THE SIGNIFICANCE OF PATTERNS OF DISTRIBUTION SHOWN BY FOREST PLANTS AND ANIMALS IN TROPICAL AFRICA FOR THE RECONSTRUCTION OF UPPER PLEISTOCENE PALAEOENVIRONMENTS: A REVIEW

by Alan Hamilton

Department of Environmental Sciences, New University of Ulster, Coleraine, Londonderry, Northern Ireland.

CONTENTS

The poverty of African forests 64
The distribution of African forest organisms 64
1. Low land forest plants 64
2. Montane forest plants 68
3. Lowland forest birds 73
4. Montane forest birds 75
5. Mammals 78
6. Butterflies 81
7. Molluscs 83
Some non-forest distributions 83
Discussion and conclusions 83
References 89

INTRODUCTION

This review covers an enormous field. During its preparation, I have become increasingly aware of my limitations, not only in knowledge, but also in ability to read even a small fraction of the literature. My research experience in this subject area is confined to studies into the vegetational history of Uganda. For other areas and for other types of life, I have tried to find publications which provide explanations for distributional patterns, rather than unassimilated data. I have also tended to consult more recent papers, relying on these, perhaps sometimes inadvisedly, to abstract previous work. My reading list, which I realize must be very inadequate, may be judged from the references. It is difficult to summarize the thorough and often detailed accounts of authors writing on their own specialities, and I suspect that there must be instances where my account gives distorted impressions of their views. In an attempt to correct this bias, I have forwarded advance copies of the manuscript to a number of experts whose opinions I have attempted to incorporate; their names are listed in the acknowledgements. If this review is justified, it is because different groups of forest organisms have lived through many of the same climatic events. Comparison of their distributional patterns should therefore be complimentary for the reconstruction of palaeoenvironments.

Place names mostly follow the Times Atlas (1967).
African forests are said to be poor in species of plants, birds, and insects (though not mammals, Boulé, 1963) compared to some other parts of the humid tropics (Carcasson, 1964; Chapman and White, 1970; Moreau, 1966; Richards, 1966). Richards (1952) considers that the environment of Africa is just as suitable as that of the other areas for development of forest at the present time and thinks that the cause of poverty must therefore be historical. Widespread extinction of lowland forest species may have occurred when the extent of lowland forest was greatly reduced (Carcasson, 1964; Chapman and White, 1970; Moreau, 1966), probably during times of extreme aridity (Carcasson, 1964). Contrary to expectations, repeated fragmentation and coalescing of forest does not seem to have increased the number of species present, perhaps because the dry periods were rather severe and because their durations were too short (for a similar view in respect to S. America, see Mayr, 1969). A different explanation for the poverty of the African forest avifauna has been advanced by Martin (1968), who wonders whether the gradual reduction of the African climax by man could be an important factor overlooked by other authors. He holds that Africa may well be saturated "at least in those groups of organisms not decimated by ancient or modern man" (p 158).

Euphorbiaceae of the East Coast (and South-East Coast) forests are very distinctive. Within the main Guineo-Congolian region, there is an important division in the Euphorbiaceae between east and west, a division not situated at the Dahomey Gap, but rather further east, in the vicinity of the Cross River (E. Nigeria). Within the Congo Forest Block, two areas are mentioned as being especially rich in endemic species, namely E. Nigeria/Mayumba (S. Gabon), particularly the Ogooué River basin (Gabon), and the forests between about 700-800 m and 1, 300-1, 400 m to the west of Lake Kivu on the east side of Zaire. The central Congo basin appears to have few endemics and several, otherwise widespread, species are lacking. This is in spite of the fact that the vegetation of the central Congo basin is of the same general type as that on its western and eastern flanks (Föret ombrophile sempervirente, ordre Glibbertioidon (sic) Macrophylum) dewerei, according to the "ecological" classification of Lebrun and Gilbert (1954); but the more detailed vegetation maps of Dandelot (1965) and Devred (1958) do show some differences. Léonard (1965) does not interpret his data in historical terms.

In West Africa, the forest of Eastern Liberia/Western Ivory Coast is very rich in endemic species of plants and mammals (Boulé, personal communication). A detailed study of the vegetation is published by Guillaumet (1967) who provides a tentative reconstruction of the vicissitudes of the West African forest block during the Pleistocene.

Gabon (Abréville, 1949) and Cameroon (Richards 1963a; Tappen 1960) are floristically very rich. Tappen stating that the forests of Southern Cameroon are floristically the richest in Africa and Richards remarking that Southern Bakundu Forest (just north of Mt. Cameroon) is floristically richer than any other African forest for which comparable data are available. Richards (1963a) suggests that the rarity or absence of many species west of the Niger is due to the climatic history of the area, rather than to present-day climatic differences. He considers that Cameroon constituted a refuge area for forest species at a time when the forest zone of Nigeria was replaced by savanna. According to Hall and Medler (1975), though without reference to Richards' paper, the refuge could have extended to the highlands of South-Eastern Nigeria (Obudu Plateau). The relative richness of Bakundu Forest (also Gabon: Abréville 1949) in tree Leguminosae, many of which have heavy seeds and are slow-growing, is attributed to their relatively slow rates of migration (Richards 1963a).

Hall and Medler (1975) mention that many Nigerian forest species have efficient dispersal mechanisms.

A quantitative analysis of the distribution of lowland forest trees in Uganda (and Kakamega Forest, Kenya) shows that they display a clearcut pattern of distribution within the country, the forests becoming poorer in species from west to east (Hamilton 1974a; Table 1). The richest areas are Impenetrable-Kayonza Forest in the south-west, Kwamba Forest to the north of Ruwenzi, and, to a lesser degree, the Sango Bay forests on the western shore of Lake Victoria. This pattern is not fully explicable by reference to present-day environmental factors and is thought to result...
Table 1

The numbers of lowland forest tree species recorded from different combinations of flora-areas in Uganda

Data from Hamilton (1974a); flora-areas after Flora of Tropical East Africa (1952 et. seq.).

<table>
<thead>
<tr>
<th>Flora-area 2 (south-west)</th>
<th>Flora-area 4 (south-central)</th>
<th>Flora-area 1 (north)</th>
<th>Flora-area 3 (south-east)</th>
<th>TOTALS</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Species found in one flora-area only.</td>
<td>46 + 10 + 0 + 0 + 56</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B. Species found in two flora-areas only.</td>
<td>87 + 7 + 0 + 0 + 97</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. Species found in three flora-areas only.</td>
<td>43 + 3 + 0 + 0 + 84</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>D. Species found in all four flora-areas.</td>
<td>56 + 1 + 1 + 1 + 56</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTALS</td>
<td>292 + 236 + 108 + 100 + 293</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

from relatively recent establishment of lowland forest in many parts of Uganda. Refuge areas are thought to have been situated at, or close to, Impenetrable-Kayonza Forest, to the west of Ruwenziro (Bwamba is not itself regarded as a refuge area), and perhaps also around Sango Bay. The Impenetrable-Kayonza refuge may have been confluent with that to the west of Ruwenziro. The date of forest spread is shown from palynological studies to have occurred at about 12,000 BP (Hamilton 1972; Kendall 1969; Livingstone 1967).

The floras of the lowland forests of the eastern side of Africa are sufficiently distinct from those of the main Guineo-Congolian Region to warrant their classification in a special domain, the Usambara-Zululand Domain (Chapman and White 1970, after Léonard 1965). The majority of species are endemics (Chapman and White 1970). Polhill (1968) recognizes two types of lowland forest in eastern Tanzania, Moist Lowland Forest, in found on the lower parts of the eastern highland (Usambara, Nguru, and Uluguru Mts; also in parts of Ulanga and Iringa Districts), and Dry Lowland Evergreen Forest, which he considers may once have been extensive in the eastern coastal and low plateau regions, but is now very fragmented. The richest areas are the East Usambaras and the Ulugurus (Chapman and White 1970; Polhill 1968). Although few species, other than pioneer species such as Trema guineensis, occur throughout the forests of the Usambara-Zululand Domain, many other species are widespread, and there is considerable floristic overlap between the forests of any one part of the total area and adjacent parts. Nevertheless it appears that of the more widespread species some have a more northern distribution extending southwards to central Mozambique and others have a southern distribution, occurring chiefly in Natal and Southern Mozambique. In Malawi both types meet" (Chapman and White 1970, pp 62-63). A floristic analysis of the East African coastal forests is given by Faden (1974), who considers that the floristic similarity between these eastern forests and those of the main Guineo-Congolian Region is due to former forest connection. He remarks that there may have been two periods of contact, one relatively recent to account for the large number of species common to both areas, and one more ancient to explain similarities at the generic level. Faden says that forest connection would require higher temperatures and a higher and more evenly distributed rainfall in the intervening area than at present.

Jebel Marra (Sudan) is an isolated volcanic complex midway between Lake Chad and Khartoum, and about 600 km north of the present lowland forest border. Wickens (1975a) has recorded a number of forest species in gallery forest, including Casuarina barteri, Maesaea lanceolata, Polyscias fulva, Saba floridat, and Trema orientalis. Saba, and also Elaeis guineensis, the latter now extinct on the mountain, have been found fossil in ash assumed from a nearby radiocarbon determination to be older than 3,500 BP. Many of these gallery forest plants have drupes or berries suitable for bird transport, while Saba fruits are readily eaten by baboons. Since internal transport by birds and mammals is believed to be only operative over relatively short distances (Wickens, in press), a northwards shift of lowland forest by about 400 km is postulated to have occurred at a time of higher rainfall. On non-distributional grounds, Wickens argues for a post-12,000 BP date for this period of forest expansion.

Aubréville (1949) has demonstrated that, in West and Central Africa, climates suitable for forest growth extend well beyond the present limits of continuous forest cover (Table 2). He argues for forest retreat at the hand of man and also proposes virtual complete destruction of a zone of dry forest which once interposed between forest and savanna. Islands of lowland forest can be found scattered through luxuriant tall grassland (Chipya vegetation) in the higher rainfall belt of Northern Zambia, from Mwinilunga to Abercorn (Chapman and White 1970) and also occur up to 4° south of the main Congo Forest Block in Zaire (Carcasson 1964), as well as in Angola (Aubréville 1949). Wild (1968) considers that the presence of Guineo-Congolian species in patches of relict forest, including riparian forest, in Rhodesia may be due to a formerly greater extent of lowland forest at a time of higher rainfall.
2. Montane forest plants

Many montane species, both forest and non-forest show disjunct distributions in Africa, occurring in two or more highland areas, but not in the intervening lowlands. Additionally, some montane areas (perhaps especially savanna areas) are rich in endemic species. No general survey study, comparable to that of the Afroalpine flora by Hedberg (1957, and other papers), of the taxonomy and distribution of African montane plants has been published (though a comprehensive survey of the entire Afrotropical forest flora is being prepared by Dr F. White). In comparison with the Afroalpine flora, there are indications that the proportion of forest species common to different highland areas is much higher and the percentage of vicarious taxa much lower (Chapman and White 1970). A common opinion (e.g. Moreau 1966; Morton 1972) is that most of the wide disjunctions shown by forest species in Africa can be attributed to previous montane forest connections at times of cold wet climate. Hedberg (1969, pp. 140-141), however, postulates that "given sufficient time most montane forest species of animals and plants should, I believe, be able to pass even a fairly wide gap without depending on continuous distribution of the whole ecosystem. Time has indeed been available here on quite a different scale from that in the formerly glaciated parts of Europe, where dispersal of plants and animals has nevertheless been markedly efficient ..."

Table 2: Estimated distances of the former extent of lowland forest beyond its present-day boundaries in various parts of Africa, based on the distribution of apparently favourable climates (from Aubréville, 1949)

<table>
<thead>
<tr>
<th>Place</th>
<th>Extension (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guinea</td>
<td>60 - 120</td>
</tr>
<tr>
<td>Ivory Coast, to the east of the Tsiassalé forest constriction</td>
<td>100 - 140</td>
</tr>
<tr>
<td>Ivory Coast, at Tsiassalé</td>
<td>240</td>
</tr>
<tr>
<td>Ivory Coast, to the west of the Tsiassalé forest constriction</td>
<td>30 - 70</td>
</tr>
<tr>
<td>Nigeria</td>
<td>20 - 120</td>
</tr>
<tr>
<td>Cameroon</td>
<td>180 - 200 on average, sometimes more</td>
</tr>
<tr>
<td>Between Cameroon and the Ouabangi River</td>
<td>100 - 140 on average, could attain 180</td>
</tr>
<tr>
<td>Northern Zaire, western part</td>
<td>100 - 160</td>
</tr>
<tr>
<td>Northern Zaire, eastern part</td>
<td>200 on average</td>
</tr>
<tr>
<td>Southern Zaire</td>
<td>160 at a minimum; 400 on average</td>
</tr>
</tbody>
</table>

Morton (1972) considers that there are four montane regions in West Africa, which he terms the Cameroons System (including Fernando Po) (maximum altitude 4,070 m) the Togoland System (875 m), the Guinea System (1,948 m), and the oceanic islands of Principe and São Tomé (2,024 m). The latter islands, which contain many endemics, have probably been colonized by long-distance dispersal across the sea; an account of their vegetation is given by Exell (1953). Morton (1972), presenting a quantitative analysis of the distribution of montane species in West Africa, observes that there are many more montane savanna than montane forest endemics. (Curry-Lindahl (1968, p 30) notes the "astonishingly high number of endemic (savanna) animal species" on Mt Nimba (on the border between Liberia, Guinea and the Ivory Coast).) Morton (1975, p 226-227) attributes the paucity of montane forest endemics to the fact that the montane forests "have always presented a closed system, which has usually been continuous with the lowland forests ... Hence no ecological vacuum existed in which accelerated speciation would be favoured, and as a result few montane forest endemics have evolved".

The origin of the montane savannas of West Africa is uncertain and may be diverse. Hall (1971) claims that the Nigerian highlands may once have been forest covered; Curry-Lindahl (1968) holds that much of the savanna of Mt Nimba may be ancient. The savanna floras consist of two main elements, species spreading up from lowland savannas and species which are confined to montane environments and which are either endemic to particular regions or which else show disjunct distributions between different highland areas (Cole 1974). Many of the latter reappear on the mountains of East and Central Africa (Cole 1974). The high degree of endemism found in montane savanna species in West Africa (Cole 1974; Morton 1972) is thought to be partly due to the effects of climatic change. In contrast to the montane forests, the montane savannas are said to present an insular situation (Morton 1972). Advances in forest at times of favourable climate would have reduced the savanna areas and probably caused extinctions; retraction during unfavourable periods would have left large savanna areas with relatively few species. It is envisaged that this ecological vacuum has been filled partly by species immigrating from both the lowlands and from other highland areas, and partly by speciation. A proposed mechanism for speciation is given in Morton (1972).

The flora of Mt Cameroon (4,072 m) contains many East African genera and species (Hall 1973; Keay 1954/55; Table 3). The number of endemics is much less than was once supposed and will probably be further reduced as species are found to be conspecific with plants occurring elsewhere or are discovered in other areas (Hall 1973; Keay 1954/55). The flora of Fernando Po, twenty miles off-shore and believed to have been connected to the mainland during times of low sea-level (Moreau, 1966), is said to be similar to that of Mt Cameroon (Bougyhe 1954/55), but the floras of the mountains of the Cameroon hinterland, offering a much greater area of habitat in the 1,830-2,440 m range, are richer (Bougyhe 1954/55; Keay 1954/55). This is chiefly due to the addition of many genera and species of East and South African affinity; species present, which are absent from Mt Cameroon, including Albizia gummifera, Arundinaria alpina, Cyathaea dregel, Dipasacus pinnatifidus, Podocarpus milanjianus, Rhamnus prin-
oides, and Xylomas monospora (the latter also on Fernando Po) (Keay 1954/55). A floristic analysis of the flora of the South-East Nigerian highlands, which are an extension of the Bamenda Highlands (Cameroon), indicates that affinities with East Africa are much less for forest than grassland species (Hall and Medler, 1975, Table 3) and the authors suggest that the forest and grassland floras have had different histories. It would be interesting to see this analysis extended to other parts of the Cameroon highland area. The scarcity of endemics on the Cameroon Highlands can be seen on Table 3 and is also mentioned by Morton (1961).

Table 3
Approximate percentages of the floras of Mt. Cameroon and the S.E. Nigerian highlands represented in the vegetation of other localities from Hall (1973) and Hall and Medler (1975).

<table>
<thead>
<tr>
<th>Mt. Cameroon</th>
<th>S.E. Nigerian highlands</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total flora</td>
</tr>
<tr>
<td>Europe</td>
<td>2</td>
</tr>
<tr>
<td>Southern Africa</td>
<td>19</td>
</tr>
<tr>
<td>Ethiopia</td>
<td>20</td>
</tr>
<tr>
<td>Eastern Africa</td>
<td>24</td>
</tr>
<tr>
<td>Fernando Po</td>
<td>47</td>
</tr>
<tr>
<td>Bamenda Highlands</td>
<td>27</td>
</tr>
<tr>
<td>Jos Plateau</td>
<td>5</td>
</tr>
<tr>
<td>Mambilla Plateau</td>
<td>6</td>
</tr>
<tr>
<td>Vogel Peak Massif</td>
<td>6</td>
</tr>
<tr>
<td>Widespread lowland vegetation</td>
<td>22</td>
</tr>
<tr>
<td>Endemic</td>
<td>5</td>
</tr>
</tbody>
</table>

According to Morton (1972), most montane disjunctions, both within West Africa and between West Africa and elsewhere have originated by withdrawal from more continuous ranges. An analysis of the dispersal methods of montane (mostly savanna) species on the Loma/Tingi Hills (Sierra Leone) indicates poor adaptation for long-distance dispersal. Lowering of vegetation by about 2,000 ft (610 m) is said to create a situation in which montane communities in West Africa would be rarely more than 100 miles (160 km) apart. "well within the range of dispersal by raving animals, birds and wind; the contestants duck or elephant then becomes a real factor in plant dispersal." A lowering of vegetation belts by 2,000 to 3,000 feet (610 to 915 m) in the area separating the Cameroon System and the mountains of East and Central Africa would have a similar effect and a series of short hops would be all that was necessary to get the present montane flora across the continent" (p 233). Morton (p 232) believes that connection with East Africa must have occurred fairly recently, since "most of the montane species have diverged but little in their disjunct populations". Many authors (e.g. van Zinderen Bakker 1967a: 1970; Welmark 1941) have envisaged that montane forest connection between the Cameroon Highlands and East Africa was by way of a corridor around the high ground to the north of the Congo basin (Carcasson 1964, Coetzee and van Zinderen Bakker 1970, and others provide hypothetical vegetation maps). The high ground to the south of the Congo basin may have carried another montane forest corridor, between the West Angolan highlands and Central Africa (see above references). Since the Cameroon montane flora is an impoverished East African montane flora, with few endemics, most species have probably spread from east to west, rather than the other way round; within West Africa, the decreasing proportion of East African species from east to west also indicates a predominantly westwards diffusion (Morton, 1972).

With regard to these opinions of Morton and others, Wickens (personal communication) writes that, in his view, the disjunctions shown by Afro-montane grassland species between West and East Africa can only be explained by long distance dispersal. A transect diagram (Wickens, in press) clearly shows that the higher ground along the Nile/Congo Divide between the Imatong and the Bongos Plateau (Central African Republic) was too low for short-distance dispersal by hill-top hopping.

In East Africa, many authors distinguish between moist and dry types of montane forest (see Hamilton 1972 for references). These two types are broadly similar to the submontane and montane forest types described by Chapman and White 1970 for Malawi). Moist montane forests differ from dry in having a much higher proportion of species with relatives in the lowland tropics (Chapman and White 1970). Within Uganda, trees of the two forest types show different patterns of distribution, species of dry montane forest tending to be widely distributed (growing on edaphically dry sites in climatically moist areas) and species of moist montane forest showing a gradient of floristic richness, the richest area being Impenetrable-Kayonza Forest, with forests becoming increasingly impoverished at greater and greater distances (Hamilton, 1974a). These patterns of distribution are interpreted as indicating that dry montane forest has been relatively widely distributed in highland Uganda in the recent past, but that moist montane forest has spread out relatively recently from a refuge in South-Western Uganda/Eastern Zaire. A change to a wetter climate on most Ugandan mountains, including Rwerenzori and Mt Elgon, is postulated. Pollen analysis provides some supporting evidence (Hamilton 1972: Livingstone, 1967; Morrison, 1968).

No detailed analysis of the distribution of montane forest species in Kenya, Tanzania, or, indeed, in East Africa as a whole has yet been published. Some highland areas are richer in species than others; the mountains of South-Western Uganda (and adjoining areas of Rwanda and Zaire) and those of Eastern Tanzania (especially the Nguru, Uluguru, and Usambura Mountains) would seem to be the principle regions of species richness and are probably the sites of former montane forest refuges, perhaps especially for moist montane forest species, during dry periods in the Pleistocene. Moreau (1966) mentions that the Uluguru and Usambara forests are richer in species and in endemics than the forests of most of the volcanic mountains, including Kilimanjaro. He also notes the many...
species of African violets, *Saintpaulia*, on the Usambaras. Several moist montane tree species show widely disjunct distributions between South-Western Uganda and Central or Eastern Kenya/Tanzania, being absent from intervening mountains, such as Mt Elgon, which provides apparently suitable habitats.

The Ethiopian montane forest flora is inadequately known, but, judging by available information, it is impoverished. Both moist and dry montane forests occur (Gillett, 1955; Logan, 1946). There is an important floristic divide between north and south (the boundary being at about the latitude of the Blue Nile), affecting species of cooler and moister vegetation types, rather than those of drier types of forest, such as *Juniperus* (Gillett, 1955). Overall, the flora of Southern Ethiopia is much more similar to that of highland Kenya/Uganda than to that of Northern Ethiopia (Gillett, 1955). Van Zinderen Bakker (1967b) considers that the interval between the Kenyan and Ethiopian mountains has been arid for a long period of time.

The montane forest tree flora of Malawi has been described at length by Chapman and White (1970; see also White, 1971). All of the 60 larger tree species, which are found in Malawi and which are regarded as being endemic to the Afromontane Region, are found outside Malawi. Malawi constitutes the southernmost limits of the ranges of several tree species of montane (dry montane) forest, including *Hagenia abyssinica*, and the northernmost limits of a few others, such as *Widdringtonia cupressoides*. Submontane (moist montane) forest shows a general southwards impoverishment within the country.

A statistical analysis of the distribution of species (of all vegetation types) in the Flora Zambesiaca area (Malawi, south to Botswana) provides evidence for a mainly north-south movement of species in the recent past, suggesting that the Zambezi and Limpopo intervals have proved ineffective barriers (Wild, 1968). It is thought that actual physical contact of the Afromontane flora of Rhodesia with those to the north and south did not occur during the Pleistocene (Wild, 1968). There are very few typically submontane (moist montane) species in South Africa, but forests of very similar floristic composition to the montane (dry montane) forests of Malawi are widespread (Chapman and White, 1970; see also van Zinderen Bakker Jr., 1973; Werger, 1973b). They include quite a number of South African endemic species (Chapman and White, 1970).

The results of Dr White’s studies on the taxonomy and distribution of montane species are awaited with interest. Meanwhile, it may be said that the two types of montane forest which are usually recognized are likely to have had different histories. The evidence suggests that, in the recent past, moist montane forest was restricted to localized refuges, from which it has subsequently spread, while dry montane forest was more widely distributed. A general change from a dry to a moister climate is suggested.

3. Lowland forest birds

A full description and analysis of the distributional patterns shown by birds in Africa has been published by Moreau (1966) to whom the reader is referred for detailed information. Also relevant is Hall and Moreau (1970), containing excellent distribution maps.

The avifauna is rather homogeneous throughout the lowland forests of West and Central Africa, with 157 (88 per cent) of the 182 species recorded from the Guinea Forest Block being also found in North-East Zaire, whereas a total of 212 species are known (Moreau 1966).

On the basis of present-day forest distribution, it might be expected that the Dahomey Gap and the Cameroons constriction would mark the sites of avifaunal change. Actually, only 9 species are endemic to the Guinea Forest Block (4 of which lack close relatives on the other side of the Dahomey Gap) and many of the species around Lagos are subspecifically identical to those in the Guinea forests. Marchant (1954) provides a quantitative analysis of avifaunal change across Nigeria (Table 4) and notes:

<table>
<thead>
<tr>
<th></th>
<th>Lagos</th>
<th>Ondo-Benin</th>
<th>Owerri</th>
<th>Kumba</th>
</tr>
</thead>
<tbody>
<tr>
<td>(W. Nigeria)</td>
<td></td>
<td>(Central</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(E. Nigeria)</td>
<td></td>
<td>Nigeria)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(W. Cameroon)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Guinea Forest Block</strong></td>
<td>52</td>
<td>40</td>
<td>29</td>
<td>12</td>
</tr>
<tr>
<td><strong>Congo Forest Block</strong></td>
<td>19</td>
<td>35</td>
<td>64</td>
<td>112</td>
</tr>
<tr>
<td><strong>Forms confined or not confined to Nigeria</strong></td>
<td>10</td>
<td>11</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td><strong>TOTALS</strong></td>
<td>81</td>
<td>86</td>
<td>103</td>
<td>126</td>
</tr>
</tbody>
</table>

* This table omits species found through Nigeria and beyond without subspecific change.

Note the decreasing proportion of Upper Guinea subspecies and the increasing proportion of Lower Guinea subspecies from west to east.

that similarity with the Guinea Forest Block decreases from west to east across Nigeria. He states that, within West Africa (Sierra Leone to Cameroon), about twice as much avifaunal change occurs within Nigeria compared with at Dahomey Gap or at the Cameroon constriction.

Moreau (1966) concludes that, in West Africa, old interruptions in the forest are more decisive for forming the modern distributional patterns.
of birds than present gaps. He considers that, although forest continued to persist in West Africa, its extent was greatly reduced during an Upper Pleistocene dry period. According to Moreau (1966), the existence of the Dahomey Gap is dependent on a very localized cold marine upwelling, rather than being due to any orographic feature. An eastwards shift of the upwelling, perhaps combined with a reduced shoreline (see Moreau [1963a] for a discussion on the origin of the coastal sands of Nigeria), might have created a forest gap in Nigeria, rather than in Togo/Dahomey.

Moreau (1966) points out that there are 6 endemic species of lowland forest bird confined to North-Eastern Zaire. A further 24 species show disjunct distributions within West and Central Africa. Moreau gives the approximate intervals of 7 such species; of these, 5 show intervals across the central Congo basin, being absent between the longitudes of about 13° and 28° East. Moreau (1966, p 164) remarks that "... it might be suggested that these restricted endemic species and these discontinuities of range are a legacy of the mid-Pleistocene fragmentation of the Congo and restriction of its species to the seaward and the eastern edges of the basin. But these effects are likely to have been obliterated by the subsequent effects of the glaciation, with the prolonged concentration of lowland life in the centre of the basin, unless some independent lowland refuge persisted on the north-eastern periphery of the area throughout the glaciation". Moreau then proceeds to discount the existence of such a refuge since the only localities which he considers to be of sufficiently low altitude is Lower Semiliki Valley/Bwamba and this contains only one of the 6 species endemic to North-Eastern Zaire. Moreau's quandary is tempered by his theories of climatic change and his views on the nature of the lowland/montane avifaunal boundary. If the distributional evidence alone is considered, there seems to be support for the existence of former lowland forest refuges on the western and eastern flanks of the Congo basin, but none for a refuge in its centre.

With the single exception of a bulbul (Phyllastrephus hypochlorus), all birds of lowland forests east of the Albertine Rift, in Uganda, Southern Sudan, and Western Kenya (Kakamega Forest), belong to species and also to subspecies found in Zaire to the west of the Semiliki River (Moreau 1966). Lowland forest in Uganda is, however, impoverished in comparison with that in Zaire, with only about half the number of species. According to Moreau (1966, p 165), there was a postglacial colonization by lowland forest birds "as montane conditions evacuated the Lake Victoria basin". The nature of the vegetation which preceded lowland forest in Uganda would not, however, seem to be especially important for explaining this lowland avifaunal distributional pattern.

Only 38 species of birds are found in the East Coast forests (Moreau, 1966). About 7 of these are exceptionally widespread, some occurring, for instance, as far south as the Cape, and are of little palaeoenvironmental significance. Of the less ubiquitous taxa, some species show well-marked disjunctions with the Congo Forest Block (three of these are subspecifically different in the two areas), and there are three or four examples in which the coastal forms are regarded as specifically distinct from their relatives in the west. Moreau considers that the avifauna of the East Coast forests provides evidence for former forest connection, perhaps on two separate occasions, with the main Guineo-Congolian forests. This would have required more and better distributed rain, and somewhat higher minimum temperatures in the intervening zone (probably Uganda/Tanzania) than now (Moreau 1963a). Moreau envisages that connection is likely to have been pre-Pleistocene.

4. Montane forest birds

Moreau (1966) considers the significance of patterns of distribution shown by montane forest birds in relation to the following seven montane regions: Cameroon. East Zaire, Kenya, Ethiopia, Angola, Tanganyika/Nyasaland, and south of the Zambezi. "Abyssinia and Southern Africa apart, the size of the common element in the bird communities (of these areas) shows that these ecological islands, however widely separated, were colonized by an already integrated community rather than by a process of random (long-distance) dispersal, as in oceanic islands" (Moreau 1963b, p 32). Contact is envisaged to have occurred during glacial maxima when "the montane areas ... [now] isolated and individually circumscribed, ... formed one great block, much of it forested, extending from Abyssinia to South Africa with an arm reaching across to the Cameroons, as shown by the 500 m contour ..." (Moreau, 1966, p 98).

In a review of Moreau's book (1966), van Zinderen Bakker (1969) advocates caution in accepting Moreau's palaeoenvironmental hypotheses. He points out that, in most cases, a decrease in temperature is insufficient in itself to allow spread of montane forest; an increase in humidity is also required. Moreover, there are important differences between the numbers of species and endemics in the different highland regions (Table 5), suggesting differences in the environmental histories both of the regions themselves and of their intervals.

All but 6 of the 43 species of montane forest birds recorded from the Cameroon Highlands are endemic species or subspecies. This proportion is so great that "if an endemics 'score' is calculated for them on the same scale as for the bird faunas of the marine islands round Africa, this land-based ecological archipelago ranks equal to the highest of them ..." (Moreau 1966, p 201). Moreau believes that contact with the east may have occurred on more than one occasion. "Probably those species which are shared, and almost certainly those which show no subspecific distinction, have had a continuous range round the northern rim of the Congo basin as recently as the last phase of the Last Glaciation, while the differentiated representatives of superspecies may derive from stocks that reached their present isolated stations during an earlier phase or an earlier glaciation" (Moreau, 1966, p 199).

The East Zaire montane region (extending south to the mountains to the west and east (Mt Kungwe) of Lake Tanganyika is richer in species than the Cameroon and has as high a proportion of endemic species. According
Table 5
The number of montane forest birds found in and shared between various montane regions of Africa. After Moreau (1966).

<table>
<thead>
<tr>
<th>Montane regions</th>
<th>Cameroon</th>
<th>East Zaire</th>
<th>Tanganyika/Nyasa</th>
<th>Kenya</th>
<th>Ethiopia</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Species shared with at least one other region</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) Subspecifically identical</td>
<td>6A</td>
<td>7A</td>
<td>17A</td>
<td>12B</td>
<td>10C</td>
</tr>
<tr>
<td>(b) Subspecifically distinct</td>
<td>2B</td>
<td>42</td>
<td>27B</td>
<td>12B</td>
<td>11C</td>
</tr>
<tr>
<td>2. Endemic species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(a) With shared superspecies</td>
<td>8A</td>
<td>21</td>
<td>6A</td>
<td>3A</td>
<td>1B</td>
</tr>
<tr>
<td>(b) Other endemic species</td>
<td>8</td>
<td>12</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>TOTAL MONTANE FOREST SPECIES RECORDED</td>
<td>43</td>
<td>63</td>
<td>64</td>
<td>47</td>
<td>19</td>
</tr>
</tbody>
</table>

A. Shared with East Zaire;
B. Shared with other regions, apart from L. Zaire;
C. Shared with Tanganyika/Nyasa.
D. Shared with Kenya

to Moreau (1966, p 201) this may be due to its great extension and to its geographically central position, the latter making these highlands "accessible as a refuge from all directions as the total montane area of Africa shrank with the post-glacial rise in temperature". Few species are found from one end of the East Zaire region to the other and, as suggested by Moreau, a detailed investigation might prove of palaeoenvironmental interest.

From an avifaunal viewpoint, the Kenyan montane region runs southwards from the Imatong, Didinga, Kulal, and Marsabit Mountains to Northern Tanzania and eastwards as far as Mts Kenya and Kilimanjaro. "It is remarkable that the entire Kenya group, though it includes numerous montane forests that are isolated today contains only a single endemic species, *Francolinus jacksoni* (and that belongs to a superspecies represented in montane forests as remote as the Cameroons, Abyssinia and Angola). Moreover, within the Kenya group as a whole subspecific variation is limited – far more so than in the Tanganyika–Nyasa group ... – even in its most isolated components, namely Kalal and Marsabit" (Moreau 1966, p 205). (The biota of Kulal, Marsabit, and other isolated montane forests reproduce that of the central Kenyan highlands in a depauperate form.) "Taking the Kenya group as a whole, the affinities of the montane forest birds with East Congo are remarkably close. Two-thirds of the forty-seven Kenya species reappear in East Congo ... A further twenty of the thirty-two species common to the main Kenya highlands and to East Congo have not diverged subspecifically in these two areas. In fact the proportion of shared subspecies is three times as great as that between Cameroons and East Congo. Two factors will have contributed to this result: one is that the Cameroons montane forests are four times as remote from East Congo as are those of Kenya. The other is that, owing to the great height of the country between Kenya and East Congo, it would have remained suitable for montane biomes several thousand years longer, before communication was broken" (Moreau 1966, p 204). A quarter of all Kenya montane forest species are neither endemics nor shared with East Zaire, but are elsewhere found on mountains in the Tanganyika/Nyasa montane region. Wickens (personal communication) points out that, although it is now recognized that a dry period in Africa should be correlated with a glaciation in Europe, and a wet period with an interglacial, nevertheless this does not upset Moreau's reasoning.

Ethiopia is very impoverished with only 19 montane forest bird species, of which 3 are endemics (2 more than the equivalent figure for the Kenyan region). The bird fauna "as a whole suggests that Abyssinia has by no means been the centre of evolution for montane forest birds that it seems suitable to be, and that very recently on the evolutionary time-scale there has been interchange of species with Kenya – possibly from Kenya rather than the other way about" (Moreau 1966, p 208), "It seems that a catastrophe must have occurred that have overtaken the Abyssinian forest bird fauna, though not so total as to eliminate Paraphasmas and the turacos (the 3 endemic species). The area is much too extensive all to have been blasted simultaneously by the vulcanicity to which parts of the plateau have been subject. Any catastrophe must surely have been climatic; cold could not have driven the montane biota lower down the slopes; an annual rainfall so low or a dry season so unmitigated as to be intolerable to evergreen forest growth remains a possibility. Are we then to believe that the evergreen forest flora of Abyssinia survived when most of the associated birds succumbed or that it derives from a subsequent re-collonization? The latter hypothesis is favoured by the high proportion of bird subspecies shared with Kenya. One would like to have a thorough analysis of other animals from this point of view" (Moreau 1966, p 209). Mani (1968) discussed shortly the various possibilities such as glaciation, desiccation, low temperature and extensive fall of volcanic dust as causes of poverty in species in the Ethiopian high mountains. Moreau (1966, p 208) believes that "the not very considerable gaps between the montane stations on the way from Kenya are so dry that they are unlikely to have been bridged by suitable vegetation at even the height of the glaciation" and therefore that colonization must have been by long-distance dispersal.

There are 18 montane forest species of birds on the highlands of West Angola. Three are endemic species, 9 are endemic subspecies, and 6 are subspecifically identical to species in other montane regions. The conditions of isolation differ in this part of Africa from those elsewhere in that ecological specification has somewhat broken down. "Thus, whereas none of the birds of the Cameroons or the East Congo montane forests have been found in the intervening lowland forests or savanna, half the typically montane species that appear in the Angolan montane forest relicts do so sporadically also in fringing forest or more evergreen thicket at lower
altitudes either elsewhere in Angola or in Zambia" (Moreau, 1966, p 210-211). Moreau is uncertain as to whether or when connection with montane forests further east occurred.

The Tanganyika-Nyasaland montane region commences on the Kasigau and Teita Hills (Kenya) and extends down the eastern side of Tanzania to the south of Malawi. The proportions of endemic species and endemic subspecies are very similar to those of Cameroon. The degree of differentiation with respect to the East Zaire montane forest avifauna suggests that past ecological barriers between the two regions have been exceptionally effective (Moreau 1966). Since much of the ground between Ulipa and the mountains round Lake Nyasa is "at about the critical level of 1,500 m, it can only have been effective (as a barrier) if it was very dry" (Moreau 1966, p 213). Some bird species range widely over the isolated mountains of the Tanganyika/Nyasaland group, but others have much more restricted distributions. The Usambaraland and Uluguru Mountains are especially rich in species and have some noteworthy endemics, and there are also strongly marked endemic species on the Teita Hills. Indeed, within the isolated forests of the Kenya-Tanganyika border (the Usambaraland, the Pares, the Teitas and Killimanjaro), an area of only about 150 by 50 miles (240 by 80 km) there is a degree of subspecific differentiation without parallel elsewhere and for which Moreau can suggest no explanation. "The gaps are all so extremely narrow that the unequivocal evidence of reduced geneflow far exceeds expectation and is at variance with the much lower prevalence of subspeciation within the whole Kenya group from the Imatongs to Killimanjaro, where geographical conditions for subspeciation would seem more favorable, above all on Marsabit" (Moreau 1966, p 215).

South of the Zambezi, montane forests contain less than half the number of species found in montane forests in Malawi. Only one species, Pogocichla swynnertoni, "has a claim to have originated south of the Zambezi" (Moreau 1966, p 216), being limited to Gorongosa and neighbouring forests on the eastern border of Rhodesia. According to van Zinderen Bakker (1969), the Limpopo Valley seems to have been a very effective barrier for preventing the southwards spread of species.

5. Mammals

Accounts of the significance of distribution patterns shown by African forest mammals are given by Bigalke (1968), Booth (1954, 1957, 1958), Dandelot (1965), Guillaumet (1967), Kingdon (1971), Rahm (1966), and Tappen (1960). Bigalke (1968) notes that, so far as mammals are concerned, the forests provide a substantially homogeneous environment at the present time and that it is therefore noteworthy that only 30 per cent of forest mammal species are found throughout the entirety of the main Guineo-Congolian forest Region. There are three main centres of endemism, Liberia Gabon/Cameroon (south of the Sanaga River) and East Zaire (Ituri/Maniema) (Bigalke, 1968; Booth, 1957; Kingdon, 1971) and it is postulated that these were probably the sites of forest refuges during dry periods in the Pleistocene (Booth, 1957). The fauna of Liberia (Guinea Forest Block) is rather poor in species; it has probably been largely isolated from the fauna of the Congo Forest Block, from which it was probably originally derived (Booth, 1957). The fauna of the East Zaire refuge has the largest number of species, perhaps because it was the largest and the ecologically most varied, and because of its central position (Kingdon, 1971). A number of species show disjunctions between Gabon/Cameroon and Ghana/Libera (Table 6) and also across the Congo basin (e.g. Gorilla

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>E. Cameroon</td>
<td>13</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>E. Zaire</td>
<td>13</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>Sangha Basin</td>
<td>13</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>Gabon/Libera</td>
<td>13</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>Togo</td>
<td>13</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>13</td>
<td>14</td>
</tr>
<tr>
<td>Benin</td>
<td>13</td>
<td>14</td>
<td>12</td>
<td>11</td>
<td>13</td>
<td>14</td>
</tr>
</tbody>
</table>

Table 6 Distribution of Primates, Sciuromorpha, Artiodactyla and Hyracoidea in high forest from Sierra Leone to Gabon.

---

78

79
Recent forest spread across Nigeria is shown by the relative poverty of their forests (Booth, 1954, 1957; Tappen, 1960; Table 6) and into the Congo basin by the rarity of endemic mammal species south of the Congo River, in spite of the barrier to dispersal that this might be supposed to present (Kingdon, 1971; Rahm, 1966: Table 7).

| Region 1: north of the Congo River and west of the Obangi River: | 11 species |
| Region 2: south of the Congo River: | 3 species |
| Region 3: east of the Obangi and Congo Rivers (lowland forest): | 7 species |
| Region 4: highlands along the western edge of the Rift (montane forest): | 8 species |
| Region 1 + Region 3: | 11 species |
| Region 3 + Region 4: | 8 species |

(No mention is made of endemic species occurring in other combinations of regions.)

A review of the geography of West African Primates is given by Booth (1958). He argues that, during dry climatic phases, the Guinea Forest Block was not only much more completely isolated from the Congo Forest Block than now, but furthermore was fragmented. One refuge was situated west of the Cavally River (Liberia) and another perhaps between the Comoé and Tano Rivers (E. Ivory Coast/W. Ghana). In these two refuges, the monkey fauna was isolated sufficiently long to enable differentiation to take place in the majority of cases. Booth thinks that, since the Volta constitutes a less formidable geographic barrier than the Niger, recolonization of the area between the Volta and Niger Rivers, which was probably completely denuded of forest at times during the Pleistocene, has been easier from the west. During the last dry phase, not all forest between the Volta and Niger was destroyed, a minor refuge persisting west of the Niger "either in Riparian Forest or in the Benin area" (Booth, 1958, p. 164). The presence of two species of Primates north, but not south, of the Sanaga River indicates that another refuge of minor importance may have been situated in Northern Cameroon, that is to the north of the main S. Cameroon/Gabon refuge (Booth, 1958). A different interpretation of primate distribution in West Africa, though without reference to Booth's papers, has been expressed by Dandelot (1965), who notes that the Sassandra River (W. Ivory Coast) provides the divide between nearly all subspecies of

forest Cercopithecidae within the Guinea Forest Block and that this is related to differences in the types of forest found on either side of the river. No indication is given that climatic changes could have influenced this pattern of distribution. Dandelot finds a similar correlation between the distribution of monkeys subspecies and forest type in the Congo forests.

The number of species of forest mammals decreases regularly from the Ituri River eastward to the Indian Ocean, the Usambara/Lower Tana lowland forests and the Kilimanjaro forests containing, for instance, only 9 per cent and 3 per cent respectively of the number of species found in the Ituri fauna (Misoon, 1963, quoted in Bigalke, 1968). Kingdon (1971) presents a detailed analysis of forest mammal distribution in East Africa. He considers that there are two colonization routes from west to east, one across Uganda to the Kenyan Highlands and the other around the south of Tanzania and on to the coast. Forests on the northern route carry mammal populations which are generally indistinguishable from those in East Zaire, implying recent spread (Kingdon, 1971; Tappen 1960). The Nile may have prevented the eastwards movement of some species. In contrast, forests on the southern route contain some endemic species and most of the remaining species are recognized as subspecifically distinct from those on the northern route; the pattern suggests spread from the west followed by a barrier of long duration (Kingdon, 1971; Tappen, 1960). (Previous connection between the main Guinea-Congolian forests and those near the east coast of South Africa has been proposed by Balinsky (1962).) There may have been a succession of forest connections along the southern route, allowing the fauna to be augmented or changed (Kingdon, 1971). The northern and southern routes meet approximately between the Usambaras and Kilimanjaro, with some overlap north of this line (Kingdon, 1971).

### 6. Butterflies

Carcasson (1964) has published an excellent paper on the significance of distributional patterns shown by butterflies in Africa. The following account is extracted from his work. Two geographical divisions for forest forms are recognized, the Lowland and Highland Forest Divisions.

Lowland forest butterflies fall into two sub-divisions, the Western Sub-division, encompassing the main Guinea-Congolian forest region, and the Eastern Sub-division, comparing the East Coast forests. The latter subdivision is poor in species, but most of those that do occur are either endemics or else very distinct subspecies of genera which are much better represented in the western forests. The distinctiveness of East Coast butterflies suggests that broad-based connections between the western and eastern forests is ancient, probably Miocene. If more recent connections occurred, they must have been incomplete and would probably have been by way of Southern Tanzania.

The distribution of butterflies in the Western Sub-division is believed to be influenced more by the positions of past forest refuges than by present-
day ecological barriers. "The vast equatorial forest itself no doubt contracted drastically during the interpluvials, possibly even breaking up into limited regions surrounding elevated areas of exceptionally high rainfall (forest refuges) … The fact that many forest butterflies are represented by fairly distinct races in Upper Guinea, in the Cameroons and Gabon and in the east Congo and Uganda, would appear to support this possibility" (p 130). Four zones of the Western Sub-division are recognized. 1. The Western Zone, which includes the Guinea Forest Block and the forests of Western Nigeria, is poor in species, but has evolved a considerable degree of subspecific differentiation and a number of endemic species. The Cross and Niger Rivers, rather than the Cameroon Highlands or the Dahomey Gap, mark the distributional limits of many West African populations. 2. The Central Zone (Cameroon and Gabon) and 3. the Congolese Zone (Zaire) are both very rich in species, the main centres of diversity lying on either side of the Congo basin. The differences between these two zones are mainly at the subspecific level. 4. The Ugandan Zone is poorer in species than the Congolese, its eastern extremity (Kakamega Forest) being very impoverished. In contrast to Southern Zaire, fragmentation of forests in Uganda has caused much peripheral subspeciation. "Much of the southern Congo is occupied by tall grasses and small, fire-resistant trees; the fact that this area enjoys a climate and soil capable of supporting true lowland forest suggests that it was covered with forest until recent times and that its denudation was the work of man (Aubréville. 1949). This is also confirmed by the many small relics separated from the main forest by up to four degrees of latitude, which show little subspeciation and seem to have suffered very little faunal impoverishment" (p 136).

The close similarity between the butterfly faunas of the various montane forests of Africa is attributed to the former connection of their biota during moist and cool pluvial phases. Despite this similarity, seven geographical montane butterfly zones are recognized (one of which, the Angolan Zone, is poorly known and is not mentioned below). 1. The Cameroon Zone is poor in species, has few endemics, and shares some species with montane zones to the east. 2. The Kivu/Ruwenzori Zone is probably the richest in species, with many endemics. This is attributed to its persistence as a refuge area for montane species. 3. The Ethiopian Zone is poorer in species than either the Kivu/Ruwenzori or Kenyan Zones, but contains a number of endemic species, as well as many endemic subspecies. The high degree of endemism gives proof of its isolation. 4. The Kenyan Zone is divided into two by the Rift. The highlands of Western Kenya and Eastern Uganda, can be regarded as an impoverished version of the Kivu/Ruwenzori Zone; the butterflies of Mt Kenya and the Aberdares are more closely related to those of the Ethiopian highlands. 5. The Tanganyika/Nyasa Zone is separated from the Kenyan Zone by a narrow strip of semi-desert north of Kilimanjaro. There are many endemic species and very distinct subspecies. The montane forests of Kilimanjaro, Meru, Ngorongoro, and the Chyulu Hills are considerably poorer in species than those along the broken eastern edge of the tableland, including those of the Nguru, Pare, Uluguru, and Usambara Mts. 6. The chief character of the South African Zone, south of the Limpopo, is its poverty and there are few endemics.

7. Molluscs

Verdier (1972) has published an account of the zoogeography of the non-marine Mollusc of East Africa. "In general the distribution of molluscs in East Africa is explainable by the great increase in the area of evergreen forests during the pluvial periods — this will also fit in with the observed affinities with the Congo, West Africa and Natal. Even where continuity was broken by drier country, connections were often available along riverine gallery forest or the distances involved were inadequate to prevent dispersal by indirect means. For instance the Kulal and Marsabit Forests could never have been in direct contact yet their fauna and that of Mount Nyeri must all have been derived from the same common source as that of the rest of the montane forests. When a more detailed knowledge of the distribution of species is available on a level with that worked out for birds and butterflies it may be possible to actually plot the approximate pathways various components of the fauna took" (p 303).

SOME NON-FOREST DISTRIBUTIONS

Similarities between the plants and animals of the south-western and northern arid regions of Africa provide evidence for a more arid climate in the intervening area in the past (Bigalke 1968; de Winter 1971; Kingdon 1971; Lebrun 1971; Monod 1971; van Zinderen Bakker 1968; Verdier 1969; Weger 1973; Winterbottom 1967). It seems that, although there has been a relatively recent connection, this was insufficiently long or the climate in the interval was insufficiently dry to allow complete exchange of biota. This is shown by the large number of endemic species in the South-West Arid Zone and, to a lesser extent, in the Somal Arid Zone (Milne-Redhead 1954/55) and by the fact that many of the disjunct species belong to sub-desert rather than true desert forms (Kingdon 1971).

There are similarities and dissimilarities between plants and animals of the northern and southern savannas, the faunal divide between the two (the Sclatere Line) running from the fringes of the Congo basin to the Tana River (Bigalke 1968; Kingdon 1971). A former eastwards extension of forest, interrupting the savanna belt, is suggested (Bigalke 1968). The great climatic and topographic diversity of the southern savannahs may account for their great number of species (Kingdon 1971).

DISCUSSION AND CONCLUSIONS

I begin with the mammalian evidence, since the uncertainties associated with the possible spread of taxa by long-distance dispersal are minimized.
According to authors, there seems little doubt that the East Coast forests have been isolated from those further west for a long time, but that at some stage forest connection or connections did occur. In the west, forest mammals and, by implication, forest have spread out fairly recently from a number of small refuges in the Guinea Forest Block and from two larger refuges situated on either side of the Congo basin. In the Southern Cameroon/Gabon area and to the west of Ruwenzi/Kivu. Despite minor recent connection, the Guinea Forest Block has been rather isolated from the Congo Forest Block; the degree of isolation is, however, less than in the case of the East Coast forests. This general picture of forest history is supported by the distributional patterns shown by lowland forest plants, birds, and butterflies. Many East Coast forms are distinctive and, in the west, there tend to be centres of endemism and species richness in the same localities as for mammals.

It could be argued that the centres of endemism and species richness mentioned above are associated with particular environmental characteristics, rather than being due to historical factors. There is probably some truth in this view, but two arguments oppose it as a general explanation. First, it conflicts with the opinions of many workers, familiar with both the taxonomy and ecology of their groups. Second, it is unlikely to account for the existence of disjunctions shown by taxa judged to be very poorly adapted for long-distance dispersal.

The reduction in extent of lowland forest which has occurred in the recent past in West and Central Africa must have been caused by climatic conditions vastly different from those which prevail at the present time. Changes in humidity are sufficient to account for the vegetational changes; depending on one's view of the lowland/montane forest boundary, it is unnecessary to invoke changes in temperature, though these could have occurred. Van Zinderen Bakker (personal communication) is of the opinion that temperature changes are primary to variations in humidity. This is well demonstrated for the last glacial maximum in Africa and also for the important onset of the general rise in temperature at about 12,000 BP.

It is fortunate that there is, by now, a substantial body of evidence relevant to the dating of at least the latter part of the period of forest contraction and of the subsequent forest expansion. Much of this has been summarized by Burke et al. (1971), De Ploey (1968), Grove (1972), Grove and Goodie (1971), Grove et al. (1975), Hamilton (1974b), Richardson et al. (1972), van Zinderen Bakker and Coetzee (1972), and Wickens (1975b). Briefly, it seems that the climate of large parts of tropical Africa was much more arid than now from before 25,000 BP to about 12,000 BP, this date marking a major change to a moister climate. There have been subsequent climatic fluctuations of a relatively minor nature; a drier period after 7,000 BP, in combination with deforestation by man, is likely to have caused the recent forest retraction noted by some authors. Pollen diagrams from Uganda show that lowland forest spread across the country at about 12,000 BP (Hamilton 1972; Kendall 1968; Livingstone 1967) and there is no reason to suppose that, elsewhere, forest expansion was not contem-
patterns shown by montane populations takes on a different hue to that subscribed to by most authors. There is a similarity between the patterns of endemism and species richness shown by montane and lowland forest organisms. The three main centres of species richness and/or endemism for montane taxa are the Cameroon Highlands (associated with the Southern Cameroon/Gabon lowland refuge), the highlands of Eastern Zaire and neighbourhood (associated with the East Zaire lowland refuge), and the Tanganyika/Nyasa highland area, especially the Usamburas and Ulugurus (associated with the East Coast lowland refuge). This coincidence can hardly be accidental and should be useful for the reconstruction of palaeo-climates. Judging by the evidence as a whole, it is postulated, first, that these three montane regions have constituted the major areas for survival of montane forest organisms during unfavourable (dry) periods during the Pleistocene and, second, that they have been isolated from one another for a long time. As with the lowland forest refuges, this generalization does not preclude the occasional movement of some species of plants and animals from one region to another. There are differences both in the degrees of differentiation of the various groups of organisms in the same region and in the degrees of distinctiveness of the biota of different regions. The former may be related to different average rates of evolutionary change in different groups and to the relative abilities of different types of organisms to travel by long-distance dispersal. The latter may be associated with the geological ages of the mountains. Inadequate knowledge of the status of the lowland/montane forest boundary and of the long-distance dispersal abilities of taxa makes it difficult to be certain whether montane forest ever extended across the intervals between these areas.

The distributional evidence is consistent with the hypothesis that many species of mammals, montane butterflies, montane birds, and moist montane forest plants have colonized the highlands of Kenya and Ethiopia from Eastern Zaire and, less importantly, from the Usambura area. Rarity of subspeciation suggests fairly recent spread and it is perhaps possible that many species migrated following the increase in humidity at 12,000 BP. However, the slow rates of differentiation in isolated populations indicated by species disjunct across the Congo basin (used as a standard for these comparisons) shows that earlier colonization by some or all species is a possibility. The wide ranges of many dry montane forest plants in the eastern half of Africa and the presence of a few endemics, most notably in (Northern ?) Ethiopia, suggests that, although conditions were unfavourable for the survival of many montane forest organisms, impoverished montane forest was able to persist, at least locally.

The absence of any suggestion in pollen diagrams that montane trees grew in lowland Uganda before invasion by lowland forest (though this evidence cannot be regarded as conclusive) and the unlikelihood, in any case, that the climates of either the Ugandan or the Kenya/Ethiopian montane intervals would have been suitable for any type of montane forest during the last 25,000 years, indicates that many montane forest species have spread from Western Uganda to the Kenyan highlands and from the latter to Ethiopia by long-distance dispersal. Actually, many authors (eg Moreau 1963b) have accepted long-distance dispersal for the crossing of the Kenya-Ethiopian interval by some montane forest species and the Ugandan interval is only slightly wider and may well have provided more favourable environments for the survival of montane species during their journeys. The distribution of mammals in Uganda and Kenya strongly supports this interpretation of montane forest history since they display a single pattern of distribution within the area, that is of increasing poverty from west to east, and since they lack both the capacity for long-distance dispersal and a clear differentiation in lowland and montane forms.

The very interesting differentiation of species on closely situated mountains in the Usambara region requires explanation since, at first sight, it would appear to oppose the arguments for mobility expressed above. I suggest that at least some of these mountains continued to carry montane forest during Pleistocene dry periods and that, although occasional individuals of montane species have travelled between them, the presence of already established populations has either opposed their survival or, if interbreeding occurred at all, that the new genes have been lost, either through sterility or through introgression with established populations. The situation is analogous to that suggested for oceanic islands by Mayr (1969).

Figure 1 illustrates some of the ideas mentioned above.

20,000 BP

8,000 BP
Today
Distribution of forest mainly follows Aubréville et al (1958), with some revision for montane areas in West Africa after Chapman and White (1970), Moreau (1966). Not all the areas marked as montane forest now carry forest, but probably did so before deforestation (minor montane areas omitted). Natural limit of forest after Aubréville (1949), with revision after Aubréville et al (1958). Dune limit after Grove and Warren (1968).

Footnote
Laurent (1973) provides a map, based on the distribution of amphibians and reptiles, showing postulated refuge areas during periods of contraction of the African lowland tropical forest.
Six areas are proposed, five of which are at the same localities (though larger in size) as those shown on the top map of Figure 1. The sixth area is situated to the south of the Congo River between the latitudes of about 10° and 26° East.

Acknowledgements
I greatly appreciate the trouble taken by the following scientists for sending me their views in connection with the preparation of this manuscript: Prof. F. Bourlière, Prof. J. de Ploey, Dr A. T. Grove, Dr P. J. Grubb, Mrs B. P. Hall, Dr J. Hall, Dr O. Hedberg, Dr B. Hopkins, Dr J. Kingdon, Dr A. Kortlandt, Prof. E. Mayr, Prof. P. J. Newbould, Dr R. M. Polhill, Prof. P. W. Richards, Dr B. T. Styles, Dr T. J. Synott, Dr B. Verdcourt, Dr M. J. A. Weger, Dr F. White, Dr G. E. Wickens, Prof. E. M. van Zinderen Bakker, Prof. J. K. Morton, also Mrs E. Doherty, Mrs I. McLean and Miss P. Galbraith for typing the manuscript at short notice.

References


Bigalke, R. C., 1968, Evolution of mammals on Southern continents, 3. The con-

Figure 1. The distribution of forest in Africa 20,000 - 0 BP, following ideas presented in the text.

Bonnefille, R., Palynological evidence for an important change in the vegetation of the Omo basin between 2, 5 and 2 million years. Manuscript.


1957 The Niger, the Volta and the Dahomey Gap as geographical barriers. Evolution, 12, 48-62.


Grove, A. T.,
Grove, A. T., Goudie, A. S.,
Grove, A. T., Pullan, R. A.,
Grove, A. T., Street, F. A., Goudie, A. S.,
Grove, A. T., Warren, A.,
Groses, C. P.,
1971, Distribution and place of origin of the gorilla. Man, 6, 44-51.
Grubb, P. J.,
Grubb, P. J., Lloyd, J. R., Pennington, T. D., Whitmore, T. C.,
Guillaumet, J. L.,
Hall, B. P., Moreau, R. E.,
Hall, J. B.,
Hall, J. B., Medler, J. A.,
Hamilton, A. C.,
Hedberg, O.,
Jardine, N.,
Keay, R. W. J.,
Kendall, R. L.,
Kenworthy, J.,
Kingdon, J.,
Kingston, B.,
Laurent, R. F.,
1973, A parallel survey of equatorial amphibians and reptiles in Africa and South America. pp 259-266, In: Tropical forest

Lebrun, J., Gilbert, G.,

Lebrun, J. P.,

Léonard, J.,
1965, Contribution à la subdivision phytogéographique de la Région guinéo-congolaise d'après la répartition géographique d'Euphorbiaceae d'Afrique tropicale. Webbia, 19, 627-649.

Liben, L.,

Livingstone, D. A.,

Logan, W. E. M.,

Mani, M. S.,

Marchant, S.,

Martin, P. S.,

Mayer, E.,

Melville, R.,

Milne-Redhead, E.,

Missonne, X.,

Monod, T.,

Moreau, R. E.,


Morrison, M. E. S.,

Morton, J. K.,


Polhill, R. M.,
Rahm, U.,

Richards, P. W.,

Serle, W.,

Tappen, N. C.,


van Zinderen Bakker, E. M., Sr,
1968, Biogeography. Palaeoecology of Africa, 4, 139-162.

van Zinderen Bakker, E. M., Sr, Coetzee, J. A.,

van Zinderen Bakker, E. M., Jr,
1973, Ecological investigations of forest communities in the eastern Orange Free State and the adjacent Natal Drakensberg. Vegetatio, 28(5-6), 299-334.

Verdcourt, B.,
1969, The arid corridor between the north-east and south-west areas of Africa. Palaeoecology of Africa. 4, 140-144.

Weimarck, H.,
1941, Phytogeographical groups, centres and intervals within the Cape Flora. Lindes Universitets Årskrift, NF, med. 2, 37(5).143 pp.
1973b, Phytosociology of the Upper Orange River Valley, South Africa. Pretoria.

West, R. G.,

White, F.,

Wickens, G. E.,
1975b, Changes in the climate and vegetation of the Sudan since 20,000 BP. Boisser. 24, 49-65.

Wild, H.,
1968, Phytogeography of South Central Africa. Kirka. 6, 197-222.

Williams, M. A. J., Adamson, D. A.,

Winterbottom, J. M.,