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The Late Quaternary history of climate and vegetation in East and southern Africa

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ABSTRACT

In the vast region of East and southern Africa the alternating glacial and interglacial periods of the Quaternary were characterized by considerable changes in temperature and precipitation. During the last glacial maximum the influence of the ITCZ was limited, while the circulation systems were strengthened. The ocean surface waters were cooler and the Benguela Current was activated. In the montane areas of East Africa and also in southern Africa the temperature dropped by about 6°C.

During this hypothermal period, rainfall on the east African plateau and mountains diminished. Summer precipitation could still penetrate the eastern half of southern Africa from the Indian Ocean, while the western half was arid to semi-arid. Cyclonic winter rain migrated further north beyond the latitude of the Orange River.

The consequences of these climatic changes during the last glacial maximum were that the woodlands of East Africa opened up. On the plateau of South Africa austro-afroalpine vegetation dominated. The south coastal plain was very windy and cold to temperate, while the Namib and Kalahari were respectively hyper-arid and semi-humid.

During hyperthermals the vegetation pattern resembled present-day conditions more closely.

RÉSUMÉ

HISTOIRE DU CLIMAT ET DE LA VÉGÉTATION À LA FIN DU QUATERNAIRE DANS L'EST ET LE SUD DE L'AFRIQUE.

Dans la vaste région de l'Afrique méridionale et orientale, les périodes glaciaires et interglaciaires du Quaternaire furent caractérisées par des changements considérables de température et de précipitations. Durant l'apogée de la dernière période glaciaire, l'influence du ITCZ fut limitée, tandis que les systèmes de circulation se renforcèrent. Les eaux de surface de l'océan devinrent plus froides et le courant du Benguela entra en activité. Dans les régions montagnerdes de l'Afrique de l'Est et aussi en Afrique méridionale, la température tomba d'environ 6°C.

Pendant la période hypothermique, la pluviosité sur les plateaux et les montagnes de l'Est africain diminua. Les précipitations d'été pouvaient encore pénétrer dans la moitié est de l'Afrique méridionale à partir de l'océan Indien, tandis que la moitié ouest était aride à semi-aride. Les pluies cycloniques d'hiver émigrèrent vers le Nord, au delà de la latitude de fleuve Orange.

Les conséquences de ces changements climatiques pendant l'apogée de la dernière période glaciaire furent que les forêts claires de l'Est africain devinrent plus ouvertes. Sur le plateau de l'Afrique du Sud, la végétation austro-afroalpine devint dominante. La plaine côtière sud fut très venteuse et froide à tempérée, tandis que le Namib et le Kalahari furent respectivement hyper-aride et semi-humide. Durant les périodes hyperthermiques, la physionomie de la végétation s'est davantage rapprochée de son aspect actuel.

INTRODUCTION

The part of Africa under discussion in this article forms a vast uplifted plateau delimited towards the oceans by raised escarpments. In Tertiary times two major periods of tectonic uplift occurred, namely in the end Miocene and terminal Pliocene, the last one of which raised the interior plateaux by about 1 000 m (King, 1978).

In east to west cross section central and southern Africa have the appearance of an enormous flat dish with a slightly raised margin. Important depressions in the surface of this dish are the early Tertiary Congo and Kalahari basins and others situated in the Karoo, the Transvaal and the river valleys of the Limpopo and Zambesi.

The high and steep monoclines of central and southern Africa, delimiting the Pliocene coastal plains from the much older interior, cut off the oceanic influence and consequently caused the southern basins to become dry and warm.

In Plio-Pleistocene times rift valleys developed in the upwarped ridges separating the basins. These elongated new valleys and the many volcanoes which were built upon their margins added to the varied topography and climate.

The vast region stretching from Kenya and Uganda down to the Cape of Good Hope has during the Quaternary witnessed impressive changes in climate and vegetation. Warmer and more humid conditions encouraged the spread of forest, woodlands and savanna. Colder and drier climates favoured enormous migrations in the reverse direction. During the Quaternary these processes have been repeated many times with different intensities, but we can only trace them with some degree of accuracy for the last 30 000 years.

The evidence for these dramatic changes of the face of Africa is provided by multidisciplinary studies. This approach has over the last twenty years provided an acceptable general model for the changes which took place although very many details remain to be cleared up.

It is convenient to separate the discussions on East and southern Africa as they represent different

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biotic and climatic regions. The part on East Africa will concentrate mainly on Kenya, Uganda and Tanzania and for southern Africa the emphasis will be laid on South Africa and Namibia as these countries have been studied in more detail than the intervening region. Moçambique will not be discussed.

EAST AFRICA

Present climate and vegetation

East Africa would in general be a semi-arid to arid part of the world if it did not have its many mountain ranges, hills and volcanoes which catch orographic rainfall. The eastern sector is under the influence of the alternating NE and SE monsoons. The SE monsoon has the longest trajectory over the ocean, but the air flow is shallow and divergent and does not meet a high coastal mountain range so that it brings only little rain to the vast plateau of the interior.

The other main source of rainfall is the monsoon which penetrates equatorial Africa from the Atlantic Ocean and loses most of its humidity over the Zaire basin and on the high mountain ridge bordering the western Rift Valley.

In the course of the last 1 000 years man has had a devastating influence on the vegetation by destruction of forest, burning woodlands and overgrazing. It would, however, be an over-simplification to assume that without human interference East Africa would have been completely covered by forest. The opening up of the vegetation is of much older age

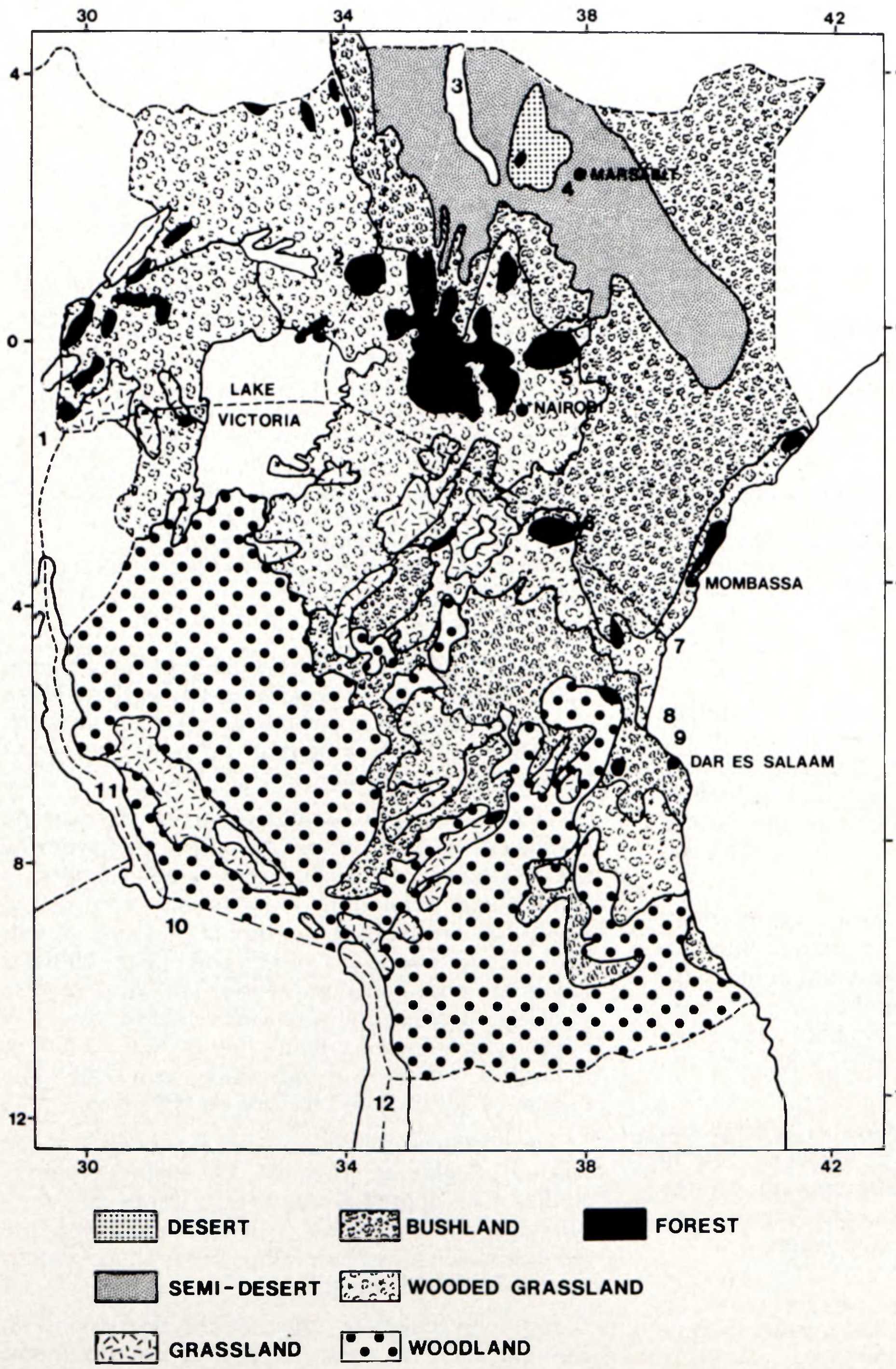

FIG. 1.—Vegetation of East Africa.

and is the consequence of the gradual desiccation of Africa which started at least during the world wide cooling in the end of the Miocene (5 My). This is also testified by the fauna of alcelaphine antelopes which are highly adapted to this open type of vegetation (Vrba, 1979, 1980).

The vegetation pattern of East Africa is one of the most varied of the world ranging from lowland rain forest with an equable warm and humid climate to sun parched semi-desert and to the highest mountains in Africa which are covered with residual glaciers right under the equator. This pattern is primarily arranged according to the availability of water. (Fig. 1).

Late Quaternary changes in East Africa

In reconstructing the Late Quaternary changes we will limit ourselves mainly to the two extreme periods known in this time span, *viz.* the hypothermal or last cold maximum and the Holocene Climatic Optimum.

During the last glacial maximum c. 18 000 yr B.P. the tropical oceans, which provide the humidity of East Africa, were colder than at present. The average ice-age zonal sea surface temperature for the entire Indian Ocean was 1,4–1,5°C cooler (Prell & Hutson, 1979). The tropical part of the Atlantic Ocean was 4–5°C colder than at present (Morley & Hays, 1979). Flohn & Nicholson (1980) calculated that, as a consequence of this, the evaporation over the tropical oceans of the world was reduced to 25–30% of the normal value. This 'ice-age aridity' can also be inferred from the low levels of practically all the lakes in tropical Africa (Van Zinderen Bakker, 1972; Butzer *et al.*, 1972). It affected nearly the whole of Africa except for the northern (Rognon, 1981) and the southern (Van Zinderen Bakker, 1976) extremities.

During the last glacial maximum the wind speed in the Northern Hemisphere was in summer accelerated by 124% and in winter by 24% (Newell *et al.*, 1981).

The lowering in temperature and the dryness of the climate were proved by pollen analytical studies of some six palynologists who worked on the East African mountains in the short period of 1961–1971 (Livingstone & Van der Hammen, 1978). Since then, very few pollen diagrams have been published from this region, but the continued interest of A.C. Hamilton in tropical palynology has done much to assess and interpret the ecological and biogeographical aspects of the data that had been collected.

The first interpretations inferring a cold and dry climate were made by Coetzee (1964, 1967) and Van Zinderen Bakker (1962, 1964), who studied pollen sequences from the Cherangani Hills and Mt Kenya. Their conclusions were based on evidence from various pollen types amongst which grass pollen played an important part. This interpretation has been criticized by Livingstone (1967) on the grounds that grass pollen in these mountains is not a valid indicator for a cold alpine environment. The climatic changes indicated by these diagrams have been re-assessed by Van Zinderen Bakker & Coetzee (1972) and by Hamilton (1974b) without taking the grass pollen into account. These new interpretations, based on studies of Hamilton (1972) on pollen deposition in the Ugandan mountains, did not change the original conclusions, *viz.* that during the last glacial maximum the climate was dry and c. 6°C colder than at present. It is strange that the use of grass pollen by Van Zinderen Bakker and Coetzee is still being attacked 'post mortem' by Livingstone (1975, 1980).

Similar results with pollen sequences have been achieved with cores from Uganda by Morrison (1968) in the Rukiga Highlands in south-west Uganda where the climate was dry and the mean annual temperature was 18 000 yr B.P. also c. 6°C lower than now. Livingstone (1967) originally explained his results in the Ruwenzori in a different way, but the re-interpretation by Hamilton (1972) came to conclusions which are practically identical to those from Kenya and the Rukiga Highlands for the last 15 500 years. More important proof for dryness on the African plateau was provided by Kendall (1969), who showed that the area round Jinja on the northern edge of Lake Victoria, where at present lowland forest is dominant, was occupied by an open arid savanna between more than 14 500 and 12 000 yr B.P.

Coetzee (1967) has designated the last cold and dry period after the type-site, the *Mount Kenya Hypothermal.* This cold maximum was coeval with the last severe maximum of the European Würm glaciation. During this time the vegetation belts on the East African mountains shifted 1 000–1 100 m downward. Similar changes have been recorded in the equatorial Andes by Van der Hammen & Gonzalez (1960).

In East Africa, the consequences of the colder and drier climates were dramatic. We will first look at the forest and the mountain vegetation. The lowland forest, being most sensitive to drought, will in tropical Africa probably only have survived in the following four areas: West Africa (west of the Togo/Dahomey gap), Cameroon/Gabon, E. Zaire and along the East African coast (Hamilton, 1974a, b; Diamond & Hamilton, 1980). The position of the refuges is also indicated by the distribution of forest mammals (Kingdon, 1971) and of endemic species of forest passerine birds (Diamond & Hamilton, 1980).

The three vegetation belts occurring on many mountains above the moist montane forest, *viz.* the dry montane forest, the Ericaceous Belt and the Afroalpine Belt, persisted at much lower altitude during the hypothermal period. The remarkable small biota of the Afroalpine Belt with their high degree of endemism remained isolated on the highest parts of the mountains and could not make contact via the lowlands. This also applies to the montane forest of the various mountains.

The opening up of the vegetation of Africa during the hypothermal period may have provided a migration route between the arid north-eastern part of East Africa and Namibia for plant and animal taxa adapted to dry conditions (*Palaeoecology of*

Africa, vol. 1, 1963, p. 188/9, vol IX 1969, chapter VI). An 'arid corridor' of this type will develop when the present rainfall diminishes and this corridor will run in a SW-NE direction passing between the lakes Tanganyika and Malawi (Van Zinderen Bakker, 1969a, b). Until some ten years ago, when the glacial periods were generally supposed to have had a wet climate, this corridor was supposed to have been of interglacial age. Hamilton (1974b) suggested that it is well possible that a connection of this kind was open or partly open at various intervals to migration during the dry period before 12 000 yr B.P.

The data on conditions on the plateau of East Africa during the hypothermal period are very scanty. The pollen record of Pilkington Bay (Kendall, 1969) and of Cherangani (Coetzee, 1967; Hamilton, 1974b) and also the low lake levels indicate that the climate was certainly dry.

The glaciation on the East African mountains came to an end some 15 000 years ago, at the same time as the Würm Glaciers in Europe and the Wisconsin counterparts in America started to wane (Livingstone, 1962). The gradual warming of the climate only had a marked effect on the vegetation near 12 600 yr B.P. at a time coeval with the Bölling-Alleröd Interstadials in Europe. The consequence of this warming up was that evaporation of the world's oceans was activated so that more moisture could reach tropical Africa from the Atlantic and Indian oceans. From that time onward, forest developed along the northern boundary of the Victoria Basin. Hamilton (1981) could show that the forest elements spread from the refuge along the western Rift Valley in an eastern direction probably mostly by long distance dispersal. At about 10 500 yr B.P., the temperature in the mountains had reached the present level. After a minimum around 10 200 B.P., very high lake levels were reached between 10 000 and 7 500 yr B.P. At about 4 600–4 000 yr B.P. the temperature in the mountains was higher than at present and the forest expansion at Pilkington Bay reached its maximum.

SOUTHERN AFRICA

Present climate and vegetation

The vegetation of southern Africa gives a very accurate image of the climatic pattern of the subcontinent. The climate is mostly arid to semi-arid and would, as in East Africa, have been drier if it was not for the orographic rainfall received by high mountains. The rainfall in the tropical part of Africa south of the equator has a zonal pattern caused by latitudinal migration of the ITCZ which follows the sun and is therefore summer rainfall. The vast zone of woodland, covering eastern Angola, Zambia, Malawi and most of Moçambique receives this precipitation which amounts from 600–800 mm per year. This rainfall pattern changes suddenly south of 20°S where the isohyets run more or less in a meridional direction. Further south the following circulation and rainfall systems dominate southern Africa (Van Zinderen Bakker, 1976):

—the mid-latitude westerlies bring cyclonic winter rain to the S.W. Cape.

—subtropical anticyclones are centred on 30°S. The stable and strong high situated near the Namibian coast over the South Atlantic produces a subsiding, divergent wind flow and is one of the main reasons for aridity in the western half of the subcontinent.

—the Benguela Current with its accompanying cold upwelling runs parallel to the Namibian coast as far north as Cape Frio and prevents moisture from penetrating the continent.

—summer rainfall reaches the interior from the Indian Ocean in an anti-clockwise airflow.

—the warm Agulhas Current along the east and south coast brings much moisture to the coastal region and the north-eastern interior.

The present-day vegetation of southern Africa presents textbook examples of extensive ecological gradients, especially on the plateau in a south-northerly and a west-easterly direction. From south to north we find the semi-arid Karoo with a BWk-climate giving way in a northern direction to grassland of the southern Highveld and the open savanna of the Kalahari basin (BSh-climate). Further north the *Brachystegia–Julbernardia* zone, with a warm Cwa-climate, runs obliquely across the continent.

In a west to east direction, the gradient is even more impressive as it is of an orographic, geological and ecological nature. The hyper-arid erg of the southern Namib Desert (BWk-climate) gradually grades in an easterly direction into the Kalahari savanna (BSh-climate). Still further east the open *Cymbopogon–Themeda* grassland covers the southern Highveld which above an altitude of c. 2 250 m is replaced by the austro-afroalpine grassland of Lesotho.

The eastern and southern coastal plains of the subcontinent form a different ecological region and conditions range in a south to north direction from temperate to tropical. The fynbos region of the SW Cape has a winter rainfall Csb-climate. This changes to an equatorial winter dry climate (Aw) of the tropical Moçambique plain. The transition from temperate to tropical biota occurs at 28° 5'S. Lat. near Lake St Lucia.

Late Quaternary changes in southern Africa

Important information about temperature changes has become available from oceanographic and terrestrial evidence especially for the last glacial maximum around 18 000 B.P.

Drastic decreases in temperature occurred in the Antarctic region, although the changes in the oceanic environment south of Africa were not very pronounced. The CLIMAP-map shows an anomaly area of more than −4°C along the south-eastern coast of South Africa (CLIMAP 1976). The Benguela Current and its cold upwelling lowered the temperature 2–5°C and penetrated much further north (Van Zinderen Bakker, 1967; De Ploey, 1969; Bornhold, 1973; Giresse, 1978). The Agulhas Current was a weak tropical current in summer and in winter was replaced by cool waters (Hutson, 1980).

Undated periglacial phenomena in the high Drakensberg, on screes and in caves along the south coast (Harper, 1969; Butzer, 1973) indicate decreases in temperature of as much as 3,5–10°C, whereas in the Wolkberg Cave well dated lowering in temperature amounted to 8–9,5°C (Talma *et al.*, 1974).

During this cold period the anticyclones were strengthened and the wind speed was accelerated by 17% (Newell *et al.*, 1981). The oceanic circulation was also intensified.

(a) *30 000–13 000 B.P.*

In recent years the following information has become available on the consequences of these climatic changes in South Central and Southern Africa. At Kalambo Falls (8° 30'S) near the south-eastern corner of Lake Tanganyika a number of isolated pollen samples show that during the 'Kalambo Interstadial' from c. 30 000 to c. 27 000 yr B.P. the climate was slightly warmer and wetter than today (Van Zinderen Bakker, 1969a). During the last cold maximum, which followed. The *Brachystegia* woodland opened up which may indicate the existence of an arid corridor. The temperature was then about 4°C lower than at present. The 22 000 year old pollen record from Ishiba Ngandu at c. 12°S on the plateau of Zambia does, however, not give information on such changes in the woodlands (Livingstone, 1971).

The history of the *Acacia-Commiphora* savanna of the Kalahari further south may more or less have followed the pattern of the Kalambo Falls sequence. During a time which immediately followed and probably overlapped with the Kalambo Interstadial the Kalahari received much rainfall which also penetrated the eastern part of Namibia and episodically even the Namib Desert proper (Heine, 1980, 1981, 1982). Lake Palaeo-Makgadikgadi gained a very high stand and tropical savanna and woodlands must have been spreading southward. During the period from 39–28 000 B.P. even the Namib Desert received more rainfall. From 28 000 to c. 25 000 B.P. rainfall increased in the catchment area of the Kuiseb River and decreased between 23 000 and 19 000 B.P. (Vogel, 1982).

During the subsequent colder period which, according to Heine (1981), lasted from 19 000–13 000 B.P., only episodically small lakes developed in the Makgadikgadi depression (Heine, 1982). Strong winds inferred from the alignment of the dunes indicate that during the last cold maximum the anticyclone over the interior was larger or had a more northerly position compared with today (Lancaster, 1979, 1981). The Kalahari and the central part of southern Africa received limited summer rainfall. This rain was generated by eastern winds drawn in from the Indian Ocean by the strengthened overland anticyclone. The drier, colder and more windy climate will have opened up the woodlands and savannas and diminished the tropical influence while drier floral elements will have invaded the Kalahari from the south.

In the southern Kalahari a more humid climate prevailed in that in winter the summer rainfall was replaced by precipitation originating from the northward displaced westerlies (Heine, 1980, 1981, 1982). The consequence of this evenly distributed low rainfall was that the Molopo could at certain times become a perennial river *(ibid)*.

These subhumid conditions of the southern Kalahari can be correlated with the impressive climatic chronology described for the Gaap Escarpment, according to which the climate during phase Vc was subhumid from ⩾ 21 000 to 14 000 B.P. (Butzer *et al.*, 1978). Before and after this more humid phase, a lower temperature is inferred from the stratigraphic evidence of the Gaap Escarpment. The dating of the older of these colder periods is not yet quite certain, but it is not well possible that it coincided with the warmer Kalambo Interstadial. The subhumid conditions must have encouraged the spread of savanna vegetation. So far no evidence from fossil pollen is available for this period.

From the fossil pollen record of the thermal spring deposits at Wonderkrater further to the east (24° 26'S), it can be concluded that during the period of c. 30 000 to c. 26 000 B.P. the climate may have been cool-temperate and the humidity did not vary much from the present semi-arid to subhumid conditions (Scott, 1982). During the last cold maximum cooler and moister conditions prevailed similar to those at present known from the lower part of the austro-afroalpine zone in Lesotho. The bushveld had changed into grassland with alpine and fynbos elements (Scott & Vogel, 1978).

A similar situation occurred on the plateau of the Orange Free State where the temperature had decreased 5–6°C (Van Zinderen Bakker, 1976). This will have caused a downward shift of the austro-afroalpine grassland of the Malutis of about 1 000 m so that the 'cold' grassland probably invaded the plateau of the Orange Free State and the surroundings. The montane forests of the valleys and ravines will have disappeared and above the altitude of 3 000 m no vegetation existed (Van Zinderen Bakker & Werger, 1974). Cottrell (1978) explains the present distribution of the southern African butterflies as a consequence of these shifts of vegetation.

The little information which is available suggests that during the Kalambo Interstadial summer rainfall could penetrate part of the Namib Desert (Heine, 1982). The climate became arid during the ensuing last cold maximum especially in the middle and northern Namib. The South Atlantic anticyclone was strengthened and strong southerly winds moved the longitudinal dunes. The Benguela Current aggravated the aridity further northward. The possibility that the westerlies could bring winter rain in the southern erg to c. 24° S. Lat. as to the southern Kalahari is still considered (Van Zinderen Bakker, 1976).

The composition of the Namib flora shows that as many as 34,5% of the species have a restricted distribution or are endemic (Robinson, 1978). The majority of these species occur in the winter rainfall area of the southern erg which points to isolation in a wide variety of habitats (Seely, 1976, 1978).

(b) *13 000 B.P. – the present*

Conditions in southern Africa changed significantly in late glacial times, especially round 13 000 yrs B.P., when the climate became warmer. At Ishiba Ngandu in Zambia such changes could, however, not be revealed by pollen analysis (Livingstone, 1971). Further south more summer rainfall reached the subcontinent. In the Kalahari these warmer and more humid conditions caused a southward migration of tropical vegetation. In the North, Lake Makgadikgadi filled up again. However, the southern region along the Orange River became semi-arid to arid (Butzer *et al.*, 1978) as the summer rains from the Indian Ocean and the cyclonic winter rain no longer reached this region. The Namib Desert, similarly, was a no-man's-land as far as rain was concerned. At Wonderkrater an important climatic change occurred at c. 12 000 B.P. The open vegetation changed to bushveld as the climate became semi-arid and cool-temperate (Scott, 1982).

During the early Holocene the temperature rose further and summer rain penetrated the subcontinent at least as far as the Orange River region (29° S. Lat.). Heine (1982) described wetter climates for the southern Kalahari (9 000–8 000 yrs B.P.) and the western Kalahari (8 705 ±165 yrs B.P.) and points out that this data fits well with slightly more humid conditions even in the southern Namib desert at Mirabib from c. 8 500–8 000 B.P.

Pollen studies at Wonderwerk Cave (Van Zinderen Bakker, in preparation) have shown that an open savanna of subtropical affinity developed in this region between 9 000 and 5 000 B.P. Subhumid conditions also existed in the Gaap Escarpment between 9 700 and 6 500 B.P. (Butzer *et al.*, 1978). In the area where the Harts, Vaal and Orange Rivers join similar conditions have been inferred by Butzer *et al.* (1979). The poorly dated member IV of the Riverton Formation also fits in this wetter episode (Butzer *et al.*, 1973; Helgren, 1978).

This early Holocene period must have been the Climatic Optimum for this region when summer rain penetrated southward at least as far as 29° S. Lat. This rain did not reach Aliwal North on the Orange River further east at 30° 19'S. Lat. as is shown by the pollen studies of Coetzee (1967). Round 9 600 yrs B.P. the climate at this site was arid.

The timing of the Climatic Optimum fits well with oceanographic evidence. In the northern Cape Basin at 25° 30'S. off the coast of Namibia the warmest temperature within the Holocene occurred at 7 000 yrs B.P. (Embley & Morley, 1980).

The climate of the early Holocene at Wonderkrater differed from the conditions described so far as it was warm and semi-arid. The surroundings of the site were occupied by Kalahari thornveld (Scott, 1982). It may well be that the anticyclone was then situated near this site.

The climatic evolution of the middle and late Holocene is not well known for southern Africa. During the middle Holocene an arid period occurred (Wonderwerk 5 000–c.3 000B.P.; Gaap 6 500–4 500 B.P.; Orange-Vaal-Hartz region about the same time as at Gaap). The climate then became subhumid with minor drier intervals in this region. The explanation of these changes requires more knowledge about palaeotemperatures, evaporation and precipitation and former vegetations.

(c) *The Cape coastal region*

This region is dominated by the westerlies especially in its western part. During colder periods this influence will have been aggravated so that the southwestern Cape received more winter rain. The southern Cape coastal region probably had a different history. Many different disciplines have provided information on the palaeoenvironments of this region (Martin, 1968; Klein, 1972, 1974; Dingle & Rogers, 1972; Schalke, 1973; Van Zinderen Bakker, 1976; Deacon, 1979). The cold glacial maxima were characterized by a low sea level, very large emerging coastal plains, a fairly cool and very windy climate and consequently an open vegetation with much grassland in which grazers such as quagga, wildebeest and springbok roamed. The adjoining colder ocean must have been responsible for a fairly dry climate. The archaeological and especially the faunal remains excavated in the many coastal caves provide important evidence for these palaeoenvironmental conditions. When the climate ameliorated from 13 000–12 000 yr B.P. onward, the sea level rose substantially, the temperature attenuated and wind force diminished so that the open grassland was replaced by a closed vegetation which supported a completely different fauna.

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