Disjunctions of montane forest birds in the Afrotropical Region

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Abstract. Geographical disjunctions of montane forest birds in the Afrotropics are explained in assuming that the crossing of the lowland forest, for example between Mt. Cameroon and the mountains around the Albertine Rift, occurred during interglacials. The probable route taken can still be seen by the present distribution of transitional forest species and it can be supposed that the montane forest birds have followed the same way. The disjunct pattern appeared when, during a subsequent glacial, the forest disappeared in most parts of the Afrotropics and the birds remained trapped on forested mountain blocks. Moreau (1966) indicated the favourable climatic conditions permitting montane forest species to reach lower altitudes, and I assume that these conditions existed during especially rainy and humid interglacials. The direction of the crossing, from east to west or vice versa, can be suggested by the general distribution of the superspecies or species in the Afrotropical Region. Most taxa seem to have crossed the lowland forest from east to west. The degree of differentiation is admitted to be correlated with the length of the isolation period. An idea of the ancientness of the crossing results from the divergence found for related taxa on the two mountain blocks.

Key words. Montane forest birds disjunctions, Afrotropics, Lowland forest crossing during interglacials.

Introduction

It has long been noted (Sharpe 1893, Reichenow 1900/01) that the forest avifaunas of Afrotropical mountain ranges are closely related and that this similarity, including highly sedentary species, could only be explained by former forest connections between the now isolated mountain blocks. Chapin (1923, 1932) suggested that climatic changes (temperature, rainfall) of the past had permitted a great extension of the montane forest, thus connecting montane areas now widely separated by lowland forest. Lönnberg (1926, 1929) particularly developed the idea that the present distribution of animals, especially birds, is the result of past climatic changes. Until recently it was believed (Moreau 1952, 1954, 1963, 1966, 1969) that these connections took place during glacials, when the cooler conditions would have permitted a greater extension of montane forests. This pluvial theory is well known and I will only give its summary. Moreau (1963) supposed that a temperature reduction of 5 ° C, during a glacial maximum, would have the effect of lowering the montane forest limits in tropical Africa from around 1500 m to 700—500 m. In the same time the decrease of the temperature was accompanied by increased precipitation. The montane forest would undergo a great extension, and free interchange between the mountain regions would have been possible during glacials. During interglacials, the climatic effects would have been the reverse of those of the glaciations. The higher temperature would have increased the lower limit of the montane forest in tropical Africa and would lead to a contraction of the present montane forest islands. The present disjunctions of montane
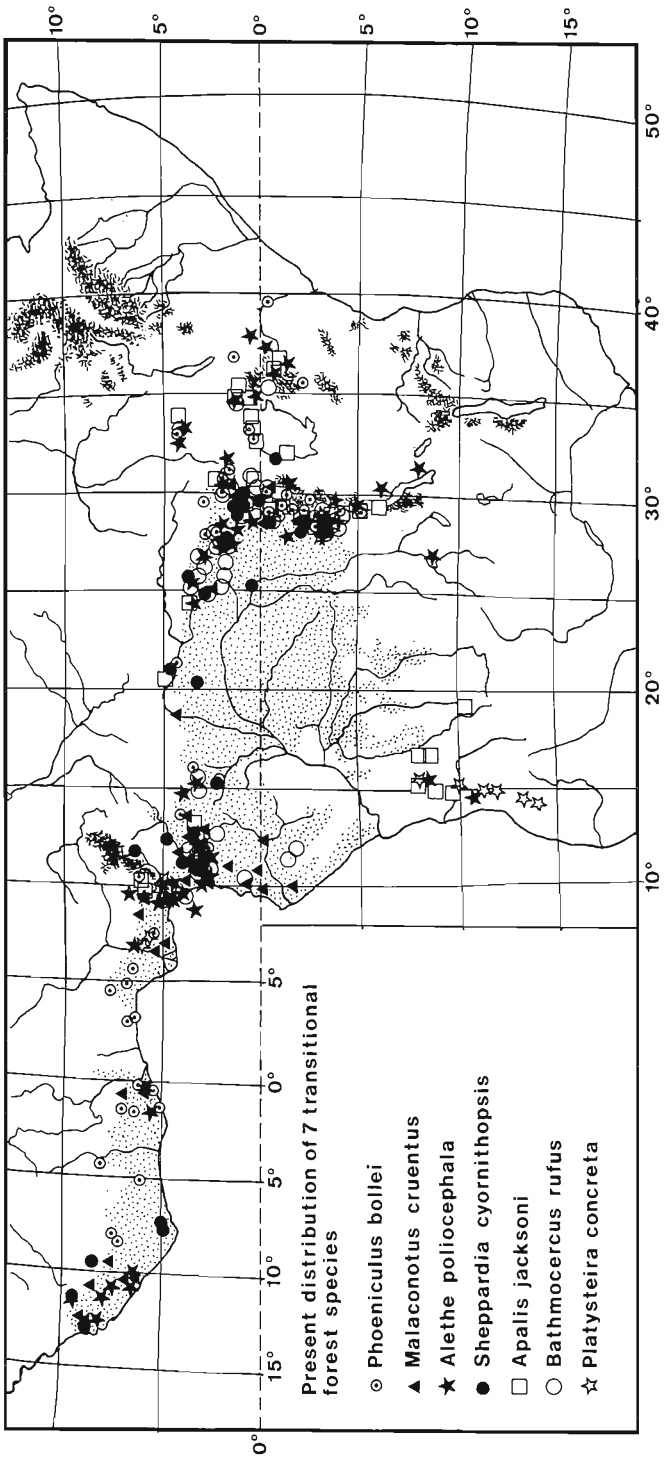
Fig. 1: Present distribution of 7 transitional forest species.

Present distribution of 7 transitional
forest species

- ⊙ Phoeniculus bollei
- ▲ Malaconotus cruentus
- ★ Alethe poliocephala
- ● Sheppardia cyornithopsis
- □ Apalis jacksoni
- ○ Bathmocercus rufus
- ☆ Platysteira concreta

forest birds are thus a consequence of the fragmentation of a continuous range existing during glacials.

Hall (1963) in her review of *Francolinus* accepted Moreau's point of view and considered the isolated populations associated with high altitude evergreen forest as relicts from a cold and wet epoch, when the montane forest and the group as a whole had a more or less continuous distribution between the extreme points where they are now found. Hall (loc. cit.) published a map of the assumed distribution of montane forest and the connections between the various mountain blocks, in a cold and wet area, and another map showing the immense area covered by forest in a warm and wet area.

Livingstone (1975) noted that many montane species are highly temperature sensitive and that some populations of the species are widely disjunct from their nearest relatives. He suggested moreover that montane forest species were able to extend their range into lowland forest, when the climate was wet between 10,000 and 7,000 B. P.

Although the distance is much shorter between East Africa and the Ethiopian highland than between central Africa and Cameroon, only few birds were able to achieve the south-north passage across very dry country, while many montane forest birds took the more humid east-west route.

Paleoclimatologists (see Livingstone 1975, for earlier references) have added new facts to our knowledge about the vegetational cover of the Afrotropical Region, during glacials and interglacials: the glacials correspond to very arid periods and even if the temperatures were low enough to move the montane forest boundaries to lower altitudes, the aridity was too high to support forest.

These climatic conditions during glacials have been accepted by all biologists, especially ornithologists dealing with the Afrotropical Region (Livingstone 1975; Hamilton 1976, Diamond & Hamilton 1980, Crowe & Crowe 1982, Diamond 1985). Thus, during the cold and arid glacials, montane forests were reduced, while lowland forests mostly disappeared except in refugia (core areas). For this reason Moreau's hypothe-
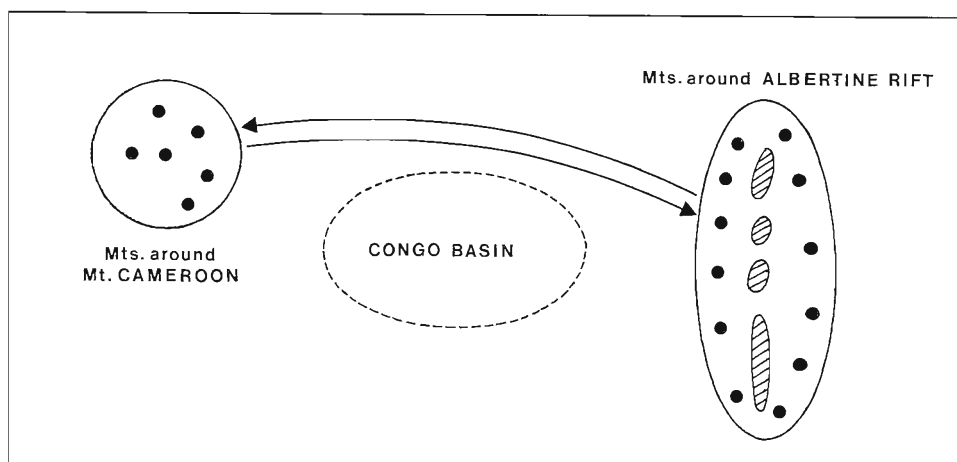

Fig. 2: Crossing the lowland forest between the mountains around the Albertine Rift and the mountains in the region of Mt. Cameroon, during especially wet interglacials. ● mountain blocks.

sis of montane forest connections during glacials cannot explain the disjunct distri-
bution of montane forest species. Necessarily, the forest species found their way to
present-day isolated montane forests not in crossing a more or less arid savanna, but
in traversing the lowland forest at suitable periods, i. e. during interglacials.

Diamond & Hamilton (1980) explain disjunct distribution by lowland forest pene-
tration of montane species when the competition was reduced, during the short period
of time when the lowland forest expanded at the end of a former dry period. Howe-
ver, the invoked lack of competition is inadequate to explain the penetration of the
lowland forest by montane forest birds, as part of the most important refugia, as the
Albertine Rift and the Cameroon-Gabon refugia, also include lowland forest. There-
fore, it can be assumed that during the expansion of the forest at low altitude, after
a dry period, the lowland forest species coming from the refugia will be the first to
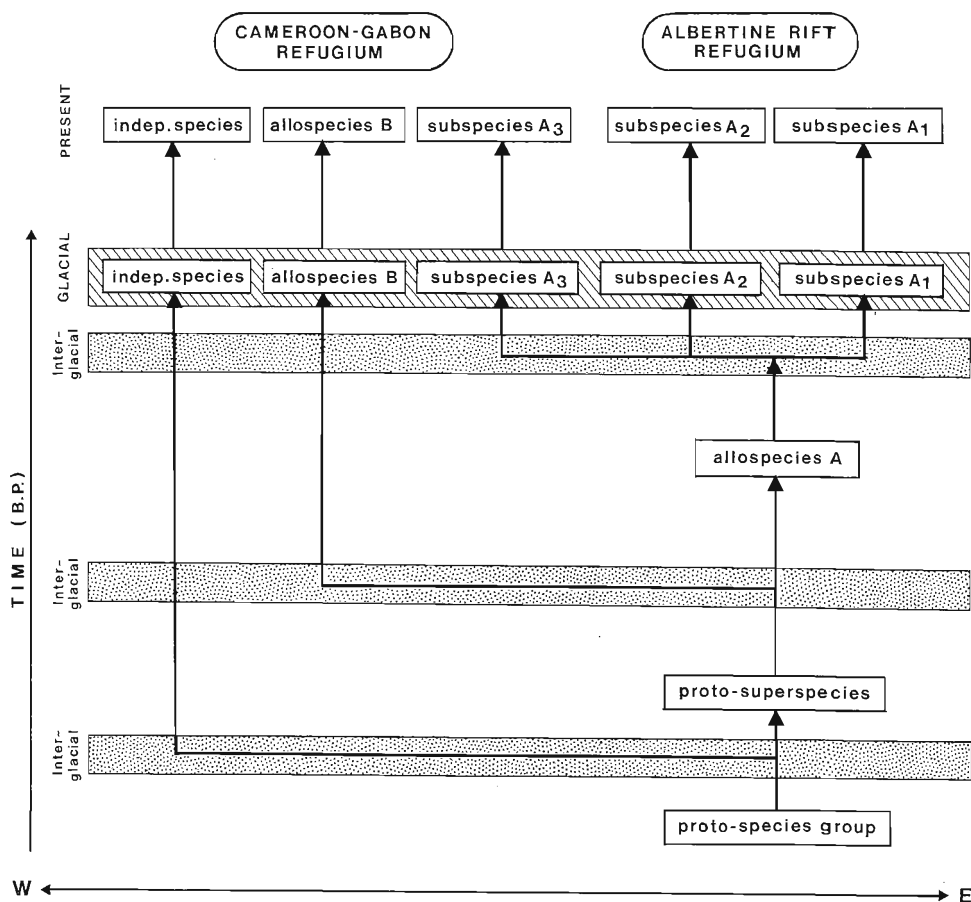occupy the new niches which appear in the expanded parts of the lowland forest.

Fig. 3: Crossing the lowland forest between the two mountain blocks at different periods: a.
crossing during the oldest interglacial for independent species; b. crossing during an intergla-
cial of medium antiquity for allospecies; c. crossing during a recent interglacial for subspecies.
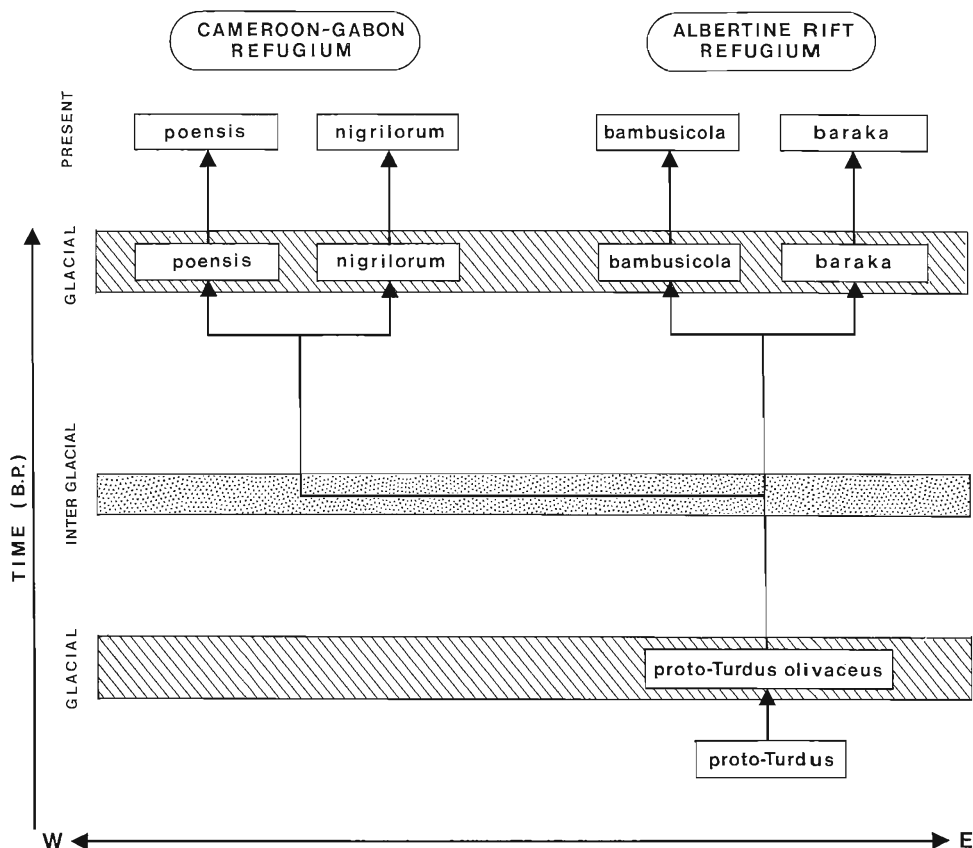Directions: W = west, E = east.

Fig. 4: Subspeciation of *Turdus olivaceus*: a. differentiation of *T. olivaceus* in the Albertine Rift refugium; b. crossing of the lowland forest during an interglacial; subspeciation in the two refugia during a subsequent glacial.

Explanation for the crossing of lowland forest by montane forest birds

How can one explain that the crossing of the lowland forest by montane forest species was possible when humid and relatively warm conditions prevailed? The answer to this question was given, in fact, by Moreau (1966) himself, who mentioned that in two regions near the tropics, where rainfall and humidity are exceptionally high, the montane birds come down to much lower altitudes than in most other places of tropical Africa where this limit is about 1500 m. This abnormal relation between the montane/lowland forest boundery and the temperature exists on the East Usambara Mts. and on Mt. Cameroon. On the East Usambara Mts. montane forest birds predominate as low as 900 m, while on the south-east face of Mt. Cameroon, where the temperature is slightly lower than on the East Usambara Mts., this limit is even 600 m.

I assume, in conformity with Moreau's findings (Prigogine, in press), that high rainfall and humidity have a great influence on the altitudinal range of montane forest

birds, and that during wet periods they would have crossed, at several occasions, the lowland forest which separates the various mountains, at altitudes of 600—900 m. Later, during a subsequent dry period, the lowland forest disappeared progressively and the stenoecious montane forest species remained isolated on the mountain they had reached.

I will limit my considerations to the mountains near Mt. Cameroon (including Fernando Po) and the mountains around the Albertine Rift. The lowland forest between these two mountain blocks represents a large distance to cross, ca. 2300 km. The altitudes in the Congo basin are below 500 m, but they rise to 500—1000 m on its northern rim. Thus the route taken by the birds crossing the lowland forest can be situated in the northern part of the principal Lower Guinea forest block where the altitudes are higher. I have chosen seven species found principally in the transitional forest of eastern Zaire (*Phoeniculus bollei, Apalis jacksoni, Bathmocercus rufus, Platysteira concreta, Alethe poliocephala, Sheppardia cyornithopsis, Malaconotus cruentus*). They are absent in the Congo basin, but they are found north of it (Fig. 1). It can be assumed that montane forest birds have taken the same way during especially humid interglacials (Fig. 2). There is no reason to suppose that these species passed round the Congo basin by the south. The distance is much greater and the floristic composition of the forest south of the Congo basin is different of that found in the north.

Different ranks of related taxa are present on the two mountain blocks. It is generally admitted (Vuilleumier 1980, Cracraft 1983) that the degree of divergence of two isolated forms, having a common ancestor, is in correlation with the length of the isolation. Therefore, for independent species forming a species group, isolated on mountain ranges, the crossing occured longer ago than in the case of allospecies. The birds having crossed the lowland forest more recently are those where the differentiation reached only the subspecific level. This is shown very schematically in Fig. 3. Yet, the various orders and families do not differentiate at the same rate and it has been suggested that non-passerines need more time for speciation than passerines (Vuilleumier 1970; Prager & Wilson 1980).

Table 1 gives a list (not complete) of related taxa which are found on or near Mt. Cameroon and on the mountains around the Albertine Rift. They are indicated in increasing taxonomic rank (populations, which may be monotypic species or same subspecies, different subspecies, allospecies, independent species) (categories D to A, see Table 2).

In order to achieve information about the passage direction, either from east to west or in the opposite direction, I have considered the general distribution of the superspecies or species. Thus, if other members of the taxon are also present on the Kenya highlands, I have assumed that it has originated in the Albertine Rift refugium. Based on this hypothesis, I suggest that most (85 %) of more or less related species have probably their origin in the Albertine Rift refugium and have crossed the lowland forest from east to west. For eight taxa I am not able to suggest the direction of their passage. Since the Albertine Rift is the most important in west central Africa near the Equator, the greatest number of forest species have their origin in this refugium (Prigogine in press) and it can be expected that, during interglacials, they colonized other mountain blocks in the tropics.

What is the ancientness of the crossing of monotypic species (category D 1)? It is possible that the gene flow still occurs between isolated populations, as for *Columba albinucha*, which has a great flying capacity, and which is able to cross great distances, and has, moreover, been collected in eastern Zaire as low as 630 m (Prigogine 1971). But, in most cases, the monotypic species are sedentary birds and gene flow is out of question. It can be presumed that the isolated populations are not exposed to a strong selection pressure and that the environmental conditions are approximately the same and do not lead to a differentiation in spite of the isolation. Thus, I cannot give an appreciation of the date when these birds (category D 1) spread out. For populations formed by the same subspecies (category D 2), in spite of the great distance separating the two mountain blocks, the crossing occurred probably quite recently and the birds had no time to differentiate on the other mountain block.

When the same species inhabits the two mountain blocks and is represented in one by one subspecies and by several subspecies on the other, it has been supposed that, during a glacial, the species crossed the lowland forest and differentiated later in subrefugia during a subsequent glacial (for example *Apaloderma vittatum* which differentiated in the region of Mt. Cameroon in *francisci*).

When the same species is encountered in the two mountain blocks and is represented by several subspecies in each, it is assumed that the species, present during a first glacial in one of the refugia, succeeded, during an interglacial, in crossing the lowland forest, then differentiated in each refugium during a subsequent glacial (Fig. 4).
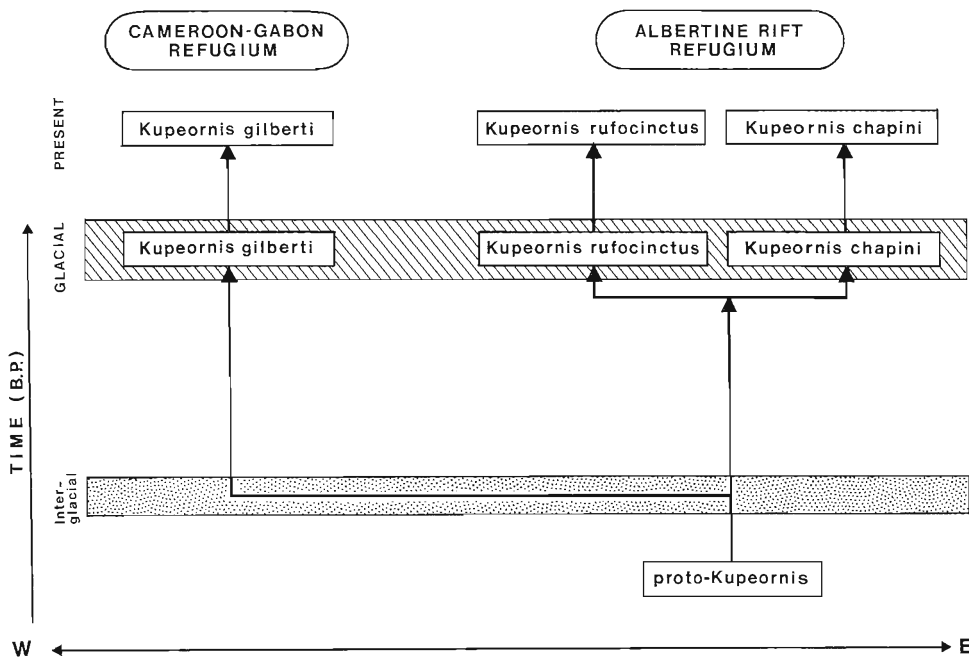

Fig. 5: Speciation of the superspecies *Kupeornis rufocinctus*: a. crossing of the lowland forest during an old interglacial by the common ancestor of the superspecies; b. evolution in one allospecies in the Cameroon-Gabon refugium, and in two taxa which are allospecies in most subrefugia of the Albertine Rift refugium, except in the Itombwe highland where they are paraspecies.

Table 1: List of taxa found in the region of Mt. Cameroon and on the mountains around the Albertine Rift.

Mt. Cameroon	Albertine Rift	Category	Direction of spread
Monotypic species		D 1	
Columba albinucha	*Columba albinucha*		W ← E
Laniarius luehderi	*Laniarius luehderi*		W ← E
Alcippe atriceps	*Alcippe atriceps*		W ← E
Kakamega poliothorax	*Kakamega poliothorax*		W ← E
Ploceus insignis	*Ploceus insignis*		W ← E
Same subspecies		D 2	
Coracina caesia pura	*Coracina c. pura*		W ← E
Apalis c. cinerea	*Apalis c. cinerea*		W ← E
Cryptospiza r. reichenovii	*Cryptospiza r. reichenovii*		W ← E
Different subspecies		C	
Aplopelia larvata simplex	*Aplopelia l. jacksoni*		W ← E
Apaloderma vittatum camerunensis *Apaloderma v. francisci* (1)	*Apaloderma v. camerunensis*		W ← E
Phoeniculus bollei okuensis	*Phoeniculus b. jacksoni*		W ← E
Pogoniulus c. coryphaeus	*Pogoniulus c. hildamariae*		W ← E
Dendropicos e. elliotii *Dendropicos e. johnstoni* *Dendropicos e. kupeensis* *Dendropicos e. schultzei*	*Dendropicos e. elliotii*		?
Smithornis sharpei zenkeri	*Smithornis s. eurylaemus*		?
Andropadus t. tephrolaemus *Andropadus t. bamendae*	*Andropadus t. kikuyuensis*		W ← E
Dryoscopus angolensis boydi	*Dryoscopus a. nandensis* *Dryoscopus a. kungwensis*		W ← E
Laniarius p. poensis *Laniarius p. camerunensis*	*Laniarius p. holomelas*		W ← E
Malaconotus m. multicolor *Malaconotus m. batesi*	*Malaconotus m. graueri*		W ← E
Malaconotus cruentus gabonensis	*Malaconotus c. adolfifriederici*		W → E
Alethe p. poliocephala	*Alethe p. carruthersi* *Alethe p. vandeweghei*		W ← E
Cossypha i. insulana (2) *Cossypha i. granti*	*Cossypha i. kungwensis* *Cossypha i. schoutedeni* *Cossypha i. kaboboensis*		W ← E
Sheppardia c. cyornithopsis	*Sheppardia c. lopezi*		W ← E
Sheppardia r. roberti	*Sheppardia r. rufescentior*		W ← E
Zoothera c. crossleyi	*Zoothera c. piletti*		W ← E
Turdus olivaceus nigrilorum *Turdus o. poensis*	*Turdus o. bambusicola* *Turdus o. baraka*		W ← E
Alcippe a. monacha *Alcippe a. claudei*	*Alcippe a. abyssinica* *Alcippe a. ansorgei*		W ← E
Bradypterus baratti camerunensis *Bradypterus b. manengubae* *Bradypterus b. lopesi*	*Bradypterus b. barakae*		W ← E
Bradypterus c. bangwensis	*Bradypterus c. cinnamoneus* *Bradypterus c. midbreadi*		W ← E
Cisticola c. discolor *Cisticola c. adametzi*	*Cisticola c. chubbi* *Cisticola c. marungensis*		W ← E

Mt. Cameroun	Albertine Rift	Category	Direction of spread
Prinia b. bairdii	*Prinia b. obscura*		W ← E
Apalis b. binotata	*Apalis b. personata*		W ← E
	Apalis b. marungensis		
Apalis j. jacksoni	*Apalis j. jacksoni*		W ← E
Apalis j. bambulensis			
Apalis p. pulchra	*Apalis p. pulchra*		W ← E
	Apalis p. murphyi		
Bathmocercus r. rufus	*Bathmocercus r. vulpinus*		W ← E
Platysteira concreta harterti	*Platysteira c. graueri*		?
Platysteira c. kumbaensis	*Platysteira c. kungwensis*		
Trochocercus a. albiventris	*Trochocercus a. toroensis*		W ← E
Nectarinia p. preussi	*Nectarinia p. kikuyuensis*		W ← E
Nectariana p. genduruensis			
Serinus b. burtoni	*Serinus b. tanganjicae*		W ← E
Linurgus o. olivaceus	*Linurgus o. prigoginei*		W ← E
Ploceus m. melanogaster	*Ploceus m. stephanophorus*		W ← E
Onychognathus walleri preussi	*Onychognathus w. elgonensis*		W ← E
Allospecies		B	
Francolinus camerunensis	*Francolinus nobilis*		W ← E
Columba sjoestedti	*Columba arquatrix*		W ← E
Campethera tullbergi	*Campethera taeniolaema*		W ← E
Andropadus montanus	*Andropadus masukuensis*		W ← E
Phyllastrephus poensis	*Phyllastrephus hypochloris*		?
Phyllastrephus poliocephalus	*Phyllastrephus flavostriatus*		W ← E
Laniarius atroflavus	*Laniarius luehderi*		W ← E
Malaconotus gladiator	*Malaconotus lagdeni*		W ← E
	Malaconotus cruentus		
Alethe poliocephala	*Alethe poliophrys*		W ← E
Kupeornis gilberti (3)	*Kupeornis rufocinctus*		W ← E
	Kupeornis chapini		
Apalis pulchra	*Apalis pulchra*		W ← E
	Apalis ruwenzorii		
Apalis sharpii	*Apalis porphyrolaema*		W ← E
Apalis bamendae	*Apalis kaboboensis*		
Batis poensis	*Batis ituriensis*		W ← E
Platysteira chalybea	*Platysteira jamesoni*		?
Platysteira blissetti			
Nectarinia oritis	*Nectarinia alinae*		?
Nectarinia preussi	*Nectarinia stuhlmanni*		W ← E
Nesocharis shelleyi	*Nesocharis ansorgei*		?
Independent species (species group) (4)		A	
Cossypha isabella	*Cossypha insulana*		?
Sheppardia cyornithopsis	*Sheppardia aequatorialis*		W ← E
Sheppardia roberti			
Phylloscopus herberti	*Phylloscopus laetus*		W ← E
	Phylloscopus budongoensis		

(1) Subspecies mostly in conformity with Jensen & Stuart (1985, 1986).
(2) *Cossypha insulana* and *C. bocagei* are not conspecific (Prigogine 1987).
(3) Field studies by J. P. Vande weghe (pers. comm.) have shown that the behaviour of the three babblers kown as *Lioptilus rufocinctus, L. gilberti* and *L. chapini* is different of that of *Lioptilus nigricapillus.* Serle (1949) described *Kupeornis gilberti* and this name is thus available for the three first babblers.
(4) Arrangements in superspecies and species groups mostly in conformity with Hall & Moreau (1970) and Snow (1978).

Table 2: Classification of taxa (Table 1) found near Mt. Cameroon and on the mountains around the Albertine Rift.

Category	Taxa	W ← E	W → E	?	Total
D 1	Monotypic species	5			5
D 2	Same subspecies	3			3
C	Different subspecies				
	One ssp. on same massif	13	1	1	15
	At least two ssp.	16		2	18
B	Allospecies				
	One sp. on same massif	9		3	12
	At least two spp.	4		1	5
A	Independent species	2		1	3
	Total	52	1	8	61

Fig. 5 represents the situation when one allospecies is found near Mt. Cameroon, while the two others inhabit the mountains around the Albertine Rift. It is supposed that the crossing of the lowland forest and the isolation of *Kupeornis gilberti* is of great ancientness, especially as *K. gilberti* is very different from *K. rufocinctus* and *K. chapini*. The question has even been raised wether *K. gilberti* is a member of the same superspecies (Jensen & Stuart 1985).

Laniarius luehderi, a monotypic species (if *L. brauni* and *L. amboimensis* are considered as different species), is found at proximity of the two mountain blocks. According to Hall & Moreau (1970), *L. atroflavus* is an allospecies of *L. luehderi*. The proto-superspecies originated in the Albertine Rift refugium and evolved later in three proto-allospecies in the same refugium: proto-*atroflavus*, proto-*mufumbiri* and proto-*luehderi*. This speciation occured at a very old period. More recently proto-*atroflavus* crossed the lowland forest and reached Mt. Cameroon. Proto-*mufumbiri* remained in the region of the Albertine Rift, while the monotypic *luehderi* crossed the lowland forest more recently.

A complicated case is given by *Cossypha isabellae* and *C. insulana* considered by Hall & Moreau (loc. cit.) as members of a species group. *C. insulana* and *C. bocagei* form a superspecies (Prigogine 1987) and therefore it can be supposed that *C. insulana* crossed the lowland forest from east to west. It is difficult to make a suggestion for *C. isabellae*. It is possible that this species had its origin in the Cameroon-Gabon refugium in a period of great ancientness, before *C. insulana* arrived in the region of Mt. Cameroon.

Discussion

Since the late seventies palynological studies have proved that, during glacials, the climate was cool and arid and that the forest disappeared in the Afrotropics except in forest refugia. However, even the climatic refugium concept (Haffer 1967) has been criticized recently (Endler 1981, Connor 1986), but Mayr & O'Hara (1986) gave strong support for the refugium hypothesis, at least for Africa. Yet, Moreau's supposition of montane forest connections during glacials can no longer be upheld. The disjunct distribution of montane forest birds needs another explanation.

My paper is based on the preponderant influence of high rainfall and humidity on the lower limit of montane forest species. The favourable climatic conditions for the crossing of lowland forest, at medium altitudes, were present during interglacials and during these periods this kind of birds reached mountain blocks situated even far away. This hypothesis is based on facts observed by Moreau (1966) in two regions of tropical Africa. Thus, the forest connections permitting the spread of sedentary birds were present, not during glacials, but during interglacials. The disjunct pattern appeared when, during a subsequent glacial period, the forest disappeared, except in the forest refugia, and the montane forest birds became isolated on the mountain ranges reached during interglacials.

In most cases the population differentiated during a glacial, sometimes even into two or more subspecies (Fig. 4). The patchy distribution between the subrefugia of the two refugia is difficult to unterstand. Probably there are several factors involved: competition, extinctions, climatic conditions (altitude and exposition), surface area (varying from one subrefugium to another).

Table 1 represents only an attempt to suggest the direction of the lowland forest crossing by various bird taxa. As already mentioned, it is based on the distribution of species or superspecies in the Afrotropical Region but it is impossible to take account of extinctions which happened probably during the Quaternary. For several taxa the direction seems evident. For others a doubt remains.

In general it appears very difficult to establish the ancientness of the crossing between the two mountain blocks followed by differentiation. Using the DNA–DNA hybridization technique Sibley & Ahlquist (1985) found for congeneric species a criterium of ca. 10-0 MYA. The upper limit corresponds to the end of the Tertiary, the Pliocene. Though the calibration of the $T_{50}H$ curve remains under discussion, it seems that the crossing of the lowland forest and the isolation of congeneric birds on another mountain block started already at the end of the Tertiary.

On the other hand, Mayr (1963) gave examples of subspeciation in birds where the isolaton was less than 10,000 years. But he added that the completion of the speciation process might take up to one million years.

For the subrefugia of the Cameroon-Gabon refugium Jensen & Stuart (1985, 1986) concluded that, since the period of isolation was relatively short, probably less than 20,000 years, most of the differentation was at the subspecific level.

It is necessary to keep in mind that the ideas developed in this paper are working hypotheses and that, possibly, other ideas will be formulated in the future, based on new facts.

Zusammenfassung

Es wurde eine Theorie vorgeschlagen, um die zoogeographische Trennung zwischen den montanen Waldvögeln in der afrotropischen Region zu erklären. Sie basiert auf der Hypothese, daß der Durchzug durch Tieflandwälder zwischen dem Mount Cameroon und den Bergen um

das Albertinrift in der Interglazialperide erfolgte. Die Route, die sie genommen haben, kann noch an der aktuellen Verbreitung der Waldvögel aus mittlerer Höhe erkannt werden, und man kann davon ausgehen, daß die Bergwaldvögel denselben Weg genommen haben. Das disjunkte Verbreitungsmodell trat auf, als während der folgenden Eiszeit die Wälder in fast allen afrotropischen Regionen verschwanden und die Vögel auf bewaldete Gebirgszüge beschränkt waren. Moreau (1966) wies auf das günstige Klima hin, das es Bergwaldvogelarten erlaubte, auf niedrigere Höhen vorzudringen, und ich nehme an, daß solche Bedingungen vor allem während der regenreichen, feuchten Zwischeneiszeiten herrschten. Auf die Richtung des Durchzugs von Osten nach Westen und umgekehrt kann man aufgrund der allgemeinen Verbreitung der Superspezies und Arten in der afrotropischen Region schließen. Die meisten Taxa überquerten die Tieflandwälder wahrscheinlich von Osten nach Westen. Allgemein gesagt, steht der Grad der Differenzierung der isolierten Taxa mit gemeinsamen Vorfahren in direktem Zusammenhang mit der Dauer der Isolationsperiode. Die Divergenz, die unter miteinander verwandten Taxa gefunden wird, gibt einen Hinweis darauf, in welch früher Periode der Durchzug erfolgt sein muß.

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