INTIMATIONS ON QUATERNARY PALAEOECOLOGY OF AFRICA*

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1. THE BIOGEOGRAPHIC PATTERN OF AFRICA

The biogeography of Africa, as compared with that of Europe is little known and it is only in recent years that more detailed studies have been made of certain areas. Taxonomists working on groups of lower plants and animals and even on flowering plants will still find many rich new areas for collecting in Africa, while the results of these taxonomic studies are the basis of any biogeographic investigation. The study of the factors responsible for the present-day pattern of distribution of plants and animals has been initiated in Africa only fairly recently. The present intimations, which are mostly directed towards botanical problems, are therefore general in nature and are often hypothetical. They are only intended to indicate possible historical approaches to the study of biogeography of Africa.

The flora and fauna of Africa, the continent for which some of the most ancient radiometric dates have been assessed, must in consequence be old in origin. The priscotropical flora of the forests, savannas, mountains and deserts of Africa has been isolated from the other continents since mesozoic times and has developed a great wealth of species especially in the Cape flora. Botanical Gondwana affinities are apparent in this southern flora, while boreal influences of a comparatively younger age are found in the mountain floras from the Sahara and Ethiopia in the north right down the length of the continent to the Drakensberg of Lesotho and South Africa. Since the breaking up of Gondwanaland the oceans have completely isolated Africa from the other Southern Continents and, during the Quaternary, the Sahara-Sindic deserts cut off, for long periods, the connections between Africa and the holarctic region. These northern routes must, however, have been temporarily open to migration of man, beast and plants during favourable intervals of the Quaternary.

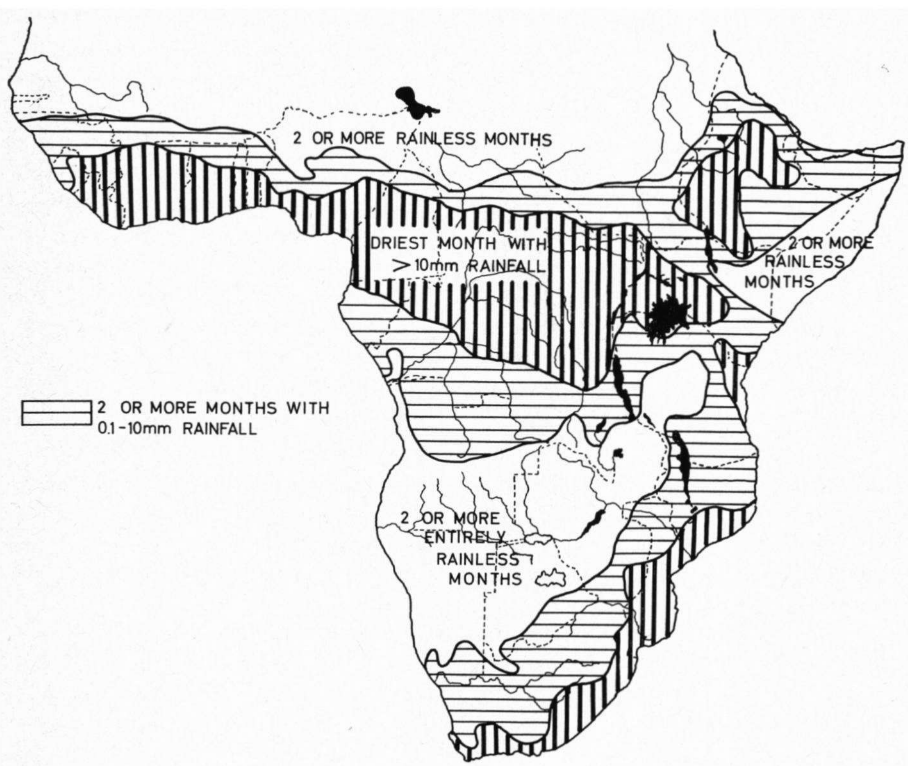
The exchange of taxa between the different areas of Africa is limited by biological, orographic and climatic barriers. Examples of the first category are the extensive tropical Congo forest, the dry south-western area of Africa and the arid north-eastern sector of Kenya and Somaliland. Deep wide valleys such

* In this survey I wish to pay homage to Professor Dr. Th. J. Stomps who stimulated my interest in plant ecology and biogeography during my study and particularly on the international excursions, which he organised with so much enthusiasm for his students. His main interest has always been with genetics and evolution and his love for these subjects and for many other facets of biology has inspired the young botanists who studied at the Hugo de Vries Laboratory at Amsterdam.

as the Limpopo valley, with a dry and hot climate are very effective barriers against the migration of temperate elements in meridional direction but provide, on the other hand, migration routes for species adapted to arid conditions.

The age of orographic features such as river valleys, coast plains and mountain chains is extremely important in the assessment of former migration routes. In this connection it is of great value to note that most of the volcanic mountains in northern and eastern Africa are, in contrast with the much older Jurassic age of the basaltic Drakensberg in southern Africa, of Tertiary and Quaternary age. These comparatively young mountain areas of the North may have served as stepping stones for certain mountain elements under different climatic conditions.

Climatic barriers can be very different in nature, as minimum or maximum temperatures, rainfall, the length of the dry season and several other factors can determine the migration of a species in different directions. Extremely interesting indications of the former existence of an arid corridor, which must have connected the arid south western region with the Kenya-Somali-Arabia arid region across Africa, have come to light through botanical and zoological surveys. From these studies it has been inferred that the taxonomic affinities of



Map 1. The arid corridor of Central Africa.

these widely separated areas cannot satisfactorily be explained by dispersal over long distances.

A large number of species of plants, birds and mammals are common to both these arid regions, but on either side of the corridor subspecies and also closely-related, but specifically distinct, populations have developed. Present day rainfall maps show that the South West and Somali Arid Districts are connected by a corridor which runs in a north-easterly direction through the Zambesi and Luangwa valleys to the area between the Lakes Tanganyika and Malawi and then right across Tanzania *(map 1)*. This possible migration route at present experiences at least two very dry months every year. Warmer and drier conditions could in the past have opened up this passage for shorter periods of time (BALINSKY 1962, DE WINTER 1966, VOLK 1964, and WINTERBOTTOM 1967).

Other important possibilities for migration and extension of areas are offered by the vast plateaux of Southern and Eastern Africa, the very elongated East Coast strip, and the mountain chains. Climatic conditions must, however, have been favourable if these routes were to be used.

2. THE CLIMATIC PATTERN OF AFRICA

As the orographic appearance of Africa has not changed considerably during the Quaternary, climatic variations are of prime importance for our comprehension of the biogeography during that period. The only realistic way to study the complex palaeoclimatic systems of the Quaternary of Africa is the actualistic approach. We have to know the present day ocean currents, wind systems and even upper atmosphere currents, the incidence of rainfall, temperature conditions and all the other climatic parameters before we can understand the changes of the past and their influences on the ecosystems. In recent years more data have been accumulated on African climates and new theories have been formulated to explain the origin of these climates. The world-wide study of the Upper Atmosphere has shown that powerful westerly air currents occur at altitudes between 2 and 20 km. These westerly vortices determine the latitudinal and longitudinal position of the pressure systems (LAMB 1961, 1964) and variations which occur in the Upper Atmosphere conditions are of great importance in determining the Earth's surface climates. This new development in climatology may in future provide an explanation of the pattern of wind systems, and consequently for the strength of the ocean currents and also for the distribution of precipitation on the Earth. Changes in temperature which are known to have occurred in the geological past may have had an overriding influence on this complex correlated system of Upper Atmosphere and surface climates.

It is interesting to note in this connection that FLOHN (1966) has recently suggested that the dryness of the Sahara and the Arabian peninsula is caused by the subsidence of the Tropical Easterly Jet stream over this region. Shifts in this system could in the past have had a profound influence on the ecology of this part of Africa and Asia.

If we consider the present day climatic pattern of Africa it becomes evident that the antarctic ice cap must be responsible for a northward shift of the climatic belts (FLOHN 1967). An arctic glaciation even if simultaneous with an extensive south polar ice sheet will have had the opposite effect. Variations of this nature are related to the momentum of the circumpolar upper winds and to the position of the troughs and ridges in these meandering windstreams. Changes in the heat budget of the Earth will have had a profound influence on the Upper and Lower Atmosphere and variations in temperature of a world-wide nature are apparently closely associated with changes in the palaeoclimates.

It has been customary in African palaeoecology to speak of pluvials and interpluvials and these pluvials were supposed to have been contemporaneous over the entire continent. Recent results indicate that this conception was wrong and that the so-called pluvials were of a regional nature (VAN ZINDEREN BAKKER 1966). The aridity or humidity of a climate depends on the interrelation of temperature, evaporation and precipitation (FLOHN 1967). The changes in the amount of rainfall are primarily dependent on shifts of the climatic belts and such shifts may bring more rain to one region and less to a neighbouring area.

3. EVIDENCE FOR QUATERNARY TEMPERATURE CHANGES IN AFRICA

Changes of humidity during the Quaternary have attracted much attention in Africa and these changes have been related directly to changes in rainfall. This is not permissible as has already been stated. Temperature changes and the consequent variations in the rate of evaporation in the extensive warm, semi-arid regions of Africa must have been of great importance from the ecological point of view. It is essential that more study should be made of the influence of the world-wide fluctuations in temperature on the ecosystems of Africa during the Quaternary. Some interesting botanical and geological evidence has in recent times become available.

3.1. Pollen analysis

The pollen analytical studies in East and Central Africa have shown that a cooler period which was synchronous with the last severe Würm-Wisconsin maximum must have occurred there. This cooler period in Africa was named the "Mount Kenya Hypothermal" at the Wenner-Gren Symposium on "Systematic Investigation of the African Late Tertiary and Quaternary" (VAN ZINDEREN BAKKER 1967b, p. 881; COETZEE 1967).

Most of the East African mountains are excellent sites for pollen analytical studies. While the vast plateaux of Africa are very dry for long periods every year, so that polliniferous material cannot be preserved, the high mountains have a much cooler and more humid climate which allows the accumulation of peat deposits and the persistence of small lakes. These sites are also very favourable for fossil pollen studies because they are situated on mountain slopes where climatic changes will have had very pronounced effects on the surrounding biota.

In the Cherangani Hills a swamp which is surrounded by montane conifer forest provided several cores the oldest of which had an age of over 27.750 ± 600 years. (VAN ZINDEREN BAKKER 1962, 1964; COETZEE 1967). Other important deposits which have also been studied at Bloemfontein have been obtained from two small lakes on Mt. Kenya (COETZEE 1964, 1967). Sacred Lake on the north eastern side of the mountain is situated in the humid montane forest, while Lake Rutundu occurs 700 m higher in the Ericaceous Belt above the tree line. The Sacred Lake core had an age of 33.350 ± 1000 years while the Rutundu sequence was calculated to be 18.000 years old. These three sites all gave identical results and could, for the last 4620 years, be compared with a core collected from a small lake situated in the conifer forest on Kilimanjaro.

The pollen diagrams indicate that during the Mount Kenya Hypothermal Period the montane forest round Sacred Lake was replaced by the higher part of the Ericaceous Belt and on the Cherangani Hills by Afro-Alpine Grassland. At a higher altitude round Lake Rutundu an Afro-Alpine Grassland indicated that dry and very cold conditions occurred. The temperature must have decreased between 5.1 and 8.8 °C compared with present day conditions as the vegetation belts had shifted about 1000–1100 m downwards. It is interesting to note that this cold phase ended simultaneously about 14.000 years ago at all three sites. This time corresponds well with the beginning of the Late Glacial in Europe and Colombia.

A gradual increase in temperature since about 10.500 years ago becomes evident in the three oldest cores at a time coeval with the Preboreal and Boreal of Europe. Besides other interesting synchronous changes it was found that the Post Glacial Climatic Optimum reached its maximum at about 4000 BP which corresponds well with the Subboreal of Europe. The correlations of the different diagrams are supported by 13 radiocarbon age determinations.

Similar results have now come from the Muchoya Swamp in Uganda where MORRISON (1968) investigated cores obtained at an altitude of 2256 m. The present day surrounding vegetation is much disturbed but appears to have been montane forest. The calculated age for this interesting profile, for which only three ^{14}C dates are available, is about 25.000 years. Before 17.000 BP volcanic activity may have influenced the vegetation, but a cold phase, with a vegetation comparable with the Ericaceous Belt of the East African mountains, is described for the period between 17.000 and 11.000 BP after which the climate ameliorated. The mean annual temperature may have been from 5 to 8 °C lower than it is today.

The results obtained by LIVINGSTONE (1967) at Lake Mahoma on Ruwenzori can be interpreted in the same way, but he prefers to explain the oldest section of his diagram not in terms of temperature decrease but as a consequence of a drier climate. It should be noted that the Afro-Alpine Grassland is not well developed on Ruwenzori because of the humid conditions on this mountain, so that indications for a colder and drier climate are not readily available.

These pollen analytical results can be correlated with others obtained in north eastern Angola (VAN ZINDEREN BAKKER & CLARK 1962), at Kalambo at the southern end of Lake Tanganyika (CLARK & VAN ZINDEREN BAKKER 1964) and, to a certain extent with those of Florisbad (VAN ZINDEREN BAKKER 1957) and Groenvlei at the southern end of the continent (MARTIN 1957).

The pollen analytical results from East, Central and Southern Africa strongly suggest that temperature changes occurred in Africa during the Upper Pleistocene and Holocene which were coeval with those in the Northern Hemisphere.

Besides the above mentioned correlations indications have been found of the Brörup Interstadial at Kalambo (zone U) and good evidence is available for the occurrence of an interstadial which was coeval with the Paudorf of Europe. This period has been named the Kalambo Interstadial in Africa and has been found at Kalambo (zone Y, COETZEE 1967), Sacred Lake (zone S), Cherangani Hills (zone S) and probably at Florisbad (VAN ZINDEREN BAKKER 1967a, p.135).

3.2. Periglacial data

Fossil periglacial or cryonival phenomena are not well known in Africa but have in recent years been described from both the northern and southern ends of the continent. Much of this evidence has not been dated with radiometric methods, but it proves beyond doubt that Africa has, like the rest of the world, been subjected to temperature fluctuations. Although solifluction, patterned soil, polygons and other indications of cold climates are described from several high mountains in tropical Africa fossil phenomena of this type have not as yet been studied from the central part of the continent.

COUVREUR (1965) has studied cryonival erosion in the Central High Atlas of Morocco and found that indications of former frost occur even at altitudes of about 1000 m.

COQUE (1969) described definite proof of gelifraction of the calcareous cliffs in the high steppe of Djebel Chambi and Bireno at an altitude of only 900–1000 m. Also near the North African coast HEY (1963) found in Cyrenaica that frost wedging occurred from 50.000 to 43.000 and from 32.000 to 12.000 BP which means that the winter temperature must have decreased by about 14 °C. Similar lowering in temperature has been described for the Iberian Peninsula, Southern France, Hungary and Southern England for the last severe Würm maximum according to FRENZEL (1967, p. 206).

In Southern Africa HARPER (1969) made an extensive study of periglaciation in the mountains of the Eastern Districts of Rhodesia and of Lesotho and Natal. He was able to distinguish two zones of intense periglacial action which must have been of Late Pleistocene age. The oldest of these periods, which occurred both in Rhodesia and in the Drakensberg, was the colder with a mean temperature some 9 °C lower than at present. During the younger period the frost wedging did not extend as low down as during the earlier period and the decrease in temperature is calculated to have been 5.5. °C. This evidence is in full agreement with similar research done by ALEXANDRE (1962) and SPARROW (1967). Additional important evidence of cryonival activity at even lower altitudes has recently been found by LINTON (1969) in South Africa.

In East Africa the bodies of glacial drift have been studied on the Ruwenzori, Kilimanjaro, Mt. Elgon and Mt. Kenya. These studies suggest that the lowering of the mean temperature was of the same order on all these mountains (BAKER 1967). On Mt. Kenya the climatic snow-line was depressed by 760–900 m during the severe Mount Kenya Hypothermal Period. It is interesting to note that the treeline had, according to pollen analytical evidence, shifted 1000–1100 m downward, as has been discussed previously (COETZEE 1967).

3.3. Sahara lacustrine deposits

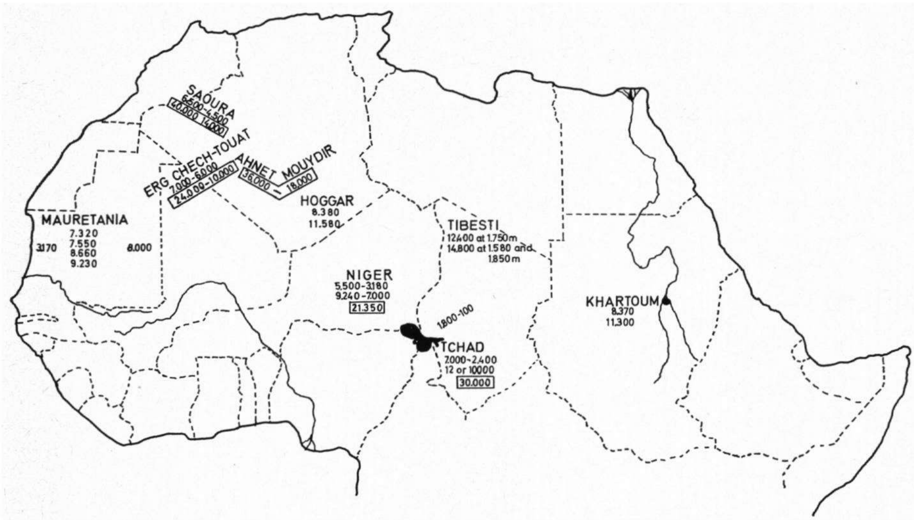
Important data on the intricate problems of the Quaternary palaeoclimates of the Sahara have been obtained through the study of biogeography, pollen analysis, geomorphology, stratigraphy and archaeology. Many radiometric dates have recently become available so that the various results can be correlated more closely. We will pay attention here only to the peculiar lacustrine phases which have in Quaternary times occurred in the driest desert of the Earth.

The latest results of research, mainly by French workers, in this field indicate that the Sahara lakes can receive their water supply in three different ways (FAURE 1967a), *viz.:*

a. directly from rainfall as the "Trou au Natron" in the Tibesti Mountains at about 1600 m altitude,
b. from rivers such as the Chari, Niger or Nile, and
c. from underground water which is fed by rainfall on a wide catchment area.

In using the changes in water level of these Saharan Lakes as indicators of former climate it should, according to Faure, be realised that correlation usually cannot be made directly with precipitation. Lakes of type b mostly do not reflect the local climatological conditions of the immediate surroundings of the lake but give more information on the distant area from where the river receives its water supply. The lakes which are nourished by subterranean water may receive a greater supply when the water mass of the lake, and consequently the pressure of the water body diminishes. This may result in this type of lake being out of phase with the climate of the surroundings.

The radiocarbon dates for the lacustrine phases of the Sahara can be arranged in two groups. (ALIMEN 1965, 1966; FAURE 1966, 1967a, b; CONRAD 1963, 1967, 1969a, b; SERVANT & FAURE 1969). The oldest group is of Upper Pleistocene age and is found in Saoura, Touat, erg Chech, the Ahnet-Mouydir basin, Niger and the Tchad Republic. This period coincides with the severely cold last Würm maximum *(map 2)*. Although it is not yet possible to give a definite explanation for every single site, the data strongly suggest that this lacustrine phase was caused by higher cyclonic rainfall as a consequence of southward displacement of the polar front during the Würm maximum. As has been discussed previously southern Europe and the Mediterranean coastlands experienced very low temperatures during this period. It is highly probable that the same cold climate reigned in the Sahara although it may have been attenuated because of the lower latitudinal position. This low temperature will have prevented rapid evaporation of the free water and will have preserved the water bodies. The cold subterranean water described by CONRAD *c.s.* (1966) from aquifers in the Hamada du



Map 2. Map giving an approximation of the ^{14}C ages (BP) of the known lacustrine periods of the Sahara. (M.H. ALIMEN 1966; G. CONRAD 1967; H. FAURE 1967a; H. FAURE & M. SERVANT 1969).

Guir and the old artesian water (25–35.000 BP) from the western Egyptian Sahara studied by KNETSCH *c.s.* (1962) probably originated during this cool lacustrine period. It is interesting that DE HEINZELIN (1967) in his study on the geomorphology and stratigraphy of the Nile sediments in Nubia came to the conclusion that during the later part of the Upper Pleistocene the water of the river was definitely colder than at present as was proved by the presence of "cold" molluscs.

During the end of the Late Glacial and Holocene a second lacustrine period occurred widespread in the Sahara. Radiocarbon dates are available from the same areas as for the older phase, and also from Mauretania, Tamanrasset and Khartoum *(map 2)*. These dates suggest that this younger lacustrine period coincided with the time of climatic amelioration which covers the European Alleröd-Subboreal or the Preboreal-Subboreal. It has been accepted by several authors that tropical rain penetrated the Sahara during this so-called Subpluvial. The ages of these lacustrine phases do not only have changes in climate to be considered but also the geomorphology, hydrology and geography of the different basins (FAURE 1967a).

In reviewing the data it is clear that much evidence for Quaternary palaeoclimates is available in Africa. The majority of these data point to changes in humidity, but good proof for variations in temperature has also come forward. These indications, especially for former cooler conditions, are of great importance both from an ecological point of view and also for the purpose of correlation with events in other parts of the world. It is understandable that as these changes in temperature are not easily detected in the fossil record of a tropical continent they have only been discovered recently. These variations should receive more attention as they may point to the real causes of the climatic changes which certainly had a profound influence on the Quaternary palaeoecology of Africa.

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