cooling affected the region profoundly within a few hundred thousand years. Thermal conditions in the Caribbean have not been assessed for the first half of the Pliocene, but in the Bahamas, reefs flourished to a greater extent than today, and the Bahama Banks comprised atolls (Beach and Ginsburg, 1980). The molluscan fauna of southern Florida differed markedly from that of the Caribbean, in sharp contrast to the situation today, when Florida shares nearly all of its strictly tropical shallow water species with the Caribbean. The distinctive Caribbean Pliocene fauna even characterized the Bahamas, which are separated from the Florida peninsula only by the narrow Straits of Florida (McNeill et al., 1988). Possibly during the highstand of sea-level of mid-Pliocene time, upwelling around Florida formed a biogeographic barrier of relatively cool water (Stanley, 1986). This may explain why, whereas hermatypic corals and many molluscan species of tropical affinities thrived in a lagoonal setting as far north as Sarasota, Florida, there was very little carbonate mud production by calcareous algae here even in the near absence of terrigineous clays. It appears that this region resembled the relatively cool but thermally stable tropical region of the modern Eastern Pacific, where upwelling also prevails (Stanley, 1986).

While the Panamanian straits connecting the Atlantic and Pacific became obstructed during mid-Pliocene time, the Bering Strait opened, to connect the two large oceans across the Arctic. This new connection apparently resulted largely from the global elevation of sea-level that ultimately inundated the eastern United States along the Orangeburg scarp. Sediments of mid-Pliocene age have been recognized at elevations in Alaska as high as 35 m above present sea-level (Carter et al., 1986). The breaching of the Bering land bridge left its mark in the stratigraphic record of northeastern Iceland, where a host of Pacific mollusk species appear abruptly in mid-Pliocene sediments (Einarsson et al., 1967).

Fossil occurrences and biogeographic distributions of molluscan species in the modern world indicate that the exchange of species between the Atlantic and Pacific was asymmetric. At least 125 species migrated from the Pacific to the Atlantic, whereas only 16 species are known to have moved in the opposite direction (Hopkins, 1967). The reason for this disparity is unclear (Vermeij, 1989), but it is significant that many groups that participated in the exchange are unable to live in most areas of the Arctic Ocean today (Carter et al., 1986). This fact, and the occurrence of a fossil sea otter on the north slope of Alaska, indicate that temperatures in the Arctic were warmer in mid-Pliocene time than they are now. At least some fringes of the Arctic were apparently ice free during at least part of the year.

The First Pulse, 3.2 to 3.1 Ma

The first events presaging the onset of the Plio-Pleistocene ice age occurred about 3.2 to 3.1 Ma, but they did not include the buildup of major ice sheets. At this time, in many low latitude areas fossil planktonic foraminifera exhibit a shift to heavier $\delta^{18}O$ values that was sustained for only about 100,000 yr. In contrast, a similar increase for deep-sea benthic foraminifera persisted, with fluctuations, to the present day (Prell, 1984). This divergence of values is taken to indicate a sustained cooling of the deep-sea where, in fact, an interval of scouring by descending cold water is also recorded (Ledbetter et al., 1978). This implies climatic cooling at high latitudes.

The temporary nature of the isotopic perturbation for planktonic fossils indicates that there was no permanent buildup of large ice sheets. Nonetheless, the oldest Pliocene tillites in northeastern Iceland occur just above a basaltic unit dated at 3.1 ± 0.1 Ma by the potassium-argon method (McDougall and Wensink, 1966) and just below the base of the Mammoth interval of reversed magnetism, dated at 3.15 Ma (Mankinen and Dalrymple, 1979). Climatic changes extended at least as far equatorward as the northwestern Mediterranean region. Here the coastal forest, dominated by cypresses, gave way to oaks and other forms of vegetation adapted to relatively drier, more seasonal climates (Suc, 1984). Statistical analysis of changes in the composition of the planktonic foraminiferal fauna of the Mediterranean reveal that a pulse of cooling between about 3.2 and 3.0 Ma reduced mean annual temperature by 2 to 4°C (Keigwin and Thunell, 1979). In northwestern Europe, several subtropical species of land plants, including palms, disappeared at the end of the Branussumian interval, about 3.2 Ma (van der Hammen et al., 1971).

Onset of the Ice Age at 2.5 to 2.4 Ma

Warmer temperatures returned temporarily to at least some regions between 3 and 2.5 Ma. Fluctuations in the composition of the planktonic foraminiferal fauna of the Mediterranean indicate oscillating temperatures for this interval (Thunell, 1979). Fossils in transgressive shallow marine strata on the north slope of Alaska reveal that sea otters were again present along the margin of the Arctic

Ocean slightly before 2.4 Ma. Fossil pollen in the same Alaskan deposits point to the presence of tundra close to sea-level, however, which means that by this time climates were deteriorating once again (Repenning *et al.,* 1987).

The cooling of climates between about 2.5 and 2.4 Ma marked the true transition to the modern ice age. Most climatic changes in the Northern Hemisphere subsequent to ~2.4 Ma reflect the pervasive influence of ice sheets. Oxygen isotopic records from deep-sea cores provide the best proxy of global ice volume (Shackleton and Opdyke, 1976), with ~50 to 70% of the late Pleistocene fluctuations linked directly to ice volume, primarily in North American and Eurasia. The remaining part of these signals was determined largely by local temperature changes, some of which tracked ice volume closely, whereas others varied independently, depending on locale.

An oxygen isotopic record covering the entire span of significant glaciation in the Northern Hemisphere is shown in Figure 7.2. Several features of this record are worth noting. First, regular cycles of rather small amplitude began at least as early as 2.7 Ma, and scattered ice-rafted debris in the North Atlantic and Norwegian Sea confirms that small ice sheets existed between 2.7 and 2.4 Ma (Jansen *et al.,* 1988; Raymo *et al.,* 1989). The 2.4 to 2.3 Ma interval included the inception of much larger cycles, in both the isotopic (Shackleton *et al.,* 1984) and the ice-rafting (Zimmerman, 1984) signals, marking the first appearance of really substantial ice sheets. For the next 1.5 m.y. (2.3 to 0.9 Ma), isotopic cycles varied mainly at the 41,000-yr period (Raymo *et al.,* 1989; Ruddiman *et al.,* 1989), and the maximum isotopic values during glacial climatic extremes generally did not exceed those near 2.4 to 2.3 Ma, except toward the end of the interval.

During the past 0.9 m.y., several isotopic cycles attained amplitudes at glacial maxima that were considerably larger than for any previous cycle, and the dominant tempo of glaciation shifted to 100,000 yr (Shackleton and Opdyke, 1976). In addition, very rapid deglaciations called "terminations" (Broecker and van Donk, 1970) began to occur at the end of the major glacial cycles.

Several other records that are continuous and span large portions of the past 3 m.y. confirm the basic climatic trends indicated by oxygen isotopes. These include sea-surface temperature records and ice-rafted fluxes in the subpolar North Atlantic Ocean (Ruddiman *et al.,* 1989); loess deposits in eastern Europe (Kukla, 1977) and south
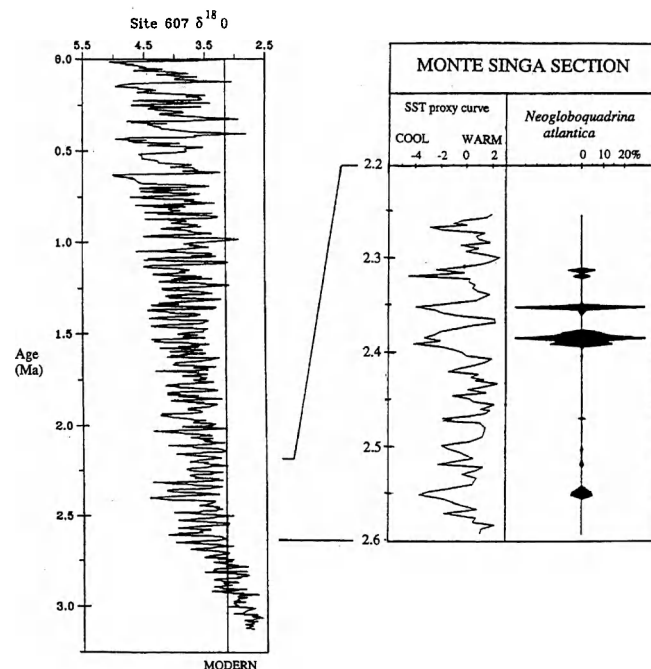

Figure 7.2 Benthic foraminiferal $\delta^{18}O$ from North Atlantic Site 607 (after Raymo *et al.,* 1990) and events between 2.6 and 2.2 Ma in the Mediterranean (Zachariasse *et al.,* 1990). This record spans the entire Northern Hemisphere ice age, at an average sampling interval of 3500 yr. The record shows the Late Pliocene initiation and mid-Pleistocene intensification of Northern Hemisphere glaciation. The sea-surface temperature (SST) proxy curve is the product of a principal component analysis of occurrences of planktonic foraminifera, based on evidence of their thermal tolerances. Relative abundance of *Neogloboquadrina atlantica, a species adapted to cool conditions, increased markedly just after 2.4 Ma and again at 2.35 Ma.*

ern China (Heller and Liu, 1982); and pollen sequences in the Netherlands, northern Italy, and Macedonia (van der Hammen *et al.*, 1971). Prominent features in these records include a large initial step toward glacial-like climates at or near 2.4 Ma, cycles of modest size and relatively high frequency until near the Jaramillo magnetic reversal (~0.9 Ma), and larger cycles displaying a 100,000-yr periodicity during the late Pleistocene.

Regions located well away from the Northern Hemisphere ice sheets might be expected to show climatic variations during the Late Pliocene and Pleistocene in response to other factors. Within middle and high latitudes of the Northern Hemisphere, however, the relatively continuous records available all appear to fluctuate sympathetically with the ice sheets. Some discrepancies may occur in the 2.3 to 0.9 Ma interval, where the isotopic record appears to detect more cycles than the loess or pollen sequences, but this may reflect different thresholds of sensitivity in the detection of small-amplitude 41,000 yr cycles.

Less continuous or well-dated stratigraphic sequences representing shallow marine and terrestrial environments yield fossils that document important climatic events. For example, the record of vegetational change along the northwestern margin of the Mediterranean at about 2.3 Ma points to a shift to drier conditions. Forests shrank and steppe vegetation, including sagebrush and weedy plants, expanded. Generally contemporaneous changes in the composition of some European floras reflect cooling (Suc, 1984). At about this time (the Praetiglian interval), what remained of the subtropical Malayan element disappeared from the flora of northwestern Europe (van der Hammen *et al.*, 1971; also see Figure 7.1). In Africa, palynofloras reveal sweeping climatic change at about 2.5 Ma., although the precise timing remains to be determined. In the Ethiopian uplands, climates became cooler and drier than today, whereas they had previously been warmer and moister (Bonnefille, 1985). Apparently this pulse of climatic change was soon partly reversed. The fact that even today, during a glacial minimum, Africa is cooler and drier than it was prior to 2.5 Ma may, however, indicate that this region has experienced a fundamental climatic change unrelated to glacial maxima.

In the Western Atlantic region and the Americas, climatic changes are less well documented, but in the high plain of Bogota, Columbia, fossil pollen records indicate cooling at about 2.5 Ma (van der Hammen, 1985). Cores obtained by drilling in the Bahamas document dramatic change a bit earlier. Here, magnetostratigraphy has provided a detailed chronology for a relatively complete stratigraphic sequence (McNeill *et al.*, 1988). Fossils in the core reveal that sea-level dropped briefly at about 2.65 Ma and San Salvador ceased to grow as a coral atoll. The fact that the biotic crisis in the Bahamas occurred as early as 2.65 Ma reflects the fact that a transition to the ice age was a complex event that spanned more than 200,000 yr (Figure 7.2). The precise chronology of climatic change remains to be established for many geographic areas, but the magnetic reversal separating the Gauss and Matuyama Chrons at 2.5 Ma should prove useful here.

BIOTIC CONSEQUENCES

The Pliocene climatic changes that affected terrestrial biotas of the North Atlantic region included a general cooling of climates, with increased seasonality in many areas and widespread aridification on the land. Among the results were the migration of many species to favorable habitats; the extinction of species unable to escape intolerable new conditions through migration; and the origin of new species adapted to the new conditions.

Terrestrial Biotas

Some of the biotic consequences of the climatic changes, in fact, represent key evidence documenting the changes. Foremost of these were previously described transformations of terrestrial floras, which we review in discussing the general topic of biotic change.

Fossil pollen have provided most of our information about Pliocene terrestrial floras of the North Atlantic region. Although the evidence assembled to date is patchy, it indicates that drying of climates was at least as significant as thermal change. Often it was an accentuation of the dry season that had the greatest impact on floras. In general, grasslands expanded at the expense of forests, which require moist conditions. Climatic changes had their primary effects on terrestrial mammals indirectly, through their influence on vegetation.

Africa

In some areas, orographic effects of regional tectonic activity had a more pronounced impact on biotas than did global climatic change. Africa, however, experienced aridification so pervasive that it could not have resulted from small-scale tectonics. Fossil pollen reveals that savannas spread at the expense of forests, not only throughout northern Africa, where the trade winds prevail, but also in Kenya (Bonnefille, 1976). The dramatic change that occurred at about 2.5 Ma entailed both cooling and drying of climates. While a slight cooling probably had some effect on African floras, aridification was the most influential climatic change. Low rainfall is the primary factor that separates grasslands from forested areas today.

The onset of the ice age had a greater impact on mammals in Africa than in Europe or North America. Presum

ably, this resulted from two conditions: (1) many species of mammals were endemic to Africa, and (2) the vegetational changes were continental in scale. Numerous forest-adapted species of antelopes died out close to 2.5 Ma, but there was a positive evolutionary response to the climatic change as well (Vrba, 1985). Several new species of antelopes adapted to savannas appeared through speciation events at about 2.5 Ma, or within 200,000 to 300,000 years thereafter (Figure 7.3). At the same time, several species adapted to grasslands invaded from Eurasia, apparently because forest barriers disappeared, at least temporarily. These species and others that evolved slightly later constitute the modern antelope fauna of the African savannas. Micromammals appear to have changed in a parallel fashion (Wesselman, 1985); in Ethiopia, numerous forest-dwelling species died out and were replaced by species adapted to drier conditions. African monkeys experienced a high rate of evolutionary turnover at about the same time, although the relationship of this change to the vegetational transition remains obscure (Delson, 1985). The dramatic effects on the history of the human family are discussed in Chapter 14 of this volume.
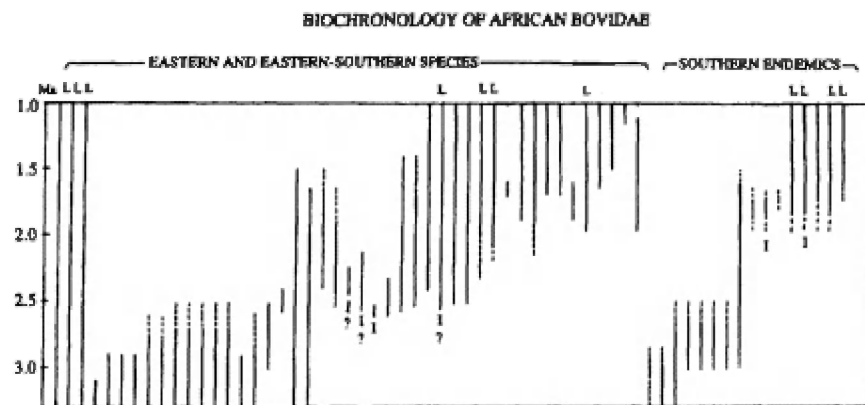

Figure 7.3 Stratigraphic ranges of antelope species in sub-Saharan Africa (I: immigrants; L:living; for identities of species, see Vrba, 1988). Most of the extinctions close to 2.5 Ma were of forest-adapted species. Most species that appeared at this time or shortly thereafter were savanna dwellers.

Europe

We have already noted the floral change along the northwestern border of the Mediterranean, where the decline of cypress-dominated forests beginning slightly before 3 Ma apparently resulted primarily from aridification but may have entailed climatic cooling as well. This region is marginal to the trade wind belt and is far more arid today than northwestern Europe. In the latter, more northerly region, cooling of climates and also divergence of seasonal extremes of temperature apparently had a stronger effect on biotas than did aridification.

We have previously noted the disappearance of the subtropical Malayan component from the flora of northwestern Europe in two pulses centered at about 3.1 and 2.5 Ma. This was not simply a matter of regional extermination: numerous endemic species suffered extinction (Leopold, 1967). As Reid and Reid (1915) noted long ago, at the time of the climatic change, southern Eurasia was spanned from east to west by a barrier of seas, deserts, and mountains unbreached by river valleys. At the same time, the increasingly dry climate of central Asia blocked eastward migration. The result was a lethal trap for many warm-adapted species, including palms. Other species, which were more widely distributed before climatic changes began, disappeared from Europe but survived in North America or China.

The floral change began earlier in northwestern Europe than in Poland (Leopold, 1967). Extinction continued into the Pleistocene Epoch, especially in Poland, but ceased almost entirely during the latter part of the Pleistocene. Floral compositions have continued to fluctuate markedly with shifts of climate, however, as a result of oscillatory migration. In Poland, for example, temperate elements have been more conspicuous during glacial minima (including the Holocene) and arctic-alpine elements during glacial maxima. In other words, the heaviest extinction occurred during the Pliocene, when numerous vulnerable species were present, and declined into the Pleistocene. By the latter part of the Pleistocene, vulnerable species had disappeared and floras consisted of species that could tolerate climatic fluctuations. Today, as a result of extinction and regional extermination, the European flora is markedly impoverished.

Mammals suffered much less heavy extinction in Europe than in Africa during the Pliocene. The strongest pulse of extinction in Europe appears to have occurred shortly after 2.0 Ma, before the existence of the faunas labeled "Tegelen"; about 15% of all known mammal species died out (Kurtén, 1968). The relatively high survivorship for the entire Pliocene Epoch probably reflected the nature of the climatic and floral changes in Europe. Whereas throughout the African continent the forest biome was constricted to a degree that was lethal for many kinds of animals, in Europe, forests changed in composition and

distribution because of temperature changes but nonetheless persisted over broad areas because aridification was less pervasive. Evidently, many species of European mammals were insensitive to changes in the composition of forests. Perhaps exemplifying the greater specificity of extinction in Europe was the disappearance of *Paraliurus anglicus*, a close relative of the extant lesser panda, which feeds exclusively on bamboo (Kurtén, 1968).

Eastern North America

Unfortunately, Pliocene terrestrial floras of eastern North America have not been well dated or extensively studied. Floras of the Great Plains, however, reveal that climates were becoming drier during the Miocene Epoch, long before the global climatic changes of mid-Pliocene time. By the Late Miocene (10 to 5 Ma), grasslands were widespread in central North America, while forests were greatly restricted (Axelrod, 1985; Leopold and Denton, 1987). As discussed later, the early spread of grasslands can be related to tectonic events in the American West. Global climatic changes of the Pliocene presumably compounded these effects, but had a less severe impact on floras in central North America than in Europe or, especially, Africa because aridification had already progressed quite far during the Miocene.

Similarly, late Cenozoic events of mammalian extinction in North America spanned a considerable interval of time: there were six such events during the past 10 m.y. (Webb, 1984). One of these was a minor episode that occurred early in Pliocene time. A more severe event took place near the end of the Pliocene, eliminating about 55 genera. This one was approximately coincident with the heaviest pulse of Pliocene extinction in Europe, but it is not clear that they shared the same cause. A striking pattern of the North American event was that many species of large mammals, among them peccaries and capybaras, survived by retreating to low latitudes. For some species the geographic shift occurred in stages. Extinction and emigration resulted in a severe impoverishment of modern mammalian faunas in the temperate zone of North America. The northward decline in diversity is especially pronounced today at latitudes above 38° (Webb, 1984).

Marine Biotas

The onset of the ice age had profound consequences for shallow water marine life of the North Atlantic, especially adjacent to North American and in the Caribbean Sea. Losses were relatively minor for planktonic species, most of which retained access to suitable biogeographic provinces, but heavy extinction left an impoverished bottom-dwelling fauna that has never recovered its diversity. Changes in sea-surface temperatures were the primary agent of extinction.

We have noted that relatively warm marine climates with low seasonality characterized mid-Pliocene waters adjacent to the eastern United States, with temperatures reaching the subtropical range as far north as Virginia near the end of Yorktown deposition, when the Gulf Stream was strengthened by closure of the Isthmus of Panama about 3.1 Ma. Thus, benthic faunas of the Western Atlantic were warm adapted and stenothermal, which means that they were highly vulnerable to climatic deterioration. The Pliocene fate of the bivalve mollusks, which has been studied in some detail (Stanley, 1986), presumably typifies the history of the benthic fauna in general.

Whereas in California and Japan, mid-Pliocene bivalve faunas contain about 70% extant species, in the Atlantic Coastal Plain only about 20% of mid-Pliocene species survive to the present. Although it might otherwise be tempting to attribute the heavy Western Atlantic extinction to the lowering of sea-level and reduction of shallow seafloor that accompanied glacial expansion during Late Pliocene time, the fact that Pacific faunas experienced no major pulse of extinction rules out eustatic change as a primary agent of extinction. In fact, a broad depositional ramp borders the west coast of Florida, whereas only narrow shelves fringe the Pacific coast of North America. Even during glacial maxima, a large area of shallow seafloor was available for colonization west of Florida; yet extinction here was as heavy as along the Atlantic coast and much heavier than in California. If we take the rate of extinction shared by California and Japan to represent a normal or "background" rate, then the Western Atlantic crisis removed about 65% of all mid-Pliocene species, whereas a much smaller fraction died out through normal attrition (Stanley, 1986).

There is strong evidence that the cooling and accompanying increase in seasonality of shallow waters in the Western Atlantic described earlier constituted the dominant cause of heavy extinction. The mid-Pliocene bivalve fauna of west-central Florida, like any marginally tropical biota, included some species restricted to very warm climates and others that ranged into the temperate zone. As it turns out, however, every one of the nearly 60 species surviving from this fauna today range into the temperate zone: around the Gulf coast to Texas or northward along the Atlantic coast at least to the Carolinas. Thus, a thermal filter removed all stenothermal species, leaving a modern fauna dominated by forms with broad thermal tolerances (see Figure 7.4).

The Plio-Pleistocene strata exposed along the Atlantic Coastal Plain represent only high stands of sea-level. Although discontinuous, the record here is consistent with the hypothesis that steps of extinction occurred during

lowstands representing glacial maxima. Extinction had ended by late Pleistocene time, however. By this time, forms unable to tolerate conditions during the pronounced glacial maxima that began about 0.9 Ma had died out (Stanley, 1986). This pattern of change paralleled that for plants in Europe. What remains is an impoverished bivalve fauna of largely eurythermal species. Many range from the temperate zone to the tropics. In addition, many bivalve species that occupied lagoonal settings before the onset of the ice age are restricted to offshore shelf areas today. Apparently these species cannot tolerate the increased seasonality (in particular, the colder winter temperatures) that now characterize nearshore waters. Only a modest number of new bivalve species evolved during Late Pliocene and Pleistocene time. The extent to which climatic changes may have initiated some speciation in the Bivalvia remains to be investigated, but the onset of the ice age has been credited with triggering the origin of several new species of Western Atlantic ostracods (Cronin, 1988).
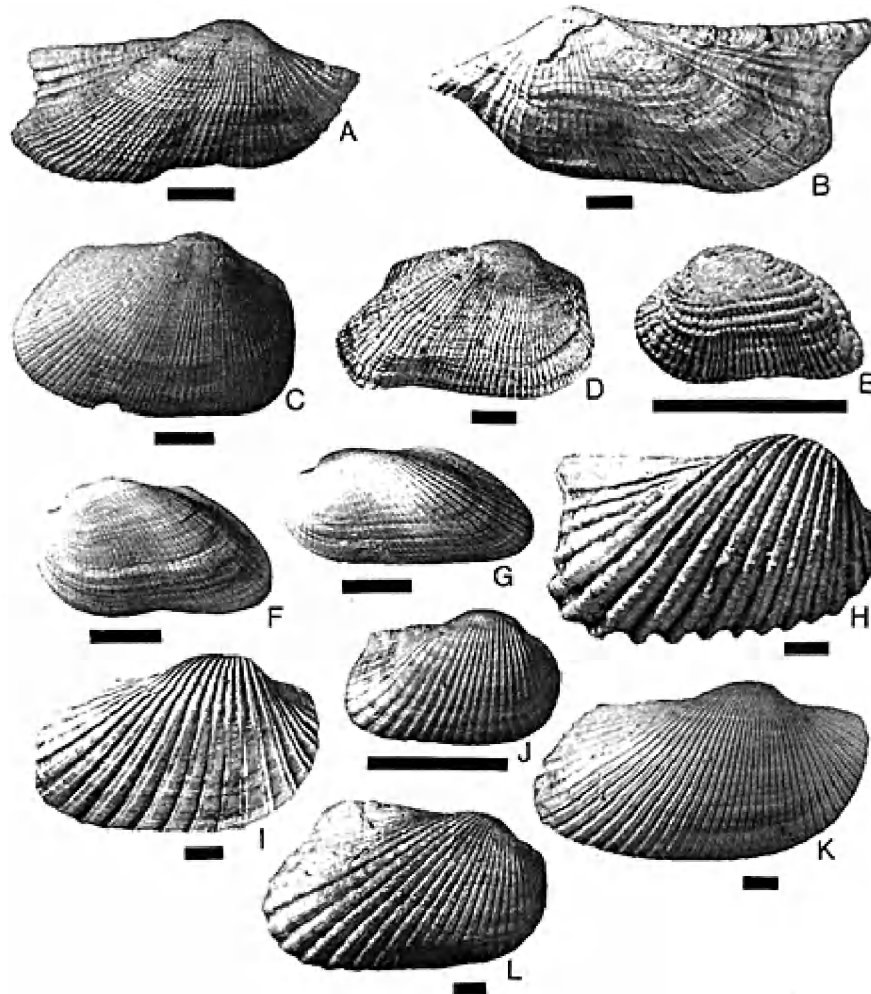

Figure 7.4 Elongate species (scale bars are 1 cm) of the family Anadaridae that lived in shallow tropical seas of southern Florida at about 3 Ma. Only two of these species (**E** and **K**) survive today, and they range into temperate waters. **A**: *Arca williamsi;* **B**: *Arca* wagneriana; **C**: *Barbatia floridana;* **D**: *Barbatia irregularis;* **E**: *Barbatia dominigensis;* **F**: *Barbatia leonensis;* **G**: *Barbatia taeniata;* **H**: *Anadara notoflorida;* **I**:*Anadara campsa;* **J**: *Anadara improcera;* **K**: *Anadara lienosa;* **L**: *Anadara propatula.*

The molluscan fauna of the Caribbean, which was largely distinct from that of eastern North America, experienced a decline that was more or less as severe, although the details remain to be brought to light. In contrast, the molluscan fauna on the Pacific side of the Isthmus of Panama has maintained its very high diversity to the present day. It may be that some of the Caribbean extinctions resulted from reduced upwelling and productivity following the uplift of the isthmus (Vermeij and Petuch, 1986), but the Caribbean fauna suffered losses as far north as the Bahamas at 2.65 Ma (McNeill et al., 1988). This occurrence and the extinction during early Pleistocene time of three species of planktonic foraminifera that were narrowly adapted to the tropical Caribbean (Stanley et al., 1988) suggest that cooling was a major cause of extinction here, as it was in the Western Atlantic. While we do not know the temporal pattern of cooling in the Caribbean, the CLIMAP study showed that during the most recent glacial maximum the sea-surface temperature in the central Caribbean dropped to a level about 4° C below that of today (Prell and Hays, 1976).

On the eastern side of the Atlantic, molluscan faunas and (by inference) marine life in general experienced significant but less severe extinction. As noted earlier, patterns of extinction of bivalves—and geographic distributions of surviving species—point to climatic cooling as the dominant agent of extinction in the Mediterranean and North Sea basins, where only 54% of the total number of Early Pliocene species survive (Raffi et al., 1985). The incidence of extinction in both regions was reduced by the ability of species to survive in the southern parts of their ranges Most species restricted to either the North Sea or the Mediterranean during Early Pliocene time died out, whereas 60 of 64 species present in both basins survive today. Even so, the total fauna declined markedly in diversity. Today it includes only 198 polysyringian bivalve species, yet 323 Early Pliocene species are known.

FORCING OF LATE CENOZOIC CLIMATIC CHANGES

In the first section of this chapter, we summarized two major regimes of late Cenozoic climatic change in and around the North Atlantic area: (1) the long-term cooling (and regional drying) that preceded Northern Hemisphere glaciation, and (2) the ice age cycles of the past 2.5 to 3 m.y. Here we provide a brief overview of some of the possible causes for these changes, with particular attention to processes affecting the North Atlantic Ocean and surrounding continents.

Tectonic Forcing of Climate (pre-2.5 Ma)

The most likely causes of climatic trends persisting for millions of years are tectonic changes in the configuration of the solid Earth that underpins the climate system, particularly changes in geography related to plate-tectonic processes. These include changes in plate position, sea-level, mountain elevations, and narrow "gateways" (sills and isthmus connections) that constrict ocean circulation. Most such tectonic changes are so gradual that it is difficult to demonstrate that they provide strong climatic forcing in the late Cenozoic. Two of these changes that may be especially relevant to climatic changes in and around the North Atlantic are the narrowing and final closing of the Isthmus of Panama and the relatively rapid uplift of plateaus and mountains in Asia and North America.

Closure of the Straits of Panamanian Isthmus

Final formation of the Isthmus of Panama occurred near 3 Ma, but was probably preceded by a long interval of gradually shallowing sill depth (Keigwin, 1982). Experiments with ocean general circulation models (OGCMs) indicate that closure should have led to a dramatic increase in the salinity of North Atlantic waters because the prior subsurface flow of low-salinity waters into the Atlantic would slow and then cease (Maier-Reimer et al., 1990). Modeling also simulates two other related changes: (1) increased formation of North Atlantic deep water (NADW), and (2) decreased formation of sea ice, resulting in a warming of circum-Atlantic waters at middle and high latitudes.

Geologic evidence confirms that a long-term increase in rates of NADW formation occurred over the past 10 or 15 m.y. (Woodruff and Savin, 1989), in agreement with the isthmus experiment. It is unclear, however, what ramifications increased NADW would have for global climate (via effects on the large oceanic carbon reservoir and thus potentially on CO_2). On glacial-interglacial time scales, increased NADW formation correlates with increased, rather than decreased, levels of atmospheric CO_2.

The simulated circum-Atlantic warming, resulting from closure of the Straits of Panama, matches neither the generally observed Northern Hemisphere trend toward cooler climates, nor the conclusion that some cooling of the North Atlantic sea surface occurred prior to glaciation (Dowsett and Poore, 1990). It does, however, match the evidence for very warm Early Pliocene ocean temperatures along the southeastern seaboard of the United States (Hazel, 1971; Stanley and Campbell, 1981; Cronin, 1988). It is also pertinent that an already-formed isthmus cannot account for the additional mid-Pleistocene cooling that led to larger glaciations over the past 1 m.y.

Plateau Uplift

Geologic data summarized by Ruddiman et al. (1989) suggest major late Cenozoic uplift of the Tibetan Plateau in southern Asia and uplift across a broad region of high terrain in the American West centered on the Colorado Plateau (although the latter is contested by Molnar and England, 1990). Experiments with global circulation models (GCMs) show that uplift of rock masses on the scale of several million square kilometers can alter the basic planetary circulation of the atmosphere, by repositioning and intensifying meanders in the midlatitude surface westerlies and jet stream flow, and creating the strong monsoonal circulations of the subtropics (Kutzbach et al., 1989). Of the many large-scale changes due to uplift that are simulated by the model (Ruddiman and Kutzbach, 1989), two are particularly pertinent to the North Atlantic region: (1) strong winter cooling over east-central North America, because prevailing winds turn from westerly toward northwesterly; and (2) increased summer (and annual) evaporation over the Mediterranean and Eastern Atlantic, due to

increased subsidence of dry air and outflow of dry air from the Asian interior (Figure 7.5).

Winter cooling over east-central North America agrees with scattered fossil evidence of the nature of Neogene continental vegetation from the Northern Plains (Thomasson, 1979) and the eastern seaboard (Rachelle, 1976; Fredericksen, 1985; Omar *et al.*, 1987). It appears to disagree with the peak shallow marine warmth attained during mid-Pliocene time in the southeastern United States (Hazel, 1971; Stanley and Campbell, 1981; Cronin, 1988).

The simulated increase in summer evaporation over the Mediterranean and Eastern Atlantic agrees with the early to middle Pliocene shift to drier summer climates recorded by North African dust (Tiedemann *et al.*, 1989) and Mediterranean vegetation (Suc, 1984). Although the ocean was not an interactive part of the uplift experiments, a drier Mediterranean and Eastern Atlantic should increase North Atlantic salinity, and, in combination with other simulated changes, could lead to increased NADW formation (Ruddiman and Kutzbach, 1989).

Most geologic data from the Northern Hemisphere indicate a large, progressive late Cenozoic cooling trend prior to Northern Hemisphere glaciations. This cooling trend appears, however, to be somewhat muted in Europe (van der Hammen *et al.*, 1971) and, as we have seen, may even be contradicted along some margins of the Atlantic.

One possible explanation for this complexity is the more regional effect of plateau uplift and the Panamanian closure on the Atlantic Ocean. Both factors seem likely to cause a stronger northward flux of salty water through the late Cenozoic. Because salty water aids deep water formation but suppresses sea-ice formation, it should increase the release of heat from the ocean to the atmosphere in winter, thereby moderating climate over and around the North Atlantic. It thus seems possible that a localized tendency toward warming around the Atlantic might attenuate the effects of an otherwise "global" cooling trend. In addition, as noted earlier, a strengthened Gulf Stream seems to account for a warming along the southeastern margin of the United States. This effect was only tempo
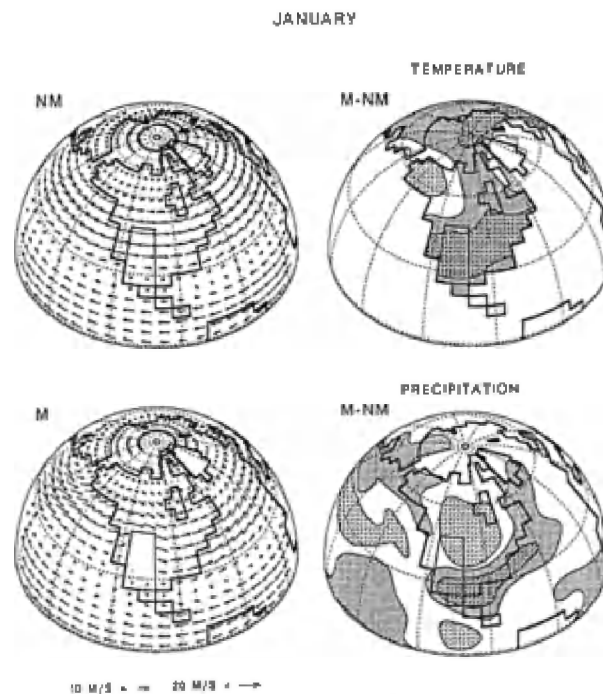

Figure 7.5 Uplift-induced changes in January atmospheric circulation over North America, based on GCM experiments summarized in Ruddiman and Kutzbach (1989). *Top left:* winds in no-mountain (NM) experiment. *Bottom left:* winds in full-mountain (M) experiment. Wind strength keyed to vectors at bottom left. *Top right:* changes in surface temperature due to uplift (M-NM difference), with cooler regions shaded. *Bottom right:* changes in precipitation due to uplift (M-NM difference), with wetter areas shaded. Regions in which temperature and precipitation changes are significant at the 99% confidence level are indicated by diagonal dashes.

rary, however; since polar regions cooled dramatically in Late Pliocene time, polar outbreaks *have* produced very cold winter temperatures in the southeastern United States.

In summary, simulation experiments using GCMs to test the climatic effects of factors such as plateau uplift and isthmus connections have yielded numerous regional trends that agree with observed climatic changes, as well as some that do not. Basically, however, these experiments support the major conclusion from earlier simulations (Barron, 1985) that changes in geography alone are inadequate to explain the large amplitude of late-Cenozoic cooling. An additional factor is needed, and the most likely explanation is a long-term decrease in atmospheric CO_2 levels. Two factors are important in determining long-term CO_2 levels: (1) rates of input from volcanoes, and (2) rates of removal by chemical weathering of silicate rocks on land.

Sea-Floor Spreading and CO_2

One hypothesis links long-term CO_2 changes mainly to rates of seafloor spreading at midocean ridge crests (Berner et al., 1983). Globally averaged spreading rates are proposed to control rates of CO_2 emission from island-arc volcanos, where ocean crust and sediments are consumed and destroyed in ocean trenches. However, over the past 30 m.y., global mean rates of seafloor spreading have been roughly constant and so cannot explain the pronounced climatic cooling.

Chemical Weathering and CO_2

A second hypothesis invokes increased chemical weathering due to uplift of plateaus and mountains as the mechanism for drawing down atmospheric CO_2 levels (Raymo et al., 1988; Raymo and Ruddiman, 1992; see also Chamberlin, 1906). As noted above, plateau uplift produces a monsoonal increase in rainfall. Uplift also exposes fresh silicate rock on faulted slopes to attack by weathering, which consumes more atmospheric CO_2 than is subsequently released to the ocean during secretion of carbonate in plankton. Whereas the Berner et al. (1983) model assumed that chemical weathering is a function of both temperature and global sea-level, the uplift hypothesis takes into account the fact that orography has a powerful control on weathering rates (Edmond, 1987). Steep slopes also flush away the products of chemical erosion, keeping weathering rates high.

An additional factor is the partitioning of carbon and alkalinity between the deep and the intermediate portions of the ocean. Because the ocean is the largest reservoir of carbon on Earth, this partitioning is potentially a critical factor in regulating atmospheric CO_2. At present, however, the partitioning even in the late Pleistocene (last glacial) ocean is poorly understood.

Whatever the ultimate cause, falling CO_2 levels during the late Cenozoic must eventually have passed through a series of critical climatic thresholds. At some point, sea ice began to expand across larger areas of the Arctic Ocean; GCM experiments show that its thickness and extent must have oscillated considerably in response to orbitally driven changes in insolation (Kutzbach and Gallimore, 1988). Modeling studies also indicate that one critical effect of more extensive sea ice would have been to increase the intensity of winter outbreaks of polar air masses across east-central North America and the rate of extraction of heat from the western North Atlantic (Raymo et al., 1990).

Ice-Sheet Forcing of Climatic Change

Variations in the Earth's orbit have affected climate throughout the history of the Earth. Changes in the Earth's inclination (or tilt) relative to the plane of the ecliptic alter seasonal insolation at high latitudes at a period of 41,000 yr. Precession of the equinoxes around the elliptical orbit influence seasonal insolation at all latitudes, mainly at periods of 23,000 and 19,000 yr. Changes in the eccentricity of the orbit at periods near 100,000 and 410,000 yr do not directly result in variations in seasonal insolation at these rhythms, but instead modulate the amplitude of the precessional signal.

Most of the clear evidence for orbital control of climate has come from continuously deposited, well-dated marine sediments of Pleistocene age (Hays *et al.*, 1976). Although orbital variations have no doubt influenced climate through all of geologic time, once ice sheets appeared in the Northern Hemisphere, they provided a particularly effective means of amplifying insolation forcing from within the climate system. For the first 1.5 m.y. or more of the Northern Hemisphere ice age, these ice sheets varied mainly at periods of 41,000 and 23,000 yr, in response to direct orbital variations in summer insolation (Raymo *et al.*, 1989). Ice-volume changes lag several thousand years behind the direct insolation forcing at 41,000- and 23,000-yr periods, because of the inherently slow time constants of ice response.

For the larger ice sheets of the past 0.9 Ma, the dominant rhythm of ice-sheet change has been centered near 100,000 yr, despite the lack of direct insolation forcing at this period (Hays *et al.*, 1976; Shackleton and Opdyke, 1976, 1977). This rhythm of change appears to reflect either a highly nonlinear response to insolation forcing (linked to the modulation of the precession signal by eccentricity) or else some kind of natural resonance that has recently developed within the climate system and is paced by insolation.

The ice sheets in turn act as a source of forcing for other parts of the climate system, through several mechanisms. Like rock plateaus, the rise of these large domes of ice can rearrange the basic circulation of the atmosphere, with major effects that are sent far downstream to the south and east. For example, both marine geologic data and GCM experiments show that cold winds from the ice sheets can chill and freeze the surface of the North Atlantic Ocean at high latitudes (Ruddiman and McIntrye, 1984; Manabe and Broccoli, 1985). GCM experiments also show that chilling and freezing of the North Atlantic can in turn cool climates substantially over maritime regions of Eurasia and southward into the Mediterranean and even northern Africa (Rind *et al.*, 1986). Loess records from China indicate that even in far southeastern Asia, aridity cycles follow the basic tempo of change in the size of ice sheets farther north (Heller and Liu, 1982; Kukla, 1987).

In addition, formation of deep water in the North Atlantic was suppressed when ice sheets were large (Boyle and Keigwin, 1985), probably because of changes in salinity created by the altered wind field (and possibly because of meltwater fluxes). Changes in rate of formation of NADW may also influence subsurface and surface circulation in the Southern Ocean (Weyl, 1968). Redistribution of nutrients and alkalinity in this region may, in turn, affect atmospheric CO_2 levels and thus global climate (Broecker and Peng, 1989). To some extent, however, CO_2 has also varied somewhat independently of Northern Hemisphere ice sheets over the past 150,000 yr (Barnola *et al.*, 1987).

SUMMARY AND CONCLUSIONS

The abrupt climatic changes that marked the onset of the Recent ice age during the Pliocene Epoch followed a long interval of widespread cooling and accentuation of contrasts between wet and dry regional climates. Nonetheless, prior to about 3.1 Ma, climates in many areas of the North Atlantic region remained warmer and less seasonal than today. The Atlantic and Pacific Oceans exchanged temperate species of mollusks by way of the Arctic, the Mediterranean Sea was marginally tropical, and shallow seas off Virginia became briefly subtropical.

Oxygen isotope ratios for marine microfossils offer the best chronological record of the present ice age. They reveal that the deep-sea became permanently cooler at about 3.2 to 3.1 Ma, which implies that there was increased cooling at high latitudes. At this time, several subtropical species of plants disappeared from northwestern Europe, and a brief pulse of cooling extended at least as far south as the Mediterranean, where changes in the planktonic foraminiferal fauna record an estimated reduction in mean annual temperature of 2 to 4°C.

Climates warmed again in at least some areas during the 3.0 to 2.5 Ma interval, but at 2.5 to 2.4 Ma the modern ice age began. Mountain glaciers had been present earlier, but the expansion of large ice sheets at this time accounted for the strong isotopic signal recorded in deep-sea cores. Subsequent isotopic cycles in these cores and in loess reveal an orbitally forced periodicity of ~41,000 yr for about 1.5 m.y. and then of ~100,000 yr between 0.9 Ma and the present.

Terrestrial biotas underwent major changes in the vicinity of the North Atlantic during Late Pliocene time, with aridification playing at least as large a role as cooling. In most areas, the greatest changes took place at about 2.5 Ma, or a bit later. Throughout Africa, forests contracted and many species of mammals that had adapted to them died out; speciation soon produced many new species adapted to the expanding savannas. In Europe forests changed their character, in part through the disappearance of subtropical taxa, but they remained widespread so that mammals were little affected. Details of floral change during the Pliocene remain poorly known for many areas of North America; grasslands were widespread before the end of Miocene time, but about 55 genera of mammals disappeared near the end of the Pliocene.

Beginning slightly before 2.5 Ma, heavy extinction of shallow marine life occurred in the Western Atlantic and Caribbean. Some species survived by migrating offshore to relatively stable thermal regimes, but nearly all strictly tropical species of Florida died out. Heavy extinction ended in late Pleistocene time, after the onset of severe climatic oscillations at -0.9 Ma. Moderately heavy extinction also occurred in the Mediterranean and the North Sea. In general, shallow water benthic faunas of the North Atlantic region are impoverished today as a result of Plio-Pleistocene extinction.

Tectonic forcing has probably been responsible for persistent, longer-term climatic trends in the North Atlantic region during late Neogene time. Formation of the Isthmus of Panama slightly before 3 Ma should have increased the formation of deep water in the North Atlantic and decreased the formation of sea ice by reducing the influx of low-salinity water to the Atlantic. In OGCMs, closure of the Straits of Panama elevates temperatures in the southeastern United States, as actually happened, but fails to produce the observed general cooling at high latitudes. General circulation models suggest that late Neogene uplift of the Tibetan Plateau and other regions should have intensified meanders in westerlies and jet stream flow, producing aridification of the Mediterranean region and reduction of winter temperatures in the southeastern United States. Both predictions match actual events, although the second change is reflected in the fossil record only after mid-Pliocene cooling at high latitudes. It appears, how

ever, that changes in geography are insufficient to account for general climatic cooling during the late Neogene time.

A trend of decreasing atmospheric CO_2 is the most likely cause of long-term climatic cooling. Spreading rates at midocean ridges have not changed enough during the past 30 m.y. to have been the primary factor. A likely cause is elevation of mountains and plateaus, which increased rates of CO_2 uptake by weathering. Since extensive sea ice and glaciers first formed at high latitudes, changes in the Earth's orbital behavior have caused their volumes to oscillate periodically and further influence climate.

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