PLEISTOCENE CLIMATIC CHANGES AND THE DISTRIBUTION OF LIFE IN EAST AFRICA

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(With one Map in the Text.)

(MS. originally received June, 1932. *Revised copy received Jan.,* 1933.)

INTRODUCTION.

No study of the distribution and ecology of living things can be made without the question arising how the present state of affairs became established. I have been brought to consider this problem in East Africa as an ornithologist with no qualification to deal with forms of life other than birds. But it will be obvious that any argument developed must be much concerned with botanical facts, and that any conclusions reached must be applicable to the distribution of animals in general and of plants as well[1]. It is for this reason that the title of the present paper is in wide terms, although the examples I shall use are mainly avian[2]. The fact that they are drawn from the most potentially mobile class of living things does not lessen their cogency. Every naturalist with field experience would agree that owing to their specialised ecology birds such as those that will be cited provide data no less acceptable for the present discussion than would a skink or a potto. Thus Chapman (1926) out of his immense experience of Andean bird distribution remarks: "There may be cases of discontinuous distribution...which are due to accidental dispersion, but, in my opinion, they are too rare to have any bearing on the general problem."

The distribution of species in East Africa raises several general problems for which no explanation can be derived from a study of the present-day conditions.

(i) Chief among them is the similarity of the fauna and flora of the mountains, a similarity that extends to all the peaks of Tropical Africa, the characteristic montane forms being wholly absent from the hundreds of miles of intervening country (cf. Bannerman (1930), pp. xl–xlii). Most of the birds

[1] I wish at the outset to express my indebtedness to Mr P. J. Greenway, Botanist at the East African Agricultural Research Station, for help in his special subject; to Mr T. W. Kirkpatrick, also of the Research Station, for valuable criticism; and to Mr C. Gillman, Chief Engineer of the Tanganyika Railways, for guidance in geological matters.

[2] For distribution in Africa generally from **Sclater** (1930), whose work provides a conspectus of the African Aves particularly apt for this purpose and not, so far as I am aware, paralleled in the literature of other classes of animals. Some of the East African data are drawn from personal observations, publication of which has been begun (**Sclater** and **Moreau**, *Ibis*, 1932, pp. 487–522, being the first of five parts).

concerned are closely associated with the montane forests, which are tall, closed, mainly evergreen communities. Indeed, as will be described later, the present physical condition of East Africa is such that, unlike West Africa, there is practically no forest of this type anywhere except on the mountains, and therefore a "forest species" nearly always connotes a montane habitat. Of this class *Heterotrogon vittatum* (Shelley), *Turdus olivaceus* Shelley, *Chlorophoneus nigrifrons* Rchw., *Onychognathus walleri* (Shelley), *Cryptospiza salvadorii* Rchw. may be quoted among many others, as being represented in one form or another, in practically every forest on the accompanying map[1] (Fig. 1). Typical examples of widespread but discontinuous distribution are afforded by *Seicercus ruficapilla* (Sundev.) from Nyasaland and the Usambaras, and *Cercococcyx montanus* Chapin, known only from Ruwenzori, Usambara and Uluguru. Some of the forest species in question live in the canopy, e.g. *Heterotrogon*, some in the intermediate strata of vegetation, e.g. *Trococercus albonotatus* Sharpe, and others, e.g. *Sheppardia cyornithopsis* Sharpe, hardly leave the thickly shadowed ground. All are bound by the closest ecological ties to the montane forests by a complex of factors which doubtless vary from species to species. The subject is a particularly difficult one that awaits critical investigation. A preliminary attempt to deal with it is being made by the writer in the Usambara Mountains, and the experience gained only deepens the impressions received from a study of the recorded distribution of the forms concerned that they disappear entirely *pari passu* with forest, and that their movement from one locality to another is only possible when a connection of forest exists. At the same time, a belt of forest may act as a barrier to the dispersal of non-forest birds. Generally speaking, a forest form seems quite incapable of adapting itself to life in any other association, even though, in an epoch like the present, when forests are progressively diminishing in area, the "economic pressure" on the birds within its limits must be strong. The converse is equally true. This is well illustrated in West Africa by Bates' recent study of differentiation (1931): the number of species represented both within and without the forest, even in different forms, is negligible compared with the long list of those entirely confined to the forest and often racially differentiated within its limits.

A few of the mountain birds are, however, associated not with the forests but with the open country above the timber line. Such are *Nectarinia johnstoni* Shelley and *Pinarochroa sordida* (Rüpp.), the first from Nyasaland to Mount Kenya, but nowhere below 8000 ft., and the second from Abyssinia to Kilimanjaro where the peaks exceed 10,000 ft.

(ii) Marked affinities with West Africa are found, among vertebrates generally, within sight of the Indian Ocean (cf. *Carnegie Institution Year Book*, No. 29, 1929–30, p. 359), and they appear to be at least as strong in the Usambaras and Ulugurus as anywhere east of Victoria Nyanza. Among birds,

[1] I am indebted to Mr F. J. Nutman for redrawing the map.

the genera *Neocossyphus* and *Hyliota*, the species *Lampribis olivacea* Dubus., *Anthreptes tephrolaema* (Jard. and Fras.), *Illadopsis rufipennis* (Sharpe), *Bubo poensis* Fraser and *Gypohierax angolensis* (Gmel.), may be quoted. Mammalian examples are afforded by *Crocidura maurisca geata* Allen and Lov. and *Otomys Kempi* Dollman (Allen and Loveridge, 1927). Among forest trees *Tylostemon Kweo* Mildb., *Englerodendron usambarense* Harms, *Schefflerodendron usambarense* Harms, *Anisophyllea laurina* R.Br., *Crotonogynopsis usambarica* Pax, are all forms of West African affinity making their appearance on the east side of the continent only in Usambara and Uluguru.

(iii) Connected with the wide but discontinuous ranges of the montane birds is the fact that most of the species have become differentiated into a number of races. It will suffice to quote as examples *Linurgus kilimensis* (Rchw. and Neum.), represented by the typical form on Kilimanjaro and by *L. k. elgonensis* v. Som., *L. k. keniensis* v. Som., and *L. k. rungwensis* Bangs and Lov., on the mountains that have given their names to the respective subspecies, and *Apalis r. ruficeps* Rchw. from the Usambaras with *A. r. altus* Friedm. from the Ulugurus. There can be little doubt that such races, especially those in close geographical proximity, were differentiated in isolation, and it becomes of interest to determine for what period of time the isolation has been effective.

(iv) Within the closed forest itself, which imposes approximate homogeneity in certain of the most important environmental factors, the bird fauna shows a definite zonation by altitude. This can nowhere be studied so well as in the Usambara Mountains, for there alone in the whole of East Africa is a practically unbroken series of forest available for observation down to within 500 ft. of sea-level. Careful examination has made it clear that a whole fauna, including representatives of such species as *Trococercus albonotatus* Sharpe, *Geokichla gurneyi* (Hartl.), *Turdus olivaceus* Linn., *Chlorophoneus nigrifrons* Rchw., *Turturoena delegorguei* (Del.), *Mesopicos griseocephalus* (Bodd.), *Alethe fülliborni* Rchw., *Alseonax minimus* (Heugl.), occupies the forest at 3000 ft. and is unknown at 2000 ft.[1] This may be called the subtropical fauna. A few species, e.g. *Apalis thoracica* (Shaw and Nodd.) seem to have their lower limit at about 4000 ft. and several, comprising a "temperate" fauna, e.g. *Laniarius fülliborni* (Rchw.), *Alethe anomala* Shelley, *Cinnyris mediocris* Shelley, *Arizelocichla nigriceps* (Shelley), *Pseudoalcippe abyssinicus* (Rüpp.), *Pholia* spp., all birds of the same fundamentally homogeneous closed forest, do not descend appreciably below 5000 ft. I believe that no comparative study of bird-zonation on African mountains has been published, but such information as is available about the limits of these species on the various mountain masses where they are represented, warrants the belief that their altitudinal relations to each other are constant. How these altitude limits exert their influence

[1] It may be noted that owing to the peculiar local conditions 3000 ft. in the East Usambaras corresponds climatically to 5000 ft. in some more inland situations.

on the organism is uncertain. It is, however, significant that some of the subtropical species flourish at sea-level in South Africa. In any case, it is clear that within the belt of mountain forests we have to deal with certainly two distinct faunae. The upper, "temperate," fauna is as widely, and even more discontinuously, distributed at the present day than the "subtropical." While the various faunal islands of "subtropical" forest are isolated from each other by non-forested areas, the "temperate" faunal islands are separated by the further barrier of the subtropical zone on every mountain where the "temperate" fauna occurs.

It is important to observe that the fauna of each zone is almost exclusively composed of *species* different from those of the contiguous zone, not merely of different races. In other words, there is no close phylogenetic relation between the faunae. It is therefore improbable that one was derived from another, even if parallel evolution on each of the isolated mountain masses were conceivable. The possibility suggests itself that the subtropical and temperate faunae were "laid down," to use a geological simile, at different epochs.

Until very recently no serious attempt was made to attack these four problems. Indeed I do not think the existence of the last one has been fully realised. Reichenow (1900) suggested that the mountains might once have formed an archipelago in the sea, all the intervening lowland being covered, and that their inhabitants had never succeeded in expanding beyond the narrow limits within which they were then confined. This hypothesis was, of course, unsupported by any geological evidence, all the facts indicating that continental Africa is a land-mass that has not been submerged since very remote geological times. Most students have preferred to postulate "climatic changes," which for years were advanced, so far as zoologists are concerned, as merely unsupported speculation. I am indebted to Mr Gillman for references which show that the German geologists (e.g. Meyer, Dantz, Uhlig, Kuntz, Jaeger) gave repeated testimony to the former existence of a pluvial. As early as 1900 Meyer published evidence of former more extensive glaciation on Kilimanjaro. The Ruwenzori evidence was even more striking: "Die ersten unzweifelhaften Beweise für die alte Vergletscherung...fand ich bei dem Abhänge von Bihunga, d. h. in einer Höhe von ungefähr 1500 Meter[1], während gegenwärtig die Gletschen nicht tiefer als bis 4200 Meter herabreichen" (Savoyen, 1909, p. 448). For some reason the zoologists seem to have been less familiar with the results obtained by these German workers than the botanists were. Writing in 1923 Chapin could only observe: "probably there were changes of topography and climate in the past which permitted extension of the mountain floral zones." So recently as 1928 Stresemann and Grote, seeking to adduce evidence of a former extension of closed forest in Equatorial

[1] **Nilsson** (1929, p. 256) on subsequent examination put the lower limit of past glaciation at 2000 instead of 1500 metres.

Africa, rely on the evidence of (then) indefinitely established pluvials in Egypt and South-west Africa, and quote Lönnberg's conclusion that it was "wohl wahrscheinlich dass auch das dazwischenliegende Land etwas ähnliches durchgemacht haben dürfte."

At last in 1929 came Lönnberg's important contribution to the problem, in which he was able to rely on Nilsson's conclusions (1929) from local geological evidence, that East Africa had witnessed not merely a single pluvial, but a succession of pluvials[1]. The last two years have seen the publication of several papers (Wayland, 1930 and 1931; Leakey, 1930 and 1931[2]) that confirm and amplify Nilsson's conclusions to a point where it appears to me that we can now estimate, with some approach to definition, the possible effect of the climatic alternations on animal distribution and the relative remoteness in time of the important changes. The conclusions reached in this discussion must be highly tentative. I cannot emphasise this too strongly, for it is not to be supposed that the last word has by any means been said on the geological premises themselves. But I feel that this paper will be justified if it helps to bring into focus the prehistoric background, hitherto absent or only adumbrated, against which any question of distribution must be viewed.

It is obvious that the key to the whole problem lies in the expansion and contraction of closed forest of one type or another. Whether the forest is completely evergreen or to some extent semi-deciduous does not seem to be important so long as it is a tall closed association that does not lose a considerable proportion of its leaves at any particular season[3]. It is proposed, then, to describe briefly the present conditions in East Africa; to give an indication of the limits of rainfall and temperature for the existing forest types; and so to obtain some idea of the climatic conditions that would be needed to bring the isolated forests of the present day into connection. The geological evidence for climatic fluctuations will then be summarised, and an attempt made to interpret the maxima and minima in terms of forest extension.

PRESENT CONDITIONS.

But little of the interior of East Africa lies appreciably below the altitude of 4000 ft. and except for the Nile basin its present aspect is primarily that of an arid savannah tending in the north-east towards desert. It is, however, narrowly edged on the coast with a more humid zone, and at comparatively

[1] I wish to express my thanks to Dr Lönnberg for his kindness in supplying me with separates of his own and Nilsson's papers.

[2] I have not had an opportunity of perusing Dr Leakey's paper given before the British Association in 1930; but I have to thank Dr C. E. P. Brooks for an extract from it, and also for aid in interpreting the results recorded.

[3] Many of the most characteristic forest species, such as *Chlorophoneus nigrifrons* Rchw., *Cryptospiza salvadori* Rchw., *Alethe poliocephala kikuyuensis* Jacks., are recorded from Nairobi, where the forests are, according to Troup, semi-deciduous.

wide intervals it bears upon its surface patches of closed forest, of many different types, but almost without exception confined to the highest ground.

The accompanying map is compiled, so far as the Kenya and Uganda Forests are concerned, from Troup's two reports (1922), and for Tanganyika from Meyer (1909) and local knowledge. The rainfall data are derived from Knox (1911)[1], Kendrew (1927), Sayers (1930), and Plate XXII of the *Meteorological Maps of the Atlas of Egypt* (1928), which supplement each other and differ in details. The small scale unfortunately makes it impossible to show more than two contours, the 3000 ft. and 6000 ft., and two isohyets, for 30 in. and 40 in. rainfalls.

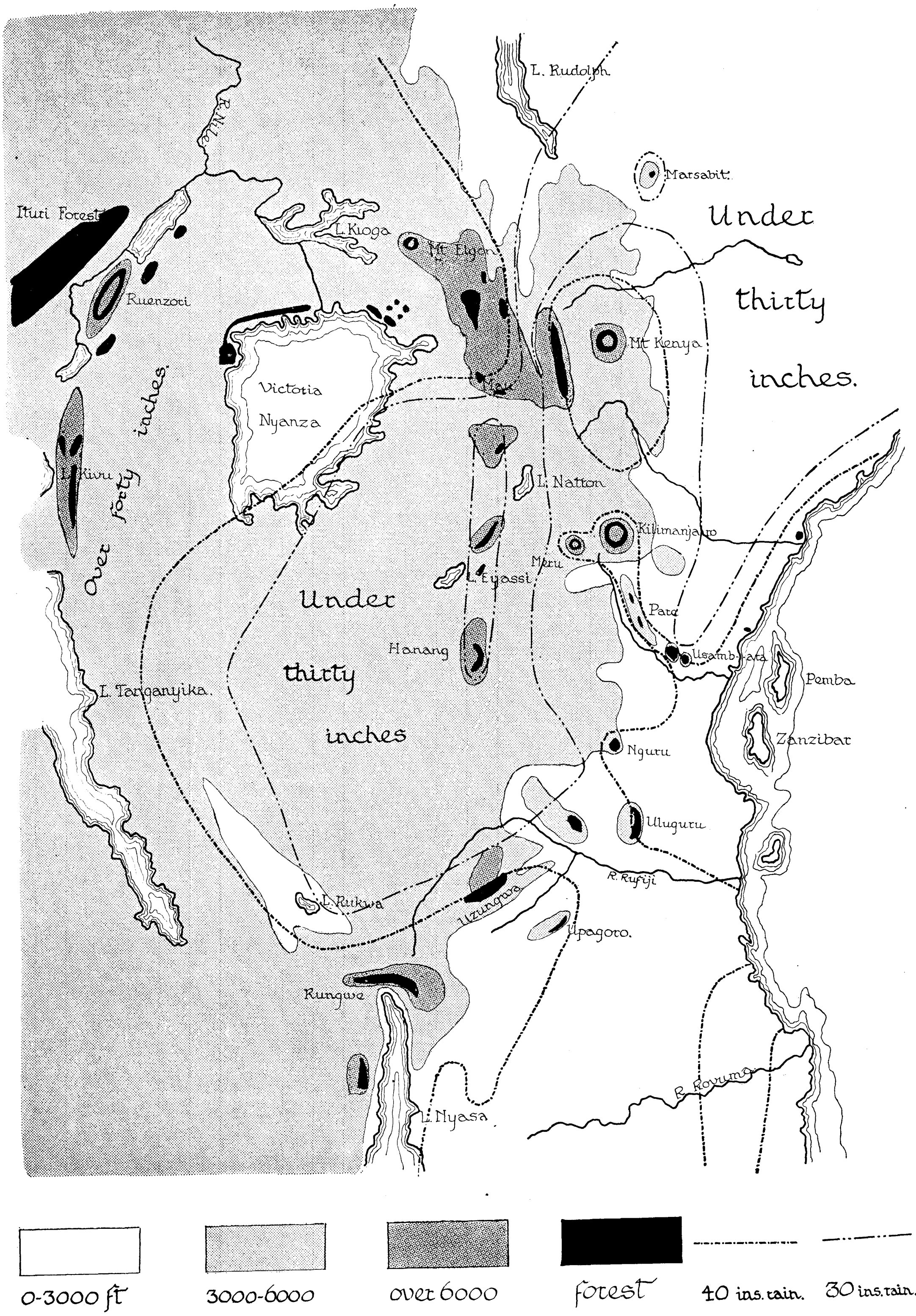
It will be seen that over practically the whole of Central Tanganyika Territory and the greater part of Kenya Colony the rainfall is under 30 in. a year. The Kenya Highlands themselves are cleft by a wedge of arid country, for the rainfall in the Rift Valley as a whole does not exceed that figure. In the catchment of Lake Nakuru, which will be frequently referred to later in this paper, it reaches 37·5 in., as calculated from the averages over a number of years given in the *Summary of Rainfall in Kenya Colony*, 1930 (B.E.A. Meteorological Service), for five local stations. The ill-effects of this generally scanty rainfall in the interior are aggravated by its bad distribution. Practically the whole of it falls in two short seasons of the year, which tend, as one travels south from the Equator, to merge into one. The effect on the vegetation is to make it impossible for any to exist that is not deciduous or xerophytic: and the overwhelmingly greater part of the East African interior is therefore occupied by grass-, thorn-, or bush-steppe, and more or less open Miombo (*Berlinia-Brachystegia*) woodland. During the dry season fires rage over this type of country, and what with the leafless condition of the trees and the scantiness of the ground cover, diurnal animals can only exist if they are at home in the full glare of the tropical sun.

Within the Nile basin the precipitation is nowhere less than 40 in., generally well-distributed under the influence of the extensive lakes and swamps: and much of the Uganda Protectorate receives nearly 60 in.

The coastal belt is also somewhat more favoured than the interior, with a rainfall exceeding 40 in. and rising opposite Pemba Island to 60 in. On the whole, moreover, it is in this belt better distributed than inland, and the prevailing winds are less desiccating than those of the interior. These conditions support along the coast a more or less deciduous bush with patches, totalling perhaps 20 square miles in Kenya Colony, of closed though not tall forest[2]. Where the eastern edge of the interior plateau faces the Indian Ocean,

[1] His Pl. I inevitably suffers from its scale. The 70–80 in. rainfall islands of the Usambaras, Ngurus and Ulugurus cannot be shown.

[2] **Troup** (1922, p. 5) gives the Arabuko "Forest Area" as 132 square miles, but much of this is *Brachystegia* woodland (Mr R. M. Graham *in litt.*) and **Hutchins** (1909) in his map appends a note to what he calls the "Arabuko and Sekoki Forest": "Estimated actual Forest 12 square miles."



MAP 1 East Africa: Mountains, Forests, Rainfall and Altitude.

and rises into mountains, such as the Usambaras and the Ulugurus, a rainfall of about 80 in. is precipitated[1], which appears to exceed anything definitely recorded elsewhere in East Africa except at the head of Lake Nyasa. The result is a magnificent forest formation at a comparatively low altitude. Apart from this, however, there is very little closed forest anywhere in East Africa below 3000 ft. and indeed by far the greater part is over 5000 ft. A large proportion of all the forest is confined to the lines of scarps looking towards the Indian Ocean. Their westward-dipping hinterlands lie in a rain-shadow where it is impossible for luxuriant vegetation to maintain itself under existing climatic conditions.

There is no doubt that the discontinuity of the forests so conspicuous on the map has been much exaggerated in recent historical times by human agency[2]. The agricultural development of the Uganda Protectorate has been at the expense of forest[3]. The Wa-kikuyu have wrought great destruction between Mount Kenya and the Aberdares. Europeans have swept away much forest west of Nairobi. The Wa-chagga have cleared the lower slopes of Kilimanjaro. The Pare Mountains have been almost completely deforested. The Wa-Bondei have cleared the eastern foothills of the Usambaras. The annual burnings by the Masai have continually eaten into the forest on the peaks along the southern end of the Rift Valley. The people on the coast have replaced the natural vegetation with cultivation.

All such operations as these have been so recent as to have no place at all on the evolutionary scale of time: we can be sure that at no earlier epoch was human agency so important. For the purposes of this enquiry the natural forest limits under present climatic conditions are correctly indicated only if we regard the map as modified to show:

(*a*) An appreciable amount of forest along the coast-line.

(*b*) A connection from Kilimanjaro to this strip, via the Pares and Usambaras, with no interruptions of greater width than 20 miles.

(*c*) A block covering most of the area Nairobi-Mt. Kenya-Aberdares.

(*d*) A more united forest west of the Rift Valley.

(*e*) Much more extensive forest between Ruwenzori and Victoria Nyanza.

The geological evidence.

Nilsson's conclusions were arrived at from a study of past glaciations on Mounts Kenya, Kilimanjaro and Elgon, and on the raised beaches of the Rift Valley lakes, Nakuru, Elmentaita and Naivasha. He found (*op. cit.* p. 255) that on Mount Kenya there were terminal moraines at about 4500 ft. ("huge"),

[1] The average at Amani, on the seaward side of the East Usambaras, is 77 in.

[2] Some idea of the forest destruction in Kenya in recent times may be obtained by comparing Troup's map (1922) with Hutchins' (1909) and Johnston's (1902, Pl. VII).

[3] Cf. **Johnston**, *op. cit.* p. 66: "Except in the northern parts of Busoga the country is still thickly forested, and it was at one time one vast tropical forest like portions of Uganda [the original Kingdom, not the Protectorate], Toro and Unyoro."

3700 ft. ("two rather large and several smaller") and 3500 ft. ("small") below the existing glaciers. Between the arrangement of these glacial maxima and that of the maxima of Lake Nakuru a striking correspondence will be found.

Wayland's work is based on a variety of Uganda data[1]. He has come to the conclusion that East Africa witnessed two major pluvials, probably corresponding with the Günz-Mindel and the Riss-Würm Glacials of Europe, and a third wet phase, not of a magnitude justifying the appellation "pluvial," which may have corresponded to the Bühl Stadium. It will be observed that the agreement between these conclusions and those derivable from Nilsson's data is close. Wayland is satisfied that climatic changes, not land oscillation, were responsible for the phenomena from which the occurrence of the two pluvials has been inferred (1930, p. 472), and that the climatic changes were not merely local. It appears, indeed, that these two pluvials in East Africa were only the local manifestations of far more extensive climatic changes. After referring to the evidence that is to be found on every continent Coleman (1932) concludes that "There can be no doubt that at least two refrigerations in the Pleistocene affected the whole world contemporaneously."

Leakey has re-examined the Rift Valley lake-basins, Nakuru and Naivasha. He has been led to conclusions more detailed in some respects than those of the other workers, and they will be considered at length. Although Leakey's findings may not command universal acceptance in detail it is satisfactory to find that the sequence of the major events summarised below is in close agreement with that of the other authorities. The lake-levels all relate to Nakuru. The Naivasha evidence is not dealt with here as the hydrography of that basin is known to have been complicated by river capture. The dates, derived except for (vii) from Brooks (1922, p. 48, and *in litt.*)[2] are, of course, only to be taken as very general indications of relative remoteness. They are based on the contemporaneity, only assumed but of strong inherent probability and generally accepted, between the East African wet and the European cold maxima. Phrases in inverted commas are Leakey's.

(i) A long and severe wet period (Kamasian) coming to a close nearly 400,000 years ago.

(ii) A dry period accompanied by tectonic action[3].

(iii) A pluvial (Gamblian) during which the lake rose to 775 ft., declined to 250 and rose again to 510, finally coming to an end somewhere about 20,000 B.C.

(iv) A period during which the lake dried up completely. "The evidence

[1] I have to thank him for separates and for a number of references.

[2] Since elaborated in Appendix B to **Leakey's** *Stone Age Cultures of Kenya Colony* (1931).

[3] Regarding this stage we know practically nothing, not even whether it was cold and dry or hot and dry: but as it will appear from subsequent discussion that its effects must have been largely overlaid by the subsequent pluvial, its importance for our present purpose is minimised.

for complete desiccation...is very strong...deposits of aeolian sand were formed."

(v) A wet phase (Makalian) marked by a rise to 375 ft. probably between 10,000 and 20,000 B.C.

(vi) A second complete disappearance of the lake. "We have further aeolian deposits at this period."

(vii) A minor wet phase (Nakuran) marked by a rise to 145 ft., the date of the climax being "estimated at 850 B.C."

(viii) At the present time Lake Nakuru is diminishing rapidly. In 1929 it nowhere exceeded 9 ft. 2 in. in depth, being 5 ft. 6 in. lower than when it was surveyed in 1906. Further, it may be calculated from the plan Leakey gives, that concurrently with this loss of depth the lake has shrunk from an area of about 21 square miles to 15·6 in the 23 years. (The former area is that delineated on the existing 1:250,000 map of the region, viz. G.S. 1764 Africa, Sheet South A-37/A dated March, 1918.) To some extent this reduction in the lake may be due to an accidental succession of dry years: but in view of the evidence for the retreat of the surviving glaciers on the peaks[1] it cannot be doubted that the shrinkage in the lake is due in part to a secular change.

The question arises of the extent to which the use of these lake-levels as criteria of pluvial intensity may be invalidated by tectonic movements. It is a fact that over a large part of the earth's surface the great differential crust movements, which had been set going in the early Tertiary, continued vigorously into the Pleistocene. East Africa in particular was the scene of tectonic activity on an immense scale. Three great shatter-belts manifested themselves, the effects of which are apparent to-day as three lines of eastward-looking scarps: (*a*) Usambara, Nguru, Uzungwa, with the secondary outlier Uluguru-Upogoro (Mahenge); (*b*) Aberdares, Mau, Mbulu, Hanang; (*c*) Ruwenzori, Kivu, Rungwe, West Nyasa. Under existing climatic conditions it is precisely on these scarps that evergreen forest maintains itself. Leakey expresses himself as satisfied that this tectonic activity was not responsible for the elevation of the Nakuru beaches for which he gives measurements, and that it may be considered as having practically come to an end before stage (iii). After stage (ii) the catchment area of Nakuru appears to have been uniform, and he believes that the physiography of the basin was not disturbed to any significant extent. It is to be noted, however, that stage (iii) is the period when Wayland concludes (1931, p. 44) that the hydrography of Uganda received its present shape. *Prima facie* this tends to invalidate the stage (iii) lake-levels as a criterion of the contemporary climate. But their status for this purpose is restored by the remarkable correspondence they exhibit with the second complex of Mount Kenya moraines. On the whole it is considered

[1] Cf. **Savoyen** (1909, p. 449): "Im übrigen befinden sich sämtliche Gletschen des Ruwenzori gegenwärtig in starken Rückgang." And for Gregory's Glacier on Mount Kenya see **Nilsson** (1929, p. 255).

that we may accept Nakuru stages (iii) to (viii) with some confidence as indices of the climate prevailing over East Africa[1].

As regards the glacial evidence, it is, of course, a fact that the terminal moraine is formed at the point where the wastage of ice exceeds the supply. In other words it is determined partly by the temperature of the environment of the glacier and partly by the snowfall on the feeder slopes above. Therefore the altitude of a terminal moraine cannot be taken as a measure of either the precipitation or the temperature, only as an integrator of both. But these two climatic factors are precisely those that in combination determine forest growth. So that, above a minimum temperature, the extent of the glaciation is, very broadly, an indication of the extent of co-existing forest growth.

FORESTS AND CLIMATE.

As a basis for arriving at the climatic requirements of closed forest, which vary with the altitude, the existing forest types and their limits may briefly be described. Most of the information regarding the Kenya and Uganda forests is derived from Troup (1922). I am indebted to Mr R. M. Graham, of the Kenya Forest Department for particulars of the coastal forests.

These are arranged in descending order of rainfall requirements.

(*a*) Magnificent evergreen forest comprising a great variety of species and very rich in endemics and West African affinities. Found only on the Usambaras, Ngurus and Ulugurus[2] with a well-distributed rainfall of at least 70 in. and a climate that is neither tropical nor subject to frosts. These conditions are found in so narrow a belt on the east side only of the mountains, that the total area of this type of forest cannot exceed 300 square miles, in three blocks 80 miles apart.

(*b*) Tall semi-deciduous forest characterised by *Sterculia appendiculata* K. Schum., *Albizzia sassa* Macbride, *Trema guineensis* Ficalho and *Chlorophora excelsa* Benth. and Hk.f. It apparently requires between 50 and 60 in. of rain in an almost fully tropical climate and is at the present day practically restricted to vestiges on the Shimba Hills near Mombasa and on the eastern foothills of the same mountains as type (*a*) forest, into which association it merges at an altitude between 2000 ft. and 3000 ft.

(*c*) "Temperate Rainforest" of Troup, a tall evergreen community in which the dominants are *Ocotea usambarensis* Engl. ("Camphor") or *Podocarpus* spp. or both. "The minimum rainfall...is probably about 55 in. to 60 in." (Troup), and the climate temperate. Much of the Mount Kenya, Aberdares, Kilimanjaro and Usambara series forest is of this type. It still

[1] Mr A. Walter, Director of the British East Africa Meteorological Service, has pointed out to me that as the area has been one of volcanic activity the possibility of an accession of water from plutonic sources into the lake at some date or other cannot be entirely excluded.

[2] These three mountains will constantly be bracketed together in the following pages and for convenience I shall refer to them as the "Usambara series."

clings to Mounts Ufiume and Hanang, south-west of Kilimanjaro (Phillips, 1929, p. 363), and it furnishes the bulk of the evergreen forests of the highlands in the south-west corner of Tanganyika Territory. The lower limit in Kenya is now 7000 ft., but it descends to 5000 ft. elsewhere.

(*d*) Semi-deciduous coastal forests (*Brachylaena Hutchinsii* Hutch., *Afzelia quanzensis* Welw. and many other species) occur in patches close to sea-level with a fairly well-distributed rainfall of about 50 in. The Sokoke-Arabuko is the only considerable area.

(*e*) The Uganda evergreen forests are various, but it appears that some of the most generally important trees are *Entandrophragma* sp., *Maesopsis eminii* Engl., *Podocarpus* spp., *Chrysophyllum* spp. Troup gives no indication of the rainfall, but from the isohyets given in the Meteorological maps of the Atlas of Egypt it appears that these forests subsist on about 50 in. at a general altitude not appreciably above 4000 ft.

(*f*) "Plateau Forests" of Troup (partly deciduous) found chiefly in the neighbourhood of Nairobi between 5000 and 6500 ft. Some typical trees are *Brachylaena Hutchinsii* Hutch., *Croton megalocarpus* Hutch., *Olea chrysophylla* Lam. Rainfall 40 in., climate equable and similar in temperature to that of type (*a*).

(*g*) "Cedar Forest" (*Juniperus procera* Hochst.) occupies a good deal of the Kenya Highlands. According to Troup its "true home is at an elevation of 7000–9000 ft. (i.e. well above the frost line) with a rainfall of 40–55 in. In the West Usambaras it is fully developed at 6000 ft., where it exists with a rainfall of under 40 in., not well distributed but supplemented by much mist.

It will be noticed that between the upper limit of type (*b*), Tall Semi-Deciduous Forest, at about 2500 ft., and the lower limit of types (*c*) and (*f*), the Temperate and Plateau Forests, which under natural conditions seems to be about 4500 ft., there is no forest in existence except that of type (*a*), which gets 70 in. of rain. There is no doubt that this is what may be described as an accidental result of the local physiography, for at the present time there is no part of the eastern half of our region between 2500 ft. and 4500 ft. that receives more than about 35 in. of rain except where the Usambara series of scarps face the ocean and precipitate no less than 70 in. But Mr Greenway informs me that if 50 in. fell anywhere between 2500 ft. and 4500 ft. the result would probably be a forest much resembling type (*b*).

From the foregoing it appears that under existing temperature conditions we can expect closed forest to cover any country above 5000 ft. that receives 40 in. of rain, and below that level 50 in.[1], provided that it is well distributed

[1] For the present purpose soil factors are ignored, especially as the majority of the East African soils are evidently capable of supporting closed forest. One apparent exception is "Black Cotton Soil" (**Nicholson**, *op. cit.* p. 21). There the inability to support forest is probably to be regarded as the result of faulty drainage, for this type of soil is developed in situations that are waterlogged during part of the year.

and probably augmented to some extent by occult precipitation. As regards the estimation of the last element, Nicholson (*op. cit.* p. 16) quotes Phillips to the effect that it may amount to as much as 25 per cent. of the precipitation measured in the rain-gauge.

The importance of a proper distribution can hardly be overestimated. Chapin (1923, p. 111) remarks that in parts of the Upper Congo (which are below 3000 ft.) with a rainfall of 65 in. "a superb unbroken forest persists because there is seldom a month without rains," whereas in parts of Sierra Leone "where there is a dry season of four months, a total annual rainfall of 170 in. does not suffice for a continuous forest growth." As regards the degree of distribution necessary, it appears from Chipp (1927) that in the Gold Coast forest of a good type maintains itself within a thousand feet of sea-level with a rainfall of no more than 50 in. falling on 75 days, divided between every month in the year, and associated with a steady high relative humidity (over 80).

Now the total rainfall in a region of mountains or within the influence of a large body of water—and such is the greater part of East Africa—consists primarily of two elements, monsoon rainfall ("the Rains") and "instability rains." The latter reduce the desiccating effects of the periods between the Rains proper and are the element in the total rainfall that gives the effect of better distribution. Nicholson (*op. cit.*) has demonstrated the important effects of montane forest in inducing instability rainfall. We may take it then that when isolated forests begin to spread, under a favourable general change of climate, from the mountain-tops to which they have been reduced in a dry period, the distribution of the rainfall undergoes local improvement and the process of reafforestation tends to be accelerated by the beneficial influence they themselves have upon the local climate. In fact, even if a favourable change of climate does not of its own nature involve a better distribution of rainfall, its secondary effects do so. Further, as the areas of forest and the rainfall increase, there is a tendency for the temperature to fall, thus reducing evaporation. Therefore once a forest sheet had been established it should be able to maintain itself after the full extent of the beneficial secular change of climate originally responsible for the forest extension had begun to wane. Moreover, any general drop in temperature would have the effect of bringing to a lower level the montane forest associations, which have smaller rainfall requirements than the lowland types.

As may be seen from the map, much of the country in the interior of East Africa receives under 30 in. of rain; but none of it is appreciably below 4000 ft. in altitude. Therefore, a general increase of between 15 and 20 in. in the rainfall should suffice to cover it in time with forest. Much of the coastal strip already receives enough rain to support forest if human intervention is eliminated, and the same applies to the country north of Victoria Nyanza. Inland from the coastal strip until the highland area is reached the rainfall in Tanganyika—e.g. between the Usambaras and the Ulugurus—is at present about 15 in. below the 50 in. required, as we have seen, to produce forest at such low altitudes, while in Kenya ("Taru Desert" and northwards) there is a deficiency of quite 25 in.

On the whole we may conclude that with a general increase of 15–20 in. in the rainfall throughout East Africa all the existing forest islands would be in communication with each other and with the Congo-West African forest. Under such conditions the low-level eastern part of Kenya would however probably still be clothed with no association more dense than Savannah. A slight general increase would of course have much more effect on forest distribution in some districts than in others. One of its first effects would be to connect the forests on both sides of the Rift Valley and to strengthen the connection across Uganda. In the next stage the Kilimanjaro-Usambara system would be brought into communication with the Kenya Highlands. But the junction of the northern and the southern mountain systems of Tanganyika Territory with the Ulugurus, and ultimately with each other, would hardly be effective until later still because of the low altitude of the country surrounding the Ulugurus.

The pluvials.

It is realised at the outset that any attempt to calculate rainfall in terms of inches from the fluctuations in the lake-levels breaks down. There are too many unknowns: for example we do not know the proportion of the total precipitation that gets into the lake or the relation that the evaporation bears to the volume of water in the lake; and both are constantly varying with the distribution of the rainfall, the vegetation of the catchment area, and the average depth of the lake. But nevertheless it is possible to draw certain conclusions for our purpose.

The Kamasian.

During this period the lower limit of the glaciers was on all the great peaks at least 4000 ft. lower than it is now. Moreover, as Nilsson deduces from the fact that the glaciers descended equally on all sides of the mountains, the precipitation must have been better distributed than at the present time. In sum, the general climate then was vastly more favourable to forest growth. If we accredit half of the 4000 ft. glacial advance to increased precipitation and half to lowered temperature we arrive at the conclusion that the climate must have been some 8° F. cooler (using the world-wide average factor of 3–4° F. per 1000 ft. altitude quoted by Willis (1922, p. 44)). In other words all the vegetation zones in East Africa were lowered 2000 ft. by the temperature factor alone, and montane forest capable of subsisting on 40 in. of rain could maintain itself down to within 3000 ft. of sea-level. But at the same time precipitation was much greater and better distributed than now. The impression is irresistible that at this epoch the whole of East Africa was covered with a sea of forest in full connection with the West African.

So far as temperature was concerned the whole of the interior plateau of Tropical Africa must have been "temperate," in enjoyment of a climate no more exacting than that now prevalent at 5000 ft. in forested districts. These conditions are held to have continued for what was, even on the geological scale, a long period. The probabilities are surely strong that what in the Introduction I have called the "Temperate" fauna of the peaks to-day is representative of that dominant throughout Tropical Africa during the Kamasian.

The only islands in this sea of forest would have been those spots where the soil was unsuitable and those above the timber-line. With the lowered general temperature this line would have fallen correspondingly, by 2000 ft. or more, so that all the country above 7000 or 8000 ft. was bare of forest. Under these conditions most of the islands of Alpine vegetation would still have been separated, although some of them, e.g. on the Mau, the Aberdares and Mount Kenya, would have been in sight of each other.

The Gamblian.

With its glacial extension only 1000 ft. less in altitude than the Kamasian and still 3000 ft. below the present, the climate of the Gamblian was evidently almost as highly favourable to forest growth as the Kamasian. Doubtless the glacial extension was due in part to increased precipitation and in part to lowered temperature. The latter factor by itself would have made it possible for montane forest requiring only 40 in. of rainfall to grow down to 3500 ft. If the concurrent increased precipitation amounted to no more than 15 or 20 in. above the present it would have sufficed, as we have seen, to link all the present forest islands. The existence of a Lake Nakuru that was 65 times as deep as the present and held several hundred times as much water derived from much the same catchment, seems to assure us of this. It is not possible to base any arguments on the actual level attained by the lake because it is not clear whether it was in connection at its maximum with Lake Naivasha, and so provided with an outlet. On the whole, the Gamblian, too, is acceptable as an epoch of continuous forest: and the probability is that to this epoch the "subtropical" fauna of the mountains owes its dispersion.

The Makalian.

The Makalian is much more difficult to evaluate. It has been comparatively easy to come to the conclusion that both the Kamasian and the Gamblian pluvials were of first importance in contributing to the present distribution of living things in Africa. We shall find equally good reason for deciding that the last wet phase, the Nakuran, was of trifling significance. But the

Makalian falls between the Gamblian and the Nakuran, in intensity as well as in time.

The most superficial comparison would seem to indicate that in degree of favourability to forest growth the Makalian was nearer to the Nakuran phase than to the Gamblian. For the Makalian lake-maximum was 375 ft., compared with 145 in the Nakuran and 775 in the Gamblian, while the glacial extension was only a few hundred feet (350 ft. on Mt Kenya) below the present, against 3000 ft. below in the Gamblian. In other words, granted that there was an increased precipitation, the temperature could not have been appreciably lower than now, and any extension of forest growth depended on the precipitation factor alone.

Any attempt to estimate the Makalian rainfall must be based on the maximum attained by Lake Nakuru. A rise to 375 ft. looks imposing, but it cannot be accepted without analysis as evidence of a climate more favourable to forest growth to a significant degree. Unfortunately analysis involves large assumptions and the calculations can only be speculative.

We have three relevant facts of importance:

(*a*) With its surface 375 ft. higher than to-day it was in connection with Lake Elmenteita.

(*b*) The area of the combined lake was slightly over 200 square miles with a catchment of some 545, compared with an area of $15\frac{1}{2}$ in a catchment of 420 in 1929[1], i.e. 13 times as great, with a catchment 30 per cent. greater.

(*c*) The present Nakuru catchment rainfall is 37·5 in., so that the general addition of 15–20 in. that we have decided would be required for continuous forest growth, would bring the Nakuru figure to about 54 in. ($=4\frac{1}{2}$ ft.).

We do not know:

(*d*) The loss by evaporation (in inches per annum) referred to subsequently as E.

(*e*) The "run-off," i.e. proportion of total precipitation reaching the lake. This will be called P. In any attempt to work out the volume of water entering the lake it must be remembered that the wastage that is the complement of P does not occur with the rain that falls on the lake surface itself. In dealing with Nakuru this is a most important reservation, because at its Makalian maximum it occupied more than a third of the catchment[2].

Now probably the only figures we have of value for E and P in the case of an Equatorial lake are those arrived at by Hurst (1925) for Victoria Nyanza, viz. 1310 mm. ($=52$ in.) and 10 per cent. respectively. We do not know how the run-off conditions of Nakuru and Victoria differ, but applying the 10 per cent. to Nakuru as a trial we can calculate that on the existing rainfall and

[1] These figures are worked out from the plan of the lake in Leakey's paper (*op. cit.*) and from G.S. map No. 1764, Africa 1:250,000 sheet South A–37/A dated March 1918.

[2] **Leakey** (1931, p. 505) notes that "during the excessively wet period from November 1928 to May 1929, when the Nakuru district got nearly treble its normal rainfall, the lake level rose only 24 in." Such definite figures aroused the hope that they might be utilised in this enquiry, but in seeking to ascertain what the "normal rainfall" for the months cited might be, I failed to find the "excessively wet period" reflected in the records at my disposal at Amani. I therefore applied to Mr A. Walter, Director of the British East African Meteorological Service, who has kindly furnished me with the figures actually recorded for each of the 7 months in question at five stations in the Nakuru catchment. They are all below the average, not 200 per cent. above. In any case, as Mr Walter points out, a lag, perhaps very considerable, is to be anticipated between abnormal downpour and lake-rise. This lag is not of course significant when we are dealing with a secular change.

lake-area E would be 130 in. a year or over 0·3 in. a day. This is about 0·1 in. less than the average rate of evaporation at Aswan[1], where the saturation deficit is certainly much greater than it is at Nakuru. This indicates that 130 in. is not too low a figure for E at Nakuru under existing conditions, but is on the contrary probably rather high. $E=100$ in. might be nearer the truth and it can be calculated that this would connote $P=6{\cdot}6$ per cent. But under the conditions of the Makalian maximum the present difference between Nakuru and Victoria in the matter of loss by evaporation could hardly persist. For, broadly, a higher rainfall is associated with a higher relative humidity, and Nakuru being at a higher altitude than Victoria, the mean temperature would be lower. Both these factors would tend to lower the saturation deficit of the Nakuru district relatively to Victoria. At the Makalian maximum, then, E for Nakuru would, by inference, have been less than the present 100 in., and may well have been as low as for Victoria now (52 in.). With the increasing size of the lake the exact value of P becomes less important for our calculation, since ultimately the rain that fell on the 200 square miles of lake-surface provided seven-eighths of all that reached the lake. If we work out the rainfall that would have been necessary to maintain the Makalian lake at its maximum (*a*) with $E=100$ in. and (*b*) with $E=52$ in., we get for (*a*) 85 in. and (*b*) 44 in. But a saturation-deficit so high as to cause a loss of 100 in. by evaporation could hardly exist with a rainfall of 85 in., so that the truth must lie nearer the 44 in. rainfall.

We may attack the problem from another side. Given a rainfall of 54 in., which is, we have decided, about the minimum conducive to a general afforestation, what value does that connote for E? For our purpose the level at any stage may be taken as constant: for although it was actually rising, several thousand years are available for the total rise of 375 ft. and the average annual change would have been only an inch or two. With the same rainfall E varies with the size of the lake. Thus with a 55 in. rainfall and the lake-area approximately 50, 100 and 200 square miles, we get evaporation figures of 80 in., 70 in. and 60 in. respectively. But it is obvious that with a rainfall of 55 in., actually higher than that of the Victoria Nyanza basin now, and a saturation deficit that should certainly have been no higher, the loss by evaporation ought to be less, not more. On these grounds therefore it seems improbable that the Rift Valley rainfall during the Makalian reached 55 in., though it may have been 12 in. or so above the present.

Speculative as all these arguments admittedly are, they point in the same direction. They all give us cause to doubt whether the Makalian rainfall was sufficiently greater than the present to permit of general forest growth. Some of the forest islands would have been linked, all those in the Kenya Highlands with each other and probably with Ruwenzori and the Kilimanjaro-Usambara Chain: but with temperatures much as they are to-day, the montane forms, "subtropical" as well as "temperate," would have remained restricted to their mountains.

The Nakuran wet phase.

A lake 145 ft. deeper than Nakuru to-day bulks large, and seems to demand a considerably increased rainfall. But between the end of the Makalian wet phase and the maximum of the Nakuran at least 10,000 years elapsed, so that 4000 may reasonably be allocated for the lake to fill up for this last wet phase. The average rate of rise would then have been about $\frac{1}{2}$ in. a year, instead of the present drop of $2\frac{1}{2}$ in. From the contours it appears that the lake at the Nakuran maximum would only have had about twice its 1906 area of 20 sq.

[1] Quoted by **Kirkpatrick** (*The Mosquitoes of Egypt*, Cairo, 1925) from *Climatological Normals for Egypt and the Sudan etc.* issued by the Physical Department, Ministry of Public Works, Egypt, 1922.

miles. How much more rain than the present annual fall would suffice to turn a deficit of $2\frac{1}{2}$ in. into a gain of $\frac{1}{2}$ in. for a lake of 40 sq. miles? The answer, using the figure of 6·6 per cent. for P that we reached in the preceding section, is barely 2 in. Doubtless the lake varied in its rate of rise and often gained more than $\frac{1}{2}$ in. in a year. But the more rapid the gain the shorter the period during which the high rate of gain can have continued. In any case, it can be calculated that even a 6 in. rise in the lake could have been accomplished on a rainfall $5\frac{1}{2}$ in. above the present. The inference is that the Nakuran wet phase had no important influence in extending forest growth.

The dry periods.

The first, post-Kamasian, dry period is quite incalculable in extent, but the next two dry periods are susceptible of some examination. At first sight the establishment of two epochs when Lake Nakuru dried up[1] would seem to indicate periods of drought severe enough to exercise a catastrophic effect on forest growth throughout East Africa. A recent reviewer of Leakey's *The Stone Age Cultures of Kenya Colony* (*Nature*, No. 3242, p. 1021), who refers to the "intensely desertic conditions" of the post-Gamblian inter-pluvial, would doubtless accept this view. Important considerations exist, however, to modify our conception of the severity of the inter-pluvials' effect on the forests.

(*a*) Although Lake Nakuru still bulks large upon the map it is, compared with its former size and depth, a mere vestige, still diminishing. During the last, and least, of the wet periods we have been considering it was over 150 ft. deep against 9 ft. 2 in. in 1929. In fact in the 23 years following 1906 it lost 5 ft. 6 in. As has been pointed out above, the deficiency in rainfall is due, in part at least, to a secular deterioration in climate. If it continues, even without intensification and with the maintenance of the existing rainfall of 37 in. a year in the catchment, Lake Nakuru will have dried up completely before the end of the present century.

(*b*) The deposits of blown alluvium in the bed of the lakes following the Gamblian and Makalian wet periods do not of necessity imply a climate much drier than the present one[2]. I am informed by eye-witnesses that in the section of the Rift Valley concerned there is already a considerable transport of soil by wind, to such an extent indeed that on one local sisal estate the soil has been compacted with heavy rollers to reduce the loss by wind-erosion.

[1] **Leakey** (*op. cit.* p. 501) refers to "complete desiccation" but it is not clear whether it has been established that the desiccation extended to the area covered by the present lake, which must presumably always have been the deepest part of the basin.

[2] Dr K. S. Sandford has pointed out to me that dust blows readily from any exposed alluvium. It forms banks of "aeolian material," which when old looks like loess and may come to be called by that name. He has recalled particularly the example of the mudbanks temporarily exposed at low Nile. The dust clouds they gave rise to as soon as the water had left them were a familiar phenomenon to us both. Thus a seasonal exposure for a few weeks every year may be capable of ultimately producing a loess-like formation in the neighbourhood.

(*c*) In the Introduction attention was drawn to the fact that the Usambara series are distinguished among East African mountains by the strength of their West African affinities, both zoological and botanical. Moreover the Usambara Series are inhabited by a surprisingly large number of distinct species, known from no localities outside these extremely restricted mountain forests. Examples are *Malaconotus alius* Friedm., *Apalis moreaui* Scl., *Ploceus nicolli* Scl., *Artisornis metopias* (Rchw.) among birds: *Pterocarpus Zimmermanii* Harms, *Cephalosphaera usambarensis* Warb., *Berlinia Scheffleri* Harms, *Sloetiopsis usambarensis* Engl., among trees.

The greatest abundance of vestigial forms, both endemic and West African, survive precisely in those spots that are unique in East Africa by reason of their copious rainfall—amounting to between 60 and 80 in. very well distributed—in a zone that is neither fully tropical nor subject to frost: and it is a legitimate inference that the forms in question are unable to survive under any more rigorous conditions. Now they are at the present day extremely restricted; any pronounced general deterioration in climate would result in the complete disappearance from East Africa of the delicately balanced conditions in which they live, and they would vanish too. Their survival till the present day tends to show that the inter-pluvials we are discussing cannot have involved very severe general desiccation.

(*d*) A general drop in rainfall sufficient to have a marked effect on the Rift Valley, which with 37 in. already shows a tendency to dry up, would not necessarily much affect the total area of the forest elsewhere. The Nakuru district would indeed be "intensely desertic" if the average rainfall fell another 10 in., but the greater part of the existing forests have as wide a margin of safety as that. Within their limits there would, of course, be some readjustment of the zones of the several types, "temperate rain-forest" for example tending to be replaced by "plateau forest" or "cedar"; but only that fringe of the forest area already maintaining itself on a minimum rainfall would be lost. If the 27 per cent. drop in rainfall which 10 in. in the Rift Valley represents were general, the effects would be more serious. Most of the existing "cedar" areas would disappear, and that association would largely replace "temperate" forest where it now occurs. Uganda, the chief corridor to the West African forests would be extensively denuded. But in comparing former dry periods with that in which we live it must constantly be remembered that the East African forests have suffered more diminution through recent human agency than they would have through an appreciable drop in rainfall.

All these considerations tend to show that the climates of the two inter-pluvials had not necessarily a catastrophic effect on forest growth. They may even not have been much more severe than that of the present day. This conclusion, in so far as it depends on consideration (*c*) applies with especial force to the post-Makalian dry period: for if the specialised forest life of the

Usambara series had been swept away in the post-Gamblian, it is just possible that the Makalian pluvial may have been long enough, and sufficiently important in extending the forest, to enable even mountains within sight of the Indian Ocean to be restocked with West African forms. But if these types had been swept away in the post-Makalian the Nakuran wet phase could have done nothing to repair the loss.

Summary of conclusions.

I desire to emphasise that in a summary of this nature the statements made must inevitably appear to be more definite and precise that I should wish or than the present evidence warrants. In particular the dates are to be understood as nothing more than indications of relative remoteness from the present. "Forest" is to be read as "Evergreen Forest."

Present forest boundaries are generally not natural. They have been reduced by human agency as much as they would have been by an appreciable drop in rainfall.

A general increase of from 15 to 20 in. in the rainfall of East Africa would be sufficient to cover practically the whole of it in time with forest.

Communication of the existing forest islands with each other and with the West African forest existed under Temperate climatic conditions for a long period prior to 400,000 years ago. To this epoch (Kamasian) is ascribed the dispersal of the species now confined to the upper part of the montane forests. Evidence that the existing Alpine areas were in direct communication during the Kamasian is, however, lacking.

After an interval of which we know nothing, Kamasian conditions were re-established in a somewhat modified form and continued until about 22,000 years ago. So recently, then, as this latter date montane forest forms—probably those now typical of the lower zones—were dominant throughout the East African interior, and West African influence could penetrate to within sight of the Indian Ocean. The subsequent dry period may have been severe enough to obliterate forests in some areas where they exist to-day, but wholesale destruction probably did not take place.

Before 12,000 years ago the forest sheet was in part re-established, but under temperature conditions similar to the present; so that montane forms were generally restricted, as now, to high ground. For these it is possible that communication was open from Elgon to Kilimanjaro and the Usambaras. But it is unlikely that the highland forms in Southern Tanganyika Territory were in communication with the Northern, or the Ulugurus with either.

The subsequent dry period may have been hardly more rigorous than that now being experienced. The wet phase that reached its maximum 2800 years ago was, beyond question, insignificant.

It follows that up till 22,000 years ago opportunities continually occurred for the flora and fauna of montanes now isolated to be assimilated with each other and with West Africa. It is only for certain during the last 12,000 years that the conditions of isolation favourable to race differentiation have been fully developed.

REFERENCES.

Allen, G. M. and **Loveridge, A.** "Mammals from the Uluguru and Usambara Mountains, Tanganyika Territory." *Proc. Boston Soc. Nat. Hist.* **38**, 413–41, 1927.

Bannerman, D. A. *Birds of Tropical West Africa*, **1**, London, 1930.

Bates, G. L. "Geographical variation within the limits of West Africa." *Ibis*, 13th series, **1**, 255–302, 1931.

Brooks, C. E. P. *Evolution of Climate*. London, 1922.

Chapin, J. P. "Ecological aspects of bird distribution in Tropical Africa." *Amer. Nat.* **57**, 106–25, 1923.

Chapman, F. M. *The Distribution of Bird Life in Ecuador*, 1926.

Chipp, T. F. "The Gold Coast Forest." *Oxford Forestry Memoirs*, No. 7, 1927.

Coleman, A. P. "Glaciation and continental drift." *Geographical Journal*, **79**, 253, 1932.

Hurst, W. E. "The lake plateau basin of the Nile. Part I." *Ministry of Public Works, Egypt, Physical Dept.*, Paper No. 21, 1925.

Hutchins, D. E. *Report on the Forests of British East Africa*. London, 1909.

Johnston, H. *The Uganda Protectorate*. 2 vols., London, 1902.

Kendrew, W. G. *The Climates of the Continents*. Oxford, 1927.

Knox, A. *The Climate of the Continent of Africa*. Cambridge, 1911.

Leakey, L. S. B. "East African Lakes." *Geog. Journ.* **77**, 497–514, 1931.

Lönnberg, E. "The development and distribution of the African fauna in connection with and depending upon climatic changes." *Ark. Zoo.* (Stockholm), **21** A, 1–33, 1929.

Meteorological Maps of the Atlas of Egypt, publ. Survey of Egypt, Cairo, 1928.

Meyer, H. *Der Kilimanjaro, Reisen und Studien*. Berlin, 1900.

Meyer, H. *Das Deutsche Kolonialreich*, **1**, Leipzig, 1909.

Nicholson, A. "Forests and Climate." *Bull. For. Dept.* Nairobi.

Nilsson, E. "Preliminary report on the quaternary geology of Mount Elgon and some parts of the Rift Valley." *Geologiske Föreningens i Stockholm Förhandlingar*, **51**, 253–61, 1929.

Phillips, J. F. V. "Some important vegetation communities in the Central Province of Tanganyika Territory." *S. Afr. Journ. Sci.* **26**, 332–72, Johannesburg, 1929.

Reichenow, A. *Die Vögel Afrikas*. Neudamm, 1900.

Savoyen, Ludwig Amadeus von, Herzog der Abruzzen. *Der Ruwenzori*. Leipzig, 1909.

Sayers, G. E. (Ed.). *Handbook of Tanganyika*. London, 1930.

Sclater, W. L. *Systema Avium Aethiopicarum*. London, 1930.

Stresemann, E. and **Grote, H.** "Verbreitung und Gliederung afrikanischen Formenkreise." *Verh. VI Intern. Orn. Kongress*, 1926, pp. 358–374 (publ. 1928).

Troup, R. S. *Report on Forestry in Kenya Colony*. London, 1922.

Troup, R. S. *Report on Forestry in Uganda*. London, 1922.

Wayland, E. J. "Pleistocene pluvial periods in Uganda." *Journ. R. Anthrop. Inst.* **60**, 467–75, 1930.

Wayland, E. J. *Summary of Progress of the Geological Survey of Uganda for the Years* 1919 *to* 1929. Entebbe, 1931.

Willis, J. C. *Age and Area*. Cambridge, 1922.