

THE ORIGINS OF THE SOUTHERN AFRICAN MAMMAL FAUNA

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Southern Africa can be geographically subdivided into different biotic zones, differing from each other climatically and vegetationally, and also in respect of the animal species occurring in them. The purpose of the present paper is to consider the nature of the mammal faunas associated with these biotic zones, and to speculate about their origins.

BIOTIC ZONES

Various attempts have been made to subdivide the Ethiopian Region (e.g. Chapin 1932, Moreau 1952). Davis (1962) reviews existing classifications, and presents a modified version of that given by Moreau. Following Davis's classification, four zones are recognised in Southern Africa, as follows (see Fig. 1):

Southern Savanna. The more moist eastern part of southern Africa, with rainfall more than 20 inches annually, extending south as far as the eastern limits of the South-West Cape (see below). The grassland zone of the southern Transvaal, Orange Free State, western Natal, Basutoland and parts of the eastern Cape Province may form a distinct subregion.

South-West Arid. The arid western part of southern Africa, with mean annual rainfall less than 20 inches. The Namib desert of the western coastal strip is in some respects distinct, and may be recognisable as a distinct subregion.

Forest. Isolated patches of montane and subtropical evergreen forest distributed in the Savanna and South-West Cape, mainly below the Great Escarpment.

South-West Cape. A climatically and biotically distinct zone, corresponding to the Cape macchia, stretching along the southern Cape coastal region from the Cape Peninsula in the west to the George-Knysna forests in the east.

CLIMATIC CHANGES IN AFRICA

It is today generally accepted that Africa underwent a succession of climatic changes during the Tertiary and Pleistocene and that these, together with the vegetational changes that accompanied them, probably affected the spread and distribution of animals. As early as 1937 Roberts surmised that the arid areas of south-west Africa and north-east Africa must at some time in the past have been continuous, and that at other times continuous forest extended "from the tropics southwards along the eastern escarpment to the southern Cape Province". Moreau (1952) assembles and discusses evidence for Tertiary and Quaternary climatic changes in Africa, pointing out amongst other things that during the early Tertiary Kalahari con-

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ditions extended as far north as the Congo basin. Leakey (1959) records the occurrence of gerenuk *Lithocranius walleri* in Middle Stone Age deposits at Broken Hill, Zambia. As this species is an arid-area form at present restricted to north-east Africa, its past occurrence as far south as the present comparatively moist Zambia suggests that more arid conditions occurred there during the Upper Pleistocene than now.

Brain and Meester (in press) point out that during the Pleistocene rainfall intensity fluctuated from roughly 10 in. below to 10 in. above present-day mean annual rainfall, and discuss how this might have affected animal distributions. Cooke (1962) and Bakker (1962, 1963) show in what manner Pleistocene fluctuations in moisture conditions and temperature may have affected the distribution of vegetation types. Bond (1963) discusses Tertiary and Quaternary climates, and points out that southern Africa was very arid during the second half of the Tertiary.

Balinsky (1962), in summing up available information on Tertiary and Quaternary climatic changes discusses the importance of periodic climatic fluctuations and displacement of vegetation zones to animal distribution patterns. Pointing out that there has existed in Africa at different times a "drought corridor" running across the continent from south-west to north-east, as well as a "rainforest belt" running from north-west to south-east, he states: "During cold and wet periods the rain forests must have expanded and closed the 'drought corridor' completely or at least narrowed it still further, enabling the animals of the wet tropics to migrate from west to east (and from east to west). During hot and dry periods, the drought corridor would have expanded allowing Kalahari and even desert conditions to surge in, linking more closely the arid south-west with the Somaliland arid area, thus accounting for the close links in the fauna of these areas . . ."

PRESENT-DAY FAUNAL DISTRIBUTIONS

While a number of southern African mammal species are largely cosmopolitan, or were so during historical times (e.g. kudu *Tragelaphus strepsiceros*, lion *Panthera leo*, baboon *Papio ursinus*, and aardvark *Orycteropus afer*), many others are to some extent confined to particular biotic zones, as shown for example by Davis (1962) for southern African Muridae (and also by Ansell 1960, for Zambian mammals). Species occurring in these zones include the following:

Southern Savanna

The greater part of the southern African mammal fauna consists of savanna species, some confined to the Southern Savanna while many others extend also further north through the Northern Savanna. Examples include the short-snouted elephant shrew *Nasilio brachyrhynchus*, red musk shrew *Crocidura flavescens*, grey musk shrew *C. silacea*, rough-haired golden mole *Chrysospalax villosus*, lesser leaf-nosed bat *Hipposideros caffer*, bush-baby *Galago senegalensis*, night-ape *G. crassicaudatus*, white-tailed mongoose *Ichneumia albicauda*, Selous' meerkat *Paracynictis selousi*, giraffe *Giraffa camelopardalis*, oribi *Ourebia ourebi*, sable antelope

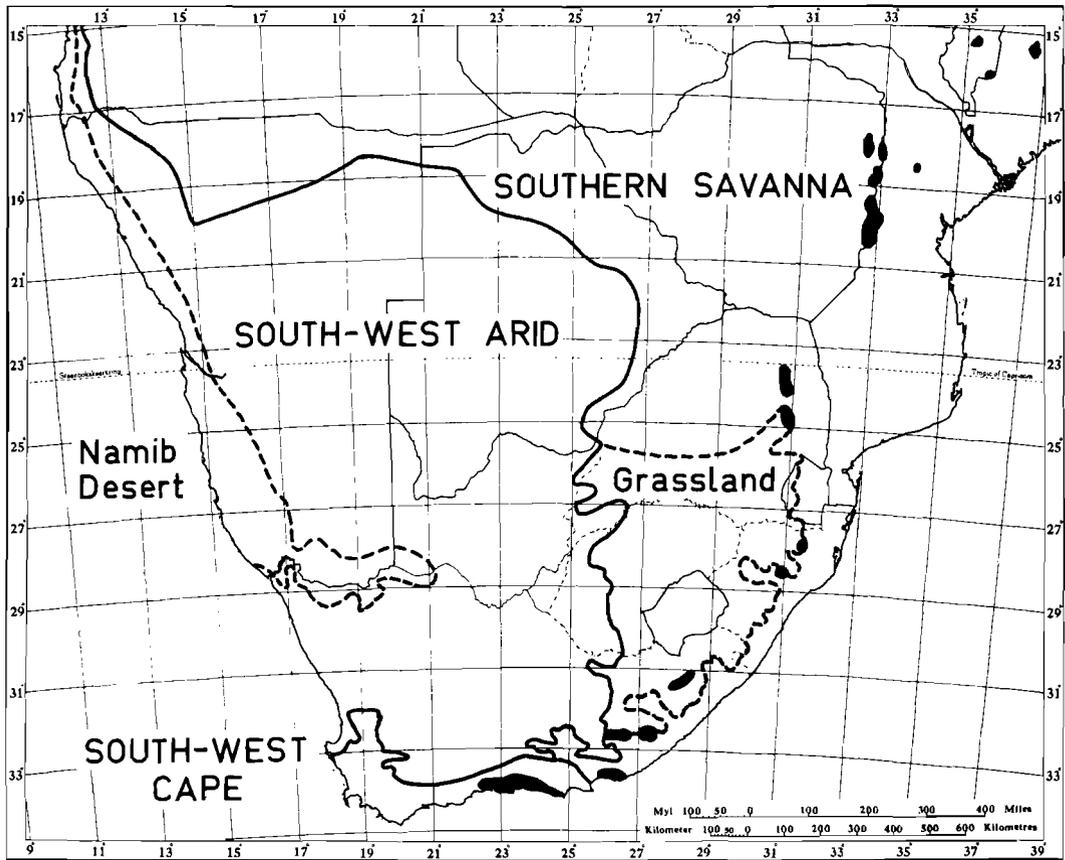


FIGURE 1. The main biotic zones of southern Africa. Forest patches are indicated in black. (After Keay 1959 and Davis 1962.)

Hippotragus niger, buffalo *Syncerus caffer*, a number of murid rodents (Davis 1962), bush squirrel *Paraxerus cepapi* and a great many others.

The grassland zone of the southern Transvaal, Orange Free State, western Natal, Basutoland and eastern Cape Province (montane, temperate and subtropical grassland—Keay 1959), although forming part of the Southern Savanna, appears to differ faunally in some respects. Some savanna species like the giraffe and red musk shrew fail to occur here, while on the other hand forms like the silver jackal *Vulpes chama*, black-footed cat *Felis nigripes*, suricate *Suricata suricatta*, springbok *Antidorcas marsupialis*, blesbok *Damaliscus dorcas phillipsi*, mouse gerbil *Malacothrix typica*, ground squirrel *Xerus inauris*, and in the past apparently also the black wildebeest *Connochaetes gnou*, and red hartebeest *Alcelaphus buselaphus*, all for the most part restricted to the South-West Arid, are (or were) also found in the grassland zone, but not elsewhere in the Southern Savanna. Similarly the white-tailed rat *Mystromys albicaudatus*, and Saunders' vlei rat *Otomys saundersae*, are common to the South-West Cape and this zone, but do not occur elsewhere in the Southern Savanna.

South-West Arid

Amongst others the following forms are more or less endemic to this area: Van Dam's elephant shrew *Elephantulus vandami*, short-eared elephant shrew *Macroscelides proboscideus*, Grant's desert golden mole *Eremitalpa granti*, De Winton's golden mole *Cryptochloris wintoni*, Cape oryx *Oryx gazella*, mountain zebra *Equus zebra*, rock rat *Petromus typicus*, pygmy rock mouse *Petromyscus collinus*, Littledale's Karroo rat *Parotomys littledalei*, and Woosnam's desert rat *Zelotomys woosnami*. Further, as shown above forms like the hedgehog, silver jackal, black-footed cat, suricate, springbok, blesbok, mouse gerbil, ground squirrel, red hartbeest and black wildebeest occur, or have in recent times occurred, both in the South-West Arid and in the grassland zone of the Southern Savanna, but not elsewhere in the latter zone.

Like the Southern Savanna the South-West Arid is not entirely homogeneous faunally. For example the kudu and the otherwise ubiquitous musk shrews (*Crocidura* spp.) do not extend into the Namib desert of the western coast, while Hartmann's mountain zebra *E. z. hartmannae* is on the other hand endemic to this zone. Other groups showing endemism are the insects, and Koch (1960) points out that the Namib desert supports a rich endemic Tenebrionid beetle fauna.

Certain similarities are apparent between the mammal fauna of the South-West Arid and those of the North-East African Somali and Sudanese Arid zones, although they are geographically separated by the intervening Northern and Southern Savanna (see e.g. Roberts 1937, Ansell 1960). The following South-West Arid forms either occur also in the North-East African arid zones, or have close relatives there, in spite of the break in their distribution: bat-eared fox *Otocyon megalotis*, gerbil (*Gerbillus paeba* in the South-West Arid, *G. gerbillus* in the Somali and Sudanese Arid), oryx (represented by *Oryx beisa* in the Somali Arid), and dik-dik *Madoqua kirkii*.

There are also several species, common to the Savanna and Arid zones, showing a similarly interrupted distribution pattern (Ansell 1960). These include the silver jackal (represented by

several related forms in North- and North-East Africa), aardwolf *Proteles cristatus*, hyaena (the brown hyaena *Hyaena brunnea*, in southern Africa, the striped hyaena *H. hyaena* in north-east Africa), black-backed jackal, baboon (*Papio ursinus* in southern Africa, the closely related *P. doguera* in East Africa and *P. cynocephalus* between them), hartebeest (*Alcelaphus buselaphus* in southern and north-east Africa, with *A. lichtensteini* between), sassaby *Damaliscus lunatus* (represented by the related *D. korrigum* in East Africa, with a gap in Zambia), steenbok *Raphicerus campestris*, ground squirrel (represented by *Xerus rutilus* in the Somali Arid), and spring hare *Pedetes capensis*.

Forest

The forest biotic zone in southern Africa contains few endemic species (e.g. dark-footed forest shrew *Myosorex cafer*, Katanga red musk shrew *Crocidura luna*, climbing shrew *Sylvisorex megalura* (although see Ansell 1960), samango monkey *Cercopithecus mitis*, palm civet *Nandinia binotata*, tree dassie *Dendrohyrax arboreus*, and sun squirrel *Heliosciurus gambianus*). A few forest species have spread into the savanna, e.g. pale-footed forest shrew *Myosorex varius*, giant musk shrew *Crocidura occidentalis*, blue duiker *Cephalophus monticola* (marginally), and bushpig *Potamochoerus porcus*.

South-West Cape

Endemic forms include the following: Verreaux's rat *Praomys verreauxi*, Cape spiny mouse *Acomys subspinosus*, Cape greater gerbil *Tatera afra*, Cape sand-mole *Bathyergus suillus*, the extinct blue-buck *Hippotragus leucophaea*, and bontebok *Damaliscus dorcas dorcas*. A few forms such as the Cape golden mole *Chrysochloris asiatica*, and white-tailed rat, although not endemic can nevertheless be regarded as typical of this area.

FAUNAL ORIGINS

The southern African mammal fauna is here considered to consist of four elements: savanna, arid, forest and archaic. Of these the first three appear to be interpretable in terms of the climatic and vegetational changes the continent has undergone (see above), and to be mainly of Pleistocene or in some cases late Pliocene origin. The archaic element, as here understood, consists of older (Miocene, and in the case of the Procaviidae, Oligocene—Hopwood and Hollyfield 1954) groups; and the factors affecting their spread and survival are no longer apparent.

Savanna element

The greater part of the fauna can be regarded as representing a savanna intrusion, which spread into southern Africa by way of the Savanna biotic zone. Although fluctuating in size this zone would have remained in existence during anything except very severe climatic fluctuations, so that it must have formed an important and fairly constant corridor for the spread and interchange of mammal species during most of the Pleistocene. However, as pointed out

by Bond (1963), during the second half of the Tertiary southern Africa was for the most part extremely arid, so that the Savanna zone was presumably very restricted or perhaps even entirely lacking, hence pre-Pleistocene savanna intrusions would probably have been rare to say the least.

The savanna element includes most of the forms at present confined to the Savanna zone, as well as some like kudu, lion, wild dog, cheetah, Burchell's zebra, gerbils (*Tatera brantsi* and *T. leucogaster*), reddish-grey musk shrew *Crocidura cyanea*, and lesser red musk shrew *C. hirta*, at present occurring also in the South-West Arid and/or the South-West Cape, into which they probably spread secondarily. However the South-West Arid species occurring in the grassland zone of the Southern Savanna (see above) are probably arid intrusions which have undergone secondary spread into the Savanna. This is probably true also of some of the species common to the Savanna and Arid zones which have their ranges interrupted in East and Central Africa, although others like the steenbok, black-backed jackal and aardwolf, whose ranges show the smallest gap (Ansell 1960) as well as the sassaby/topi, are probably savanna species. The two grassland species which occur also in the South-West Cape, i.e. white-tailed rat and Saunders' vlei rat, are regarded by Davis (1962) as Savanna species with relict populations in the South-West Cape. However, the white-tailed rat may, as here suggested, form part of the archaic element, in which case both grassland and South-West Cape populations of this species should probably be regarded as relict.

Arid element

The similarities between the faunas of the at present isolated arid areas (South-West Arid in the south, Somali and Sudanese Arid in the north), in respect of such animals as the banded fox, *Gerbillus*, oryx and dik-dik (see above) confirm the past existence of a "drought corridor" allowing the spread and interchange of arid-area species during dry periods of the Pleistocene and presumably also the Tertiary. The arid element consists of those species which spread into southern Africa along this drought corridor, and includes not only most species at present endemic to the South-West Arid but also some which are common to the South-West Arid and Southern Savanna zones and are separated by a gap in Central and East Africa from close relatives in North-East Africa, for example silver jackal, brown hyaena, chacma baboon, red hartebeest and ground squirrel. The presence of these species in the Savanna zone probably represents secondary spread into those parts of this zone where rainfall and other environmental factors permit. The spring-hare, however, although it has a similar break in its distribution, is here regarded as belonging to the archaic, rather than the arid, element.

Of the species common to the South-West Arid and Southern Savanna zones which have their ranges interrupted in East and Central Africa the silver jackal, red hartebeest and ground squirrel occur (or occurred) only in the grassland zone of the Southern Savanna, as do the blackfooted cat, suricate, springbok, blesbok, black wildebeest and mouse gerbil, all of which are regarded as forming part of the arid element.

Forest element

As stated above, during moist periods in the past the present isolated forest patches were

probably continuous, providing a route by means of which forest species were able to spread from the lowland forest of equatorial Africa, down the eastern part of Africa and southward as far as the southern Cape Province. The blue duiker has followed this route as far south as the Outeniqua forest on the southern Cape coast; other forest species have followed it for varying distances, the Katanga red musk shrew, palm civet and sun squirrel for example reaching no further south than the Melsetter district on the eastern escarpment (and Beira in the case of the last two species).

As pointed out above southern Africa was very arid during the latter part of the Tertiary. During the Pleistocene, however, conditions favouring the spread of forests arose repeatedly during successive pluvial periods. Presumably, therefore, the southern African forest element is of Pleistocene age. It is furthermore probable that more than one invasion is represented, and Meester (1958) points out that the relationships of the pale-footed and dark-footed forest shrews can be best explained by assuming that they represent successive invasions of the same parent stock.

Species like the Katanga red musk shrew, climbing shrew, samango monkey, palm civet, tree dassie and sun squirrel, which are restricted to the forest habitat must be regarded as having a relict distribution in southern Africa, like the forests they inhabit.

Archaic element

This element includes those groups or forms at present occurring in southern Africa which, on present evidence, appear to have had a long independent evolutionary history here. Distribution patterns are frequently of a relict type, and whatever climatic factors may have been operative in shaping their distribution patterns are no longer apparent. Examples include the golden moles (Chrysochloridae) and elephant shrews (Macroscelididae), both of which are known as far back as the Lower Miocene of Kenya (Butler and Hopwood 1957), the dassies (Procaviidae), known from the Lower Oligocene of Egypt and the Lower Miocene of South-West Africa (Hopwood and Hollyfield 1954), the aardvark and spring-hare, with closely related ancestral forms from the Miocene of East Africa (MacInnes 1956, 1957), and possibly also the white-tailed rat and rock rat, which appear to be phylogenetically isolated, without close African relatives (although the rock rat may be related to the cane rat *Thryonomys swinderianus*).

In most of these cases the assumption is made that as they occurred elsewhere in Africa during the Miocene they also occurred in southern Africa at that time. Unfortunately the fossil record is too incomplete to indicate whether or not this assumption is correct. However, as they are for the most part arid-area forms, or at least include arid-area species in the case of the more widespread groups, it is reasonable to suppose that they would have been able to survive the arid conditions of the southern African Tertiary. (In this connection the difference between the archaic and arid element is mainly one of timing, and forms here regarded as belonging to the arid element may well prove to be archaic.)

The golden moles are for the most part confined to southern Africa but appear to have undergone secondary spread during comparatively recent times, extending as far north as

Uganda and Tanganyika in the east (*Chlorotalpa*—Allen 1939), and the Congo and south-eastern Cameroons in the west (*Chrysochloris*—Allen 1939). *Chrysochloris*, an arid-area group occurring in the South-West Arid and South-West Cape may have spread northwards during an arid period when Kalahari conditions extended into the Congo basin, while *Chlorotalpa*, which has a partly montane distribution, may have spread north by mountain-hopping during a moister period, when montane forests were more extensive than at present.

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