Annals of the South African Museum. Annale van die Suid-Afrikaanse Museum.

Cape Town :South African Museum,1898-2004.
https://www.biodiversitylibrary.org/bibliography/6928

v.66 (1974-1975): https://www.biodiversitylibrary.org/item/127147

Page(s): Page 109, Page 110, Page 111, Page 112, Page 113, Page 114, Page 115, Page 116, Page 117, Page 118, Page 119, Page 120, Page 121, Page 122, Page 123, Page 124, Page 125, Page 126, Page 127, Page 128, Page 129, Page 130, Page 131, Page 132, Page 133, Page 134, Page 135, Page 136, Page 137, Page 138, Page 139, Page 140, Page 141, Page 142, Page 143, Page 144, Page 145, Page 146, Page 147, Page 148, Page 149

This page intentionally left blank.

THE ZOOGEOGRAPHY OF THE SOUTH AFRICAN AVIFAUNA

By

J. M. WINTERBOTTOM

South African Museum, Cape Town

(With 9 maps and 6 tables)

[*MS accepted 1 November 1973*]

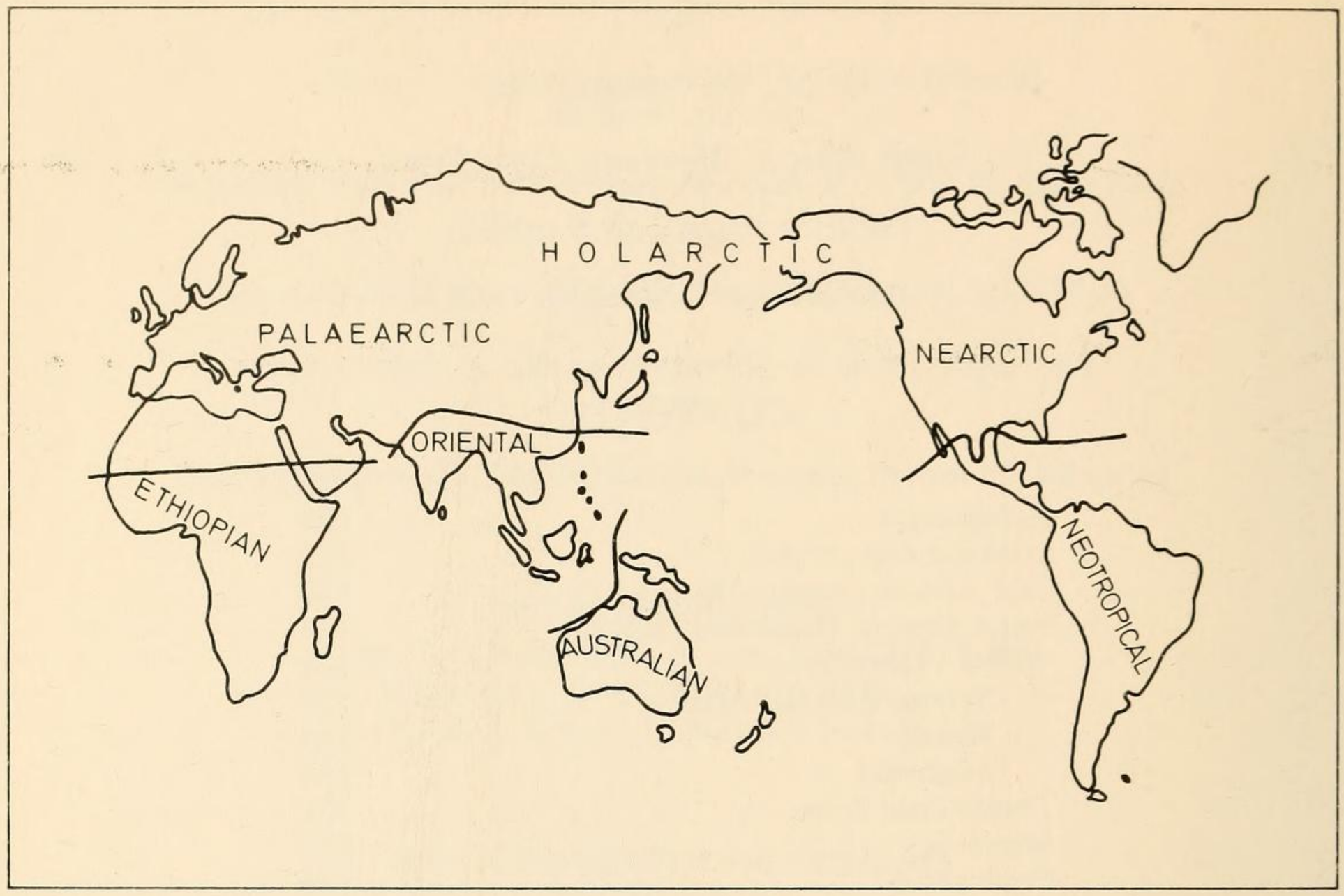
CONTENTS

INTRODUCTION

From the days of P. L. Sclater (1858) and A. R. Wallace (1876), Africa south of the Sahara has been recognized as one of the major faunal regions of the globe. Wallace, in subdividing this, the Ethiopian Region, constituted the area south of the Zambezi and Kunene Rivers as the South African Sub-region and this is the part of the continent dealt with in this paper.

The fauna of any area depends partly on geography and partly on climate, the latter working on animals chiefly through the vegetation. South Africa is the southern extremity of a continent separated on three sides from other land masses by a wide expanse of ocean and on the fourth by deserts. It is generally agreed that the African fauna has most in common with that of the Oriental Region, especially in the case of the forest fauna (De Beaufort 1951); and that the land fauna is sharply divided into forest and non-forest. It is also frequently stated (e.g. by De Beaufort 1951 and Cloudesley-Thompson 1969) that the forest fauna is the older of the two, but I have recently (Winterbottom 1973) given reasons for doubting this. The Ethiopian Region was isolated from the north by the Tethys Sea until the Miocene and by that time had developed its

Ann. S. Afr. Mus. **66** (6), 1974: 109–149, 9 maps, 6 tables.



Map 1. Zoogeographical regions of the world.

own individuality. The great expansion of grasslands during this period must have led to considerable speciation (Brodkorb 1960). Although there were times, at least during the Pleistocene, when the present Sahara Desert was inhabitable for a wide range of animals, it is important to note the very considerable climatic differences between north and south. The present bird and butterfly fauna of North America is almost entirely Palaearctic, showing that the Ethiopian elements cannot compete with them in the temperate climate north of the Sahara and the Palaearctic fauna is at a similar disadvantage in the tropical Sudan. It is important to stress this becase the temperate areas south of the Equator are inhabited by a fauna totally distinct from the Palaearctic and clearly derived from the tropical fauna to the north. Much of South Africa has a temperate climate and its fauna, though related to the tropical fauna to the north, has obviously been in existence for a long time, since it has allowed the evolution of at least one distinct family, the Promeropidae, and a number of distinct genera, such as *Geocolaptes* and *Chaetops*. Hall (1970) finds that the African passerine fauna is relatively rich, as compared with the Oriental and Palaearctic, in fruit-eaters (8%) and seed-eaters (24%). The South African avifauna, with only 2% fruit-eaters and 18% seed-eaters, is markedly less so than the African fauna as a whole.

As with the temperate fauna in the extreme south-west, the desert fauna of South Africa has long been isolated, or almost isolated, from the deserts to the north, and genera such as *Namibornis*, *Lanioturdus* and *Philetairus* have evolved

there. The genus *Namibornis* is a particularly enlightening one in this respect, since it appears to be intermediate between the Turdine genus *Cercomela* and the Muscicapine genus *Melaenornis*, so its ancestors must have arrived before the groups diverged (Jensen & Jensen 1971). The question of links with the north-eastern desert area of Somaliland is discussed below.

Of the endemic South African species, the majority, as might be expected, have their nearest relatives either in South Africa itself or in adjoining areas to the north. Apart from the southwest–northeast species pairs, which are discussed below, there are five whose nearest relatives occur in the Palaearctic and about 14 whose affinities are obscure but which have obviously had a long history in South Africa.

In summary, the terrestrial avifauna of South Africa contains 6% of species which are found in other zoogeographical regions, 33% which range widely over the whole Ethiopian Region, and 34% which occur also in East as well as South Africa (Table 1). Among the non-passerines, the figures for the first two of these categories are higher than in the passerines, being 12% for cosmopolitan and 40% for Ethiopian species.

Table 1

Geographical affinities of breeding South African land birds (percentages)

	Cosmo-politan	Ethio-pian	South & East Africa	S.W.–N.E. only	West Central Africa	South Africa	Total No. of Species
Non-passerine	12	40	32	½	0	15	225
Passerine	2	28	35	2	2	31	241
All species	6	33	34	1	1	25	466

If we consider the South African terrestrial avifauna at the generic level, we need to use wider categories. These, as used in Table 2, are: Cosmopolitan, being genera represented in both Old and New Worlds and in at least four

Table 2

Geographical affinities of genera of breeding South African land birds (percentages)

	Cosmopolitan	Old World	Pan-tropical	Ethiopian and Oriental	Ethiopian and Palaearctic	Ethiopian and Neotropical	Ethiopian	South and East Africa	South Africa	Total No. of Genera
Non-passerine	22	22	3	1	4	1	44	0	1	96
Passerine	7	16	0	6	4	0	58	2	7	120
All species	13	19	1	4	4	1	53	1	5	216

zoogeographical regions; Old World, being genera represented in at least three of the four regions of the Old World; Pan-tropical Old World, genera represented in the Ethiopian, Oriental and Australian Regions but not in the Palaearctic; Ethiopian and Oriental; Ethiopian and Palaearctic; Ethiopian and Neotropical; Ethiopian, being genera widespread in the Region; South and East African; and South African. As at the species level, the percentage with Cosmopolitan affinities is markedly higher among the non-passerines than among the passerines (to obtain a comparable total to the Cosmopolitan species in Table 1, the first six columns of Table 2 should be summed); but the percentage of Ethiopian genera is much higher than the percentage of Ethiopian species (as might be expected) and is higher in the passerines than in the non-passerines; but the percentage of South African genera is small, confirming the view that South Africa does not merit rank as a major division of the Ethiopian Region.

Udvardy (1969) analyses the tendency for species to change their range by the use of what he terms 'dynamic potential'. Species with distribution limits in the area being considered constitute the Intrinsic Dynamic Potential; species which moved their limit during the time period considered represent the Realized Dynamic Potential and those which did not move, the Unrealized Dynamic Potential. He gives a table to show this in respect of the Carpathian Basin, 1860–1960. However, the application of this type of analysis to South Africa is complicated by several factors:

(i) Lying as it does at the end of a continent, all the breeding species on the South African list (665, excluding sea birds) find their limits in the area, so that the Intrinsic Dynamic Potential is 665.

(ii) Since the area is bounded by the sea on the west, south and east, all movement must be from the north.

(iii) Owing to the great size of the area, it is necessary to introduce an additional category to those used by Udvardy, namely species advancing in the area. There are 8 of these for the period 1900–1970; 9 are receding; 3 are sporadic breeders; and 1 is newly arrived, giving a Realized Dynamic Potential of 21 (Carpathian Basin, 37). This suggests that the South African avifauna as a whole is rather static.

In discussing the zoogeography of southern Africa, it is essential to realize that five different patterns are involved, since the barriers which are effective for one set of species are the areas of distribution of others. This is obvious if we consider the sea and the land, the former being a barrier to land birds and the latter to sea birds. The five patterns here mentioned are:

(i) oceanic birds;
(ii) coastal birds;
(iii) freshwater birds;
(iv) montane birds;
(v) the rest.

These patterns become more and more complicated as one proceeds from (i) to (v) and, especially in (v), it is exceedingly difficult to disentangle geographical from ecological factors. Since (v) is much the most widespread and has excited greatest comment, I propose to deal with these patterns in the reverse order to that listed above.

LOWLAND AND PLATEAU

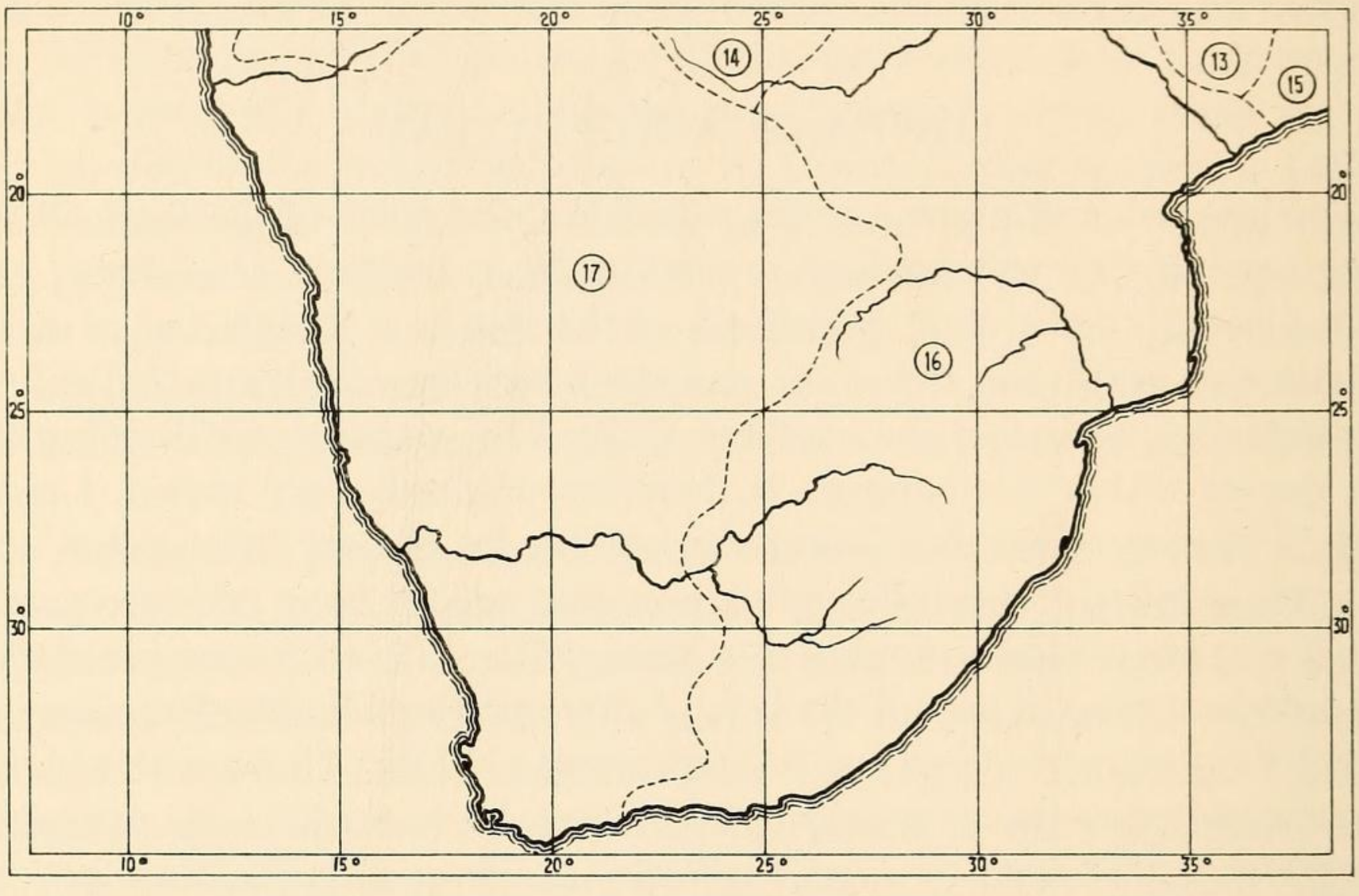
The lowland and plateau areas, which occupy most of the land of South Africa, vary in their climate and vegetation from the bare sand-dunes of the Namib Desert* to the close woodland of the *Baikiaea* 'mutemwa' of western Rhodesia and north-east Botswana and the sometimes impenetrable thickets of the macchia vegetation of the southern Cape. The geographical distribution of avian species within this complex is therefore naturally very varied. I made a list of 51 species which are found throughout, or almost throughout, South Africa; but it by no means follows that because a species has a wide geographical range, it also has a wide ecological tolerance. Of the 51 species mentioned above, three do not appear in any of the lists of dominant or abundant species in the different habitats considered by Winterbottom (1972*b*). Those with much the widest ecological tolerance appear to be the two doves *Streptopelia capicola* and *S. senegalensis*, followed by *Lanius collaris*, *Dicrurus adsimilis*, *Ploceus velatus* and *Sylvietta rufescens*. Generally speaking, therefore, even species very widespread geographically are limited to one or a few habitats and occur only in them, so that, in effect, their distribution is patchy rather than general.

There have been a number of attempts to deal with the zoogeography of South Africa. Wallace (1876) made it one of the four sub-regions into which he divided the Ethiopian Region; Chapin (1932) divided it into the South West Arid and South East Veld Districts, the boundaries of each of which he extended rather beyond Wallace's (and our) limits of the Zambezi and Kunene. Bowen (1933) produced an entirely different arrangement. Unfortunately, his maps are on so small a scale that it is extremely difficult to make out the boundaries he proposes; within our area, however, he recognizes two zones, four 'climates' and five districts. Of these, his Rhodesian Savanna District is roughly equivalent to our South Central Highlands; his Southeast Veldt to our Macchia and Highveld, with the southern Karoo and Rhodesian plateau added; and his East African Lowland to the two northern divisions of our East African Coastal. In the south-west, he divides the area in two by a line running down the centre of Damaraland—an impossible division: but if more realistically adjusted, this may be taken as marking the boundary between our South Temperate and South West Arid Districts. He leaves the coastal areas from Beira to Cape Town as a transition zone, 'in which both Tropical and Subtropical Zone species may occur'.

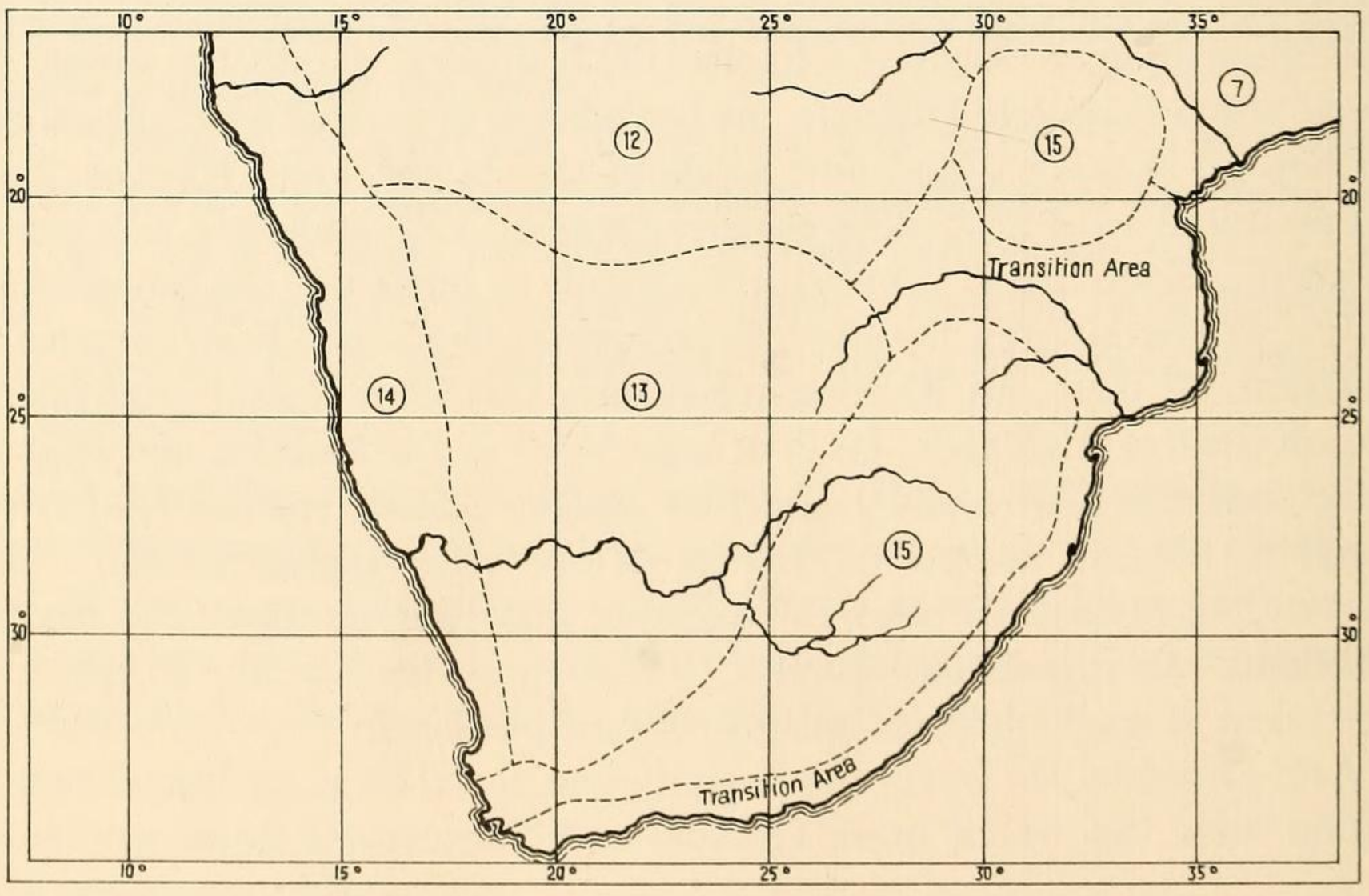
Moreau (1952) divided South Africa in three, splitting off the south-west

* Places mentioned in the text are shown on Map 9.

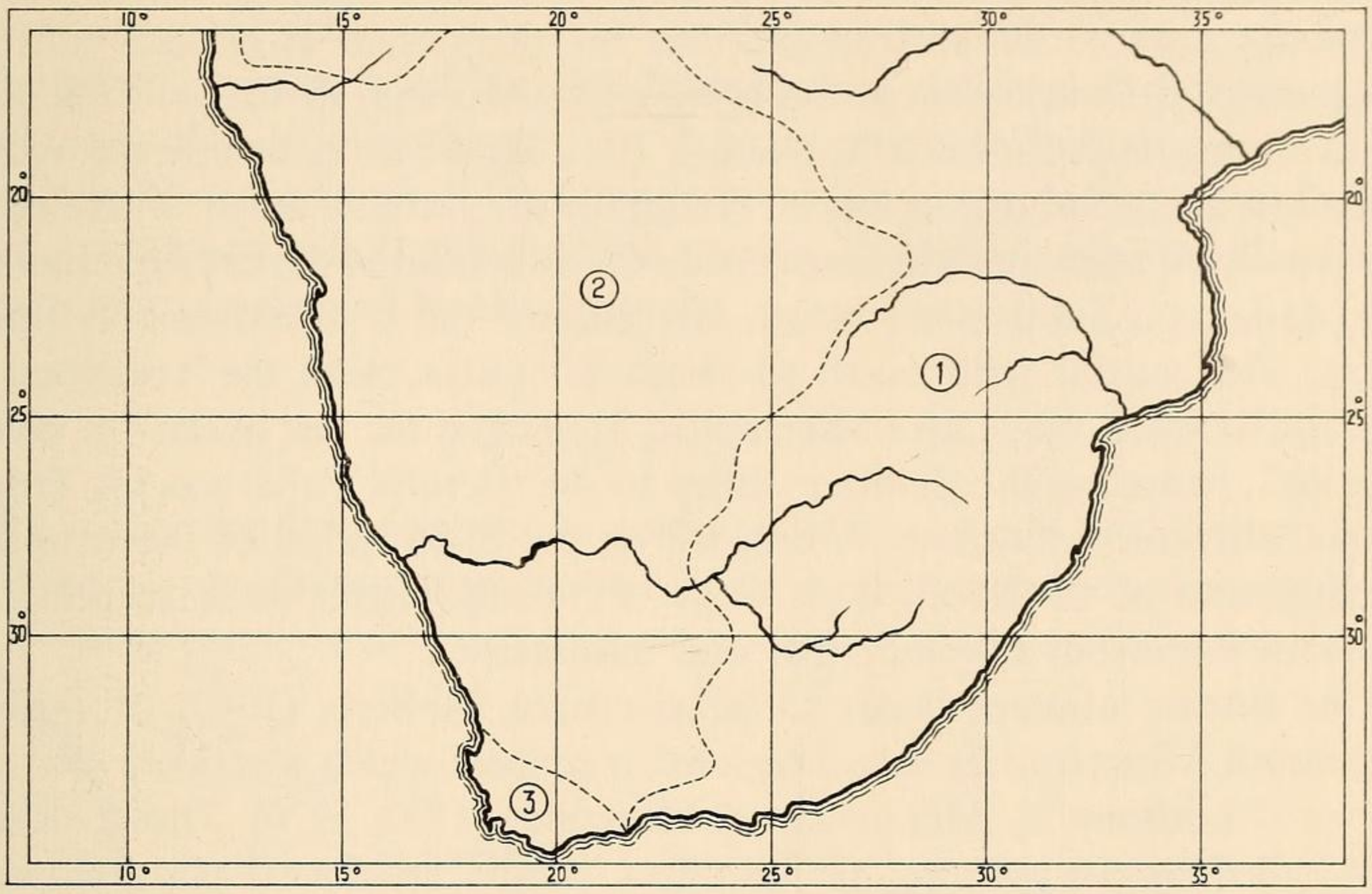
Map 2. Zoogeographical divisions of South Africa according to A. Chapin; B. Bowen; C. Moreau; D. Poynton.



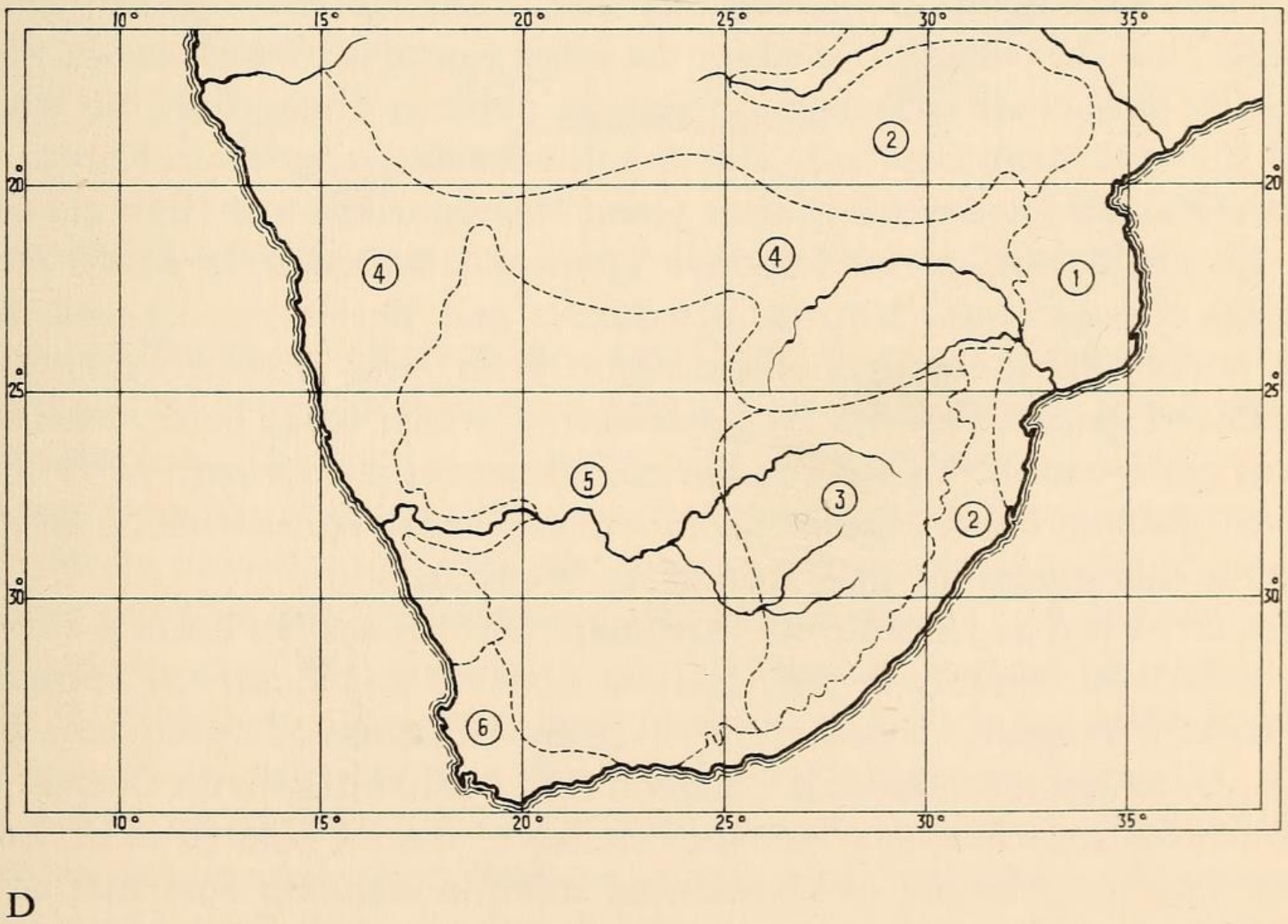
Map A



Map B



Map C



Map D

Cape from the rest and uniting Chapin's South East Veld with vast areas the to north as a Southern Savanna District. Winterbottom (1959) removed the Highveld grasslands from Chapin's South East Veld to his South West Arid and divided the rest of that district between his Rhodesian Highlands and East African Coastal Districts. Poynton (1964), like Moreau, divided off the south-western Cape; he put most of the South West Arid into a Temperate Western and the rest into a Subtropical Arid, except for the extreme north, where he proposed a division running right across from Ovamboland to the eastern Highlands of Rhodesia as a Subtropical Moist. He retained the highveld as a Temperate Eastern. The coastal strip north to about St. Lucia, with the Transvaal and Swaziland lowveld, made up a Subtropical Moist and the rest of the low country on the east, including the Zambezi valley to the Victoria Falls, was his Tropical division. Poynton's divisions were based on the distribution of the Amphibia. His distinction of the South-West Cape is entirely justifiable in respect of its amphibian fauna but not for birds and mammals.

One further attempt needs to be discussed. Roberts (1940) proposed to divide South Africa into 21 'small regions', a concept which was taken over, with minor modifications, by McLachlan & Liversidge (1957, 1970). These, although not so called by the authors, are, in effect, 'biotic provinces' as developed by Dice (1952). Of the divisions they propose, their Southern and Eastern Evergreen Forest, Southern and South-western Cape and a few others have some validity, though the detailed evidence on which they are based has never been published. Many of the others, however, have no biological reality at all and the birds which the authors cite, when they do list any, do not support their conclusions. Thus the only bird listed for the Little Karoo is *Circus maurus*, which I personally have never seen there, though no doubt it does occur; but which is found all over their Southern and South-western Cape, their Karoo, their Eastern Grassveld and much of their Great Namaqualand and Highveld Grassveld. They cite four species for their Thornveld Kalahari, *Turdoides bicolor*, *Laniarius atrococcineus*, *Mirafra africanoides* and *Erythropygia paena*, all of which occur almost throughout the South West Arid District. Among their Damaraland species, they list *Tockus bradfieldi*, whose range barely reaches the extreme north-east of this division but extends across the northern parts of their Sandveld Kalahari and Ngamiland to western Rhodesia and which they also list as the sole species for their Rhodesian Woodlands.

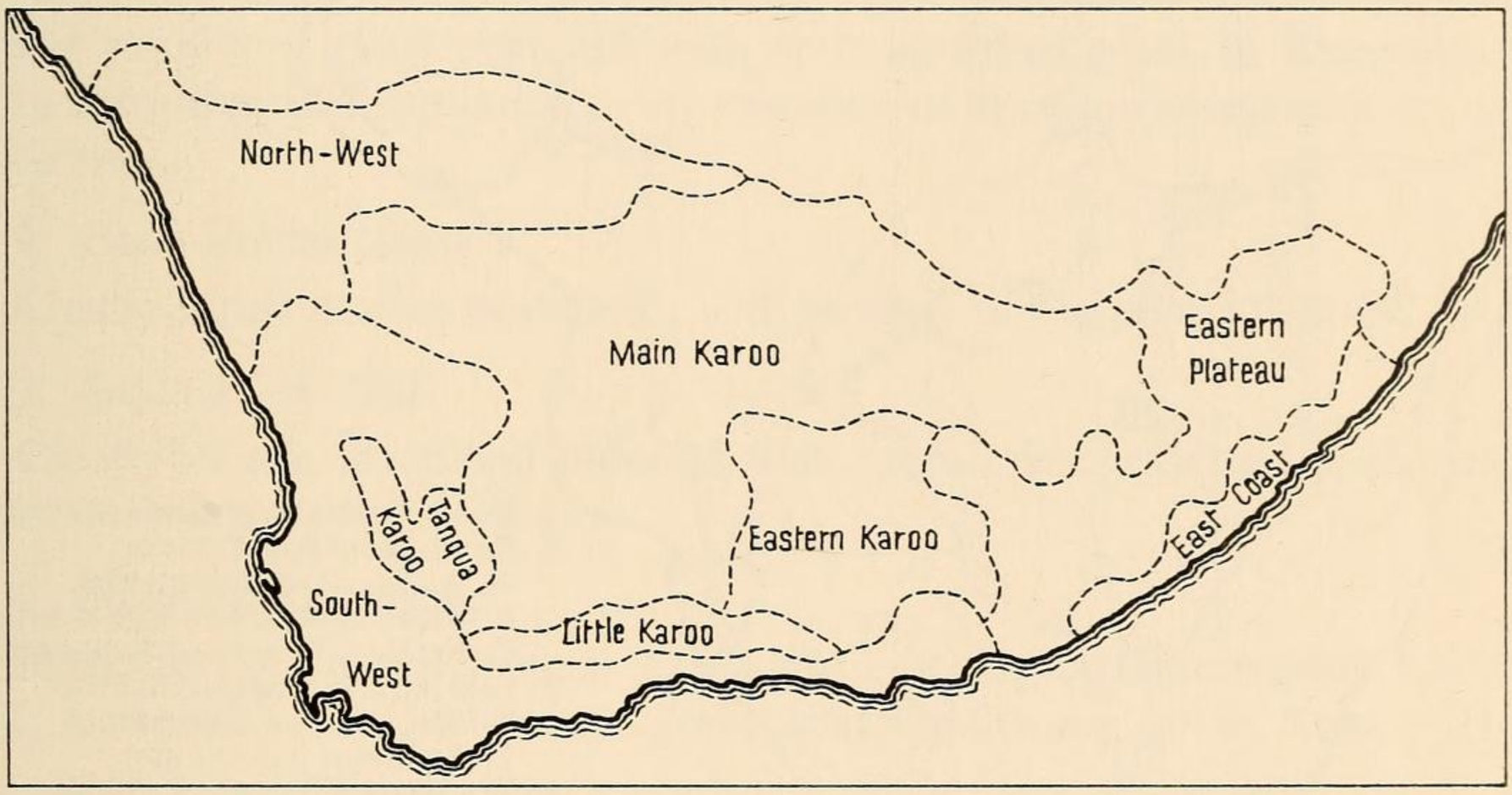
As far as can be judged from their map, Durban and St. Lucia are in their Eastern Littoral, Ndumu in their Eastern Lowveld and Lourenço Marques in their Eastern Tropical Littoral. Analysis of the avifaunas of these places shows that St. Lucia has much more in common with Ndumu than with Durban; that Lourenço Marques has an avifauna as similar to that of Ndumu as St. Lucia's is; and that the avifauna of Durban has more in common with that of East London than with that of St. Lucia. This is in accord with the suggestions made below, which would group St. Lucia and Ndumu with Lourenço Marques in one sub-district of the East African Coastal District and Durban and East

London in another, with the area between St. Lucia and Durban as a transitional zone.

In an endeavour to apply McLachlan & Liversidge's concepts more closely, to see what would come of a detailed analysis, I drew up a list of species not distributed all over South Africa; listed those which occurred in each magisterial district (and sub-district in the western Cape, as set out in Winterbottom, 1968*b*) in the Cape Province south of the Orange River; and compared the lists for each district so obtained with those of all the adjoining districts, using the Co-efficient of Community as defined by the formula:

$$\frac{c}{n_1 + n_2 - c} \times 100$$

where c is the number of species in common and n_1, n_2 are the numbers in the smaller and larger faunas respectively. Lines were then drawn through district



Map 3. Avifaunal areas of the Cape Province south of the Orange River.

boundaries where the co-efficients indicated faunal change. The results are shown in Map 3 and differ considerably from McLachlan & Liversidge's 'small regions' for the same area. The number of species used in the analysis was 329.

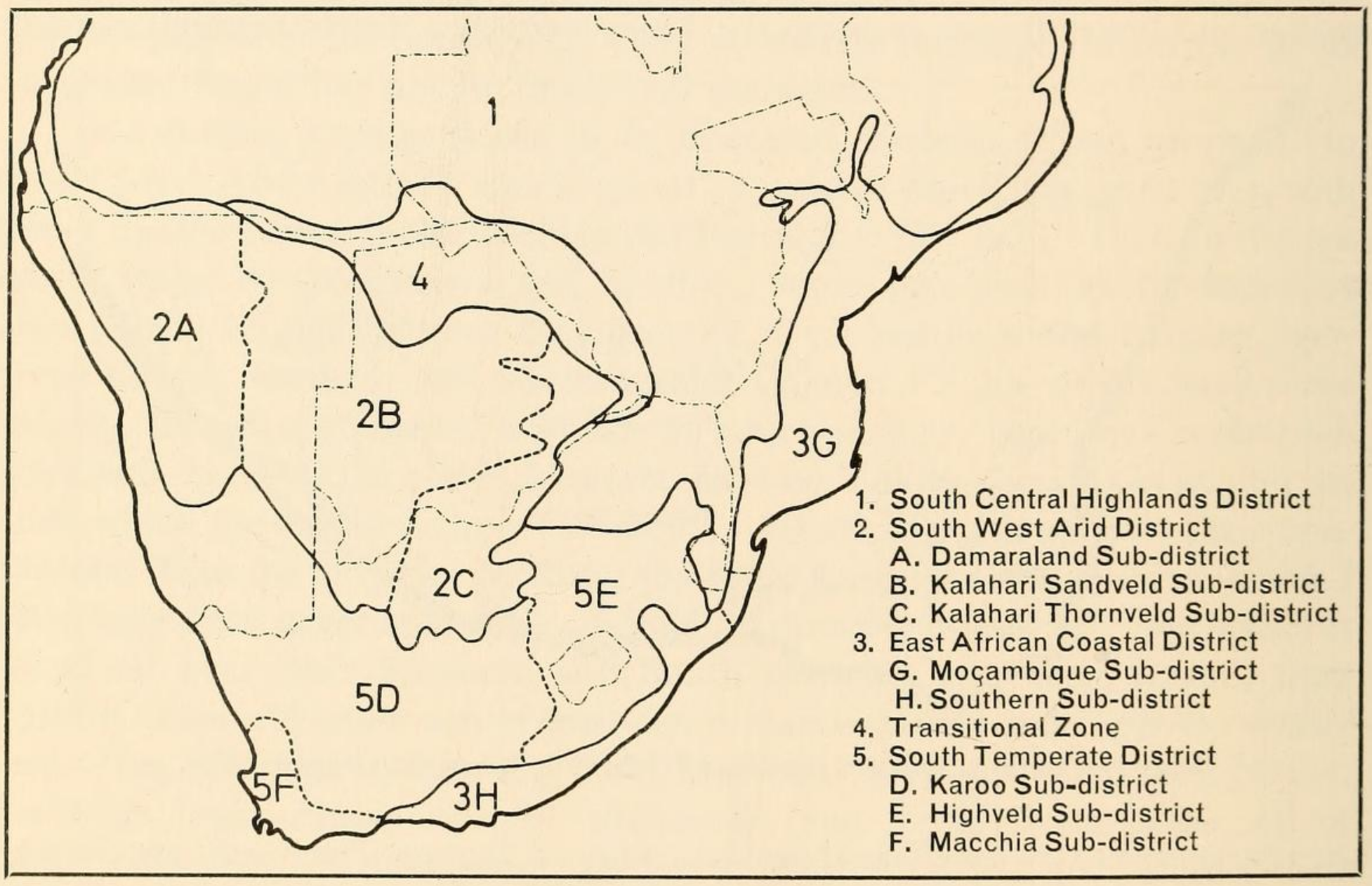
Apart from the unsatisfactory nature of the actual divisions proposed, the whole concept of biotic provinces, like those of life zones and faunal groups (on the second of which, see Winterbottom 1965), is an attempt to find a way out of the difficulties—very real difficulties—of the classical method of regions and districts. Unfortunately, however, these methods, at least to my mind, produce results even less satisfactory than those they were designed to supersede.

It will be realized from what has been said above and what follows, that modern zoogeographers reject Wallace's division of South Africa as a distinct sub-region of the Ethiopian Region and that the boundaries of the various zoogeographical areas which have been proposed do not coincide with the Zambezi and Kunene Rivers at any point. For various reasons, the present paper is

primarily concerned with Wallace's sub-region, to which about 130 species are restricted, but it is appreciated that all those subdivisions which reach the Zambezi or Kunene continue north of the rivers, though the avifauna of these northern areas is not considered in detail here.

My own views on the zoogeographical subdivisions in South Africa are shown in Map 4. It will be seen that there are four districts (apart from montane forest) partly or wholly within the area: the South Central Highlands, the East African Coastal, the South West Arid and the Southern Temperate; plus an extended Transitional Zone between the first and third. Comments on, and justification of, the establishment of these districts follow.

The most fundamental pattern in bird distribution in South Africa is the dichotomy between east and west. I have listed 106 species whose distribution



Map 4. Zoogeographical regions of South Africa.

does not extend west of the main eastern escarpment, though some of them occur in the montane forest of that area; and 103 whose distribution, at least north of Port Elizabeth, does not extend east of the same escarpment. There is a third common pattern, that of species which occur in the north, often south to the Limpopo or even the northern Transvaal, in the west but extend further south, into Natal and sometimes the eastern Cape, in the east. These are species whose main centre of distribution lies north of our limits.

Although the discussion in this paper is mainly of the geographical distribution patterns, these must obviously be influenced by ecological conditions. They are not discussed in detail here since that has already been done elsewhere (Winterbottom 1972*a*). Hall & Moreau (1970) say 'It is the distribution of

vegetation which governs the geographical lines along which speciation has taken place'. But things are by no means as simple as this, as perusal of my ecological paper will show. In fact, Hall & Moreau use as their base map (as does Moreau 1966) a map produced by Cooke (1962) which is by no means always suitable to show the relations between bird and plant distribution. This is particularly the case with the 'Dry Woodland, etc., mostly Acacia', which is extended east to include the highveld grasslands and thus obscures the ecological preferences of over 40 species.

It is nevertheless important for zoogeographical purposes to know something of the major habitats available to birds in each of the areas delimited in Map 4.

1. *South Central Highlands*

Most of the area is covered with *Brachystegia* woodland (miombo), fairly close woodland of rather small, deciduous trees with grass ground cover. There are also stretches of *Baikiaea* woodland of somewhat similar character and of mopane woodland, more open and with more scattered grass. In Rhodesia, and also in extra-limital Zambia, there are stretches of open grassland with scattered *Acacia* trees.

2. *East African Coast*

Chiefly scrub *Acacia* woodland, with patches of temperate forest.

3. *South West Arid*

Chiefly *Acacia* woodland on sand, with more open grassland in the south-east.

4. *Southern Temperate*

Macchia—bushes of *Protea*, *Erica*, etc.—in the extreme south; Karoo—small, scattered bushes; with bare gravel and sand-dunes in the Namib; Highveld—open grassland.

The climatic vicissitudes of the Pleistocene must have changed the distribution of these vegetation types; but it would not appear to have eliminated or drastically reduced or seriously fragmented any of them. Clark (1967) produces a map showing the vegetation at 50% of the present rainfall; and while it is unlikely that the rainfall decreased simultaneously over the whole continent, Clark's map does support the conclusion that an arid corridor linked, or almost linked, the South West Arid District with the Somali Arid, perhaps several times. This explains the curious relationships between the avifaunas of the two districts. The following species are found in both, but not in the intervening areas:

Poliohierax semitorquatus, *Eupodotis ruficrista*, *Mirafra africanoides*, *Turdoides melanops*, *Nectarinia mariquensis*, *Ploceus rubigenosus*, *Passer motitensis*, *Bubalornis albirostris*, *Estrilda erythronotus* and *Amadina fasciata*.

A number of other species (e.g. *Pterocles gutturalis*, *Francolinus sephaena*) have been excluded because they range rather far beyond South West Arid limits. In addition, there are over 20 cases of closely-related pairs of species,

some of which some systematists regard as conspecific. Yet the presence of endemic genera in each area suggests that there was only a limited exchange of fauna. The question has been more fully discussed elsewhere and an analysis of the avifaunas of the South West Arid and Southern Temperate Districts (Winterbottom 1972*c*) shows that of the 90 characteristic species, 34 are specifically identical or closely allied to species otherwise found in the Somali Arid District; 24 are nearly related to species which occur further east in South Africa; and the 32 remaining forms are peculiar to these districts and their origins are in many cases obscure. Several of them, however, suggest more than one invasion from the north and/or radiation in the south-west. The Pleistocene arid periods, when the Kalahari sands were blown deep into the Congo basin, have left south-west arid relicts further north—the populations of *Certhilauda albofasciata* in Angola and Tanzania are examples.

While the temperate forest faunas have been repeatedly isolated and then joined again, a process which facilitates and accelerates speciation, this has not been the case with the non-forest habitats. Keast (1972) has pointed out that in Australia the desert is central and as it expanded and contracted, the fauna of the more mesic habitats were alternately driven into 'refuges' and then brought together again, while the desert fauna itself remained undivided and was presented with little opportunity for speciation. In Africa, however, it is the deserts which are peripheral. Contact between the northern deserts and those of the south-west has been minimal and the faunas are decidedly different (Winterbottom 1972*c*). The two existing deserts in the south-west are separated by the somewhat less arid Karoo and are decidedly different in character. The Namib, as shown by its remarkable flora and arthropod and herpetological fauna, is very old; but it appears to have always been of very restricted area. The Kalahari, by contrast, has undoubtedly fluctuated greatly in size. At the height of arid periods, Kalahari-type vegetation apparently extended right across the continent in the Limpopo basin to the Indian Ocean and northward deep into the Congo basin. At such times, the south-western portions were under a much more severe desert regime than they are today. On the other hand, during pluvial periods, the northern and north-western parts of the present desert would have been bushveld. Nevertheless, at no time would either desert have been fragmented.

The avifauna of the Namib contains several endemic bird species; that of the Kalahari does not—its avifauna is merely an impoverished version of that of the *Acacia* steppe further west.

EAST AFRICAN COASTAL DISTRICT

The two major groups of east and west mentioned above characterize what Winterbottom (1959) defined as the South West Arid and South East Coastal Districts. The latter has two sub-districts within our limits, besides a third north of the Rovuma River in East Africa. The division between the other sub-districts may be drawn at St. Lucia, south-west of which there is a rapid fall-off in tropical species; but the area from St. Lucia to Durban is regarded as a transi-

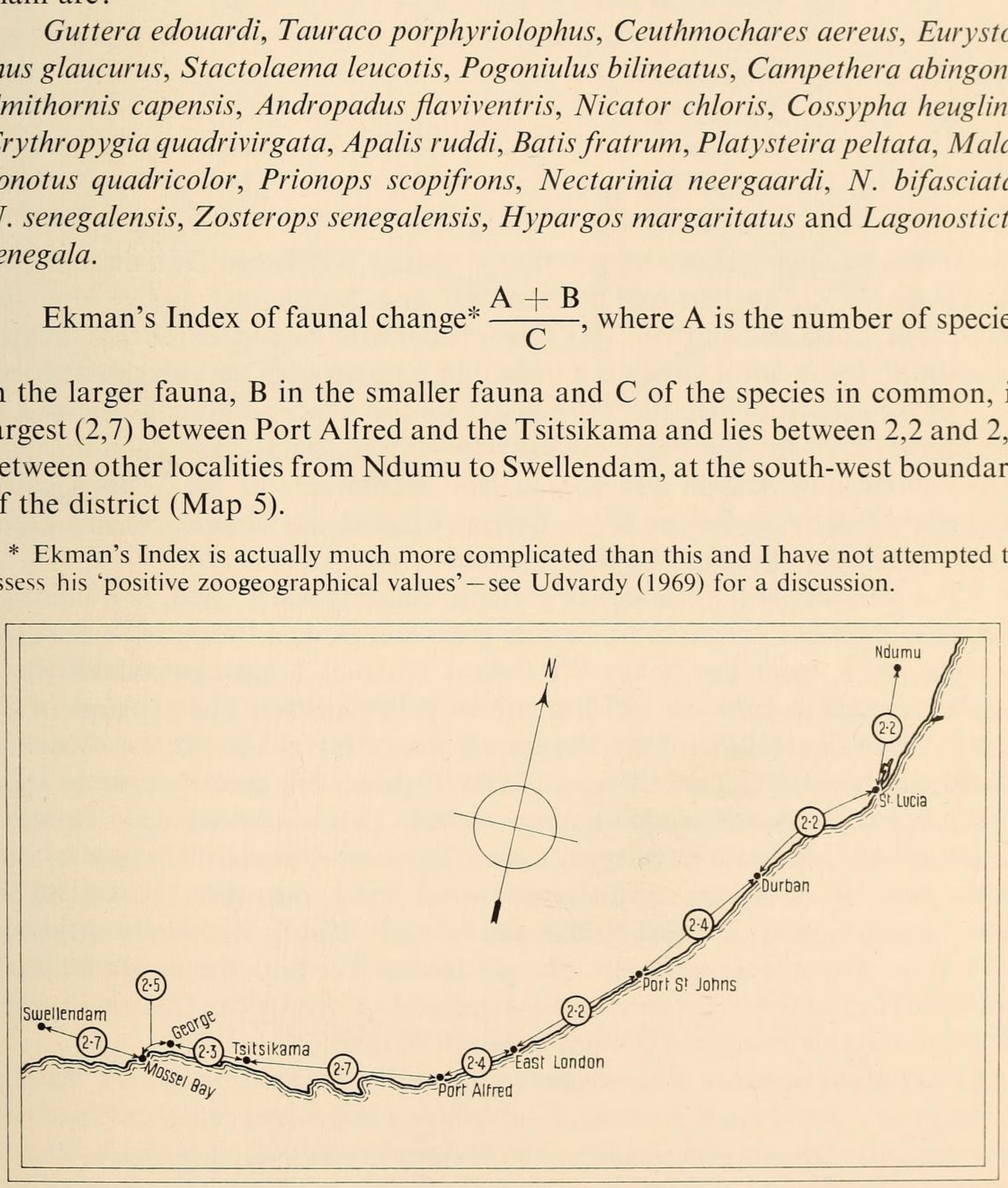
tional zone between the two; and, as will be seen below, the fixing of the boundary is by no means as simple as some authors have assumed, the whole of the southern part being, as it were, a subtraction zone at the end of the tropical belt further north.

Of the characteristic species of the northern of the two sub-districts, two drop out between Ndumu and St. Lucia, nine between St. Lucia and Durban and 12 between Durban and Port St. Johns (these figures are based on Pooley & Dixon (1966) for Ndumu; Natal Parks Board (undated) for St. Lucia; Lawson (1971) for Durban; and McCulloch, Skead & Winterbottom (1970) for Port St. Johns). The 23 tropical species which drop out along this stretch of coastal plain are:

Guttera edouardi, *Tauraco porphyriolophus*, *Ceuthmochares aereus*, *Eurystomus glaucurus*, *Stactolaema leucotis*, *Pogoniulus bilineatus*, *Campethera abingoni*, *Smithornis capensis*, *Andropadus flaviventris*, *Nicator chloris*, *Cossypha heuglini*, *Erythropygia quadrivirgata*, *Apalis ruddi*, *Batis fratrum*, *Platysteira peltata*, *Malaconotus quadricolor*, *Prionops scopifrons*, *Nectarinia neergaardi*, *N. bifasciata*, *N. senegalensis*, *Zosterops senegalensis*, *Hypargos margaritatus* and *Lagonosticta senegala*.

Ekman's Index of faunal change* $\frac{A + B}{C}$, where A is the number of species in the larger fauna, B in the smaller fauna and C of the species in common, is largest (2,7) between Port Alfred and the Tsitsikama and lies between 2,2 and 2,4 between other localities from Ndumu to Swellendam, at the south-west boundary of the district (Map 5).

* Ekman's Index is actually much more complicated than this and I have not attempted to assess his 'positive zoogeographical values'—see Udvardy (1969) for a discussion.



Map 5. Ekman's Index along the south-east coast.

Another method of measuring faunal change is by Schilder's Index (Udvardy 1969). The Percentage Occurrence Index derived from this, in respect of the East African Coastal District between Ndumu and Swellendam would consist, for each station, of the number of species present at Ndumu but not at Swellendam in each plus the number of species present at Swellendam absent from the other stations, expressed as a percentage of the Ndumu figure (which will, obviously, be 100%). The full list is:

Ndumu	100
St. Lucia	92
Durban	79
Port St. Johns	52
East London	47
Port Alfred	31
Tsitsikama	24
George	19
Mossel Bay	11
Swellendam	0

It will be seen that the biggest faunal change is between Durban and Port St. Johns (27%), not between Port Alfred and Tstisikama, and is high too between St. Lucia and Durban. This agrees better with the suggestion that the area between St. Lucia and Durban is a transition zone between the two sub-districts.

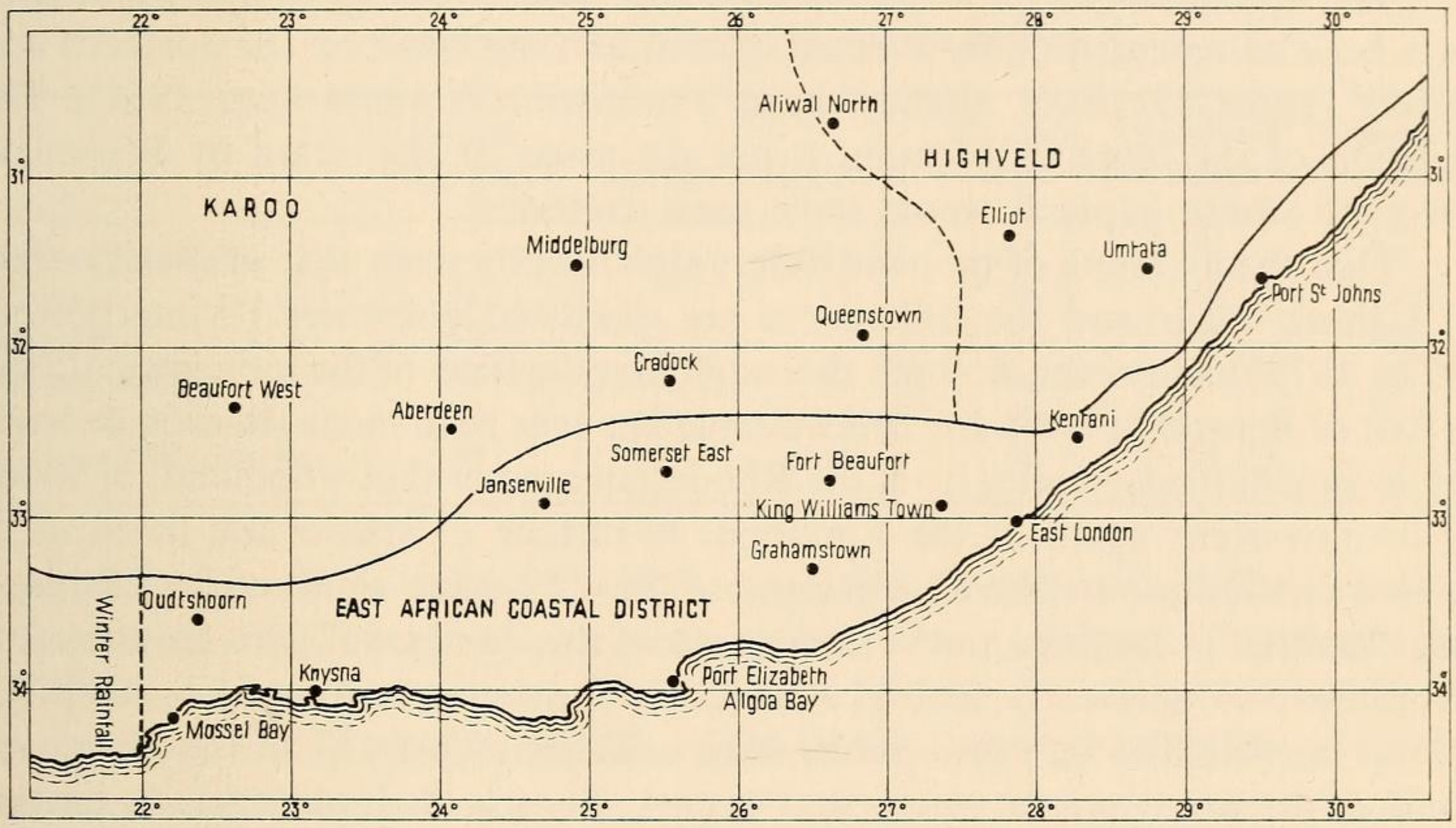
As mentioned above, there are many species which, although confined to the east south of the Limpopo, extend westwards across the Rhodesian plateau into Zambia and Angola and are, in fact, inhabitants of the South Central Highlands District as well as of the Eastern Coastal. To what extent, therefore, are we justified in keeping the two separate?

The avifauna of the Rhodesian plateau, omitting water birds, non-breeding migrants, montane forest and montane grassland birds and species which just impinge on it from the South West Arid District, I have calculated (from Smithers, Irwin & Paterson 1957) to consist of 296 species. The avifauna of the East African Coastal area from the Save River to Natal I count as 324 species (based on Pinto 1953, and Clancey 1953). Of these, 236 species occur in both. This gives a Coefficient of Community of 61,4. This is a little below the figure usually taken to indicate identity of fauna (Hagmeier & Stults 1964); and in view of the fact that both Pinto and Clancey cover areas some distance west of the East African Coastal District, so that some South Central Highlands birds may have crept into the Coastal list, the distinction between the two districts is justified. The following key species characterize the East African Coastal District, those in brackets being extralimital to South Africa:

Francolinus rovumae, *Poicephalus cryptoxanthus*, (*Tauraco fischeri*), *Halcyon senegaloides*, *Pogoniulus pusillus*, *P. simplex*, *Campethera notata*, (*Turdoides squamulatus*), *Lioptilus nigricapillus*, *Phyllastrephus debilis*, *Andropadus importunus*, *Turdus fischeri*, *Cossypha dichroa*, *Erythropygia signata*, *E. quadrivirgata*, *Sheppardia gunningi*, *Bradypterus barratti*, *B. sylvaticus*, *Apalis ruddi*, (*Erythro-*

cercus holochlorus), *Batis fratrum*, *Erythrocercus livingstonei*, (*Anthus melindae*), (*A. sokokoensis*), (*Macronyx aurantigula*), *Tchagra tchagra*, *Malaconotus quadricolor*, *Prionops scopifrons*, *Lamprotornis corruscus*, (*Spreo fischeri*), (*Nectarinia pembae*), *N. neergaardi*, *N. veroxii*, *Anthreptes reichenowi*, (*A. neglectus*), *Ploceus subaureus*, (*P. golandi*), (*Euplectes nigroventris*), *Hypargos margaritatus* *Serinus scotops* and *S. citrinipectus*.

As I have shown elsewhere (Winterbottom 1965), there are two centres of species concentration in the East African Coastal District, one in Mozambique and the other opposite Zanzibar and Pemba; though further exploration of the



Map 6. Lines of Maximal Faunal Change, south-east Cape.

coastal belt in northern Mozambique may show that this bipolarity is due to imperfect knowledge.

The boundary of the South East Coastal District at its southern extremity is based on a map (Map 6) showing the range-limits of 234 species by 1° squares. This somewhat rough-and-ready method simplifies an exceedingly complicated pattern. The northward bulge in the boundary between 24° and 27°E. is due to the extension of the distribution of many coastal birds into the lush vegetation of the inland mountains, while Karoo birds infiltrate south in the drier valleys between the ranges. In the square 32–33°S., 26–27°E. this phenomenon is particularly marked, for 125 species find their limits in this square.

SOUTH CENTRAL HIGHLANDS DISTRICT

Where my proposals differ most radically from those of previous workers is in the extent of the South Central Highlands District. Benson & Irwin (1966), in their fine paper on the *Brachystegia* avifauna, tentatively suggest that the whole extent of this woodland might be regarded as forming a zoogeographical unit, which would fuse Chapin's Rhodesian Highlands and his East African High-

lands Districts (except that part of the latter north of the Equator) and would add the Rhodesian plateau to the district too. I am in complete agreement with these suggestions, which, indeed, I had recommended in part over 30 years ago (Winterbottom 1942), but it will be noted that I have (i) carried the zoogeographical districts across the Luangwa and Zambezi rifts, where the vegetation is dominated by the mopane *Colophospermum mopane*; and (ii) taken it further south to include the middle Limpopo valley and the Transvaal and Swaziland lowveld, some of which is also dominated by *Colophospermum mopane* and the rest by *Acacia* and other trees.

The differences in the avifauna east and west of the Lebombo mountains have been commented on by Vincent (1951); and my views on the northern and eastern Transvaal have already been expressed (Winterbottom 1962). The question of the mopane avifauna is not discussed in any detail by Benson & Irwin, to whose paper it would have been irrelevant.

That the avifauna of mopane differs significantly from that of *Brachystegia* is, I think, clear and the differences are discussed elsewhere (Winterbottom 1972*a*, 1972*b*). However, no such thorough investigation of the mopane avifauna as that of Benson & Irwin for *Brachystegia* has ever been made. Benson & Irwin list 96 *Brachystegia* species from the Rhodesian area of that woodland, of which 19 do not occur south of the Limpopo. A further 13 species are listed as of limited distribution in *Brachystegia* and of these 12 occur south of the Limpopo and the other is confined to the area north of the Zambezi. There are therefore altogether 109 species typical of Rhodesian *Brachystegia*, of which 90 (83%) extend beyond that belt into South Africa. These include 17 of the 29 species confined to *Brachystegia* where that occurs. Benson & Irwin exclude raptors from their list; and these would swell the number of species common to *Brachystegia* and the area south of the Limpopo and to the mopane woodland further north to a significant extent.

I believe, therefore, that the inclusion of the mopane areas of the Zambezi and Luangwa valleys and of the southern lowveld within the South Central Highlands District is justified.

Excluding forms extra-limital to our area, such as *Seicercus laurae*, *Cisticola dambo* and *Myioparus boehmi*, species confined to the South Central Highlands, or virtually so, are as follows:

Centropus cupreicaudus, *Coracias spatulata*, *Stactolaema whytii*, *Campethera bennetti*, *Pinarornis plumosus*, *Monticola angolensis*, *Thamnolaea arnoti*, *Camaroptera stierlingi*, *Cisticola pipiens*, *Lanius souzae*, *Parus rufiventris*, *Lamprotornis acuticaudus*, *Ploceus olivaceiceps* and *Serinus mennelli*.

It will be noted that by no means all of these are birds of the *Brachystegia*.

WESTERN DISTRICTS

As already indicated, Chapin (1923) placed all that part of South Africa west of the highveld grasslands and the Rhodesian plateau in a single district, the South West Arid; Moreau (1952) split off the macchia areas of the extreme

south-west; and Winterbottom (1959) extended Chapin's original district to include the highveld as well as the macchia. There are some 37 species which are widespread in this extended South West Arid District and virtually confined to it:

Melierax canorus, *Francolinus levaillantoides*, *Otis kori*, *O. ludwigii*, *Eupodotis afra*, *Cursorius rufus*, *Pterocles namaqua*, *Colius colius*, *Mirafra apiata*, *M. sabota*, *Certhilauda albofasciata*, *Calandrella starki*, *C. conirostris*, *Eremopterix verticalis*, *Hirundo spilodera*, *Anthoscopus minutus*, *Pycnonotus nigricans*, *Parisoma subcaeruleum*, *Melaenornis silens*, *M. infuscatus*, *Batis pririt*, *Oenanthe monticola*, *Cercomela schlegelii*, *Myrmecocichla formicivora*, *Prinia flavicans*, *P. pectoralis*, *Laniarius atrococcineus*, *Malaconotus zeylonus*, *Onychognathus nabouroup*, *Lamprotornis nitens*, *Nectarinia fusca*, *Sporopipes squamifrons*, *Amadina erythrocephala*, *Uraeginthus granatinus*, *Serinus flaviventris*, *Emberiza impetuani* and *E. capensis*.

Table 3

Coefficients of Community: western districts

	Winter Rainfall	Karoo	Highveld	Damara-land	Sandveld Kalahari	Kalahari Woodland
Winter Rainfall . .	—	51	55	25	24	34
Karoo	51	—	57	46	46	32
Highveld	55	57	—	52	46	46
Damaraland . . .	25	46	52	—	60	60
Sandveld Kalahari .	24	46	46	60	—	51
Kalahari Woodland .	30	32	46	60	51	—

Nevertheless, there are differences between one part of this area and another and Winterbottom (1969) accordingly divided it into six sub-districts: Winter Rainfall; Karoo; Highveld; Damaraland; Sandveld Kalahari; and Kalahari Woodland. Later, Winterbottom (1970) suggested that these sub-districts fell into two groups and proposed to separate the first three as a Southern Temperate District.

If we analyse the faunas of these various sub-districts, using the Coefficient of Community and omitting aquatic forms, we find that the group consisting of the Winter Rainfall, Karoo and Highveld have coefficients of 51–57 *inter se*; and the Damaraland and two Kalahari divisions have coefficients of 51–60 *inter se*. Except in the case of Damaraland and the Highveld, between which the coefficient is 52, the coefficient between divisions in different groups in no case exceeds 46 (Table 3). Inspection of Table 3 also shows that the Winter Rainfall area is the most distinct (average coefficient 37) and the Highveld least (average coefficient 52,8).

The anomalously high coefficient between Damaraland and the Highveld is due to the fact that each contains a higher percentage of species of wide range in the Ethiopian Region further north but which do not penetrate as far south as the other subdivisions. McLachlan & Liversidge (1970) say of the Sandveld

Kalahari 'perhaps mainly characterised by its lack of birds'; and it is, in fact, merely an impoverished version of the Damaraland fauna, 95% of its species being recorded from Damaraland too.

Cooke (1962) produces a map showing the hypothetical vegetation at 50–60% of the present rainfall. This shows that the Karoo would be divided into a northern and a southern section by a broad corridor of desert across Great Namaqualand, linking the Namib with the Kalahari. I can find no trace of this in the present bird distribution, and it is odd that, of the list of Namib birds given by Willoughby & Cade (1967), not a single one is confined to the Namib and Kalahari; all are either Namib endemics or widely distributed in other parts of the south-west.

In commenting on his previous suggestions, Chapin (1932) remarked, with his usual perspicacity, that his treatment of South Africa was the least satisfactory part of his classification and that more districts might be needed. If we split the enlarged South West Arid District on the lines proposed above and confirmed by the figures in Table 3, we find three genera confined to the restricted South West Arid and four to the Southern Temperate; with one (*Philetairus*) occurring in parts of each. The endemic genera and species of these two districts are:

South West Arid District

Genera: *Namibornis*
Achaetops
Lanioturdus

Doubtful genus: *Aethocichla*

Species:
Francolinus hartlaubi
*F. adspersus**
Pterocles burchelli
Poicephalus rueppellii
Agapornis roseicollis
Tockus monteiri
*T. bradfieldi**
Mirafra chuana
Turdoides bicolor
T. gymnogenys
Monticola brevipes
Melaenornis mariquensis
Erythropygia paena
Namibornis herero
Achaetops pycnopygius
Lanioturdus torquatus
Laniarius atrococcineus
*Lamprotornis australis**
Vidua regia

In addition, the Southwest–Northeast species *Poliohierax semitorquatus*, *Turdoides melanops*, *Bubalornis albirostris*, *Estrilda erythronotos* and *Ploceus rubiginosus* are confined to this district in South Africa.

Southern Temperate District

Genera: *Geocolaptes*
Calendula
Chaetops
Stenostira

Doubtful genera: *Sigelus*
Euryptila

Species: *Circus maurus*
Francolinus africanus
F. capensis
*Bubo capensis**
Eupodotis vigorsii
Merops apiaster
Geocolaptes olivaceus
Certhilauda curvirostris
C. albescens
Calendula magnirostris
Eremopterix australis
Hirundo albigularis
Macronyx capensis
Chaetops frenatus
Parisoma lyardi
*Melaenornis silens**
Stenostira scita
Cercomela sinuata
C. tractrac
Monticola rupestris
M. explorator
Erythropygia coryphaeus
Cisticola subruficapilla
Prinia maculosa
P. substriata
*Tchagra tchagra**
Spreo bicolor
*Ploceus capensis**
Serinus tottus
S. alario
S. albogularis

Species marked * extend somewhat beyond the boundaries of the district in which they are listed. Not included in the Southern Temperate list are species confined, or virtually confined, to one sub-district (18 in all). These will be discussed later. *Merops apiaster*, of course, also breeds in the Palaearctic and is widespread in Africa as a non-breeding migrant; and we might have added *Ciconia ciconia* to the Southern Temperate list, since it does the same, though its breeding population in South Africa is very small.

Table 4

Zoogeographical affinities: western species

District	% of Avifauna					
	Cosmo-politan	Ethiopian	S. & E. African	S.W.–N.E. only	S.W. Endemic	Sectional Endemic
South West Arid . .	11	37	24	3	16	9
Southern Temperate .	11	33	23	3	16	14

In Table 4, the zoogeographical affinities of the avifauna are set out. Six categories have been used: Cosmopolitan, being species found in the Ethiopian and one or more other regions; Ethiopian, being species of wide distribution within that region; South and East African, being species of wide distribution in South and East Africa but not extending to West Africa; Southwest–North-east only, being species found in south-western and north-eastern Africa but not in the intervening area; South West endemics, which are found in both western districts; and sectional endemics, found in only one or the other of these two districts. It will be seen that the Southern Temperate District contains a higher

percentage of endemics and a lower percentage of Ethiopian species than the South West Arid.

Moreau (1966) analyses faunas in five categories: A, aquatic birds; B, raptorial and scavenging birds; C, game and other ground birds; D, other non-passerines; and E, passerines. Omitting category A, the results for the two districts of the south-west area are set out in Table 5. It will be seen that the two present rather different faunas, the first having more ground birds and passerines and the second more raptors and 'other non-passerines'. That the Southern Temperate should have more ground birds is to be expected in view of the small extent of woodland in its area, nearly all of which is more or less open country. Moreau (1966) has drawn attention to the relative decline in group D species as one proceeds further from the Equator; and the Southern Temperate District is almost wholly extra-tropical, whereas much of the South West Arid is within the tropics, so that the difference in Group D is to be expected. Moreau attributes the decline to the relative paucity of large insects, which are a major food requirement for many Group D species, in more temperate regions. Many of these species are also dependent on tree-holes for nest-sites and these, too, are in shorter supply further from the Equator.

Table 5

Numbers and percentages of species by categories

District	No. of Species					Percentage			
	B	C	D	E	Total	B	C	D	E
Southern Temperate . .	29	41	44	165	279	10	15	16	59
South West Arid . . .	45	31	58	154	288	16	11	20	53
Somali Arid	39	24	68	161	292	13	8	23	55
Sudanese Arid	42	29	74	163	308	14	9	24	53

I have included in Table 5 an analysis on similar lines of the avifaunas of Chapin's Somali Arid and Sudanese Arid Districts. These figures show that the South West Arid avifauna is intermediate between these wholly tropical faunas and that of the Southern Temperate District in respect of group D. All three of the more tropical faunas have fewer passerines and ground birds but more raptors than the southern fauna. The relationships between these arid faunas are more fully discussed elsewhere (Winterbottom 1972*c*).

Moreau (1966) uses the same classification as that discussed above to analyse the faunas of 'sample-areas' in certain vegetation types. He gives one example for the South West Arid District. This relates to *Acacia* woodland in the central Kalahari and, as may be seen from Table 6, represents a decidedly impoverished fauna when compared with Damaraland areas further west, even with Valencia, on the borders of the Namib (Kemp & Kemp 1972); or with the

Kalahari Gemsbok National Park further south (Prozesky & Haagner 1962), but not with the miserable fauna recorded from Tsabong (Pianka & Huey 1971). Moreau explains that the poor fauna of his Kalahari sample is partly because it

Table 6

Numbers of species in sample areas, South West Arid District

Locality	Latitude	Longitude	C	D	E	Total
Central Kalahari . . .	*c.* 24°S.	*c.* 23°E.	12	16	43	71
Sturmfeld	21°38′S.	18°51′E.	14	28	58	100
Sissekab.	19°22′S.	17°11′E.	16	38	65	119
Otjivasandu.	19°12′S.	14°28′E.	14	22	61	97
Gemsbok Park	26–27°S.	20–21°E.	25	20	66	111
Valencia.	23°10′S.	16°25′E.	9	23	46	78
Tsabong.	26°08′S.	22°28′E.	6	7	19	32

contains only the birds present in the dry season and therefore omits all breeding migrants. However, this cannot account for Pianka & Huey's results.

Similar lists for 12 Karoo localities in the Southern Temperate District have an average for groups C–E species of 45,6, with a range of 32–61. They are markedly inferior to the South West areas in all groups. Six Winter Rainfall localities have an average for the same groups of 48,3, with a range of 38–59, suggesting a similar type of avifauna to that of the Karoo. A single sample from the Highveld (based on Boddam-Whetham 1965) has 88 species in groups C–E, including 22 in group D; and is thus intermediate between the Karoo areas and those of the South West Arid. Thus the Southern Temperate District in general contains rather fewer species as a whole than the South West Arid (Table 5) and decidedly fewer in any one locality.

The inter-relations of the various sub-districts of the South West Arid and Southern Temperate Districts have been discussed above and also elsewhere (Winterbottom 1968*b*, 1971*a*). However, some comments may be made on the Southern Temperate sub-districts and particularly on the Highveld.

Winter Rainfall Area

There are six indigenous species in the Winter Rainfall area: *Anthus crenatus*, *Pycnonotus capensis*, *Bradypterus victorini*, *Promerops cafer*, *Nectarinia violacea* and *Serinus leucopterus*. It is, as remarked above, the most distinct of the three Southern Temperate sub-districts and only 13 of the widespread south-western birds (p. 125) but 25 of the Southern Temperate endemics occur as breeding species. That this avifauna is primarily derived from areas further north and east, especially the Karoo and the South Eastern Coastal District, is shown by the fact that an analysis of the terrestrial birds in Moreau's groups C, D and E gives the proportions of one indigenous species to five found also in other South Temperate divisions to 11 widespread in South Africa. In view of the marked individuality of the lower vertebrates and of the plants of this area, some explanation would seem to be needed; and I have suggested (Winterbottom

1968*c*) that the most important factors may 'have been the same ones, whatever they are, which have been responsible for the reduction in size of the avifauna as one proceeds from low latitudes to high; with the relatively lesser ecological diversity of the vegetation type as a contributing factor'.

Karoo

Five species are endemic to the Karoo; *Alaemon grayi*, *A. burra*, *Calandrella sclateri*, *Camaroptera subcinnamomea* and *Eremomela gregalis*. Of these, *A. grayi* is confined to the Namib. No less than 35 of the 37 south-western endemics occur widely on the Karoo; and 26 of the Southern Temperate endemics.

Highveld

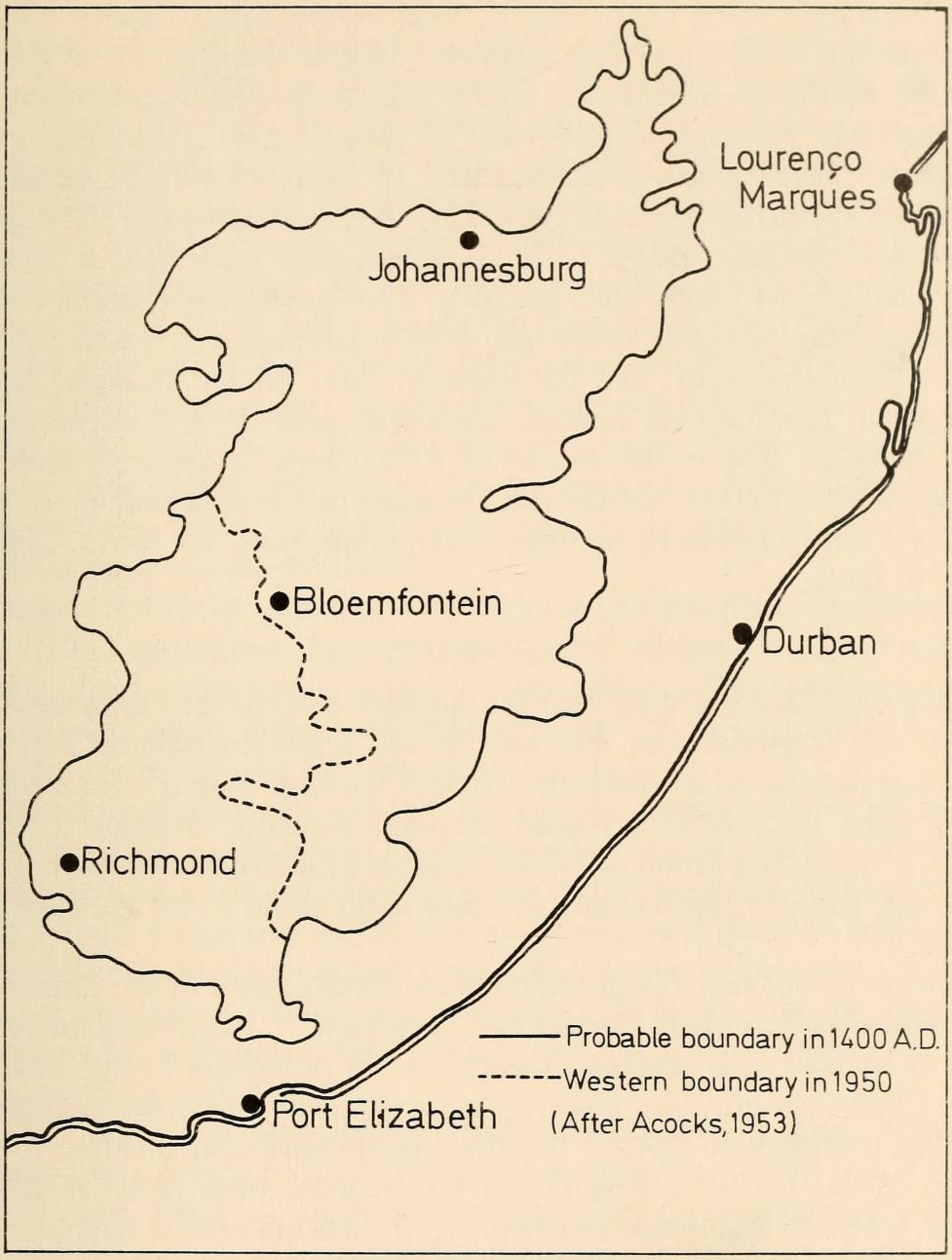
The highveld grasslands of South Africa have their closest, and virtually their only, counterpart in the rest of the Ethiopian Region in the high grasslands of Ethiopia, from which they are cut off by some 2 500 miles (4 000 km) of intervening tropical and subtropical vegetation. Nevertheless, out of 143 terrestrial species listed by Urban & Brown (1971) for the highland grasslands of Ethiopia, 77 (54%) are recorded for the Orange Free State (Van der Plaat 1961) and/or Lesotho (Jacot-Guillarmod 1963).

In considering the avifauna of the highveld and its affinities, two recent man-made changes must be taken into consideration. The first, in point of beginning, is the progressive degradation of the grassveld and its replacement by Karoo as a consequence of 300 years of over-grazing and other agricultural malpractices. Acocks (1953), our chief authority on such matters, believes that the Karoo has advanced at least 2° eastward in the last 450 years (Map 7). The original westward boundary of the grassveld coincides with a climatic change from temperate to tropical. It is necessary to bear this in mind since a number of typical highveld birds, such as *Eupodotis caerulescens*, *Anthropoides paradisea*, *Hirundo spilodera* and the nominate race of *Certhilauda albofasciata*, still inhabit this former grassveld area. This is in significant contrast to the Karoo enclave in the Breede River valley, which is natural Karoo and where, for instance, the subspecies of *Serinus flaviventris* and *Certhilauda curvirostris* are the Karoo forms *quintoni* and *gilli* respectively and not the subspecies of the surrounding macchia, *flaviventris* and *curvirostris*.

The second change has been the considerable planting of trees, mostly aliens, round houses and as wind-breaks, which has led to the invasion of, or at least increase in numbers in, this originally treeless area by arboreal species previously rare or absent (see, e.g., Freer 1965).

Both these changes affect attempts to assess the composition of the highveld avifauna, the first by suggesting that some highveld endemics or near-endemics range to a considerable distance beyond the grassveld; and the second by suggesting that a number of woodland species inhabit the highveld too.

A full list of the characteristic birds of the grasslands will be found in Winterbottom (1972*a*) but for zoogeographical purposes, there are six species confined, or almost confined, to this division. They are:



Map 7. Highveld Grassland.

Geronticus calvus, *Eupodotis caerulescens*, *Calandrella fringillaris*, *Mirafra ruddi*, *Anthus chloris* and *Promerops gurneyi*.

The last of these is not an inhabitant of grassland but of *Protea* bush and it reappears in the *Protea* bush of the eastern highlands of Rhodesia. It is obviously closely related to *P. cafer* of the Winter Rainfall area, with which it occasionally hybridises in the King Williams' Town area, where the two species are sympatric (Skead 1964).

TRANSITIONAL ZONE

This comprises a mosaic of *Baikiaea*, *Acacia* and mopane woodland, open grassland, flood plains and swamps. Examination of the ranges of individual

species show that many characteristic birds of the South Central Highlands extend into this zone, where they meet other forms characteristic of the South West Arid. This is, for instance, the area of overlap between *Pycnonotus barbatus* and *P. nigricans*; *Melierax metabates* and *M. canorus*; *Tockus alboterminatus* and *T. bradfieldi*; *Mirafra rufocinnamomea* and *M. apiata*; *Turdoides jardeneii* and *T. melanops*; *Prinia subflava* and *P. flavicans*; *Laniarius aethiopicus* and *L. bicolor*: though some of these species pairs are ecologically separated. It marks the southern limit in the west of such species as *Streptopelia semitorquata*, *Poicephalus robustus*, *Macrodipteryx vexillarius*, *Merops pusillus*, *Andropadus flaviventris* and *Monticola angolensis*; and the northern limit of, for example, *Laniarius atrococcineus*, *Lamprotornis australis*, *Bubalornis albirostris*, *Pterocles namaqua* and *P. burchelli*. The mixed nature of its avifauna is apparent from these examples. Smithers (1964) divides the Botswana part into several areas, but the Coefficients of Community between these range from 60 to 75, indicating identity of fauna.

MONTANE

Chapin (1932) pointed out that the montane areas of the Ethiopian Region, scattered and fragmented as they are, formed a zoogeographical unit with a distribution pattern quite distinct from that of the lower country. He accordingly grouped them together as a Humid Montane Province, dividing it into two districts, a Cameroon Montane District and an East African Montane District. He did not, however, include any montane areas south of the Zambezi in this province.

Moreau (1966) remarks of the montane forests south of the Zambezi that they contain 'less than half [the number of species] . . . occupying the montane forests of Malawi' and dismisses them from his discussion in two brief paragraphs. Closer investigation, however, suggests that Moreau was exaggerating. I compiled from Benson (1953) a list of 91 species inhabiting montane forests in Malawi; of this list, 68 species (75%) are recorded from forest in Rhodesia and/or southern Mozambique and 58 (64%) from south of the Limpopo. One or two species (e.g. *Pogonocichla swynnertoni* for Rhodesia and *Cossypha dichroa* for South Africa) must be added to obtain the total avifaunas of these southern forests but it is clear that at least the Rhodesian montane forests and that of Gorongoza must be included in the same zoogeographical division as the montane forests further north. Dowsett (1971) agrees.

As one proceeds south, the situation is complicated by the fact that the forests descend to lower and lower altitudes and finally merge with the lowland forest of the East African Coastal District to form a Southern Temperate Forest (Liversidge 1959*b*; Winterbottom 1968). It is still further complicated by differences in the ecological preferences of species in tropical and temperate areas. The Limpopo and Zambezi valleys must always have isolated these southern montane forests into two blocks, cut off by the Zambezi from the montane areas to the north. Whether one is justified in splitting off the montane

and temperate forests south of the Limpopo as a distinct South Temperate Forest District or whether it is better to regard them as a sub-district of the East African Montane District is a moot point, but as they include a number of endemic species, such as *Cossypha dichroa*, *Bradypterus sylvaticus* and *Erythropygia signata*, besides lacking many forms widespread further north (e.g. *Alethe* spp., *Arizelocichla* spp., *Cryptospiza* spp.), they cannot be 'lumped' with the East African Montane forests without some distinction being drawn.

In an endeavour to find out what might have become of our temperate and montane forests in South Africa during the Pleistocene, I first tried to ascertain the factors controlling their natural distribution at present (i.e. ignoring the effects of human interference). Acocks (1953) suggests that the minimum rainfall for forest is 30–35 inches (*c.* 762–889 mm) per annum. But it is clear, from the absence of forest at high altitudes on the Drakensberg and the mountains of the south-west Cape, that some other factor must be involved as well. The most probable of these is temperature.

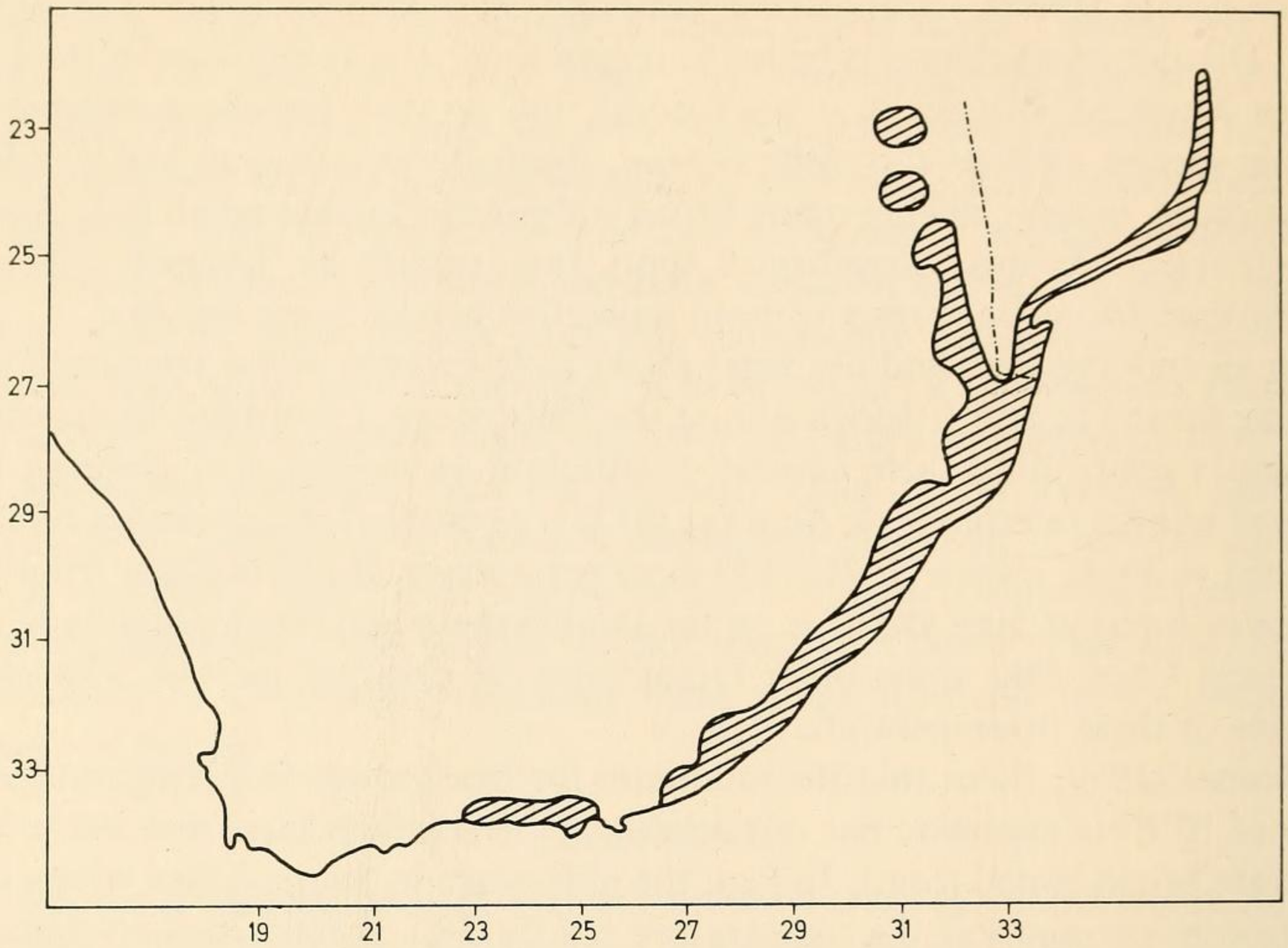
Zeuner (1959) states that the minimum for tree growth is a temperature in excess of 10°C. in summer; but this relates to the northern taiga and not to the temperate broad-leafed forest. In fact, the only place in South Africa where this condition might apply if the temperature fell by 5°C. is Port Nolloth and the rainfall there is inadequate for tree growth anyway.

I therefore plotted the rainfall against the average minimum monthly temperature of the coldest month for those meteorological stations in the vicinity of which forest occurs or was known to occur in the recent past. The bulk of these fell into a zone demarcated by the 850 mm isohyet and the 8°C. isotherm; but in the extreme south, forest could occur with 700 mm of rain and a minimum average temperature of 7°C. in the coldest month. In South America, *Nothofagus* forest occurs at much lower temperatures than this but *Nothofagus* apparently never occurred in Africa.

I then made the assumptions that during a hypothermal period, the temperature would drop 5°C. and the effectiveness of the rainfall would increase by 25%. Cooke (1962) has produced a map showing the hypothetical vegetation with a rainfall of 150% of that at present, but this seemed to me excessive.

The next step was to plot those meteorological stations which met these two requirements—i.e. those with a minimum monthly average temperature of 13°C. or more in the coldest month and a rainfall of at least 640 mm.

The map so obtained (Map 8) suggests that, except close to sea-level, forest could not grow along the south coast except between Knysna and Humansdorp; that there would be a block of forest along the coastal lowland from Alexandria to St. Lucia and thence west of the Lebombo Mountains to about 24°30′S., though the forest may not have been completely continuous. There would be further montane forest blocks in the north-eastern Transvaal, major enlargements of the existing Woodbush and Soutpansberg forests but lower down the mountains, though not descending into the Limpopo valley. It also appears that the Kasane area, at the junction of the Zambezi and Chobe, would have been



Map 8. Suggested forest country during a pluvial period.

able to support forest—there is, of course, riverine ('gallery') forest there today. This forest would not reach as far east as the Victoria Falls; and as its postulated existence depends on the assumption that the increased effectiveness of the rainfall would be the same there as in the south, the suggestion is decidedly speculative.

The big coastal block referred to above is mapped by Cooke (1962) as 'Tropical forest-savanna mosaic' and he extends it up into coastal Mozambique as far as Beira. I did not carry my own investigations into Mozambique but the rainfall map of the South African Weather Bureau supports Cooke's idea that the conditions along the coast there would be much the same as in Natal and Zululand and this has been adopted in my map.

The southern (Knysna) forest block of my map is shown by Cooke as 'Subtropical mixed woodland', which seems to me unlikely.

My map suggests that the temperate (montane) forest and the tropical lowland forest would merge along the Pongola River about latitude 27°S., which is some 4–5° further north than they do today. In East Africa, including Rhodesia, a faunal change in continuous forest cover occurs rather abruptly at an altitude which naturally varies according to the latitude; but this change does not coincide with any change in the botanical nature of the forest. Further south, where lowland and montane forest are separated by drier areas, the avifaunas of the two differ somewhat but chiefly at the subspecific level. Further south still, the two forest types merge into a temperate lowland forest and the avifauna

contains elements of both, plus some endemics. It would presumably be forest of this type which extended north to Zululand in the Pleistocene hypothermals and its greater extent and fragmentation during arid periods would give more scope for the development of these endemics.

I have not considered here whether the lowering of the sea level, and the consequent exposure of much of the present Agulhas Bank, would affect the issue. This has been discussed briefly elsewhere (Winterbottom 1968) and my conclusion was that it would be unlikely to be important.

The avifauna of the montane grasslands and heath-*Protea* complex in Rhodesia includes one endemic species, *Prinia robertsi*; a number of species of wider distribution further south but confined to this area in Rhodesia, such as *Sarothrura affinis*, *Sphenoeacus afer*, *Malaconotus zeylonus*, *Promerops gurneyi*, *Nectarinia famosa*, and *Serinus canicollis*; and montane species of East Africa, here at the southern end of their range, like *Apus myoptilus* and *Nectarinia kilimensis*. Of a list of 58 non-forest montane species in Malawi (based on Benson 1953), ten (17%) do not occur south of the Zambezi.

In the montane non-forest areas south of the Limpopo, there are a number of other species restricted to this type of habitat there but occurring down to sea-level further south. Examples are *Geocolaptes olivaceus* and *Serinus tottus*.

Although the montane forests north of the Limpopo are regarded as a distinct district, this is not the case with the lowland forests of East Africa. These differ from the West African lowland forests in their broken and slighter extent, so that many of the species extend out of the forest into dense scrub. I have listed only six species (*Neocossyphus poensis*, *Bias musicus*, *Malacocincla rufipennis*, *Dicrurus ludwigii*, *Nectarinia olivacea* and *Mandingoa nitidula*) which occur in the West African forests and again in the coastal forests of the east but not in between, and two cases in which one member of a superspecies inhabits the West African forests and another the East African (*Macrosphenus concolor* and *M. kretschmeri*; and *Erythrocercus mccalli* and *E. holochlorus*), so that the avifaunas of the two are quite distinct and it is simplest to regard the East African coastal forests as a habitat of the East African Coastal District. This difference between montane and lowland forest becomes intelligible if we realize that when forest was at its maximum, during a pluvial, the lower temperature would favour montane, rather than lowland, forest; that the avifaunas of the two forest types are largely distinct (Moreau (1952) estimates that 90% of the montane forest avifauna is confined to that habitat and does not occur in lowland forest); and that therefore there is unlikely to have been any direct connection between the lowland forest of east and west.

FRESHWATER

As I have shown elsewhere (Winterbottom 1967), the freshwater avifauna of eastern and northern South Africa forms part of the East African tropical aquatic avifauna; but that of the west and south-west is rather different.

The tropical avifauna, which extends south to St. Lucia, has been fully

discussed and described elsewhere (Winterbottom 1967, 1972*a*). It comprises 52 species, excluding Palaearctic migrants and species characteristic of reed-beds (e.g. *Acrocephalus* spp.). A further ten species are sufficiently widespread to suggest that they, too, should be included. The fauna, which has already been set out in papers cited above and also in Ruwet (1965), is:

Phalacrocorax lucidus, *P. africanus*, *Anhinga rufa*, *Pelecanus rufescens*, *Nycticorax nycticorax*, *Butorides striatus*, *Ardeola rufiventris*, *A. ralloides*, *A. ibis*, *Egretta ardesiaca*, *E. garzetta*, *E. intermedia*, *E. alba*, *Ardea cinerea*, *A. melanocephala*, *A. goliath*, *A. purpurea*, *Ixobrychus minutus*, *Scopus umbretta*, *Ibis ibis*, *Leptoptilos crumeniferus*, *Ephippiorhynchus senegalensis*, *Anastomus lamelligerus*, *Threskiornis aethiopica*, *Plegadis falcinellus*, *Bostrychia hagedash*, *Platalea alba*, *Thalassornis leuconotus*, *Sarkidiornis melanotos*, *Dendrocygna viduata*, *D. bicolor*, *Nettapus auritus*, *Plectropterus gambensis*, *Anas erythrorhyncha*, *Rallus caerulescens*, *Limnocorax flavirostra*, *Gallinula chloropus*, *Porphyrio porphyrio*, *Balaearica pavonina*, *Actophilornis africanus*, *Vanellus senegallus*, *V. armatus*, *V. crassirostris*, *Himantopus himantopus*, *Gallinago nigripennis*, *Larus cirrocephalus*, *Glareola pratincola*, *Chlidonias leucoptera*, *Alcedo cristata*, *Ceryle rudis*, *C. maxima*.

For southern African areas, we should add *Pelecanus onocrotalus*.

The temperate aquatic avifauna of the south-west, based on species occurring in at least 5% of 1 210 lists, consists of 49 species, as follows:

Podiceps cristatus, *P. nigricollis*, *P. ruficollis*, *Pelecanus onocrotalus*, *Phalacrocorax lucidus*, *P. africanus*, *Anhinga rufa*, *Ardea cinerea*, *A. melanocephaal*, *A. purpurea*, *Egretta garzetta*, *E. intermedia*, *Ardeola ibis*, *Nycticorax nycticorax*, *Scopus umbretta*, *Threskiornis aethiopica*, *Platalea alba*, *Phoenicopterus ruber*, *P. minor*, *Plecotropterus gambensis*, *Alopochen aegyptiacus*, *Tadorna cana*, *Anas smithii*, *A. undulata*. *A. erythrorhyncha*, *A. capensis*, *Netta erythrophthalma*, *Oxyura punctata*, *Haliaeetus vocifer*, *Circus ranivorus*, *Limnocorax flavirostra*, *Porphyrio porhpyrio*, *Gallinula chloropus*, *Fulica cristata*, *Charadrius marginatus*, *C. pecuarius*, *C. tricollaris*, *Vanellus armatus*, *Gallinago nigripennis*, *Recurvirostra avosetta*, *Himantopus himantopus*, *Burhinus vermiculatus*, *Ceryle rudis*, *Alcedo cristata*, *Riparia paludicola*, *Acrocephalus gracilirostris*, *Bradypterus babaecalus*, *Cisticola tinniens* and *Motacilla capensis*.

Non-breeding migrants from the Palaearctic, visitors from the sea-coast (e.g. *Larus novaehollandiae*) and species which forage on the shores but breed elsewhere (e.g. *Macronyx capensis*) are excluded.

Of the above 49 species, only 22 (45%) occur also in the tropical list and the Coefficient of Community is 25; so that the two are very distinct.

I have also suggested that the Karoo-Damaraland water birds may form a distinct assembly. The fauna, based on South West African and Karoo lists, numbers 28 species, namely:

Podiceps ruficollis, *Phalacrocorax lucidus*, *P. africanus*, *Ardea cinerea*, *A. melanocephala*, *Scopus umbretta*, *Ciconia nigra*, *Ibis ibis*, *Platalea alba*, *Alopochen aegyptiacus*, *Tadorna cana*, *Anas smithii*, *A. undulata*, *A. sparsa*,

A. capensis, *A. erythrorhyncha*, *Oxyura punctata*, *Gallinula chloropus*, *Fulica cristata*, *Charadrius pecuarius*, *C. tricollaris*, *Vanellus armatus*, *Recurvirostra avosetta*, *Himantopus himantopus*, *Larus cirrocephalus*, *Acrocephalus baeticatus*, *Cisticola tinniens* and *Motacilla capensis*.

The Coefficient of Community between this fauna and that of the south-west is only 43; but Simpson's Coefficient:

$$\frac{c}{n_1} \times 100$$

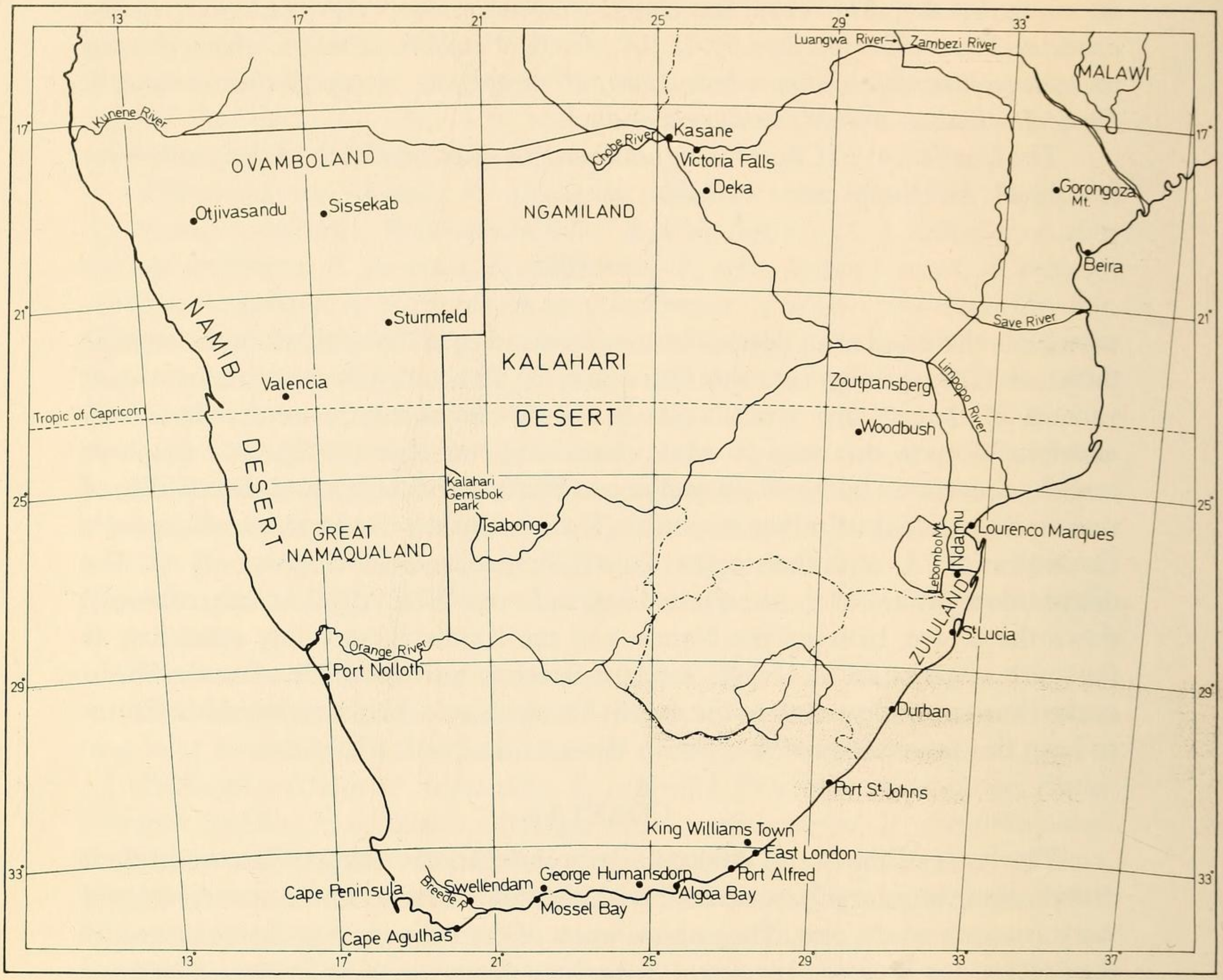
where c is the number of species in common and n_1 is the number in the smaller fauna, is 82, suggesting that this fauna may be little more than an impoverished version of that of the south-west. It should be noted, however, that *Anas undulata*, despite the map in McLachlan & Liversidge (1970), and *Cisticola tinniens* occur only in the south and not in South West Africa and the validity of their inclusion is thus rather doubtful. Their exclusion would reduce Simpson's Coefficient to 75. With the tropical fauna, Simpson's Coefficient is only 43. The distribution pattern of most aquatic birds in South West Africa is a narrow strip down the centre, between the Namib and the Kalahari, and only extending as far south as about 25°S., though some of this may be due to lack of observations at the time water is present in the south. On the whole, I think it would be better to keep this fauna distinct as a South West Arid aquatic avifauna.

COASTAL

The birds of the South African coasts show an east–west difference in their distribution, very largely correlated with the cold current on the west coast and the warm one on the east. The rich avifauna of the west coast is characterized by the presence as breeding species of *Spheniscus demersus*, *Sula bassana*, *Phalacrocorax lucidus*, *P. capensis*, *P. neglectus*, *P. africanus coronatus*, *Haematopus moquini*, *Charadrius marginatus*, *Larus novaehollandiae*, *L. dominicanus*, *Sterna bergii* and *S. balaenarum*. The section from Cape L'Agulhas to Algoa Bay may be regarded as a transition zone, east and north of which the coastal fauna is an impoverished one, with, from Zululand north, a small tropical component *Dromas ardeola*, *Sterna fuscata* and *S. benghalensis* being the most important; but none of these breeds within our limits. The only coastal-breeding species given by Clancey (1971) for southern Mozambique are *Charadrius marginatus*, *Sterna bergii* and *Hydroprogne caspia*.

OCEANIC

As Liversidge (1959*a*) has pointed out, oceanic waters in South Africa belong to the Southern Oceans of Alexander (1955). The Southern Oceans are characterized by the wealth of Sphenisciformes and Procellariiformes, plus a few species of other groups, such as *Sterna vittata*. The only uncertain point is just where this Southern Oceans avifauna gives place to that of the Tropical Oceans. Serventy, Serventy & Warham (1972) have placed the limit of the



Map 9. Places mentioned in the text.

Sub-Antarctic avifauna at the Sub-tropical Convergence; but have, in effect, admitted the invalidity of this by extending the boundary northwards to include the southern coasts of Australia. The idea that the Sub-tropical Convergence constitutes a faunal boundary for birds no doubt stems from Murphy (1936), who considered that 'the majority of oceanic birds are bound as peons to their own specific types of surface water'. This is an exaggeration (Winterbottom 1971*b*). In the Atlantic, the boundary between the Southern Oceans and the Tropical Seas appears to be about the Tropic of Capricorn; on the east coast, it may be about the same latitude—of the 13 species recorded by Rand (1962) in a transect along 28°S., all but *Sterna fuscata* were birds of the Southern Oceans fauna; but the breeding sea birds of Europa Island, in about 22°S., are tropical—*Sula sula*, *Fregata minor*, *Phaethon* spp. and *Sterna fuscata* (Malzy 1966). The distribution of marine birds in the Indian Ocean is poorly known (Watson, Zusi & Storer 1963) but of the 18 tropical species, ten have been recorded within South African limits, mostly as stragglers.

Of the predominantly marine families, the Spheniscidae, Diomedeidae, Procellariidae, Hydrobatidae, Sulidae, Phalacrocoracidae, Stercorariidae and Laridae, South African seas are inhabited by 54 species, excluding such fresh-water forms as *Larus cirrocephalus* and *Chlidonias* spp. in the Laridae and the tropical terns, boobies, tropic-birds and frigate-birds which reach the area only marginally. Of these, 11 species breed (and are more typical of the coasts than the ocean) and another 11 are migrants from the north. The remaining 32 species all breed in the south, ten of them (plus *Larus dominicanus*, which also breeds in South Africa) south of 60°S. Attempts to divide the avifauna of the south into Antarctic and Sub-Antarctic have been made by Murphy (1964) and Voous (1965) but there are only three marine birds whose breeding is wholly confined to the Antarctic (*Thalassoica antarctica*, *Fulmarus glacialoides* and *Pagodroma nivea*) and the first two of these range far to the north out of the breeding season. It may therefore be doubted if it is really profitable to make such a distinction. As I have pointed out elsewhere (Winterbottom 1971*b*), the influence of surface waters has been over-emphasized (except possibly in the case of penguins, whose distribution when not breeding is very poorly known) and I agree with Alexander in including all waters south of the Tropical Convergence in a single zoo-geographical district, the Southern Oceans. To this district, South African off-shore waters belong. It should be noted, however, that not a single species of the Procellariiformes breeds in South African waters.

SUMMARY

South Africa forms part of the Ethiopian Zoogeographical Region. Its birds exhibit five distinct patterns of geographical distribution: oceanic birds, coastal birds, freshwater birds, forest birds and the rest.

Almost the whole of oceanic waters off the South African coast are inhabited by birds of the Southern Oceans Zoogeographical Region.

Coastal birds show a difference between east and west correlated with the warm and cold currents; the eastern avifauna is impoverished and, in the north, has a small tropical element.

Freshwater birds fall into three groups, an eastern tropical, a southern temperate and a western.

The avifauna of the mountain forests of Rhodesia and Mozambique forms a sub-district of the East African Montane District of Chapin (1932). The avi-fauna of the temperate forests south of the Limpopo is rather more distinct; but the tropical forests of the lowlands of Mozambique and Zululand are best regarded as a habitat of the East African Coastal District.

For the remaining land birds, the pattern suggested by their distribution comprises four districts, three of which extend beyond the borders of South Africa, and a transitional zone. Sub-districts are recognizable for three of these districts.

The districts and sub-districts are:

South Central Highlands District
South West Arid District
    Damaraland Sub-district
    Kalahari Sandveld Sub-district
    Kalahari Thornveld Sub-district
East African Coastal District
    Mozambique Sub-district
    Southern Sub-district
South Temperate District
    Karoo Sub-district
    Highveld Sub-district
    Winter Rainfall Sub-district

The transition zone lies between the South Central Highlands and the South West Arid Districts.

ACKNOWLEDGEMENTS

In matters of past plant distribution, I have had the advantage of conversations with Professor E. M. van Zinderen Bakker and Professor E. Schelpe, who must not, however, be held responsible for the views expressed here. I have also had discussions and correspondence on zoogeography with Dr J. C. Poynton, whose views I have found stimulating—especially when I disagreed with them! My colleagues, Professor W. R. Siegfried and Mrs M. K. Rowan, read the whole MS and made helpful suggestions.

For anything concerning the distribution of passerine birds I have found Hall & Moreau (1970) invaluable—without it, this paper would have contained many more inaccuracies than no doubt it does. For non-passerines, I have used White (1965), also a useful work of reference. For the detailed distribution of birds within South Africa, I have used the various numbers of the *South African Avifauna Series*, published by the Percy FitzPatrick Institute of African Ornithology, and the numerous MS lists filed in the Institute, especially my own and those of C. J. Skead, whose meticulous work on the birds of the eastern Cape Province has been invaluable.

The section on the western districts incorporates most of a paper presented at the XV Congressus Internationalis Ornithologicus, where my views on the desirability of two districts in this area were first put forward (Winterbottom 1970).

REFERENCES

Acocks, J. P. H. 1953. Veld types of South Africa. *Mem. bot. Surv. S. Afr.* **28**: i–iv, 1–192.
Alexander, W. B. 1955. *Birds of the ocean*. 2nd ed. London: Putnam.
Benson, C. W. 1953. *A checklist of the birds of Nyasaland*. Blantyre, Lusaka: Nyasaland Society.
Benson, C. W. & Irwin, M. P. S. 1966. The *Brachystegia* avifauna. *Ostrich, Suppl.* **6**: 297–321.

BODDAM-WHETHAM, A. D. 1965. The birds of Kirklington, O.F.S. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **32**: 1–35.
BOWEN, W. W. 1933. African bird distribution in relation to temperature and rainfall. *Ecology* **14**: 247–271.
BRODKORB, P. 1960. How many birds have existed? *Bull. Fla St. Mus. biol. Sci.* **5**: 41–53.
CHAPIN, J. P. 1923. Ecological Aspects of bird distribution in tropical Africa. *Am. Nat.* **59**: 106–125.
CHAPIN, J. P. 1932. Birds of the Belgian Congo. Part 1. *Bull. Am. Mus. nat. Hist.* **65**: i–x, 1–756.
CLANCEY, P. A. 1953. *A preliminary list of the birds of Natal and Zululand.* Durban: Durban Museum.
CLANCEY, P. A. 1971. A handlist of the birds of Moçambique. Part 1. *Mems Inst. Invest. cient. Mocamb.* 10(A): 145–302.
CLARK, J. D. 1967. *Atlas of African prehistory.* Chicago, London: University of Chicago Press.
CLOUDESLEY-THOMPSON, J. L. 1969. *The zoology of tropical Africa.* London: Weidenfeld & Nicolson.
COOKE, H. B. S. 1962. The Pleistocene environment in southern Africa: hypothetical vegetation in southern Africa during the Pleistocene. *Ann. Cape prov. Mus.* **2**: 11–15.
DE BEAUFORT, L. F. 1951. *Zoogeography of the land and inland waters.* London: Sidgwick Jackson.
DOWSETT, R. J. 1971. The avifauna of the Makutu Plateau, Zambia. *Revue Zool. Bot. afr.* **84**: 312–333.
EKMAN, S. 1952. *Zoogeography of the sea.* London: Sidgwick.
FREER, J. S. 1955. Reaction of birds to habitation. *Bokmakierie* **7**: 48–49.
HAGMEIER, E. M. & STULTS, C. D. 1964. A numerical analysis of the distribution patterns of North American mammals. *Syst. Zool.* **13**: 125–155.
HALL, B. P. 1970. Causal ornithogeography of Africa, *Int. orn. Congr.* **15** (Abstr.): 33–36.
HALL, B. P. & MOREAU, R. E. 1970. *An atlas of speciation in African passerine birds.* London: British Museum (Natural History).
JACOT-GUILLARMOD, C. 1963. Catalogue of the birds of Basutoland. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **8**: 1–111.
JENSEN, R. A. C. & JENSEN, M. K. 1971. First breeding records of the Herero Chat *Namibornis herero*, and taxonomic implications. *Ostrich, Suppl.* **8**: 105–116.
KEAST, A. 1972. Faunal elements and evolutionary patterns: some comparisons between the continental avifaunas of Africa, South America and Australia. *Int. orn. Congr.* **15** (Proc.): 594–622.
KEMP, A. C. & KEMP, M. I. 1972. The birds of Valencia Ranch, South West Africa. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **82**: 1–15.
LAWSON, W. J. 1971. Check list of the birds of Durban. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **73**: 1–80.
LIVERSIDGE, R. 1959*a*. The place of South Africa in the distribution and migration of ocean birds. *Ostrich, Suppl.* **3**: 47–57.
LIVERSIDGE, R. 1959*b*. Tropical mountain birds south of the Zambesi. *Ostrich, Suppl.* **3**: 68–78.
MCCULLOCH, D., SKEAD, C. J. & WINTERBOTTOM, J. M. 1970. The birds of Port St. Johns. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **71**: 1–34.
MACKWORTH-PRAED, C. W. & GRANT, C. H. B. 1955. *African handbook of birds.* Ser. 1, **1**. *Birds of eastern and north eastern Africa.* London: Longmans, Green.
MCLACHLAN, G. R. & LIVERSIDGE, R. 1947. *Roberts Birds of South Africa.* Johannesburg: Central News Agency.
MCLACHLAN, G. R. & LIVERSIDGE, R. 1970. *Roberts Birds of South Africa.* 3rd ed. Johannesburg: Central News Agency.
MALZY, P. 1966. Oiseaux et mammifères de l'Île Europa. *Mém. Mus. natn. Hist. nat., Paris* (n.s. A) **41**: 23–27.
MOREAU, R. E. 1952. Africa since the Mesozoic. *Proc. zool. Soc. Lond.* **121**: 869–913.
MOREAU, R. E. 1966. *The bird faunas of Africa and its islands.* New York, London: Academic Press.
MURPHY, R. C. 1936. *Oceanic birds of South America.* New York: American Museum of Natural History.
MURPHY, R. C. 1964. Systematics and distribution of Antarctic petrels. *In:* CARRICK, R., HOLDGATE, M. & PREVOST, J., *eds. Biologie Antarctique*: 349–358. Paris: Hermann.

PATERSON, J. M. 1958. *Check list of birds of the eastern Cape Province*. Port Elizabeth: Eastern Cape Wild Bird Society.

PIANKA, E. R. & HUEY, R. B. 1971. Bird species density in the Kalahari and the Australian deserts. *Koedoe* **14**: 123–129.

PINTO, A. A. DA R. 1953. Uma lista sistemática das aves da região do extremo sul da Provincia de Moçambique. *Bolm Soc. Est. Moçamb.* **23** (77): 1–72.

POOLEY, A. C. & DIXON, J. E. W. 1966. A check list of the birds occurring in the Ndumu Game Reserve in Northern Zululand. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **39**: 1–38.

POYNTON, J. C. 1964. The biotic divisions of southern Africa as shown by the Amphibia. *In:* DAVIS, D. H. S., *ed. Ecological studies in southern Africa:* 206–218. The Hague: Junk. (*Monographiae biol.* **14**.)

PROZESKY, O. P. M. & HAAGNER, C. H. 1962. A check list of the birds of the Kalahari Gemsbok Park. *Koedoe* **5**: 171–182.

RAND, R. W. 1962. Sea-birds south of Madagascar. *Ostrich* **33** (3): 48–51.

ROBERTS, A. 1940. *The birds of South Africa*. London: Witherby; Johannesburg: Central News Agency.

RUWET, J. C. 1965. Les oiseaux des plaines et du lac-barrage de la Lufira supérieure (Katanga meridional). Liège: Editions F.U.L.R.E.A.C.

SCLATER, P. L. 1858. On the general geographical distribution of the members of the class Aves. *J. Linn. Soc.* (Zool.) **2**: 130–145.

SERVENTY, D. L., SERVENTY, V. & WARHAM, J. 1972. *Handbook of Australian seabirds*. Sydney: Reed.

SHORT, L. L. 1970. The affinity of African with Neotropical woodpeckers. *Ostrich, Suppl.* **8**: 35–40.

SKEAD, C. H. 1964. Sugarbirds in the Amatole Mountains, King William's Town, Cape Province. *Ostrich* **35**: 236.

SMITHERS, R. H. N. 1964. *A check list of the birds of Bechuanaland Protectorate and the Caprivi Strip*. Salisbury: National Museums of Southern Rhodesia.

SMITHERS, R. H. N., IRWIN, M. P. S. & PATERSON, M. L. 1957. *A check list of the birds of Southern Rhodesia*. Salisbury: Rhodesian Ornithological Society.

UDVARDY, M. D. F. 1969. *Dynamic zoogeography*. New York: Van Nostrand Reinhold.

URBAN, E. K. & BROWN, L. H. 1971. *A check list of the birds of Ethiopia*. Addis Ababa: University Press.

VAN DER PLAAT, A. 1961. Lys van wilde voëls vir die Oranje-Vrystaat. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **2**: 1–69.

VINCENT, J. 1951. Note on some Swaziland birds. *Ostrich* **22**: 123–125.

VOOUS, K. H. 1965. Antarctic birds. *In:* MIEGHEM, J. VAN & OYE, P. VAN, *eds. Biogeography and ecology in Antarctica:* 649–689. The Hague: Junk. (*Monographiae biol.* **15**.)

WALLACE, A. R. 1876. *The geographical distribution of animals*. London: Macmillan.

WATSON, G. E., ZUSI, R. L. & STORER, R. 1963. *Preliminary field guide to the birds of the Indian Ocean*. Washington: Smithsonian Institution.

WHITE, C. M. N. 1965. *A revised check list of African non-passerine birds*. Lusaka: Government Printer.

WILLOUGHBY, E. J. & CADE, T. J. 1967. Drinking habits of birds in the central Namib Desert of South West Africa. *Scient. Pap. Namib Des. Res. Stn* **31**: 1–35.

WINTERBOTTOM, J. M. 1942. A contribution to the ornithology of Barotseland. *Ibis* (14) **6**: 18–27.

WINTERBOTTOM, J. M. 1959. Some zoo-geographical remarks on the South African avifauna. *Ostrich, Suppl.* **3**: 40–46.

WINTERBOTTOM, J. M. 1962. The zoo-geographical affinities of the avifauna of the northern and eastern Transvaal. *Ostrich* **33** (2): 32–37.

WINTERBOTTOM, J. M. 1965. Faunal groups in the avifauna of southern Africa. *Revue Zool. Bot. afr.* **71**: 157–170*ter*.

WINTERBOTTOM, J. M. 1966. Avifaunal resemblances between the Neotropical and Ethiopian Regions. *Hornero* **10**: 209–214.

WINTERBOTTOM, J. M. 1967. The relationships of some African aquatic avifaunas. *Revue Zool. Bot. afr.* **75**: 148–155.

WINTERBOTTOM, J. M. 1968*a*. Remarks on some forest avifaunas of southern Africa. *Ostrich* **39**: 146–149.

WINTERBOTTOM, J. M. 1968*b*. A check list of the land and fresh water birds of the western Cape Province. *Ann. S. Afr. Mus.* **53**: 1–276.
WINTERBOTTOM, J. M. 1968*c*. Remarks on the avifauna of the macchia of the southern Cape Province. *Revue Zool. Bot. afr.* **77**: 221–235.
WINTERBOTTOM, J. M. 1969. *Check list of the birds of South Africa*. Cape Town: South African Ornithological Society.
WINTERBOTTOM, J. M. 1970. The zoogeography of the south west arid area of Africa. *Int. orn. Congr.* **15** (Abstr.): 238.
WINTERBOTTOM, J. M. 1971*a*. *A preliminary check list of the birds of South West Africa*. Windhoek: S.W.A. Scientific Society.
WINTERBOTTOM, J. M. 1971*b*. The position of Marion Island in the sub-Antarctic avifauna. *In:* VAN ZINDEREN BAKKER, E. M., WINTERBOTTOM, J. M. & DYER, R. A., *eds. Marion and Prince Edward Islands:* 241–248. Cape Town: Balkema.
WINTERBOTTOM, J. M. 1972*a*. Ecological distribution of birds in southern Africa. *Monogr. P. Fitzpatrick Inst. Afr. Orn.* **1**: i–vii, 1–82.
WINTERBOTTOM, J. M. 1972*b*. The Mopane avifauna. *S. Afr. Avifauna Ser. P. Fitzpatrick Inst. Afr. Orn.* **87**: 1–19.
WINTERBOTTOM, J. M. 1972*c*. The avifaunas of the arid districts of Africa. *Revue Zool. Bot. afr.* **85**: 131–141.
WINTERBOTTOM, J. M. 1973. The antiquity of the African avifauna. *Ostrich* **44**: 139.
ZEUNER, F. E. 1959. *The Pleistocene period*. London: Hutchinson.

APPENDIX

English names of birds mentioned in the text

Achaetops pycnopygius—Damara Rockjumper
Acrocephalus baeticatus—South African Marsh-Warbler
gracilirostris—Cape Reed-Warbler
Actophilornis africanus—African Jaçana
Agapornis roseicollis—Rosy-faced Lovebird
Agalaius phoeniceus—Red-winged Blackbird
Alaemon burra—Red Lark
grayi—Gray's Lark
Alcedo cristata—Malachite Kingfisher
Alopochen aegyptiacus—Egyptian Goose
Amadina erythrocephala—Red-headed Finch
fasciata—Cut-throat Finch
Anas capensis—Cape Teal
erythrorhyncha—Red-billed Teal
smithii—Cape Shoveller
sparsa—Black Duck
undulata—Yellow-billed Duck
Anastomus lamelligerus—Openbill
Andropadus flaviventris—Yellow-breasted Bulbul
importunus—Sombre Bulbul
virens—Little Greenbul
Anhinga rufa—African Darter
Anthoscopus minutus—Penduline Tit
Anthreptes neglecta—Ulunguru Violet-backed Sunbird
reichenowi—Blue-throated Sunbird
Anthropoides paradisea—Blue Crane
Anthus chloris—Yellow-breasted Pipit
crenatus—African Rock-Pipit
melindae—Malindi Pipit
sokokensis—Sokoke Pipit
Apalis ruddi—Rudd's Apalis
Apus myoptilus—Scarce Swift
Ardea cinerea—Grey Heron
goliath—Goliath-Heron
melanocephala—Black-headed Heron
purpurea—Purple Heron
Ardeola ibis—Cattle-Egret
ralloides—Squacco Heron
rufiventris—Rufous-bellied Heron
Balaearica pavonina—Crowned Crane
Batis fratrum—Woodwards' Batis
pririt—Pririt Batis
Bias musicus—Black-and-White Flycatcher
Bostrychia hagedash—Hadeda
Bradypterus babaecalus—African Sedge-Warbler
barratti—Scrub-Warbler
sylvaticus—Knysna Scrub-Warbler
victorini—Victorin's Warbler
Bubalornis albirostris—Buffalo-Weaver
Bubo capensis—Cape Eagle-Owl
Burhinus vermiculatus—Water-Dikkop
Butorides striatus—Green-backed Heron
Calandrella conirostris—Pink-billed Lark
fringillaris—Botha's Lark
sclateri—Sclater's Lark

Calandrella starki—Stark's Lark
Calendula magnirostris—Thick-billed Lark
Camaroptera stierlingi—Stierling's Barred Warbler
subcinnamomea—Cinnamon-breasted Warbler
Campethera abingoni—Golden-tailed Woodpecker
bennetti—Bennett's Woodpecker
notata—Knysna Woodpecker
Centropus cupreicaudus—Coppery-tailed Coucal
Cercomela schlegelii—Karoo Chat
sinuata—Sickle-winged Chat
tractrac—Tractrac Chat
Certhilauda albescens—Karoo Lark
albofasciata—Spike-heeled Lark
curvirostris—Long-billed Lark
Ceryle maxima—Giant-Kingfisher
rudis—Pied Kingfisher
Ceuthmochares aereus—Green Coucal
Charadrius marginatus—White-fronted Plover
pecuarius—Kittlitz's Plover
tricollaris—Three-Banded Plover
Chlidonias leucoptera—White-winged Black Tern
Ciconia ciconia—White Stork
nigra—Black Stork
Circus maurus—Black Harrier
ranivorus—African Marsh-Harrier
Cisticola dambo—Black-tailed Cisticola
juncidis—Fan-tailed Cisticola
pipiens—Chirping Cisticola
subruficapilla—Grey-backed Cisticola
tinniens—Le Vaillant's Cisticola
Colius colius—White-backed Mousebird
Coracias spatulata—Racket-tailed Roller
Cossypha dichroa—Chorister-Robin
heuglini—Heuglin's Robin
Cursoirus rufus—Burchell's Courser
Dendrocygna bicolor—Fulvous Tree-Duck
viduata—White-faced Duck
Dicrurus adsimilis—Fork-tailed Drongo
ludwigii—Square-tailed Drongo
Dromas ardeola—Crab-Plover
Egretta alba—Great White Egret
ardesiaca—Black Heron
garzetta—Little Egret
intermedia—Yellow-billed Egret
Emberiza capensis—Cape Bunting
impetuani—Lark-like Bunting
Ephippiorhynchus senegalensis—Saddle-billed Stork
Eremomela gregalis—Karoo Green Warbler
Eremopterix australis—Black-eared Finch-Lark
verticalis—Grey-backed Finch-Lark
Erythrocercus holochlorus—Little Yellow Flycatcher
livingstonei—Livingstone's Flycatcher
mccalli—Chestnut-capped Flycatcher
Erythropygia coryphaeus—Karoo Robin
paena—Kalahari Robin
quadrivirgata—Bearded Robin
signata—Brown Robin
Estrilda erythronotos—Black-cheeked Waxbill
Euplectes axillaris—Red-shouldered Widowbird

Euplectes nigroventris—Zanzibar Red Bishop
Eupodotis afer—Black Korhaan
caerulescens—Blue Korhaan
ruficrista—Red-crested Korhaan
vigorsii—Karoo Korhaan
Eurystomus glaucurus—Broad-billed Roller
Francolinus adspersus—Red-billed Francolin
africanus—Grey-winged Francolin
capensis—Cape Francolin
hartlaubi—Hartlaub's Francolin
levaillantoides—Orange River Francolin
rovumae—Rovuma Francolin
sephaena—Crested Francolin
Fregata minor—Greater Frigatebird
Fulica cristata—Red-knobbed Coot
Fulmarus glacialoides—Antarctic Fulmar
Gallinago nigripennis—Ethiopian Snipe
Gallinula chloropus—Moorhen
Geocolaptes olivaceus—Ground-Woodpecker
Geronticus calvus—Bald Ibis
Glareola pratincola—Pratincole
Gutter edouardi—Crested Guineafowl
Haematopus moquini—Black Oystercatcher
Halcyon senegaloides—Mangrove-Kingfisher
Haliaeetus vocifer—Fish-Eagle
Himantopus himantopus—Black-winged Stilt
Hirundo albigularis—White-throated Swallow
spilodera—Cliff-Swallow
Hydroprogne caspia—Caspian Tern
Hypargos niveoguttatus—Red-throated Twinspot
Ibis ibis—Wood-Ibis
Ixobrychus minutus—Little Bittern
Lagonosticta senegala—Red-billed Firefinch
Lamprotornis acuticaudus—Sharp-tailed Starling
australis—Burchell's Starling
corruscus—Black-bellied Starling
mevesii—Long-tailed Starling
nitens—Cape Starling
Laniarius aethiopicus—Tropical Boubou
atrococcineus—Crimson-breasted Shrike
bicolor—Western Boubou
Lanioturdus torquatus—White-tailed Shrike
Lanius collaris—Fiscal-Shrike
souzae—Souza's Shrike
Larus cirrocephalus—Grey-headed Gull
dominicanus—Southern Black-backed Gull
novaehollandiae—Hartlaub's Gull
Leptoptilus crumeniferus—Marabou
Limnocorax flavirostra—Black Crake
Lioptilus nigricapillus—Bush-Blackcap
Macrodipteryx vexillarius—Pennant-winged Nightjar
Macronyx aurantigula—Pangani Longclaw
capensis—Orange-throated Longclaw
croceus—Yellow-throated Longclaw
Macrosphenus concolor—Grey Longbill
kretschmeri—Kretschmer's Longbill
Malacocincla rufipennis—Pale-breasted Illadopsis
Malaconotus quadricolor—Gorgeous Bush-Shrike
zeylonus—*Bokmakierie*

Mandingoa nitidula—Green Twinspot
Melaenornis infuscatus—Chat-Flycatcher
mariquensis—Marico Flycatcher
silens—Fiscal-Flycatcher
Melierax canorus—Chanting Goshawk
metabates—Dark Chanting Goshawk
Merops apiaster—European Bee-eater
pusillus—Little Bee-eater
Mirafra africanoides—Fawn-coloured Lark
apiata—Clapper-Lark
chuana—Short-clawed Lark
ruddi—Rudd's Lark
rufocinnamomea—Flappet-Lark
sabota—Sabota Lark
Monticola angolensis—Angola Thrush
brevipes—Short-toed Rock-Thrush
explorator—Sentinel Rock-Thrush
rupestris—Cape Rock-Thrush
Motacilla capensis—Cape Wagtail
Myioparus boehmi—Böhm's Flycatcher
Myrmecocichla formicivora—Ant-eating Chat
Namibornis herero—Herero Chat
Nectarinia bifasciata—Purple-banded Sunbird
famosa—Malachite Sunbird
fusca—Dusky Sunbird
kilimensis—Bronze Sunbird
mariquensis—Marico Sunbird
neergaardi—Neergaard's Sunbird
olivacea—Olive Sunbird
pembae—Pemba Sunbird
senegalensis—Scarlet-chested Sunbird
veroxii—Grey Sunbird
violacea—Orange-breasted Sunbird
Neocossyphus poensis—White-tailed Ant-Thrush
Netta erythrophthalma—Southern Pochard
Nettapus auritus—Pygmy-Goose
Nicator gularis—Yellow-spotted Nicator
Nycticorax nycticorax—Night-Heron
Oenanthe monticola—Mountain-Chat
Onychognathus nabouroup—Pale-winged Starling
Ortygospiza locustella—Locust-Finch
Otis kori—Kori Bustard
ludwigii—Ludwig's Bustard
Oxyura punctata—Maccoa Duck
Pagodroma nivea—Snow-Petrel
Parisoma layardi—Layard's Tit-babbler
subcaeruleum—Tit-babbler
Parus rufiventris—Rufous Tit
Passer motitensis—Great Sparrow
Pelecanus onocrotalus—White Pelican
rufescens—Pink-backed Pelican
Phalacrocorax africanus—Reed-Cormorant
capensis—Cape Cormorant
lucidus—White-breasted Cormorant
neglectus—Bank-Cormorant
Phoenicopterus minor—Lesser Flamingo
ruber—Greater Flamingo
Phyllastrephus debilis—Slender Bulbul
Pinarornis plumosus—Boulder-Chat

Platalea alba—African Spoonbill
Platysteira peltata—Black-throated Wattle-eye
Plectropterus gambensis—Spur-winged Goose
Plegadis falcinellus—Glossy Ibis
Ploceus capensis—Cape Weaver
golandi—Clarke's Weaver
olivaceiceps—Olive-headed Weaver
rubiginosus—Chestnut-Weaver
subaureus—Yellow Weaver
velatus—Masked Weaver
Podiceps cristatus—Great Crested Grebe
nigricollis—Black-necked Grebe
ruficollis—Dabchick
Pogonocichla swynnertoni—Swynnerton's Robin
Pogoniulus bilineatus—Golden-rumped Tinker-Barbet
pusillus—Red-fronted Tinker-Barbet
simplex—Green Tinker-Barbet
Poicephalus cryptoxanthus—Brown-headed Parrot
robustus—Cape Parrot
rueppellii—Rüppell's Parrot
Poliohierax semitorquatus—Pygmy-Falcon
Porphyrio porphyrio—Purple Gallinule
Prinia flavicans—Black-chested Prinia
maculosa—Karoo Prinia
pectoralis—Rufous-eared Prinia
robertsi—Roberts's Prinia
subflava—Tawny-flanked Prinia
substriata—Namaqua Prinia
Prionops scopifrons—Chestnut-fronted Helmet-Shrike
Promerops cafer—Cape Sugarbird
gurneyi—Gurney's Sugarbird
Pterocles burchelli—Spotted Sandgrouse
gutturalis—Yellow-throated Sandgrouse
namaqua—Namaqua Sandgrouse
Pycnonotus barbatus—Black-eyed Bulbul
capensis—Cape Bulbul
nigricans—Red-eyed Bulbul
Rallus caerulescens—Cape Rail
Recurvirostra avosetta—Avocet
Riparia paludicola—African Sand-Martin
Sarkidiornis melanotus—Knob-billed Duck
Sarothrura affinis—Striped Flufftail
Scopus umbretta—Hamerkop
Seicercus laurae—Mrs Boulton's Warbler
Serinus alario—Black-headed Canary
albogularis—White-throated Seed-eater
citrinipectus—Lemon-breasted Canary
flaviventris—Yellow Canary
leucopterus—Protea Seed-eater
mennelli—Black-eared Seed-eater
scotops—Forest-Canary
tottus—Mountain-Siskin
Sheppardia gunningi—Gunning's Robin
Smithornis capensis—African Broadbill
Spheniscus demersus—Jackass-Penguin
Sphenoeacus afer—Grassbird
Sporopipes squamifrons—Scaly Weaver
Spreo bicolor—Pied Starling
fischeri—Fischer's Starling

Stactolaema leucotis—White-eared Barbet
whytii—Whyte's Barbet
Stenostira scita—Fairy-Flycatcher
Sterna balaenarum—Damara Tern
benghalensis—Lesser Crested Tern
bergii—Swift Tern
fuscata—Sooty Tern
vittata—Antarctic Tern
Streptopelia capicola—Cape Turtle-Dove
semitorquata—Red-eyed Dove
senegalensis—Laughing Dove
Sturnella magna—Meadowlark
Sula bassana—Cape Gannet
sula—Red-footed Booby
Sylvietta rufescens—Long-billed Crombec
Tadorna cana—South African Shelduck
Tauraco fischeri—Fischer's Turaco
porphyriolophus—Purple-crested Lourie
Tchagra tchagra—Tchagra
Thalassoica antarctica—Antarctic Petrel
Thalassornis leuconotus—White-backed Duck
Thamnolaea arnoti—Arnot's Chat
Threskiornis aethiopica—Sacred Ibis
Tockus alboterminatus—Crowned Hornbill
bradfieldi—Bradfield's Hornbill
monteiri—Monteiro's Hornbill
Turdoides bicolor—Pied Babbler
gymnogenys—Bare-cheeked Babbler
jardineii—Arrow-marked Babbler
melanops—Black-faced Babbler
squamulatus—Scaly Babbler
Turdus fischeri—Natal Thrush
Uraeginthus granatinus—Violet-eared Waxbill
Vanellus armatus—Blacksmith-Plover
crassirostris—White-winged Plover
senegallus—Wattled Plover
Vidua regia—Shaft-tailed Whydah
Zosterops senegalensis—Yellow White-eye