Alex L. du Toit Memorial Lectures 17 : 1-19

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THE EVOLUTION OF MAN IN AFRICA: WAS IT A CONSEQUENCE OF CAINOZOIC COOLING?

by

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CONTENTS

I. INTRODUCTION

Alexander Logie du Toit, in whose memory and honour this lecture is given, was a remarkable geologist with very wide interests in the earth sciences (Gevers, 1950) — interests which included questions of human evolution. Dr Du Toit was, for instance, a founder member of the South African Archaeological Society and was elected its second President in 1946. A year before his death in 1948, Dr Du Toit gave his Presidential Address to this society on *Palaeolithic environments in Kenya and the Union — a contrast* (Du Toit, 1947) in which he pleaded for "more facts and less speculation" on the part of geologists and archaeologists dealing with problems of correlation. The theme of this 17th memorial lecture would therefore not have been alien to Dr Du Toit's thinking and I have no doubt that he would have taken pleasure in hearing of recent research results to be reviewed here, if he were able to be with us now.

II. THE OBJECTIVE OF THIS CONTRIBUTION

The aim of this lecture is a simple one — *to draw the attention of those interested in human evolution to a remarkable record of past global temperatures that has recently become available, and to point out that certain low temperature episodes, reflected in this record, could well have served as stimuli for critical steps in hominoid evolution.* The record of past global temperatures, to be described here, is based largely on isotope compositions of foraminiferal tests preserved in deep-sea sediments. Fluctuations in global temperature are regarded as *primary environmental changes* which then led to *secondary effects,* such as rainfall and vegetation changes. In the case of many African habitats, the secondary effects could well have been more important as evolutionary stimuli than were the primary temperature fluctuations.

III. SOME EVIDENCE FOR GLOBAL COOLING DURING THE CAINOZOIC ERA

A. Evidence from Deep-sea Sediments: Historical Notes

During the last century it has become clear to geologists that a remarkable record of the earth's history has been preserved in deep-sea sediments. Such sediments are accumulating steadily in a protected environment that covers a large part of the globe's surface. They are often undisturbed, but have the disadvantage of being covered by a layer of water up to 3 km or more in depth. Special technology is required if the detailed history of deep-sea sediments is to be read.

Towards the end of last century studies had already begun on the composition of deep-sea sediments. Sir John

Murray (1880, 1897) concluded that temperature was particularly important in determining the species distribution of planktonic foraminifera. He also observed that the ocean floor surrounding Antarctica was covered by a deposit of glacial-marine sediments, while diatomaceous ooze occurred slightly further to the north. This in turn was followed by foraminiferal ooze.

Further sea-bed samples were collected by the German South Polar expedition of 1901–1903, including short cores. These were studied by Philippi (1910) who observed that, in some of them, diatom ooze lay *below* glacial marine deposits, while in others foraminiferal ooze lay *above* diatom ooze. Philippi concluded that, during the last glacial period, the depositional belts in the southern ocean had shifted. He demonstrated for the first time that cores of deep-ocean sediment can be used in the reconstruction of past climates.

Concerning the subsequent progress of deep-sea coring, Emiliani (1955, p. 546) wrote:

> "Methods have been developed only recently to sample appreciable lengths of the sedimentary column of the sea bottom. Schott (1935) worked with cores less than a meter long. A few years later Piggot succeeded in raising cores 3 m in length. The most important step in sampling deep sea sediments was the invention of the piston cores by Kullenberg (1947), which made possible the recovery of cores more than 20 m long and eliminated compaction due to coring. The Kullenberg corer was extensively used by the Swedish Deep-Sea Expedition of 1947–1948, which brought back about 300 long cores. With the Kullenberg corer, however, up to 40–50 cm of sediments may be lost at the top. This incompleteness was compensated by sampling the top 50 cm of submarine sediments with short pilot cores, usually raised at the same locations. Recently, Ewing has modified the original Kullenberg design so as to prevent the loss of surface material (Ewing *et al.*, 1954)."

Technology required for deep-sea coring was gradually being developed as part of the offshore drilling programmes of the petroleum industry, so that in the late 1950s some of the techniques could be applied for scientific purposes in "Project Mohole", supported by the National Science Foundation.

This project pioneered much of the technology essential for the subsequent climatic interpretation of deep-sea sediments (Van Andel, 1968), making use of the drilling-barge *Cuss I* which drilled five experimental holes in about 1 000 m off San Diego, followed by another five in much deeper water near Guadaloupe Island. In such deep water the vessel could not be anchored, but its position was controlled dynamically by taut-wire buoys and the feasibility of scientific deep-sea drilling was demonstrated.

As Project Mohole continued to concentrate on the deep penetration of sub-oceanic rocks, several other initiatives started whose aim was to unravel the history of more recent deep-sea sediments. During 1962, through the enthusiasm of Cesare Emiliani, a committee known as LOCO was formed to arrange drilling in the Caribbean and western Atlantic. This was followed in the same year by another organisation known as CORE, but neither group received the necessary financial backing. However, in 1964 a more successful co-operative venture was launched, involving marine scientists from the University of Miami, Lamont Geological Observatory, Woods Hole Oceanographic Institution and the Scripps Institute of Oceanography. These four institutions signed a formal agreement called JOIDES, the Joint Oceanographic Institutions Deep Earth Sampling, to co-operate in deep-sea drilling. Its first venture was the drilling and coring of six holes on the Blake Plateau off the south-eastern coast of the United States, with funds from the National Science Foundation. The success of this venture led to much more generous funding of a JOIDES ocean-drilling project managed by the Scripps Institute. A contract was signed with Global Marine Inc. of Los Angeles to provide and operate the drilling vessel *Glomar Challenger* which was commissioned in 1968. Since then a remarkable series of holes has been drilled in sediments beneath the Atlantic, Pacific, Indian and Antarctic oceans, with each drilling cruise consisting of a two-month "leg". When the Deep Sea Drilling Project came to an end in 1975, 44 legs had been completed. JOIDES has subsequently been joined by institutions from various other countries and has entered the International Phase of Ocean Drilling, or IPOD (Uyeda, 1978).

B. Evidence from Deep-sea Sediments: Oxygen Isotope Ratios in Foraminifera

Sediment cores from the deep ocean, layers in which may be dated in a variety of ways, have many uses. When the aim is to reconstruct past sea temperatures, the calcareous tests of foraminifera are of great value. Protozoans of the Order Foraminiferida are currently classified in the Superclass Rhizopoda of the Phylum Sarcomastigophora (Levine *et al.*, 1980). They are almost exclusively marine animals which construct a species-typical test or skeleton which generally survives in oceanic sediments. Of the five suborders of Foraminiferida, representatives of three construct their own tests out of calcium carbonate deposited by their living protoplasm (see Fig. 1). The process whereby calcium carbonate is laid down from solution in water may be expressed by the following equations:

$$H_2O + CO_2 \rightleftharpoons 2H^+ + CO_3{}^{--}$$
$$Ca^{++} + CO_3{}^{--} \rightarrow Ca\,CO_3 \downarrow$$

The oxygen in the calcium carbonate of foraminiferal tests will consist of two isotopes: oxygen-16, the common one, and oxygen-18, about 500 times less common. Atoms of these two oxygen isotopes are diagrammatically represented in Fig. 2. It will be seen that an atom of oxygen-16 has eight protons and eight neutrons in its nucleus, while one of oxygen-18 has eight protons but 10 neutrons. Thus the rarer isotope is the heavier one.

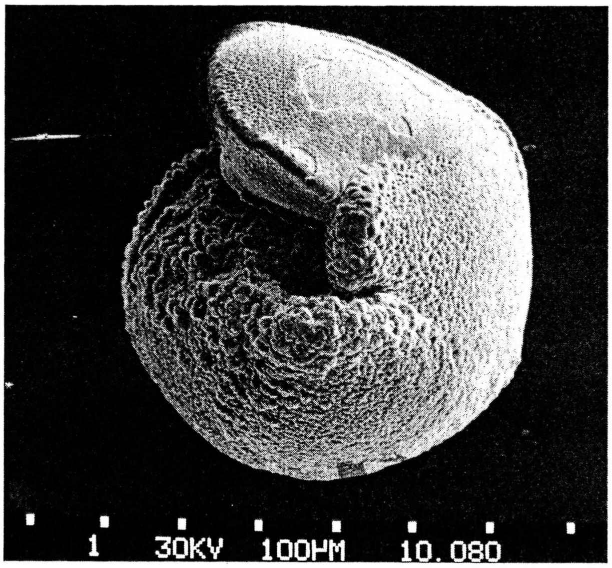

Figure 1
S.E.M. photograph of the calcareous test of a foraminiferan, *Globorotalia truncatulioides* in ventral view. The species is characteristic of transitional waters in the temperature range 10–18 °C. Photo by courtesy of Prof. R.V. Dingle and D. Salmon.

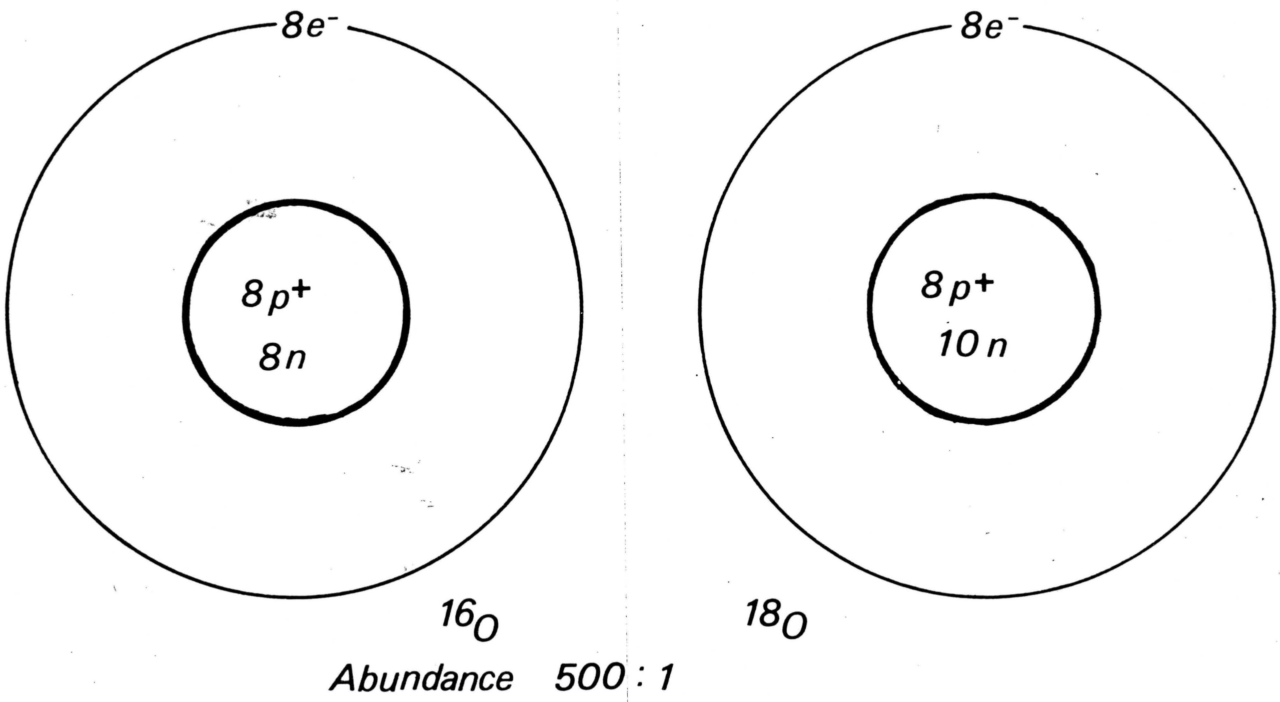

Figure 2
Diagrammatic representation of atoms of two isotopes of oxygen: ^{16}O with eight protons and eight neutrons in the nucleus and the much rarer, heavier isotope ^{18}O, with eight protons and 10 neutrons in the nucleus.

As was first pointed out by Urey (1947), thermodynamic theory predicts that the ratio of these two oxygen isotopes in calcite will vary according to the temperature at which the mineral is deposited. For this reason, analyses of the isotope ratios in the calcitic tests of foraminifera preserved in deep-ocean cores should provide a measure of the sea temperatures prevailing when the foraminifera were alive.

Cesare Emiliani, then of the University of Chicago, was one of the first to use oxygen isotope ratios in foraminiferal skeletons from deep-sea cores in reconstructing sea temperatures. At his disposal were 12 cores, eight from the Swedish Deep-Sea Expedition of 1947–48 and four provided by the Lamont Geological Observatory. From each level of the core, a sufficient number of shells of the desired foraminiferal species was selected under the microscope. Depending on their size, about 100–400 shells were required to make up the 5 mg of calcium carbonate necessary for each isotopic analysis (Emiliani, 1955).

> "The foraminiferal samples were crushed, washed in distilled water in an agitator for 15 minutes to loosen whatever foreign material might be inside the tests, dried at 90°C, pulverised in an agate mortar, heated at 475°C in a stream of helium for an hour and fifteen minutes to remove the organic material, treated with 100 per cent H_3PO_4 at 25°C, and the CO_2 gas thus obtained analysed by mass spectrometer." (Emiliani, 1955, p. 548).

Emiliani was able to conclude that the superficial waters in the equatorial Atlantic and Caribbean underwent periodic temperature oscillations during the Pleistocene with an amplitude of about 6 °C. These conclusions, drawn from oxygen-isotope analyses, confirmed earlier ones based on foraminiferal faunal analyses, that there had been a number of alternating warmer and colder stages (Phleger, 1948; Arrhenius, 1952; Schott, 1952, 1954; Ericson, 1953; Hough, 1953; Phleger *et al.*, 1953). Furthermore, it seemed feasible to correlate these alternations between widely separated cores.

It was proposed by Arrhenius (1952) that the alternations should be numbered back from the present, with the contemporary warm phase designated no. 1. Warm periods would thus have odd numbers and cold phases even ones. The system was accepted by Emiliani (1955) who wrote:

> "Ideally, in a sinusoidal change of temperature with time the boundaries between succeeding stages may be established at the midpoints between temperature maxima and minima. The terms "anathermal" and "catathermal" (abbreviated respectively to An and Ct) may be conveniently used to define the intervals of rising and declining temperatures, which include adjacent halves of neighbouring stages." (Emiliani, 1955, p. 547).

So it became apparent that the determination of oxygen isotope ratios in foraminiferal skeletons could be of great value in reconstructing sea temperatures of the past. This is a fact, but there is a complication, namely, that in relating isotope-ratio to temperature, it is essential to know what the isotopic composition of the sea water itself is. For the contemporary ocean, direct measurement is possible, but can we assume that isotope concentrations in the seas of the past were unchanged? We certainly cannot. The reason for this is related to the so-called "ice-volume" effect, depicted diagrammatically in Fig. 3.

When water is evaporated from the surface of the sea, it is those molecules of water containing the *lighter* isotopes of oxygen that are selectively vapourised. When this water vapour is then redeposited on land in the form of snow, to build up for instance the Antarctic ice-cap, an interesting situation develops. The sea water becomes progressively enriched in the heavier isotope oxygen-18, while the land ice is selectively enriched in the lighter oxygen-16. It is therefore clear that during a glacial period when extensive continental ice-caps build up, water in the oceans will show an oxygen-18 enrichment. We are therefore dealing with two influences: a pure temperature effect on the oxygen isotope ratio in deposited calcite, and an "ice-volume effect" influencing the isotope ratio in the

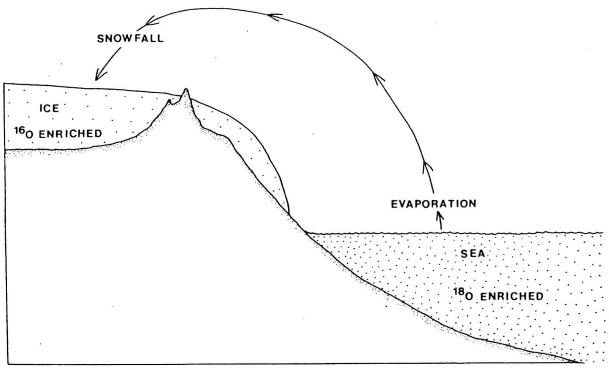

Figure 3
Diagrammatic representation of the "ice-volume effect" in which evaporation from the surface of the sea leaves the ocean water enriched in the heavier isotope of oxygen, ^{18}O, while ice formed from snowfalls on land is selectively enriched in the lighter ^{16}O.

sea water. Since the foraminifera are living in the sea water, the isotopic content of their skeletons will naturally be affected by that of this medium. The two influences are clearly closely linked, but there has been a good deal of controversy as to which is dominant. Emiliani (1955, 1966, 1971) has been of the opinion that the variations in isotopic content of sea water between glacial-interglacial extremes contributed little to the observed isotopic variations in foraminiferal shells. An opposite view has been taken by other workers, e.g. Olausson (1965), Craig (1965), Shackleton (1967), Dansgaard and Tauber (1969), Broecker and Van Donk (1970), Shackleton and Opdyke (1973) and Imbrie *et al.* (1973), who have interpreted changes in isotope ratio in foraminiferal shells as reflecting ice-volume fluctuations rather than pure temperature effects.

An opportunity to test the relative significance of the two influences was provided by analyses on core V16-205 described in detail by Van Donk (1976) and extensively discussed later in this lecture. This core covered a time period of 2,3 Ma and, from it, samples of planktonic foraminifera were analysed for oxygen isotopes throughout. In addition to this, however, data on the abundance of planktonic foraminifera from the core were used by Briskin and Berggren (1975) to provide curves of summer temperature, winter temperature and salinity in the sea water throughout the accumulation period of the cored sediment. For this purpose, the quantitative palaeoenvironmental model of Imbrie and Kipp (1971) was used. A comparison of the curves obtained by Briskin and Berggren with those of oxygen isotope ratios for the same core allowed Van Donk (1976) to conclude:

> "Thus 80 to 90% of the variation in the oxygen isotope composition of the foraminiferal shells is due to a change in the isotopic composition of sea water. This in turn results from the waxing and waning of large continental glaciers. Therefore the 0–18 curves based on isotope analyses of foraminiferal shells represent ice volume curves."

An alternative answer to the question can be found in a comparison of isotope ratios in shells of surface-living or planktonic foraminifera with those in the skeletons of bottom-living or benthonic forms (Streeter, 1980). When examining a suite of foraminiferal forms preserved in a sediment, it is possible to say which species were planktonic and which benthonic. If a sample of each is therefore selected and analysed for oxygen isotope ratios, a measure of surface relative to bottom ocean water can be obtained. When the sample is taken in very deep water, in excess of 3 km, the benthonic foraminifera will have been living in water of almost constant temperature, beneath the permanent thermocline. When the oxygen isotope ratios in the shells of these forms is compared with those from foraminifera living at the surface, very little difference is typically encountered. During a glacial-interglacial cycle, the isotope changes observed in surface and deep water foraminifera shells run parallel, suggesting that such changes reflect "ice-volume" rather than pure temperature effects. It is reasonable to regard the ocean as a well-mixed reservoir, even down to its greatest depths, in which changes resulting from land-ice volume are rapidly communicated throughout the entire mass. According to Van Donk (1976), complete oceanic mixing occurs in less than 1 500 years.

Another factor that must be taken into account, when interpreting oxygen isotope ratios, is that the calcite making up foraminiferal skeltons has been laid down by living protoplasm and, in some species, this protoplasm is able to actively influence the isotope ratio in the shell. It is therefore useful to know whether a particular species deposits its calcium carbonate in isotopic equilibrium with the surrounding water or whether it shows a consistent offset from equilibrium. Duplessy *et al.* (1970) and Vinot-Bertouille and Duplessy (1973) have shown that certain benthonic plankton consistently deposit calcium carbonate out of isotopic equilibrium with that of the surrounding water and similar observations on planktonic foraminiferal tests have been made by Shackleton *et al.* (1973). A good deal of research on this topic is now being undertaken as well as on other aspects of the use of foraminifera in temperature reconstructions (e.g. Savin *et al.*, 1975 and Kennett, 1978a).

C. A Temperature Record for the Cainozoic Era

In 1980, Streeter was able to report that, at that time, over 70 isotopic time series of varying length and detail had been published, coming from all parts of the deep ocean. In this consideration of a temperature record for the Cainozoic Era, attention will be focused particularly on results from five drilling sites, four in the southern Ocean and one in the tropical Atlantic. The results have been presented by Shackleton and Kennett (1975a, b) and Van Donk (1976).

1. Deep-sea drilling project sites 277, 279 and 281

The purpose of the investigation by Shackleton and Kennett (1975a) on these three cores was "to evaluate the high-latitude climatic record of the Cenozoic and to investigate the history of Antarctic glaciation in this interval". The positions of these drilling sites, which were cored as part of Leg 29 operations, are shown in Fig. 4. Particulars are as follows:

Site	Latitude	Longitude	Water Depth m	Metres Cored	Metres Recovered
277	52°13,43'S	166°11,48'E	1 222	434,5	258,5
279A	51°20,14'S	162°28,10'E	3 368	110,0	79,8
281	47°59,84'S	147°45,85'E	1 591	169,0	105,6

Samples of both plantonic and benthonic foraminifera were extracted from each level studied in the three overlapping cores, covering the last 55 Ma with a sampling interval of less than one million years. Procedure was described as follows:

> "Samples comprised between about 0.1 and 0.4 mg carbonate after cleaning. Adhering fine-grained matter was removed by ultrasonic cleaning in Anal R grade methanol. Samples were roasted in vacuo at 450°C for 30 minutes to eliminate possible volatile contaminants, and carbon dioxide evolved by the action of 100 percent orthophosphoric acid at 50°C. Isotope analyses were performed in a VG Micromass 602 C mass spectrometer and calibrated by analysis of standard carbonate samples under identical conditions."

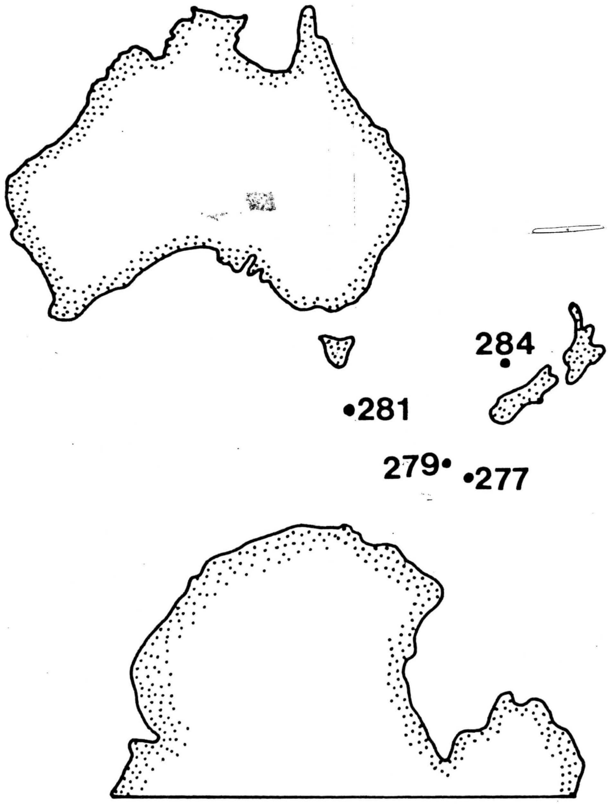

Figure 4
Map, redrawn from Kemp (1978), showing positions of deepsea drilling sites 227, 279, 281 and 284 referred to in the text.

The temperature curve obtained by Shackleton and Kennett (1975a) from cores at the three overlapping sites 277, 279 and 281 is shown in Fig. 5. It reflects sea-surface temperatures and is similar in general form to a second curve, based on benthonic foraminifera and reflecting bottom-water temperatures. The surface-temperature curve indicates that in the Late Paleocene and Early Eocene the temperature of surface water was 18–20 °C. This conclusion is very similar to that reached by Douglas and Savin (1973) on the basis of their study of isotope ratios in Cretaceous and Tertiary foraminifera from cores in the tropical Central North Pacific. The temperature appears to have dropped in a series of steps to a value of about 7 °C in the Oligocene, with a most dramatic drop at the Eocene–Oligocene boundary. This "terminal Eocene event" will be further considered later, but it is of interest that the temperature drop had been noted some years previously in the course of isotope measurements on Tertiary fossils from New Zealand by Devereux (1967).

During the Early Miocene there was a rise in surface temperature, followed by a decline and another rise early in the Middle Miocene. Shackleton and Kennett consider that the part of the curve above this, covered largely by core 281, has been seriously influenced by a major change in ocean isotopic content resulting from the accumulation of Antarctic ice.

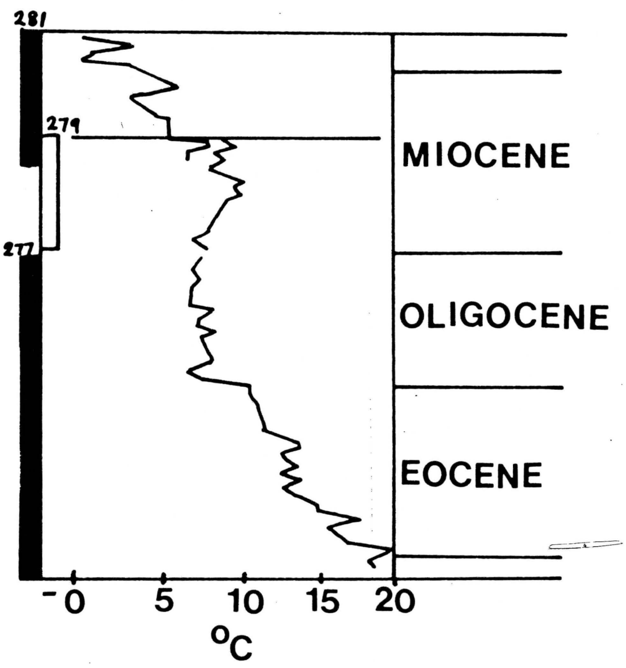

Figure 5
Diagram giving an indication of surface water temperatures in the southern ocean derived from oxygen isotope determinations on planktonic foraminifera in cores from sites 277, 279 and 281. Redrawn from Shackleton and Kennett (1975a).

2. D.S.D.P. Site 284

Better resolution during the last 6 Ma timespan has been obtained from analyses on cores from Site 284 covering the interval from Late Miocene to Early Pleistocene, or from about 6–1,5 Ma b.p. The site is located at 40°30,48′S, 167°40,81′E in a water depth of 1 068 m. The 22 cores obtained covered 166,8 m of the 208 m penetrated (Shackleton and Kennett, 1975b). Stable isotope analyses on both oxygen and carbon were made on 39 samples of benthonic foraminifera of the genus *Uvigerina* and the results were compared with percentage abundance figures for the planktonic cool water foraminifer *Neogloboquadrina pachyderma.* These abundance figures were obtained by Kennett and Vella (1975) who state that increases in the percentage abundance of *N. pachyderma* represent cooler intervals.

The conclusions that may be drawn from these curves are that the end of the Miocene is marked by a cold period during which a major expansion of the Antarctic ice sheet occurred. During the Pliocene, temperatures rose again but declined sharply at the end of the Pliocene when, at about 2,6 Ma b.p. the first Northern Hemisphere glaciation took place.

3. Core V16-205 from the Equatorial Atlantic Ocean

Van Donk (1976) has provided an oxygen isotope record for the entire Pleistocene Period. He described his analytical technique as follows:

"Core V16-205, with a total length of 1,232 cm, was raised in the tropical Atlantic Ocean (lat 15°24′N, long 43°24′W) from a depth of 4,045 m. A single species of Planktonic foraminifera, *Globigerinoides sacculifer,* was extracted from samples at 10-cm intervals and in several sections at 3-cm intervals. A total of 136 samples were analysed. The samples were lightly crushed and cleaned ultrasonically. They were then acidified with 100% H_3PO_4 at 25°C and converted into CO_2 gas according to the procedure established by McCrea (1950), but without having been roasted. The gas was analysed in a commercial Nuclide dual-collector mass spectrometer. The overall analytical precision of the isotope values is 0.12‰ for a single analysis." (Van Donk, 1976, p. 148).

As mentioned earlier, it is considered that the observed changes in isotope ratio have resulted very largely from the "ice-volume" effect and represent the waxing and waning of large continental ice-masses. Van Donk wrote: "twenty one isotopically determined interglacial stages are defined for the past 2.1 m.yr. with an equal number of isotopically determined glacial or near-glacial stages, although many of the latter are much less pronounced than the most recent glacial maximum". Van Donk goes on to point out that there was a prolonged near-interglacial stage, numbered 27, which lasted from about 1,2–1,0 Ma b.p.

The record from core V16-205 has been compared with three other O^{18} records of *G. sacculifer:* that of core V28-238 from the equatorial Pacific (Shackleton and Opdyke, 1973), V12-122 from the Caribbean (Imbrie *et al.*, 1973) and P6304-9 also from the Caribbean (Emiliani, 1966). A remarkable correspondence of warm and cold stages is apparent (see Van Donk, 1976, Fig. 3).

4. Correlation with European Continental Deposits

It is possible to correlate the temperature record derived from deep-sea cores with the record preserved in European continental deposits as Kukla (1977, 1978) has shown. In this attempt Kukla used piston core V28-238, referred to above, as a type section. Described by Shackleton and Opdyke (1973), this 16 m-long core was raised in 3 120 m of water in the equatorial Pacific. It provides evidence of eight completed glacial cycles, and nine terminations, in the last epoch of normal polarity which lasted approximately 0,7 Ma. Kukla pointed out that there are three kinds of land-based deposits capable of providing a climatic record comparable with that from the deep-sea cores. These are pollen-rich lake beds, continental ice sheets and deposits of alternating loess and soils. It is the last kind of deposit that is of special relevance here. Kulka (1977, p. 322) wrote:

> "The great advantage of loess sequences is that they are essentially continuous. With the help of magnetostratigraphy and observed parallels in climatic history they can be directly correlated with deep-sea sediments (Kukla, 1970, 1975). They are also stratigraphically related to the terraces of rivers flowing through formerly glaciated areas. In this way a link is provided for a direct correlation of the deep-sea record with classical glacial stages."

Kukla points out that more than 100 localities with well-developed loess sequences have been described in Czechoslovakia and Austria during this century. He continued (Kukla, 1977, p. 323):

> "The periglacial area around Prague, Brno and Nitra in Czechoslovakia, as well as around Krems and Vienna in Austria, was never glaciated. When the Alpine and Fennoscandinavian ice sheets reached their maximum extents, loess accumulated in this region influenced by a highly continental periglacial climate. During the interglacials the climate was of the Atlantic type, similar to the present one, or warmer and wetter. Deciduous forests spread, leaving behind the characteristic *parabraunerde* soils. Thus in favorable desposition basins, glacial-interglacial cycles were recorded by repeated alternation of loess and forest soils. The deposits are frequently associated with river terraces because the steep cliffs of abandoned river banks provided ideal sedimentary traps for the windblown dust. The terraces around Prague were formed by a tributary of the Labe (Elbe) river which flows into the region of Fennoscandinavian glacial deposits. The terraces around Brno, Nitra, Krems and Vienna belong to the tributaries of the Danube. The Danube also drains the Alpine foothills where classical Alpine glacial stages were defined by Penck and Brückner (1909). Thus the correlation of loess sequences with glacial deposits in northern Europe and in the Alps is possible . . . (p. 329): A surprisingly close correspondence of sedimentary sequences of different ages has been observed in the region around Prague and Brno. This observation led to the definition of sedimentary cycles of the first and second order and later, to a regional lithostratigraphic system naming the soils according to their cyclic position in the sequence (Kukla, 1970). Cycles of the first order are called glacial cycles, and are delimited by marklines. Those of the second order are stadial cycles or subcycles and are delimited by submarklines. Each cycle and subcycle starts with a thin deposit of hillwash loam (phase 1), succeeded in turn by a forest soil of braunerde type (phase 2), steppe soil of chernozem type (phase 3), marker (phase 4), pellet sand (phase 5) and loess (phase 6). Some members of the sequence may be missing, but within the studied area the successive order of the phases always remains identical."

A remarkable record of alternating loess and forest soil at Krems in Austria is shown in simplified diagrammatic form in Fig. 6. Fink and Kukla (1977) described the site in detail, noting that the Pleistocene sediments fill an abandoned river meander 60 m above the present Danube. The conclusion was reached that at least 17 times during the past 1,7 Ma the deposition of loess containing characteristic cold-resistant gastropods was interrupted by the development of temperate interglacial forests. This means that the total number of glacial cycles after the Olduvai

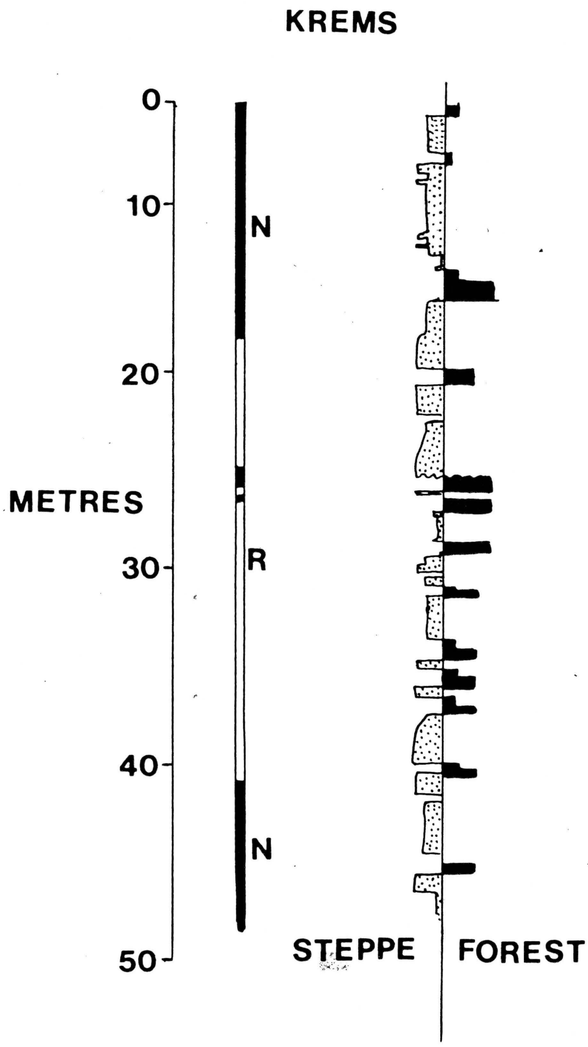

Figure 6
A simplified profile from a terrace of the Danube River at Krems in Austria described by Fink and Kukla (1977). The profile indicates that on at least 17 occasions during the last 1,7 million years, the deposition of glacial period loess was interrupted by the development of temperate interglacial forests.

Event was at least 17 and that individual cycles had a mean duration of 100 000 years. This very remarkable conclusion prompted Kukla (1977) to write:

"Only four glacials and three interglacials were recognised by classical Alpine and north European subdivisions of the Pleistocene. The classical units are correlated with continuous oxygen isotope records from the oceans, using loess sections and terraces as a link. It is found that: (1) the terraces representing the four Alpine 'glacial' stages fully cover the last 0,8 million years but correspond to both glacial and interglacial climates; (2) the Alpine 'interglacial' stages do not represent episodes of interglacial climate but probably intervals of accelerated crustal movements; (3) the physical evidence on which the north European classical subdivision is based accounts for only about 15% of the time represented. This has led to serious miscorrelations.

It is urgently recommended to abandon the classical terminology in all interregional correlations and to base the chronostratigraphic subdivision of the Pleistocene on the ^{18}O record of deepsea sediments". (Kukla, 1977, p. 307).

D. A Generalised Climatic Curve

The conclusions reached in the investigations which have just been reviewed may be presented in the form of a simplified curve shown in Fig. 7. The curve is based on evidence from both hemispheres and from marine and terrestrial deposits. It is therefore a composite curve intended to reflect a global temperature trend, though it has been established that changes in southern hemisphere sea temperatures may precede those in the northern hemisphere (Salinger, 1981).

The major feature of the temperature curve presented in Fig. 7 is of a progressive decline in temperature from the Paleocene until the end of the Miocene, followed by a series of subsequent oscillations. The tentative temperature values in degrees C would apply to southern ocean surface temperature, as reflected at D.S.D.P. sites 227, 279 and 281. These values would naturally not be applicable in lower or higher latitudes, though the form of the curve would hopefully have relevance to the global environment as a whole. Some particular features of the curve, their possible causes and implications, will now be discussed.

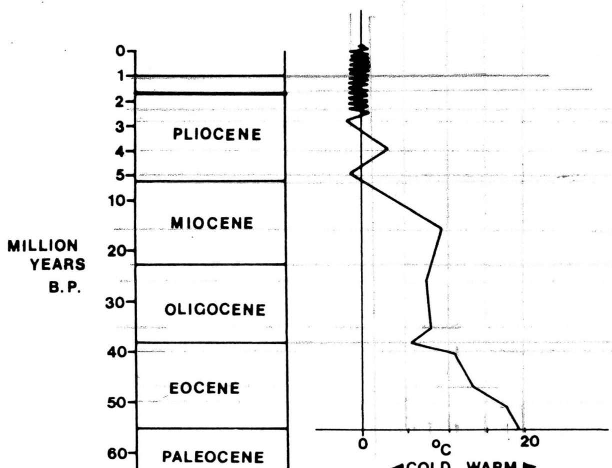

Figure 7

A simplified diagrammatic representation of global temperature changes during the last 60 million years, based on evidence from various sources discussed in the text. The temperature calibration is applicable to sea surface temperatures at high latitudes in the southern ocean but the trends of the curve hopefully have worldwide application.

1. The "Terminal Eocene Event"

The term "terminal Eocene event" was first used by Wolfe (1978) for what he regarded as the most dramatic climatic event to have occurred in mid-Tertiary times. He based his conclusion on Northern Hemisphere fossil floras and wrote:

"In middle to high lattitudes of the Northern Hemisphere, the vegetation changed drastically. Within a geologically short period of time, areas that had been occupied by broad-leaved evergreen forest became occupied by temperate broad-leaved deciduous forest. A major decline in mean annual temperature occurred — about 12–13°C at latitude 60° in Alaska and about 10–11°C at latitude 45° in the Pacific Northwest. Just as profound, however, was the shift in temperature equability: in the Pacific Northwest, for example, mean annual range of temperature which has been at least as low as 3–5°C in the middle Eocene, must have been at least 21°C and probably as high as 25°C in the Oligocene." (Wolfe, 1978, pp. 699–700).

In the southern ocean, evidence for an apparent dramatic temperature drop at the end of the Eocene, about 38 Ma ago has been obtained from cores raised at D.S.D.P. site 277, described earlier. Kennett and Shackleton (1976) have made a particular study of this part of the record. The striking isotopic change observed in the tests of benthonic foraminifera deposited at this time occurs in a sediment thickness of only 170 cm which, at an estimated sedimentation rate of about 1,6–2,2 cm per 1 000 years, suggests a temperature change duration of 75 000–100 000 years. During this brief interlude, bottom water temperature in this part of the southern ocean decreased by 5 °C. Kennett and Shackleton (1976, p. 515) wrote as follows:

"Our interpretation of the latest Eocene–earliest Oligocene oxygen isotope change is that it reflects a decrease in Antarctic surface-water temperatures to feeezing and the production of extensive sea ice. This also marks the development of the psychrosphere (the present-day system of bottom waters of the world ocean). The oxygen isotope evidence indicates that no significant ice sheet formed at this time, and that the ice volumes on Antarctica remained relatively small until the Middle Miocene. Ice-rafted debris in cores of Eocene and Oligocene age from the Southern Ocean off West Antarctica record limited glaciation at this time, probably associated with alpine glacial development of West Antarctica, although others have suggested the presence of substantial thicknesses of ice since the beginning of the Oligocene. In East Antarctica, ice conditions in the Palaeocene are unknown, but if glaciers were present, they did not reach sea level.

The drop in bottom water temperatures in the earliest Oligocene caused a major crisis for the bathyal to abyssal benthonic fauna of the World's oceans including ostracods and benthonic foraminifera. The impact on planktonic fauna and flora was less dramatic . . ."

Particularly clear evidence of the terminal Eocene temperature drop in the northern hemisphere has come from an oxygen isotope study of molluscan shells from various localities on the continental shelf of western Europe, made by Buchardt (1978). His results indicate at least a 10 °C drop in sea temperature over the Eocene–Oligocene boundary.

The sudden and short-lived temperature fall at the end of the Eocene appears therefore to have affected both hemispheres simultaneously. The cause of this episode has elicited a good deal of speculation. Wolfe (1978) was of the opinion that the terminal Eocene event came about as a result of a rapid shift in the inclination of the earth's rotational axis. He wrote (Wolfe, 1978, p. 702):

> "If the major climatic trends during the Tertiary were largely the result of inclinational changes, then from the Paleocene to the middle Eocene, inclination decreased gradually from a value of perhaps 10° to a value approaching 5°. The inclination then began to increase slightly until the end of the Eocene, when the inclination increased rapidly to 25–30°. Since then, the inclination has gradually decreased to the present average value of 23,5°."

Although it seems to be accepted that changes in inclination have occurred in the past, these are thought to have taken place very slowly, in fact too slowly to have caused the terminal Eocene event (O'Keefe, 1980). As an alternative, O'Keefe suggests that the latter low-temperature event was the result of a comet's collision with the earth. This possibility had in fact been suggested before. Urey (1973) proposed thatt tektites (glass-like particles) were produced by cometary collisions with the earth and that the ages of tektite-strewn fields correspond with the terminations of certain geological periods.

This concept was supported by O'Keefe who wrote:

> "The largest known strewn field is dated at −34 Myr, close to the time of the terminal Eocene event. It has been called the North American strewn field; but Glass *et al.* (1977, 1979) found that it extends from the Caribbean through the central Pacific to the Indian Ocean, and that its total mass is 1–10 × 10^9 tons. Glass and Zwart have shown, from bottom ocean cores, that five abundant species of Radiolaria, comprising two thirds of the total radiolarian population, disappear or nearly disappear at the level at which the microtektites appear." (O'Keefe, 1980, pp. 309–310).

It has been suggested that during the terminal Eocene low temperature event winters became very severe while summer temperatures were little affected. O'Keefe (1980) suggests the tektites and microtektites that accompanied the fall described above, but which missed the earth, organised themselves into a ring system like that of Saturn. The shadow of the rings fell on the winter hemisphere and so produced the observed cooling, lasting between one and several million years.

There has been discussion on the origin of the tektites, with King (1980) questioning the suggestion that they were of cosmic origin. He thinks it more likely that they were produced by a meteorite's impact on terrestrial tuffs or tuffaceous sedimentary rocks. Such a possibility was vigorously denied by O'Keefe in his reply to King's letter.

2. Temperature Decline During the Miocene

The progressive decline in southern ocean temperatures that has been inferred during the course of the Miocene was apparently strongly influenced, if not mediated, by the isolation of Antarctica through continental drift. As Kennett *et al.* (1972) have documented, Australia began its northward drift from Antarctica in the early Eocene, about 55 Ma ago. Throughout the ensuing time, Antarctica apparently remained relatively stable in its current polar position.

Kennett (1978b) has pointed out that the present South Tasman Rise, that incorporates the island of Tasmania, is a continental crustal feature which would have obstructed the passage between Australia and Antarctica for a considerable time. It was not until about 38 Ma ago that Australia's northward drift had proceeded far enough for the South Tasman Rise to clear Victoria Land in Antarctica. Kennett (1978b) suggested that during the time interval 38–22 Ma b.p. a deep seaway between Antarctica and the South Tasman Rise would have developed.

The only other obstruction in the way of a circum-Antarctic current would have been the Drake Passage, between the southern tip of South America and Antarctica. Kennett (1978b) provided evidence to suggest that this opening occurred no later than 21 Ma ago, while Barker and Burrell (1976) consider that the main opening started in the Middle Oligocene, about 30 Ma ago.

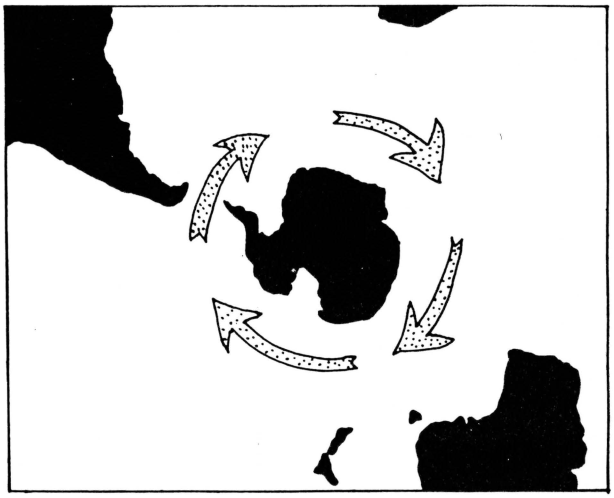

Figure 8
Diagrammatic representation of the circum-Antarctic current which started to flow once the northward drift of Australia, and the creation of the Drake passage, had opened a seaway around Antarctica.

In their discussion of the development of the circum-Antarctic current, Kennett *et al.* (1974) conclude that this current, which today transports a larger volume of water than any other — about 20 × 10^6 m^3 per second — has flowed for the last 30 Ma (see Fig. 8). Its development led to a fundamental change in the world's oceanic circulation, whereby Antarctica was effectively isolated from contact with warmer sea water that formerly had penetrated southwards from lower latitudes. As a result of this isolation, progressive cooling of Antarctica appears to have set in. It has been suggested by Savin *et al.* (1975) that an immediate effect of the circum-Antarctic current ~~was to~~ uncouple high- and low- latitude temperatures for a while, with the result that Antarctic cooling initially had little effect on areas closer to the equator.

A good deal of evidence has been assembled, relating to the establishment and growth of the Antarctic ice cap. Some of this evidence concerns former vegetation of Antarctica described by Kemp and Barrett (1975) and Kemp (1978). Pollen and spores were recovered from site 270, which was drilled off the edge of the present Ross Ice Shelf, and some of the sediments, dated at about 26 Ma, are from a period before glaciation occurred. Pollen and spores are, however, particularly abundant in sediments that accumulated soon after glaciation of the area started. Numerically the assemblages are dominated by pollens of *Nothofagus* type but pollen of Proteaceae and other plants, as well as fern spores, also occur. Such vegetation apparently persisted in Antarctica until the end of the Oligocene at least, whereafter it was eliminated by increasing cold.

So it was clearly during the course of the Miocene that the establishment and growth of the Antarctic ice cap occurred. An alternative model, proposed by Matthews and Poore (1980) suggesting that the earth has had a significant ice budget at least since Eocene and perhaps even throughout much of Cretaceous time, does not seem to be supported by evidence from oceanic cores. For instance a recent report by Woodruff *et al.* (1981) draws some significant conclusions on the timing of Antarctic ice-cap build-up. The Deep Sea Drilling Project site 289 in the western equatorial Pacific has yelded an extremely detailed record of the carbon and oxygen isotopic changes in the Miocene deep ocean. Woodruff *et al.* (1981) conclude that the transition from a relatively unglaciated world to one similar to today, in the southern hemisphere at least, occurred between 16,5 and 13 Ma b.p. with the greatest change occurring between about 14,8 and 14,0 Ma b.p. At this time the earth's climatic system seems to have become extremely unstable and, perhaps for a million years, it oscillated back and forth between glacial and interglacial modes. After about 14 Ma b.p. the glacial mode in southern high latitudes appears to have been firmly established and has persisted ever since.

As had been pointed out by Drewry (1978), the Antarctic ice sheet may be divided into two principal but unequal portions. In East Antarctica there is currently about 10,2 million km^2 of ice grounded largely above sea level, while the much smaller West Antarctic ice sheet, covering about 1,6 million km^2 is grounded mainly below sea level and possesses floating ice shelf extensions into both the Ross and Weddell seas. Drewry (1978, p. 31) concludes:

> "By Mid-Late Miocene times substantial ice sheets were developing in East Antarctica, discharging ice through gaps in the southern Transantarctic Mountains into an open Ross Sea. Other coastal upland areas of Marie Byrd Land supported growing ice fields (e.g. Jones Mountains) but a full-bodied West Antarctic ice sheet was not yet present."

This conclusion that the formation of the East Antarctic ice sheet antedates that of the West Antarctic one by as much as eight or nine million years is supported by Mercer (1978).

3. The "Terminal Miocene Event"

Mention has already been made of evidence obtained by Shackleton and Kennett (1975b) from D.S.D.P. Site 284 suggesting that the end of the Miocene was marked by a cold period during which a major expansion of the Antarctic ice sheet occurred. Such a conclusion had already been reached by Hayes *et al.* (1973) in their preliminary assessment of Leg 28 deep sea drilling in the southern ocean.

Mercer (1978) has provided and discussed evidence to show that, at the end of the Miocene, the West Antarctic ice sheet developed rather rapidly, linking the ice-covered island with the main mass of East Antarctica to form the continent of Antarctica as we know it today. The cold episode that was responsible for this ice sheet expansion was apparently a widespread one, affecting large areas of the globe. For instance, Loutit and Kennett (1979) record a distinct carbon 13/carbon 12 isotopic shift in the light direction in a shallow marine sedimentary sequence of Late Miocene age at Blind River, New Zealand. This may be correlated with a similar shift in Late Miocene Deep Sea Drilling Project sequences throughout the Indo-Pacific, dated at about 6,2 Ma. The shift is interpreted as resulting from a distinct Late Miocene cooling event, together with a marked drop in sea level at 6,1 Ma b.p. caused by a sudden build up of Antarctic ice. The shallowest water depths recorded at Blind River occurred at about 5,6 Ma ago, when the sea level drop was between 40 and 70 m.

A comparable sea level decline has been documented in sediments of south-western Spain where foraminiferal assemblages have been used as indicators of sea water depth at the time of accumulation (Van Couvering *et al.*, 1976; Berggren and Haq, 1976). In the upper part of the Late Miocene Andalusian Stage stratotype section, water depths are thought to have declined rather abruptly about 5,5 Ma ago from about 70–100 m to about 20–30 m. This eustatic sea level change can almost certainly be correlated with that already described at Blind River in New Zealand, while Hendey (1981a) has speculated that it was responsible for the regression observed in the sediment sequence at Langebaanweg on the western Cape coast, between the Gravel Member and the Quartzose Sand Member of the Varswater Formation.

But certainly the most dramatic result of the Terminal Miocene sea level decline appears to have been the salinity crisis in the Mediterranean, which has been documented in detail by Hsü *et al.* (1977) and Adams *et al.* (1977). It was as a result of drilling by the Glomar Challenger in 1970 that the presence of vast deposits of salt beneath the Mediterranean was demonstrated. Furthermore it was established that these evaporite deposits were of Messinian (Late Miocene) age and that they had been laid down in a comparatively brief period of time, somewhere between 6,5 and 5 Ma ago. As Adams *et al.* (1977) have stated:

> "The salinity crisis occurred after the western Tethys lost its last connection with the Atlantic about 6,2 Myr B.P., its connection with the Indo-Pacific having been severed about the end of the Early Miocene some 10 Myr earlier. The Iberian Portal, as the hypothetical last connection with the Atlantic is often known, must have existed somewhere between the Iberian Maseta and the Moroccan Maseta and could have been any one of the former Betic, Gibraltar, or Rif straits, although Benson now believes that its connection to the Atlantic lay across Andalusia and was therefore the northernmost of the three passages. Isolation of the ancient Mediterranean from the world ocean resulted in the precipitation of more than 10^6 km^3 of gypsum, halite and other salts from a volume of seawater estimated to be equivalent to thirty times that contained in the present Mediterranean basins."

Although the terminal Miocene eustatic sea level drop was almost certainly responsible for the final isolation of the Mediterranean, it could not have had this effect if the previously existing Atlantic–Mediterranean connection had been a very shallow one. So, in the model proposed by Van Couvering *et al.* (1976), the Atlantic–Mediterranean connection is visualised as being over a sill that was slowly lifted tectonically. Gradually, as this happened, the Mediterranean water was transformed from normal sea water to highly concentrated brine, formed by refluxive concentration. When the terminal Miocene sea level drop cut off the Mediterranean's connection with the open Atlantic, the complete evaporation of the Mediterranean brine is thought to have occurred between 5,5 and 5,0 Ma ago.

The almost unbelievable magnitude of the Mediterranean salt deposits has been discussed by Ryan (1973). He pointed out that these deposits had an estimated volume of more than one million cubic kilometres and that this represents more than six per cent of the dissolved salts in the entire world's oceans. He writes:

> "As a consequence of being drained of more than six percent of its dissolved salts, the World Ocean turned more alkaline and its deep waters became noticeably more undersaturated in calcium carbonate. It is believed that the concurrent freshening of its surface water layer may have enhanced the formation of high latitude sea ice in Late Miocene times, an event which could have led to the great burst of glaciation recorded on the continent of Antarctica at that time."

If Ryan's suggestion is valid, the scenario is a most intesting one. Gradually between 6,5 and 5 Ma ago, refluxive concentration of the Mediterranean removed up to six per cent of the world ocean's salt, resulting in extensive formation of sea ice around Antarctica at a higher temperature than would otherwise have been possible. This, in turn, increased the earth's albedo, thereby reducing air temperatures over Antarctica and promoting rapid enlargement of that continent's ice cap. The effect of this ice build up on land was to reduce global sea levels by between 40 and 70 m, a lowering sufficient to isolate the Mediterranean completely from the Atlantic, and to convert it into an evaporite basin.

The complete drying up of so large a body of water as the Mediterranean, over a brief geological period, must have had dramtic physical and biological consequences. Some of these have been mentioned by Hsü *et al.* (1977), for instance the fact that the lowering of the base level of erosion led to the deep incision of rivers that drained into the Mediterranean, while a dry-land connection between Africa and Europe permitted free exchanges of fauna and flora. Hsü *et al.* (1977) visualise a cool, more arid climate around the desiccated Mediterranean and, to my knowledge, these authors were the first to speculate as to whether this aridity, caused by the Messinian salinity crisis, had not perhaps been responsible for the spread of East African savannas which in turn promoted the evolution of man from his pre-human ancestors.

4. The First Northern Hemisphere Ice Sheet

There is abundant evidence from various parts of the world to indicate that the terminal Miocene sea level drop was short-lived on the geological timescale and that a warmer period with rapid regression of Antarctic ice followed. In the Andalusian Stage stratotype of south-western Spain for instance, Van Couvering *et al.* (1976) report that, by the beginning of the Pliocene at 5 Ma ago, the sea had returned to the level it had stood at before the terminal Miocene regression. The result was that a connection was once again established between the Mediterranean basin and the Atlantic, via the straits of Gibraltar. At present the Gibraltar Sill has a depth of 320 m which allows a reflux of higher salinity (38 parts per thousand) intermediate water, as a consequence of excess evaporation over river run off and precipitation in the Mediterranean region (Adams *et al.*, 1977).

Thunell (1979) has used planktonic foraminifera from cores taken at D.S.D.P. sites 125 and 132 to monitor the climatic evolution of the eastern and western Mediterranean during the last five million years. He reports that, following the re-establishment of the Mediterranean, a gradual warming of its surface waters occurred throughout the early Pliocene. This was followed by a 3–4°C drop in surface water temperatures during the early part of the late Pliocene, the onset of this cooling being dated to approximately 3,2 Ma, and thought to be related to initiation of Northern Hemisphere glaciation.

Evidence for the first onset of glaciation in the Northern Hemisphere has been summarised by Thunell (1979, p. 73) as follows:

> "The late Pliocene is marked by a global climatic cooling that has been observed and dated in a variety of ways. In the Sierra Nevada region of California, a glacial till is incorporated in a quartz latite that has been radiometrically dated at 3,0 to 3,1 m.y. B.P. (Curray, 1966). Likewise, the oldest glacial deposit in Iceland lies immediately above a lava that has been dated paleomagnetically at 3,1 m.y. B.P. (McDougall and Wensink, 1966). Berggren (1972) concluded that continental glaciation developed in the Northern Hemisphere about 3,0 m.y. B.P. based on the first appearance of ice-rafted debris in the North Atlantic. This late Pliocene cooling was also observed by Shackleton and Kennett (1975b) as a significant enrichment in the ^{18}O content of benthonic foraminifera and interpreted as reflecting the first accumulation of a Northern Hemisphere ice sheet. A similar isotopic event has been recorded in the equatorial Pacific and dated paleomagnetically at 3,2 m.y. b.p. (Shackleton and Opdyke, 1977). Finally, intensification of abyssal circulation at 3,3 m.y. b.p. (Ledbetter *et al.*, 1978) may also be intimately linked with the onset of Northern Hemisphere glaciation".

The paper of Shackleton and Opdyke (1977), referred to above, and entitled *Oxygen isotope and palaeomagnetic evidence for early Northern Hemisphere glaciation* is an extremely important one in the context of this discussion. Their evidence comes from Core V28-179, raised in the equatorial Pacific through a water depth of 4 509 m, and suggests that prior to 3,2 Ma ago no Northern Hemisphere ice sheet had formed and that the world was experiencing a period of stable "interglacial" or "preglacial" climate. Following the establishment of the northern ice cap, however, which occurred between 3,2 and 2,6 Ma ago, the pattern of oscillation between glacial and interglacial interludes was established. Shackleton and Opdyke (1977, p. 218) wrote:

> "Thus we have clear evidence that glaciations of a magnitude of at least two-thirds that of the late Pleistocene glacial maxima were occurring at the time interval from 2,5 to 1,8 Myr ago. This was probably the scale of glaciation throughout the Lower Pleistocene. Evidently a major change in the character of glaciations occurred at about 2,5 Myr ago. The substantial carbon isotopic event at this point may represent a large drop in the continental biomass and may have been associated with significant floral extinctions under severe environmental pressure."

As the surface of the earth cooled progressively from Eocene times onward, why did the formation of an Antarctic ice sheet so long precede that of an Arctic one? The reason is simply that, for geographic reasons, the southern polar regions experience much lower mean annual temperatures than do the northern polar areas (Flohn, 1978).

5. Glacial-interglacial Oscillations: Some Evidence from Africa

A variety of evidence has now been presented in support of the simplified representation of global temperature change shown in Fig. 7. The discussion which follows will focus on Africa, particularly Africa south of the equator and will aim to show how the recorded temperature changes may have affected atmospheric and oceanic circulation patterns, rainfall, vegetation and, finally, what influence all these changes may have had on the course of human evolution. First, however, a short review will be given of some evidence for low temperature episodes on the African continent, particularly in the southern regions. The subject has enjoyed a good deal of attention over many years by such people as Bond (e.g. 1962, 1965) and Van Zinderen Bakker (e.g. 1962, 1975, 1976) who has done so much, not only by way of his own researches, but also through his stimulation and co-ordination of work on past climates and environments in Africa and its surroundings. The many volumes of *Palaeoecology of Africa and the Surrounding Islands and Antarctica* edited by E.M. van Zinderen Bakker will stand as a permanent witness to his interest and activity.

Flint (1959) discussed the evidence available at that time from the high mountains of equatorial East Africa and concluded that, at certain times in the past, the limits of glaciations and of snow lines had been lower. On the basis of these lower limits, he suggested a temperature reduction of about 5°C for Mount Kenya and of about 7°C for Kilimanjaro. Following more detailed work on Kilimanjaro, Downie (1964) concluded that, on that mountain, six glacial episodes could be recognised and, of these, the third was the most severe.

Detailed studies of a pollen profile taken from a core put down into Sacred Lake in the rain forest zone of Mount Kenya have produced some significant results of relevance here (Coetzee, 1964, 1967). Coetzee concluded that during the decline of the last glacial there was a depression of vegetation belts on Mount Kenya of at least 1 000 m, indicating a probable drop in temperature of about 8°C. Analysis and dating of cores taken in glacial lakes on the Ugandan side of the Ruwenzori range by Livingstone (1962) showed that the decline of the last glacial period, about 15 000 years ago was essentially synchronous on these equatorial mountains and in the high latitudes of the northern hemisphere.

Turning to southern Africa, evidence for periglacial conditions during the Pleistocene has been assembled by Harper (1969). He examined the higher mountain areas of the eastern escarpment and found evidence both in the eastern districts of Zimbabwe and in the Drakensberg. The Zimbabwean evidence was in the form of frost-wedged rock but in the Drakensberg, evidence of two cold episodes was found, the earlier apparently more intense than the later one. Harper concluded that, during the older cold period, the mean temperature was 9°C lower than present, with the results that the higher peaks were above the climatic snowline. Below this was a broad periglacial zone extending some 915 m (3 000 ft.) lower, characterised by intensely frost-wedged rock. During the younger cold period, the estimated temperature depression was about 5,5°C.

Butzer (1973a) provided a critical review of Pleistocene periglacial phenomena in southern Africa. He was inclined to dismiss the Zimbabwean evidence of Harper's as unreliable, as he did some evidence of periglacial phenomena on the Transvaal highveld reported by Linton (1969). He was, however, in broad agreement with Harper's conclusions for the mountains of Natal, Lesotho and the eastern Cape. During the 1970s Butzer and his collaborators published a good deal of evidence for low temperature episodes from a variety of sedimentary contexts in southern Africa. In their paper on the Late Cainozoic evolution of the Cape coast between Knysna and Cape St Francis, Butzer and Helgren (1972) had this to say:

> "Perhaps the most surprising conclusions, at least to the writers, are those concerning repeated and drastic changes in vegetation and climate in what today is the most mesic environment in southern Africa. The evergreen Knysna and Tzitzikamma Forests were essentially eliminated on several occasions, e.g. during the accumulation of the Keurbooms fanglomerates, the Formosa land rubble, the Brakkloof eolanite and the pre-Brenton slope breccias and colluvia. In other instances, e.g. during the early phases of the Würm glacial and probably also contemporary with the Formosa land rubble, frost weathering was so potent in what is now an equitable, mesothermal climate, that a 10°C drop in winter temperature must be postulated".

Some remarkable evidence for cyclical cold and warm periods was described by Butzer *et al.* (1978b) following their study of lime tufa accumlations along the edge of the Gaap escarpment in the north-eastern Cape. At four sites they were able to discriminate six major depositional complexes, characterised by basal cryoclastic breccias or coarse conglomerates that reflect frost shattering and torrential runoff, followed by sheets and lobes of tufa generated in an environment substantially wetter than that of today. Of the six depositional phases described, Butzer *et al.* (1978b) wrote:

> "The best-developed cryoclastic breccias of the escarpment are those of phases 1A and 1C, probably synchronous with one or both of the late Miocene to early Pliocene cold intervals. However, Phases II, III, IVa and Vb also include comparable facies wherever exposures in former scarp proximity are adequate. Basal, cryoclastic beds are the rule rather than the exception in the standard depositional hemicycle of the Gaap Escarpment".

A similar record of cyclic episodes of cold and warm climate was deduced by Butzer *et al.* (1978a) from the sediments in Border Cave, KwaZulu. Here their detailed lithostratigraphic and sedimentological study identified eight Pleistocene sedimentary cycles, including six major cold phases. The cold interludes are represented by layers rich in angular rubble — spalls produced from the ryolite cave walls and roof by frost shattering and identified as typical *éboulis secs.* Butzer *et al.* (1978a) point out that the present-day winter temperatures at Border Cave could not cause frost effects there and that a depression of winter minimum temperatures of at least 8 °C would be required. The authors do make the important point however that so great a depression of *mean annual temperature* is not implied, because the effect of Pleistocene glacials was to increase *continentality,* that is, to increase the daily and seasonal *range* of temperatures experienced at any one place.

A similar concentration of frost-shattered rock pieces had been described earlier by Butzer (1973b) from the sediment preserved in Nelson Bay Cave on the Robberg Peninsula near Plettenburg Bay. The best evidence for frost action at present-day sea level is found in Black Loam layers I–III, containing Middle Stone Age artefacts and equated by Butzer with the Lower Würm Pleniglacial. Less well-preserved *éboulis secs* have been described from the Middle Stone Age horizon in Die Kelders Cave near Hermanus by Butzer (1979).

Evidence of a different kind has come from oxygen isotope analyses of stalagmites in the Wolkberg Cave in the north-eastern Transvaal (Talma *et al.,* 1974). Analyses were done on stalagmites dated to 29 600 and 19 800 years b.p. and these showed that, during those glacial times, ground water temperatures in the caves were between 8,3 and 9,4 °C lower than they are today.

This review of some recent evidence has made it clear, I think, that at least some of the global low-temperature events reflected in the deep-sea record have left recognisable traces on the African continent. We already have traces of six cold episodes preserved in southern African Pleistocene deposits, and further research will doubtless bring more to light.

In conclusion, therefore, one may safely say that African habitats have been repeatedly affected by low-temperature episodes during the last few million years. Those episodes of which we have traces suggest that minimum winter temperatures were depressed by between 5 and 10 °C on each occasion.

IV. SOME EFFECTS OF LOW-TEMPERATURE EPISODES ON AFRICAN ENVIRONMENTS

Although low-temperature episodes will have affected the entire earth, the focus on this discussion will be particularly on Africa. Similarly, although there have been many low-temperature periods, or glacials, during the Quaternary Period, the last which had its maximum about 18 000 b.p. is the most accessible to investigation. Some probable effects of this last cold phase, with particular reference to Africa, will therefore be considered first.

In 1975 Williams wrote as follows:

> "We propose that the increasing evidence from Africa, India, South America and Australia provides further support for the view that there was widespread tropical aridity in both hemispheres during the late Pleistocene . . . Taken together, the evidence from pollen analysis, geochemistry, geomorphology, marine geology and isotope chemistry is entirely consistent with low latitude aridity in Africa, India, South America and Australia during the uppermost Pleistocene. The essential problem now is to select from among the many models a mechanism capable of reducing effective pre-

cipitation throughout the tropics during the latter stages of an ice age". (Williams, 1975: pp. 617–618).

Climatic conditons during the last glacial maximum have been the subject of an investigation by CLIMAP Project members (1976), CLIMAP being a multi-institutional consortium of scientists studying long-term climatic change and using quantitative evidence to reconstruct boundary conditions for the climate of 18 000 years ago. The four boundary conditions considered necessary to simulate the 18 000 b.p. atmospheric conditions were (i) the geography of the continents; (ii) the albedo of land and ice surfaces; (iii) the extent and elevation of permanent ice, and (iv) the sea-surface temperature pattern of the world ocean. Following their investigation, the project members concluded:

> "In the Northern Hemisphere the 18 000 B.P. world differed strikingly from the present in the huge land-based ice sheets, reaching approximately 3 km in thickness, and in a dramatic increase in the extent of pack ice and marine-based ice sheets. In the Southern Hemisphere the most striking contrast was the greater extent of sea-ice. On land, grasslands, steppes and deserts spread at the expense of forests. This change in vegetation, together with extensive areas of permanent ice and sandy outwash plains, caused an increase in global surface albedo over modern values. Sealevel was lower by at least 85 m".

In the same year Gates (1976a, b) published a numerical simulation of ice-age climate with a global general circulation model. The global distribution of July climate was simulated with a two-level atmospheric general circulation model using the surface boundary conditions of sea-surface temperature, ice-sheet topography and surface albedo assembled by the CLIMAP project members. Compared with the simulation of present July conditions, the ice-age atmosphere was found to have been substantially cooler and drier with surface air temperatures between 4,9 and 5,8 °C lower than present.

Heath (1979) made simulations of a glacial palaeoclimate by three different atmospheric general circulation models and concluded that all models showed less precipitation during the last glacial than today and were unanimous in predicting less rainfall in subtropical Africa than is now experienced.

The reason for dry tropical conditions during a glacial period have been considered in detail by Manabe and Hahn (1977). They wrote:

> "Numerical time integrations of a general circulation model of the atmosphere are performed with both modern and ice age boundary conditions. It is shown that the climate of continental portions of the tropics in the ice age simulation is much drier than that of the modern climate simulation. According to camparisons of results from the two experiments, tropical continental aridity of the ice age results from stronger surface outflow from (or weaker surface inflow into) continents. The intensification of outflow from (or weakening of inflow into) tropical continental regions results from the fact that in response to ice age boundary conditions, atmospheric temperature is reduced more over continents than over oceans."

But the evidence seems to suggest that ice age effects on precipitation varied from place to place on the African continent. While inter-tropical areas were experiencing dryness, sub-tropical regions could well have been moister. Some direct evidence for tropical dryness has come from systematic studies of dated lake levels. Butzer *et al.* (1972) compared such records for Lakes Rudolf, Nakuru, Naivasha, Magadi, Rukwa and Chad and concluded that these lakes were much enlarged during the period 10 000–8 000 b.p., a time corresponding with the warm climatic optimum. Further back, during glacial maximum times, the lake levels were found to have been low.

These studies were extended by Street and Grove (1976) who compiled published lake level data from 58 African basins in a simple cartographic form to emphasise regional patterns of surface water availability over the past 21 000 years. Their results reflected low lake levels from all tropical basins between 21 000 and 10 000 b.p. spanning the peak and decline of the last glacial maximum, followed by an abrupt change to wetter conditions. Street and Grove divided the time involved into four periods: (1) the glacial mode (21 000–12 500 b.p.), (2) the late glacial (12 500–10 000 b.p.), (3) the interglacial mode (10 000–5 000 b.p.) and (4) the irregular decline from full interglacial conditions (5 000–0 b.p.). According to Street and Grove, desert and semi-desert conditions expanded over large areas of tropical Africa during Period 1. They suggest that equatorial lowland forest was drastically reduced in extent and was restricted to refuges in West Africa and eastern Zaïre. In the Sudan, desert conditions penetrated up to 450 km southwards into present semi-desert grassland, scrub and thorn savanna areas. This reduction in effective plant cover substantially increased albedo from sand-covered areas.

During Period 2, there was a general restoration of forest vegetation across central Africa, while in the Sahara, semi-desert grassland, scrub and thorn savanna invaded huge expanses of former aeolean sands. Lowland forest species advanced 300–400 km north of their present limits in the Sudan.

This trend is thought to have continued into Period 3 so that biological productivity and biomass was greatly increased in tropical Africa, while surface albedo was diminished by expansion of open water, marshes and forests. These general conclusions have been confirmed by Selby (1977).

In contrast to this apparently consistent evidence from the tropics, different indications have been forthcoming from the southern African region. Butzer *et al.* (1973) made a detailed study of a pan at Alexandersfontein, near Kimberley. Although this is an unimpressive feature at present, it was found to have harboured a +19 m lake with a surface area of 44 km^2 shortly before 16 000 b.p. Assuming a temperature depression of 6 °C at that time, calculations show that the rainfall must have been about twice that of today.

Similar evidence for widespread humidity in the Kalahari during the period 17 000–15 000 b.p. has been collected by Lancaster (1977, 1979a, b). He studied a series of now-dry pans along the main Kalahari watershed between latitudes 23–26 °S. From one of these, known as Urwi Pan, Lancaster recovered stromatolites dated by 14C at around 16 000 b.p. and indicating, apparently, permanent wave agitated water in the pan at that time. Such conditions would have required considerably increased rainfall and much reduced evaporation coupled with lower temperatures.

A model that could account for increased precipitation over southern Africa during glacial times has been devised by Van Zinderen Bakker (1976). The main feature of this model is that the belt of westerly winds, with their associated cyclonic depressions, that today bring winter rains to the Cape, would have been displaced far to the north. Van Zinderen Bakker visualises winter rainfall carried by cold fronts or cyclonic depressions as penetrating as far north as the Tropic of Capricorn during glacial winters.

The Van Zinderen Bakker model has been widely accepted and only superficially modified by other writers (e.g. Tankard and Rogers, 1978; Grindley, 1979). However, some doubts have been expressed as to whether winter rains did, in fact, penetrate deep into the interior during glacial times. For instance Hays *et al.* (1976) have pointed out that the position of the polar front in the southern ocean, the generating area of the rain-bearing cyclonic depressions, hardly moved northwards at all south of Africa during the last glacial maximum. From his detailed studies at the Boomplaas Cave in the Cango valley near Oudtshoorn, Deacon (1979) and Avery (1982) have concluded that glacial winters there, while certainly cold, were not wet.

It is clear that the detailed picture of glacial period climatic conditions in southern Africa will have to be worked out on the basis of meticulous investigations at securely dated sites.

Before leaving this topic it is perhaps worth mentioning some consequences of earlier low temperature episodes on African habitats. In particular, the effects of late Miocene cooling on habitats along the west coast of Africa are of note. It is well known that the Namib is desertic for two reasons — as a consequence of its position on the African continent relative to the persistent sub-tropical anticyclones and, secondly, as a result of the influence of the cold Benguela current. This current transports cold, upwelling Antarctic water along the African west coast and its history, in geological terms, has been studied by Siesser (1978, 1980). He made use of cores taken on the Walvis Ridge Abutment and used, among other techniques, total organic carbon content as a measure of past biological productivity in the sea, and thus of upwelling. Siesser was able to show that the cold Benguela current had its origin in early Late Miocene times about 10 Ma ago, but that the production of organic carbon in the core studied increased dramatically at the end of the Miocene about 5 Ma ago. It thus seems likely that the extreme aridification of the west coast does not extend further than about 10 Ma back, though it may have been greatly intensified at the time of the terminal Miocene event. (~5 Ma)

It is very probable that the progressive aridification of west coast habitats led to the extinction of some of the remarkable Miocene mammals known, for instance, from Arrisdrift at the mouth of the Orange River (Corvinus and Hendey, 1978; Hendey, 1978) and from Langebaanweg (Hendey, 1981a, b, 1982). Evidence for related vegetational changes in this regiom has been forthcoming from the fossil pollen studies of Coetzee (1978a, b; 1980).

An interesting aspect of the relationship between low temperature episodes and extinctions such as those just referred to has been raised by Mörner (1978a, b). He points out that any marked lowering of sea level, such as that which occurred at the end of the Miocene and during subsequent glacials, will have also affected the ground water table under the continents by geoid changes. Such a lowering of the water table would drastically affect vegetation and animals dependent on it, according to Mörner, and the effect would be independent of any other climatic or environmental change that the reduced temperature might bring about.

V. HOW THE EFFECTS OF LOW-TEMPERATURE EPISODES MAY HAVE SERVED AS EVOLUTIONARY STIMULI IN AFRICA

There are probably many ways in which a changing environment may serve as an evolutionary stimulus. The one to be discussed here, however, is how environmental change may break up a once continuous distribution of an organism into discontinuous patches and thus serve as a mediator of allopatry. Two examples will be considered: one from the African tropics and the other from sub-tropical southern Africa.

The possible effect of glacial-induced climatic changes on African vegetation has already been touched upon. However, the evidence for the tropical regions has been considered in detail by Hamilton (1976). His conclusions are summarised in Fig. 9 where the extent of lowland forest in tropical Africa today is contrasted with that visualised for glacial maximum conditions 20 000 b.p. and for warm, climatic optimum conditions 8 000 b.p. It will be seen that, according to Hamilton, forest areas suffered considerable contraction during glacial times, with the lowland forest block becoming broken into two separate pieces, on the east and west. By contrast, during the warm climatic optimum times 8 000 b.p., the forest areas expanded beyond their present limits, while lakes, such as Lake Chad shown in the reconstruction, were considerably enlarged.

Apparently it was not only on the African continent that tropical forests suffered such dramatic reductions. Shackleton (1977) has reviewed evidence for similar glacial-period forest shrinkages in South America, Java, Sumatra, Borneo and Malaysia. He has furthermore linked the expansions and contractions of the world's forests to changes in carbon isotope ratios in the tests of benthonic foraminifera. Contrary to expectations, the ratio of 13C in dissolved oceanic CO_2 can undergo significant changes within a few thousand years, and Shackleton suggested that such changes are a consequence of changes in the terrestrial plant biomass. Thus it appears possible to detect past expansions and contractions of tropical forests through the study of carbon isotope ratios in deep-sea foraminifera.

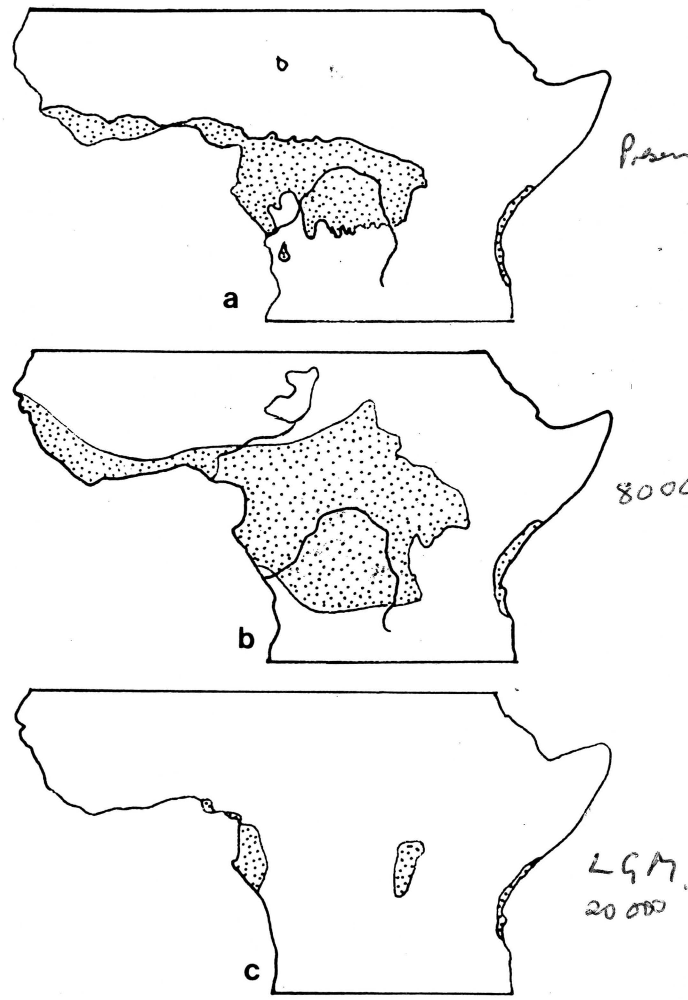

Figure 9

Three maps of tropical Africa indicating (a) the present extent of lowland forest, (b) the reconstructed extent of lowland forest during the warm climatic optimum 8 000 years ago, and (c) the extent during the last glacial maximum, 20 000 years ago. Redrawn from Hamilton (1976).

Let us turn now from the tropical forests of Africa to the vegetation of the interior of southern Africa. Elsewhere (Brain, *in press*) I have considered the close correspondence that exists between the distribution of temperate grassland in southern Africa and that area of southern Africa which receives frost on at least 100 nights per year. This relationship has been considered by Werger and Coetzee (1978) who point out that, although frost alone may be an important factor in maintaining a grassland, the combination of *frost and fire* is much more significant. Frequently, woody vegetation is not able to survive fire when it has been severely frosted.

Making use of figures for mean daily minimum temperatures during the coldest month (July) over southern Africa provided by Jackson (1961), the isothermal maps shown in Figs. 10a and b have been drawn. Figure 10a shows the area of southern Africa experiencing mean minimum temperatures for the coldest month of below 0 °C at present, while Fig. 10b indicates how far this zone would spread if the mean temperature were to fall by 5 °C. On the assumption that there is a direct link between low winter temperatures and the presence of grassland in southern Africa, considerable expansion of the present grassland area shown in Fig. 10c presumably occurred during glacial periods. Direct evidence for such grassland spread is starting to accumulate. For instance with reference to the Cape Ecozone, Klein (1980) remarked that "cooler intervals repeatedly witnessed an increase in grazing ungulates relative to browsers" while in the central Transvaal, in an area now covered with bushveld, a pollen profile from Wonderkrater shows that the area was devoid of bushveld trees during the last glacial maximum (Scott and Vogel, 1978).

It seems extremely likely that the distributions of certain plants and animals in Africa will have expanded and contracted repeatedly in response to temperature cycles. From the point of view of this discussion, however, it is important to notice that such expansions and contractions will have been topographically intricate with the result that once-continuous distributions will have been fragmented for varying lengths of time. It is precisely in such circumstances of allopatry and small population size that speciation events are likely to occur (e.g. Futuyma and Mayer, 1980; Paterson, 1981).

VI. WHICH LOW-TEMPERATURE EPISODES ARE LIKELY TO HAVE SERVED AS EFFECTIVE EVOLUTIONARY STIMULI IN AFRICA?

From the evidence and discussion presented earlier, it is likely that the following low-temperature episodes were significant as evolutionary stimuli for hominoids in Africa (reference should be made to Fig. 7).

A. Mid-Miocene Temperature Oscillations

It will be recalled that Woodruff *et al.* (1981) presented evidence for the establishment of the East Antarctic ice cap between 16,5 and 13 Ma b.p. with the greatest change occurring between about 14,8 and 14,0 Ma ago. At this time the earth's climatic system seems to have become extremely unstable and to have oscillated back and forth between glacial and interglacial modes for perhaps a million years.

Just what effect this episode might have had on tropical habitats is difficult to visualise. It may well have fragmented areas of tropical forest although mean global temperature was still presumably fairly high.

B. The Terminal Miocene Event

This very well-documented low-temperature episode occurred between 6,5 and 5 Ma b.p. and had world-wide repercussions as discussed earlier. Not only did global temperature drop dramatically, leading to the establishment of the West Antarctic ice cap, but sea levels were lowered by as much as 70 m. This lowering contributed to the Messinian salinity crisis of the Mediterranean and effects on African habitats were probably strongly marked. It is very likely that the tropical forest block was broken up and that open habitats spread at the expense of wooded ones.

C. The First Establishment of a Northern Hemisphere Ice Sheet

The evidence discussed earlier indicates that when the next severe low-temperature event came round between 3,2 and 2,6 Ma b.p., global temperature had declined sufficiently to allow an ice sheet to develop in the Northern Hemisphere, in addition to that in the south, for the first time. Effects on African habitats may have been even more marked than had been the case with the terminal Miocene event.

D. Glacial-Interglacial Oscillations

As discussed earlier it appears that for the last two million years the earth's climate has oscillated back and forth between glacial and interglacial modes, with each cycle taking perhaps 100 000 years. Vegetation zones will have repeatedly migrated to and fro across Africa in response to changes in temperature and moistness. Animals dependent on the vegetation in these zones will have moved with them, often finding themselves cut off from the rest of their populations in island refuges of various sizes.

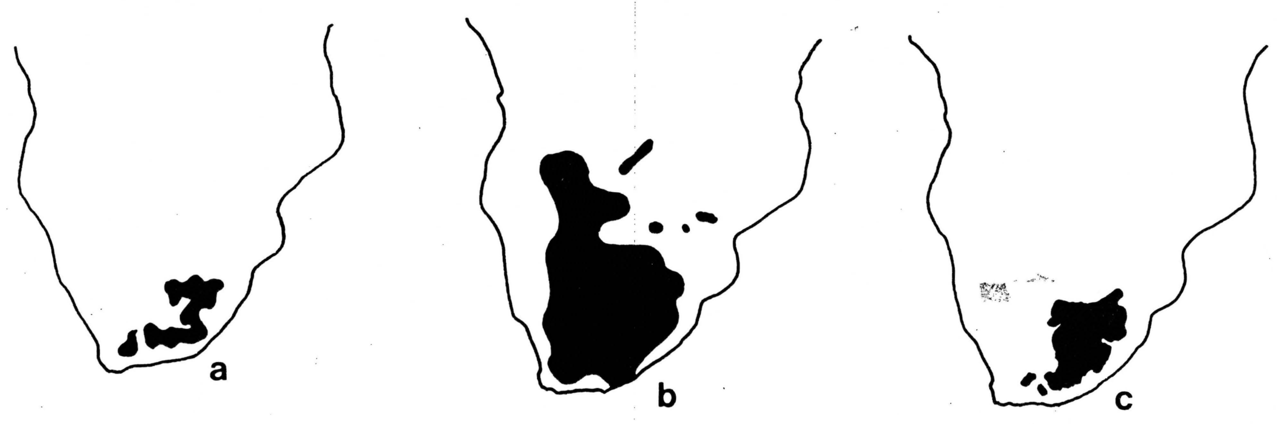

Figure 10

(a) The area of southern Africa experiencing mean minimum temperatures for the coldest month (July) of below 0 °C at present. (b) The area that would experience mean minimum temperatures during July below 0 °C if winter minimum temperatures were to drop by 5 °C. (c) The area of southern Africa currently occupied by temperate grassland.

VII. A POSSIBLE CORRELATION BETWEEN SOME CRITICAL EVENTS IN HOMINOID EVOLUTION AND LOW-TEMPERATURE EPISODES

A. Mid-Miocene Temperature Oscillations

The recent description of new and reasonably complete fossil skull material of *Sivapithecus* from the Middle to Late Miocene of Pakistan (Pilbeam and Smith, 1981; Pilbeam, 1982) has thrown most interesting new light on an early phase of hominoid evolution. The traditional view, held by many palaeoanthropologists over a number of years, was that *Ramapithecus* was a direct ancestor of *Australopithecus* and thus of man. However, the new Pakistan finds suggest that *Ramapithecus* is very similar to *Sivapithecus* (Andrews, 1982; Andrews and Cronin, 1982) and that it is more closely related to the ancestry of the orang-utan than it is to that of man.

A good deal of biomolecular evidence has been accumulating during the last twenty years to clarify the past branching sequence or cladistics of the hominoids, as well as the timing of branchings. This evidence illuminates three cladogenic events in hominoid evolution: first the separation of the gibbon lineage from that leading to the great apes and man; second, the subsequent divergence of the orang-utan lineage from that linking the African apes and man; and thirdly, evidence from molecular comparisons that man, chimpanzee and gorilla shared a substantial lineage before their subsequent divergence (Andrews and Cronin, 1982, p. 541).

In addition to defining the sequence of branchings, molecular anthropology has also been used to date these events, using the so-called "molecular clock". Present estimates for the three events are: gibbon divergence 12 ± 3 Ma b.p.; orang-utan divergence 10 ± 3 Ma b.p.; and man–African ape divergence 5 ± 1,5 Ma b.p. (Andrews and Cronin, 1982, p. 452).

The Mid-Miocene temperature oscillations referred to in the last section between 16,5 and 13 Ma b.p. might conceivably have been something to do with the two cladogenic events representing the gibbon and orang-utan divergences. However, resolution in this part of the temperature record is not good enough at present to provide anything more than tantalizing indications.

B. The Terminal Miocene Event

As discussed earlier, the evidence for this dramatic low-temperature event between 6,5 and 5 Ma b.p. is good and the chances are that it had a dramtic effect on African habitats. The time coincides with that suggested by the "molecular clock" for the separation of the australopithecine lineage from that leading to the chimpanzee and gorilla. The palaeontological evidence of *Australopithecus afarensis* (Johanson *et al.,* 1978; Johanson and White, 1979) and of hominid footprints from the same time period (Leakey and Hay, 1979; Day and Wickens, 1980; White, 1980) indicate that at between 3,5 and 4 Ma b.p. hominids were already bipedal. It appears therefore that the most obvious anatomical change to have taken place between the australopithecine and African ape lineages at about 5 Ma b.p. was the acquisition of erect posture in the former lineage (Fig. 11). This evolutionary development could well have been mediated by environmental changes induced by the terminal Miocene event. Fragmentation of once continuous forest and woodland areas at that time could well have separated the ancestral australopithecine population from its ape contemporaries

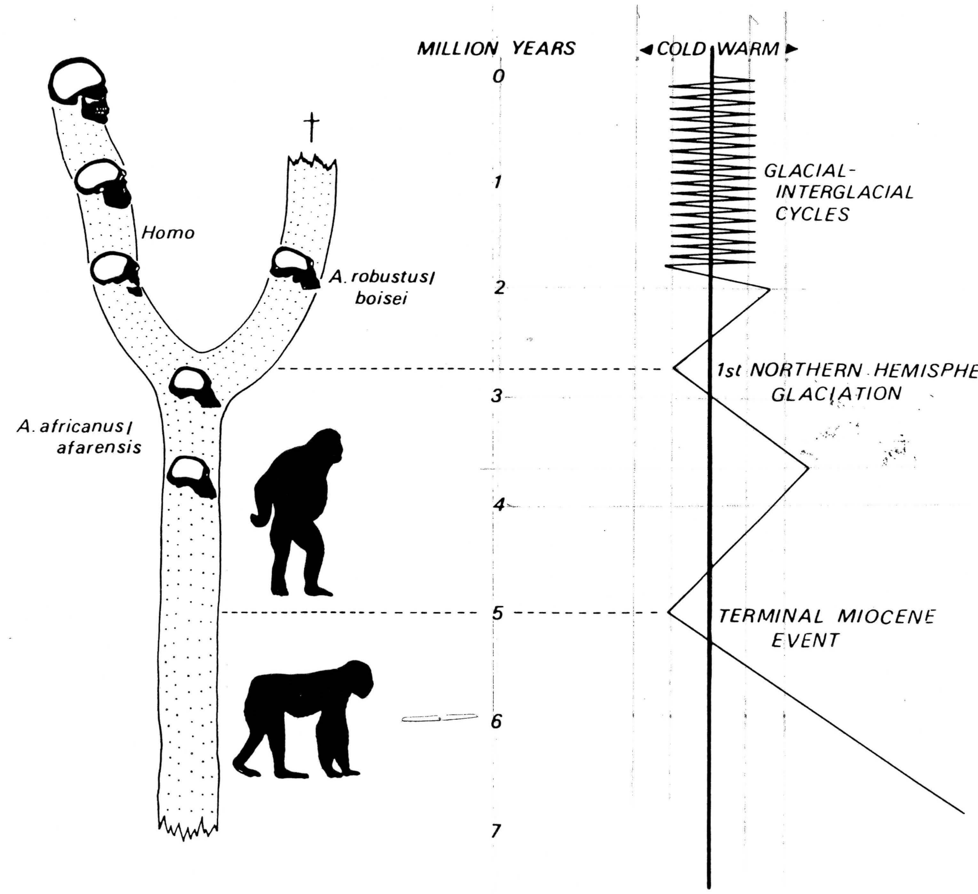

Figure 11

A suggested correlation between events in hominid evolution and low-temperature episodes. The Terminal Miocene Event is correlated with the acquisition of erect posture and with the separation of the African great ape lineage from that of the australopithecines (the split is not shown here). The first Northern Hemisphere glaciation is correlated with the separation of the *Homo* and robust australopithecine lineages.

and in this way facilitated a speciation event involving bipedality.

C. The First Establishment of a Northern Hemisphere Ice Sheet

As discussed earlier, this low-temperature episode appears to have occurred between 3,2 and 2,6 Ma b.p. This time coincides with the split, documented on palaeontological grounds between *Homo* and the australopithecine lineages. As pointed out by Johanson and White (1979) opinions vary as to the precise nature, in taxonomic terms, of this split. Johanson and White visualise *Australopithecus afarensis* leading directly to *Homo*, with *A. africanus* and *A. robustus/boisei* on a side-line, while Tobias (1980) for instance regards *A. africanus* as the direct ancestor of the *Homo* lineage.

Again this cladogenic event could very well have been brought about by temperature — induced environmental changes, leading to range fragmentation.

D. Glacial-interglacial Oscillations

As discussed earlier, the last two million years has seen perhaps 20 glacial-interglacial cycles, each causing profound expansions and contractions of vegetational zones. During these times the *Homo* lineage progressed from *H. habilis*, through *H. erectus* to *H. scapiens*, making use of increased intelligence, culture and technology to cope with problems of survival. The australopithecine lineage on the other hand adopted a different strategy — that of increasing its body size as well as the grinding area of its teeth and the power of its jaw muscles. That African habitats were becoming progressively more open is suggested by studies of the antelope tribe Alcelaphini — that to which the wildebeest and hartebeest belong. Vrba (1979) has shown that all 28 known fossil and modern species of these grazing antelopes evolved in Africa within the last five million years, most of them coming into being during the last three million. These speciation events were very probably promoted by repeated fragmentation of grassland ranges. In the same way it was probably the demands of survival in progressively more open habitats that promoted both brain expansion in *Homo* and a trend to robusticity in *Australopithecus*. Of the two opinions, the human one has, thus far, proved the more appropriate.

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