EFFECTIVE TEMPERATURE AS AN ECOLOGICAL FACTOR IN SOUTHERN AFRICA

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INTRODUCTION

The tremendous volume of scientific research on thermobiology, prompted partly no doubt by man's own inefficient, subjective performance as a thermometer, bears witness to the ultimate utter dependence of all organisms on solar radiation. It is well known that the adaptation of animals to thermal factors is unequal and varied, and that this is demonstrated by the way in which temperature may act as a limiting factor, either alone or as one environmental component interacting with others. Clearly, a consideration of the broader ecological implications of temperature is germane to an understanding of the formation, evolution and interrelation of faunal aggregations in the biosphere.

Surprisingly enough, there are relatively few studies on temperature as a faunistic factor in Africa. This does not reflect any inherent lack of interest which the continent may have for investigators. On the contrary, Africa is climatically unusual among the continents in that its montane areas are relatively small and discontinuous, and it does not extend sufficiently far south or north for latitude to have in present climatic circumstances an especially marked influence. Approximately bisected by the equator, Africa is, as Flint (1959: 347) says, "... the world's warmest continent". South of the Zambesi and Cunene Rivers ecological conditions are particularly interesting on account of their varied nature which is a consequence partly of a wide range of rainfall and the various seasons of its occurrence, and partly of the presence of highlands, the most important of which are asymmetrically placed on the wetter eastern and southern sides of the subcontinent. The altitude of these highlands creates climates much cooler than those that would stem from latitudinal effects alone, though they are not sufficiently high to eliminate the positive isonomaly that exists over most of southern Africa because of continental heating to the north. These factors of rainfall and orographically determined temperature gradients correlate with the distribution of the fauna and flora. Despite many obvious faunal discontinuities in southern Africa, few attempts have been made to explain these in ecological terms other than aspects of vegetation and rainfall. This may be because so many conflicting opinions exist as to which parameters of temperature express best its role as a contributory determinant of zoogeographic boundaries. Studies by Bowen and Poynton seem to be the only ones so far which deal with temperature from that point of view, and I propose to discuss their approach to the subject and their results.

The main purpose of this paper is to ascertain whether a concept developed by an American Geographer, Professor H. P. Bailey of the University of California, concerning the biological importance of the warm period of the year, can meaningfully be applied to southern Africa. Effective Temperature, the numerical expression of this concept, does in fact seem to quantify an ecological factor important to some of the major biogeographic sectors of the fauna. It also provides possibly unexpected insights into the thermal characteristics of South Africa during the last glacial period of the Pleistocene.

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PREVIOUS STUDIES ON THE ECOLOGICAL IMPORTANCE OF TEMPERATURE IN SOUTHERN AFRICA

A study by Bowen

Bowen (1932) presents a scheme of climatic classification for Subsaharan Africa which he states to be relevant to bird distribution. He claims that the distribution of many African birds may be explained by reference to temperature zones, though rainfall must also be considered in an explanation of the distribution of certain species. Bowen favours the idea that temperature extremes, rather than any levels obtained by methods of temperature summation such as those of Köppen or Merriam, are important limiting factors, and assumes that the effect of temperature is direct, whereas rainfall appears to affect bird distribution chiefly through its influence on vegetation. He mentions humidity, nature of soils, and atmospheric pressure as other possible determinants of distribution.

For establishing ecological divisions of the Ethiopian Faunal Region, Bowen uses the following parameters in various combinations: mean annual temperature; mean minimum temperature of the coldest month; mean maximum temperature of the hottest month; annual range of temperature; mean annual rainfall; seasonal duration of rainfall. Subsaharan Africa is divided into five zones—Tropical, Transitional, Subtropical, Temperate and Alpine—of which the Tropical and Subtropical areas are subdivided quite elaborately. Bowen's maps (his Figs. 5 c, d) show southern Africa in the Subtropical Climate category except for a narrow strip of Transitional Zone climate which borders the southern and south-eastern coasts from the Cape Peninsula in the west, and is contiguous with the Transitional Climate of Moçambique and the Limpopo Valley. The area with Subtropical Climate is divided into three sub-categories; there is Highland Climate over most of Rhodesia, the South African Highveld, Great Escarpment and eastern plateau slopes, interrupted by the extension of Transitional Climate along the Limpopo. Within this zone is an area of Temperate Climate over Lesotho and the Drakensberg Escarpment. Westward, reflecting increasing aridity, is a central Kalahari Arid District, then a Damara Arid District which borders the Atlantic from almost the Cape Peninsula to about lat. 12°S.

This climatic scheme is relatively complex and is of special interest in that parameters of both rainfall and temperature are used. However, it seems to have been completely ignored by ornithologists; thus in Moreau's (1966) recent comprehensive study of African birds, Bowen's paper is not even mentioned. The reason for this probably lies in the many unsatisfactory features of Bowen's scheme. In the first place, Bowen presents no direct evidence why his chosen temperature parameters might be limiting factors for African birds, other than to state that the ranges of many species coincide with the climatic types which he defines. Secondly, he gives no consideration to non-climatic factors which are known to influence bird distribution. As examples, physiographic features (such as rift valleys—see Benson, Stuart-Irwin and White 1962) may be mentioned, also certain vegetation types such as *Brachystegia* and Mopane Woodland which are avoided by some species of birds, other vegetation types such as montane forest to which some birds are strictly confined (see Hall & Moreau 1962), and the close association that exists between certain plants and bird species (examples are given by Liversidge 1962: 147).

The parameters chosen by Bowen are open to question on other grounds. The mean minimum temperature of the coldest month is based on night temperatures during that month, and therefore is of doubtful significance for many species of birds which seek out and regularly use sheltered roosting places. Moreover, many species of birds probably avoid the coldest time of year in their normal breeding grounds by migration, a factor largely ignored by Bowen who says, "In discussing zoogeography such species must be considered independently". In fact, seasonal movements seem to feature in the lives of many African birds, though the matter is at present poorly known and documented (see the thorough discussion by Moreau, 1966: Chap. 13). Winter movements, nearly always to warmer areas, however need not always be prompted by cold but may result from food shortages occurring before the colder months of the year. Similarly, the mean maximum temperature of the hottest month is a factor of problematic significance; indeed it probably is important in regions of low or unreliable rainfall, but may be of less moment where birds have water supplies adequate to help them withstand the effects of high temperatures.

Bowen's maps (his Figs. 5 c, d) are on a scale so small that few details can be shown in the distribution of the zones. Nevertheless, a study of the climatic features on which he defines the zones indicates inaccuracies and omissions. Too much country is included in the Southeast Veldt District division of the Highland Climate, the Cape fold mountains are ignored, and the intrusion of a strip of low rainfall from the Karroo to the shores of Algoa Bay is not taken into account. Deficiencies in the scheme are revealed by the failure to represent the winter rainfall of the south-west Cape, and by the inclusion of an entire southern coastal strip, starting at the Cape Peninsula in the west, in the climatic type characteristic of coastal Natal and Zululand, the Moçambique plain and Limpopo Valley.

More detailed criticism from the strictly ornithological point of view is possible but not appropriate here. Perhaps the fairest conclusion to be drawn about Bowen's scheme is that its validity should be tested by an application to animal groups other than birds, and that up till now its value is unproven. Bird distribution is a subject in many ways uniquely complex. I accept the conclusions of Liversidge (1962) on the matter, especially that "dominant climatic factors in a region influence the birds of that area and where these dominant climatic factors vary from region to region, the main factors influencing bird distribution of these regions also vary".

Studies by Poynton

Poynton, who has been considerably influenced by Bowen's work, has contributed an important series of papers on the distribution of Anura in southern Africa in which temperature is frequently invoked as a limiting factor. These papers are largely repetitive and only the more recent (1962, 1964a and 1964b) will be referred to here. Poynton's contribution to this field can be summarised by a series of quotations from his works:

1. "From the distribution of the Amphibia, it is . . . concluded that the biotic pattern of southern Africa is primarily determined by the thermal pattern, and secondarily the distribution of rainfall. The greater part of southern Africa is regarded as being non-tropical, the truly tropical portion being restricted to the Moçambique plain. This tropical-non-tropical differentiation is determined by the thermal pattern". (1964b: 216)
2. "There are no evident changes in the ecological composition of the vleis and rivers along the length of the eastern and southern lowlands, nor are there any evident changes in the ecological characteristics of the amphibians occupying these habitats; yet the taxonomic composition of the amphibian fauna changes completely. The only environmental feature that tends to show a fairly direct and consistent correlation with this faunal change is temperature". (1964a: 230)
3. ". . . the pattern shown by the mean midwinter months (July) surface isotherms fits the distribution pattern extraordinarily well. This is especially true of the 18°C isotherm

which cuts the east coast in the region of Lake St. Lucia, and then runs northwards along the western edge of the Moçambique plain. This isotherm marks the belt of precipitous subtraction at the edge of the main concentration of the tropical fauna. Another isotherm which shows a particularly clear correlation with the pattern of amphibian distribution is the 13°C July isotherm. On the eastern slopes it marks the division between the tropical transitional and the temperate transitional faunas, and also marks the easterly limit of the Cape fauna". (1964b: 210)

4. ". . . these midwinter isotherms do seem to be reliable climatic indicators, *summarising the climatic complex* that appears to be decisive in limiting the distribution of Amphibians, despite the generalised type of habitat preference that these animals show. The value of mean midwinter temperature conditions as general climatic indicators was stressed by Köppen, and indeed he defined a tropical climate as one in which the coldest month has a mean temperature of over 18°C. It therefore seems realistic to make use of these mean isotherms in defining biotic divisions, provided that they are understood to be *symptomatic of a climatic complex*, and not in themselves causative factors in distribution". (1964b: 210; *my italics.*)

In considering the theses outlined in these quotations, I will deal first with Poynton's conclusion that the biotic pattern of southern Africa is primarily determined by the thermal pattern and secondarily by the distribution of rainfall. My view is exactly the opposite one, for reasons the following illustration will reveal. Both Durban (Natal Coast) and Upington (Northern Cape Province) have exactly the same mean annual temperature of 20·5°C, but their mean annual rainfall is widely different, 1,008 mm. at Durban, 156 mm. at Upington (data from WB 19*). The climax formation, in the classification of Acocks (1953), at Durban is Coastal Tropical Forest, and at Upington is Karroo Bushveld, and these localities have almost nothing in common in their fauna and flora. If, by some hypothetical climatic catastrophe, the rainfall distribution should be reversed, the vegetation at Upington in time would probably succeed to forest, whereas at Durban near-desert conditions would prevail. This would merely be another instance of the well-known phenomenon that the growth form of vegetation almost anywhere, except in polar, near-polar and high altitude regions, is largely dependent on the amount and seasonal distribution of rainfall. ". . . the rainfall and the presence or absence of desiccation will determine the growth of trees, grass or desert. . ." (Story 1952: 31). Where rainfall is considerable, forest usually will develop, but if it diminishes markedly xerophytic plant forms appear (the reverse situation has occurred in the Congo where part of the present forest is rooted in Kalahari Sand—Moreau, 1966: 51), and the distribution and evolution of the fauna will be closely associated with such changes.

Southern Africa is progressively more arid from east to west; a true desert occurs on the west coast, and an arid environment exists over the Karroo southwards to the Cape fold mountains. The contrast between east and west coasts is profound in terms of rainfall and its attendant effects, and this is reflected in the completely different fauna and flora of those

*Two publications of the South African Weather Bureau, in its series *Climate of South Africa*, will be referred to as WB 19 and WB 28 respectively; the first is a book of climate statistics and is anonymous, the second is a general survey of the South African climate and is by B. R. Schulze.

areas. A rainfall gradient so great is beyond the range of adaptability of very many animals. Admittedly the eastern fauna is sparsely represented in the west by elements capable of meeting the hostile arid environment, but the most important influence which aridity has on the taxonomic composition of the fauna is not mere depauperisation. This is an ancient desert focus (Bond 1963), populated by a very considerable, highly specialised, obviously old, indigenous fauna, members of which commonly are taxonomically distinct at the generic level and in some groups even at the tribal (eg. Tenebrionidae) and subfamily (eg. Bombyliidae) levels. It is well known that components of this fauna have affinities with the fauna of Mediterranean deserts and the Horn of Africa.

The fundamental division of the biota of southern Africa is into dry western, humid eastern, and part dry-part humid southern sections. This is reflected in the trichotomy of the flora into (1) Karroo, (2) tropical or subtropical forest, savanna and grassland, and (3) macchia, and evidently is a long-standing situation probably extending back over most of the Tertiary (Levyns 1962). The southern latitudinal extension of South Africa evidently is not great enough to impose an overriding thermal influence, and the thermal pattern therefore is considered to be secondary, modifying the distribution pattern mainly within the eastern and southern regions where highlands and especially prominent mountain ranges are present. This is as true for Amphibia as it is for other groups.

I must deal next with a technicality, namely the distribution of the 18°C mean July isotherm in Zululand.* Poynton (1964b: legend to Fig. 2) states that the isotherms he draws are based on data from the South African Weather Bureau. However, the published data are not adequate for the course of this isotherm to be determined. It is true that in WB 19 the station at Cape St. Lucia lighthouse records mean temperatures for both June and July as 17·9°C, but this is misleading because, though at the coast, that station in fact is on the summit of a large dune and has an altitude of 111 m. In such a situation the minimum temperatures recorded will always be too high because cool night air is continuously drained away; the measurements actually are a better guide to free air conditions at that altitude. The monthly means for the station are thus too high. Unpublished data for Charters Creek, supplied by the Natal Parks, Game and Fish Preservation Board, covering the eight-year period 1959-1966, give a mean July temperature of 16·5°C; the station is at a very low altitude on the shore of Lake St. Lucia, 30 km. north of the lighthouse. This mean seems a little low, and the station may be affected by its proximity to the lake, but even so the figure compares well with the July mean of 16·8°C over eight years for Dukuduku cited in WB 19, a station at 70 m. about midway between the other two.

Poynton seems to have overlooked the study by Schulze (1947) who presents two climatic maps of South Africa based on the classifications of Köppen and Thornthwaite respectively. Schulze shows the boundary of Köppen's *A Type Tropical Rain Climate* crossing the coast of Zululand at about 27°30'S, in the vicinity of Sordwana Bay. The likelihood of this being nearly correct is shown by unpublished data for the Mbazwane Forest Station just south of Lake Sibayi, at 68 m., where the July mean for the four years 1963-1966 was

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*Zululand is the territory between the Tugela River and the Swaziland and Moçambique borders.

18·1°C. That is not a long enough period for the mean to be satisfactorily assessed, but the true value must be close to that figure, possibly a little lower. Therefore it seems reasonably certain that the 18°C mean July isotherm crosses the coast a full half-degree of latitude north of the position indicated by Poynton.

Poynton specifically stated that no direct biological significance can be attributed to the mean July isotherms, but (witness the fourth quotation above) he considers that they summarise or are symptomatic of a climatic complex. The latter is a surprising point of view to advance as it is one which can so easily be disproved. In the following table pairs of stations which have about the same mean July temperature are listed with various climatic data (taken from WB 19).

TABLE 1

	Mean July Temp.	*Mean Annual Temp.*	*Mean Annual Number of Days with frost*	*Number of Days Mean Max. > 30°C*	*Mean Annual Rainfall*	*Number of Months Rainfall < 10 mm.*	*Relative Humidity at 0800*	*Number of Rains ⩾ 2 mm.*	*Altitude M*
Port Elizabeth..	13·3	17·3	0·2	11·6	576	0	81	100·6	58
Ghanzi	13·5	20·7	9·5	166·1	470	5	61	53	1,131
George	13·0	16·4	0·[illegible]	12·5	860	0	76	124·4	221
Windhoek ..	12·9	18·8	1·3	69·3	362	5	44	54·5	1,728
Ladysmith ..	11·9	18·6	14·2	87·4	788	1	75	92·6	1,061
Port Nolloth ..	11·9	14·1	0·1	12·2	61	12	88	35·0	7
Durban ..	16·5	20·5	0·0	6·0	1,008	0	75	116·2	5
Ondangua ..	16·4	22·5	0·5	179·7	517	5	—	55·6	1,095

It is immediately obvious from this table that isotherms based on mean July temperatures cannot possibly be used as indicators of a climatic complex. This is also true for any other isotherm.

In another statement, Poynton (1964b: 214) refers to "the tropical fauna, which is limited by the thermal conditions summarised by the 18°C mean July isotherm". This is confusing in view of his first statement discussed above, because thermal conditions are only a part of any climatic complex. As the table above shows, in a general sense no isotherm can summarise all the thermal conditions of all stations embraced by it. In respect of thermal conditions which might be summarised by the 18°C July isotherm only, the situation differs in degree as only places with a relatively hot climate are now included. However, even for different stations on that isotherm, other thermal parameters are unlikely to be the same unless the stations are very close together. One must also beware the fascination of whole numbers. Köppen originally chose the 20°C mean July isotherm as the limit for a tropical climate and subsequently dropped the figure to 18°C (his possible reason for this choice is mentioned later), but no abrupt boundary was implied and of course there can be none.

To demonstrate this, the table given below lists a series of stations with July means lying on each side of 18 °C; several other temperature parameters are given for each station, and these show gradual but unequal and uncorrelated changes.

TABLE 2

		July Temperatures				°C	*Annual Temperatures*			
	Mean	*Mean Max.*	*Mean Min.*	*Absolute Max.*	*Absolute Min.*	*Mean*	*Mean Max.*	*Mean Min.*	*Absolute Max.*	*Absolute Min.*
Komatipoort	17·5	26·4	8·6	35·0	−1·7	23·0	30·3	15·8	47·7	−1·8
Messina ..	17·8	24·5	11·4	32·6	3·9	23·3	29·4	17·2	43·3	2·7
Otobotini	18·1	24·6	11·6	34·4	4·4	22·7	28·4	16·9	44·4	4·4
Punda Maria	18·4	25·3	11·4	32·2	5·0	22·9	29·4	16·4	43·3	2·7
Wankie ..	19·0	27·5	10·5	31·5	6·5	24·5	32·0	17·5	42·5	2·2

Having dealt with some of the climatological aspects of Poynton's studies, it remains to consider some of the biological aspects and especially his attempt to explain anuran distribution in Zululand as a consequence primarily of certain thermal factors. Concerning this region, Poynton (1964a: 230-1) says: "It is . . . seemingly impossible to attribute the precipitous subtraction of the tropical fauna in the Lake St. Lucia region to contemporary ecological factors. No explanation in terms of habitat, prey or predators seems to offer itself. This dramatic zoogeographic change can only be interpreted in the light of the faunal pattern shifting with oscillations in the general thermal pattern. . ."

The first comment to be made is that it is misleading to group together all the species that Poynton calls "tropical" for the purpose of discussing anuran distribution in Zululand (see Poynton 1964a: Fig. 123). As a consequence of his definition of a "tropical" species,[*] species with widely differing ranges are included in that category. Of the 41 Anuran species which he considers "tropical" (1964a: 223), 33 are present in northern Zululand, but only 15 of these are in fact distributed (as far as is known) only on the coastal plain (*Xenopus muelleri*, *Breviceps mossambicus*, *Pyxicephalus marmoratus*, *Ptychadena oxyrhynchus*, *P. mascariensis*, *P. taenioscelis*, *Phrynobatrachus acridoides*, *Arthroleptis stenodactylis*, *Leptopelis concolor*, *Hylambates maculatus*, *Afrixalus fornasinii*, *Hyperolius puncticulatus*, *H. tuberilinguis*, *H. pusillus*, *H. nasutus*). The remaining 18 occur elsewhere in South Africa as well, notably in the central, northern and eastern parts of the Transvaal, in places where they are subjected to thermal conditions considerably dissimilar to those in Zululand. And of these 18, 10 (marked + in the following list) occur not only on the Zululand coastal plain but also range into Natal and further south, away from the coast: *Bufo +regularis*, *B. pusillus*, *B. +carens*, *B. garmani*, *Phryonomerus bifasciatus*, *Pyxicephalus +adspersus*, *P. +delalandei*, *Rana +angolensis*, *Ptychadena anchietae*, *P. +porosissima*, *P. vernayi*, *Phrynobatrachus*

[*] A tropical form is here taken to be a form at least a substantial part of whose range is included in an area experiencing a tropical climate as defined by Köppen, i.e., in which the coldest month has a mean temperature of over 18°C (64·4°F). (Poynton, 1964a: 223)

+natalensis, *P. ukingensis*, *Chiromantis xerampelina*, *Hemisus marmoratum*, *Kassina +senagalensis*, *Afrixalus +brachycnemis*, *Hyperolius +marmoratus*. Thus, if thermal conditions are limiting factors in Zululand, only 15 of the 33 "tropical" species there are likely to be affected; the remainder show by their wider distribution that they have spread independently of the scale of thermal conditions found in Zululand. In addition, the "non-tropical" *Bufo vertebralis fenoulheti* ranges over central South Africa into the Eastern Cape Province, but is not known from Natal except in Zululand and apparently has entered that area from the north. Full details on the distribution of these species are presented by Poynton (1964a); some additional localities given by Bass (1966) for Zululand species do not alter the picture very much.

An examination of the data presented by Poynton (1964a) and Bass (1966) shows that the number of "tropical" species entering Zululand from the north decreases quite rapidly southwards. Between 27°S and 28°S latitude the decrease is fairly small, then there is a great reduction between 28°S and 29°S, a further considerable reduction between 29°S and 30°S, and thereafter a regular but small decrease in the species count. Poynton's maps show that the faunistic change southwards is a step-like or clinal one, which is to be expected as no two species will have exactly the same range in a gradually changing environment (Peters 1955). If the 18°C mean July isotherm is correctly located on the coast at about 27°30'S, it lies near the beginning of the zone of rapid subtraction. The question to be answered now is—are there no factors other than thermal ones which can cause the subtraction in numbers south of latitude 27°S?

A possible factor which immediately comes to mind is that the coastal plain itself gradually narrows southwards and eventually almost disappears; indeed, Poynton (1964a: 224) says, "the initial western subtraction of the tropical fauna is associated with the rising of topography inland from the Moçambique plain. . ." This rise of the land to the west becomes progressively greater southwards and at the same time approaches the coast more and more. At about the vicinity of Eshowe the 2,000 ft. contour is about 48 km. inland if measured along the latitude line, but at and about Durban is only 25 km. from the sea. The change in topography is due to the presence of erosion-resistant Table Mountain Sandstone which occurs in a series of outcrops running roughly north-south (Fig. 1). Northernmost outcrops are between 28°S and 29°S, and are displaced to the west by faulting; there is an extensive outcrop east of Melmoth, forming the elevated landscape west of Eshowe, extending progressively nearer the coast to the south, and forming the mountainous country inland of Durban; south of Durban, from Amanzimtoti to about Port Shepstone, much of the sandstone has been removed by erosion, but further south a long, continuous outcrop borders the coast from Port Edward to Embotji at about 31°30'S.

It is well known that a correlation exists between area and number of species, a larger self-contained area carrying more species than a smaller one broadly equivalent ecologically, and it is also established empirically that as the area of sampling increases, the number of species increases in an approximately logarithmic manner; this is discussed, *inter alia*, by Preston (1962), Wilson (1961), MacArthur and Wilson (1963), and Darlington (1957: 568-570). A possible explanation of the subtraction of "tropical" species would be that those which

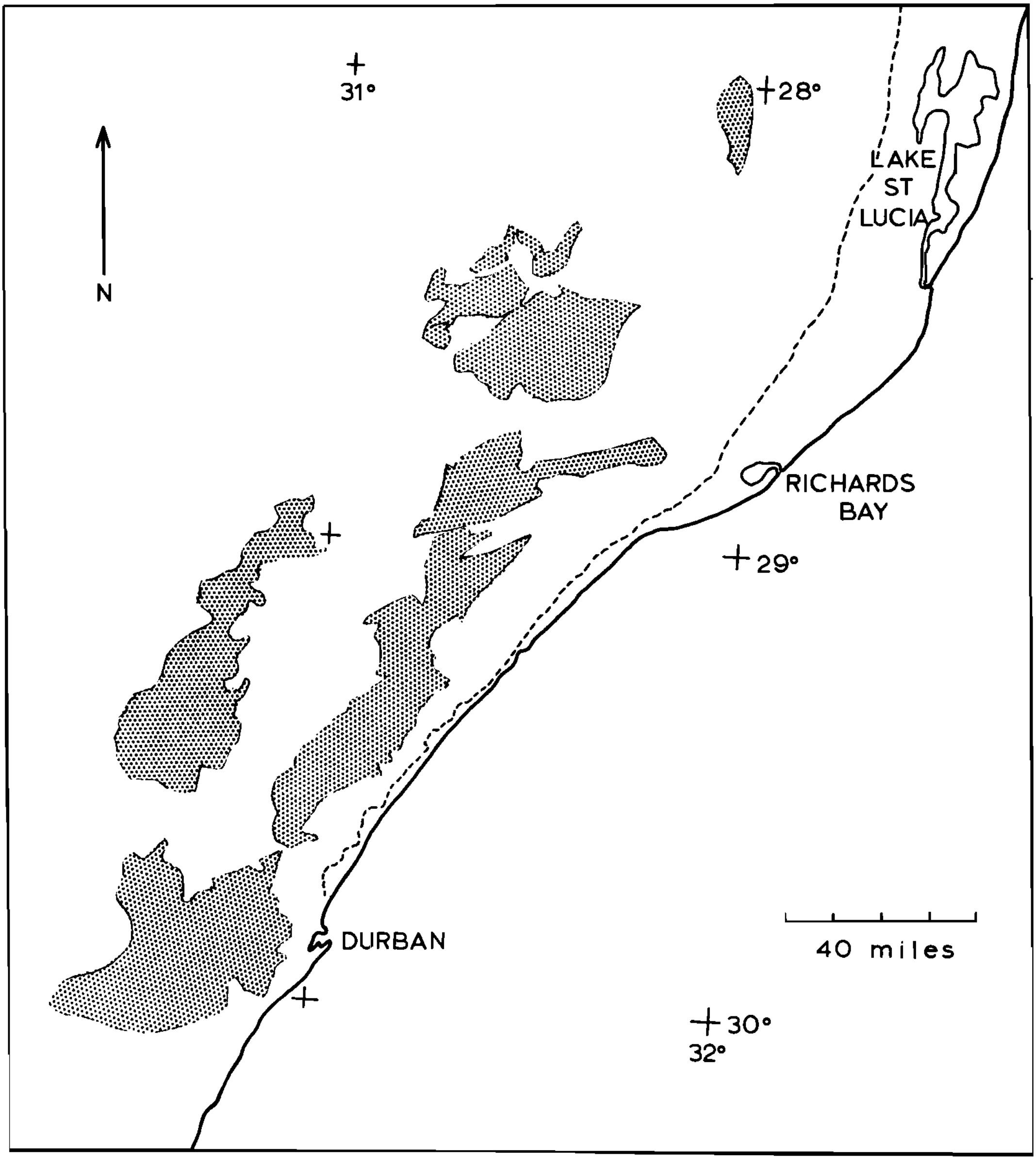

FIGURE 1
Map showing the distribution of Table Mountain Sandstone (stippled patches) in middle and northern Natal. The dotted line marks the western limit of marine Tertiary and Cretaceous sediments. (From 1 : 1,000,000 geological map of South Africa, Government Printer, Pretoria, 1955.)

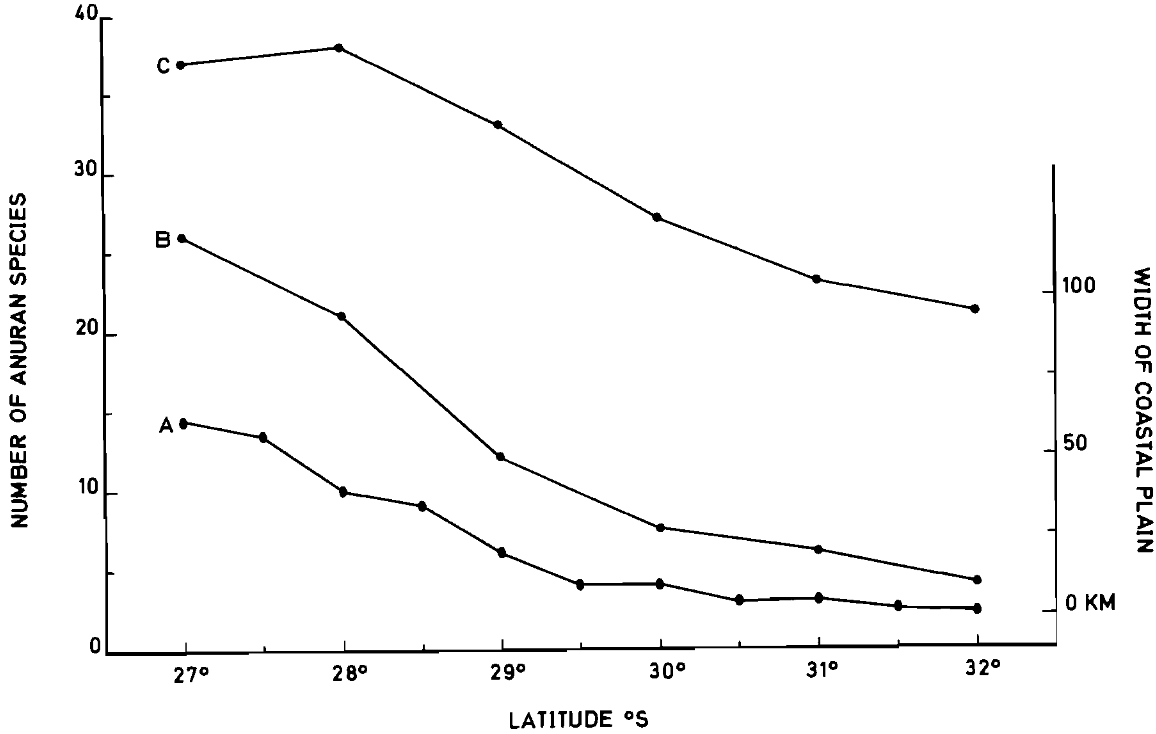

FIGURE 2

Diagram showing the decrease in width of the coastal plain in Natal and Zululand (line A) and associated decrease in number of anuran species (lines B and C, see text), at various latitudes.

on present records appear to be confined to the coastal plain are in fact limited in their range by a preference for ecological conditions offered by this plain, and that as the plain diminishes and therefore can carry fewer individuals, so the number of species will decline. In order to test this possibility, the width of the coastal plain was measured as the distance from sea level to the 500 ft. contour along the line of latitude for each degree and half-degree, on the topographic 1 : 500,000 maps issued by the Government Printer, Pretoria. For present purposes, width of the plain is considered to be a direct index to area. In Fig. 2 the width of the coastal plain is plotted (A) between 27°S and 32°S. The lines B and C represent the numbers of frog species (taken from Poynton, 1964a, with a few modifications from Bass, 1966), the distribution of which has been plotted on a $\frac{1}{4}$° square grid, selected on the following basis: B, the 15 "tropical" species listed above, plus 8 "tropical" species (those without + in the second list above) which in Zululand are more or less restricted to the plain as here defined, but which range quite widely into the Transvaal; C, the total number of all frog species on the coastal plain as here defined.

Line B is the one with which we are concerned; this represents the "tropical" species with a coastal plain distribution in Natal and Zululand. The three lines have a generally

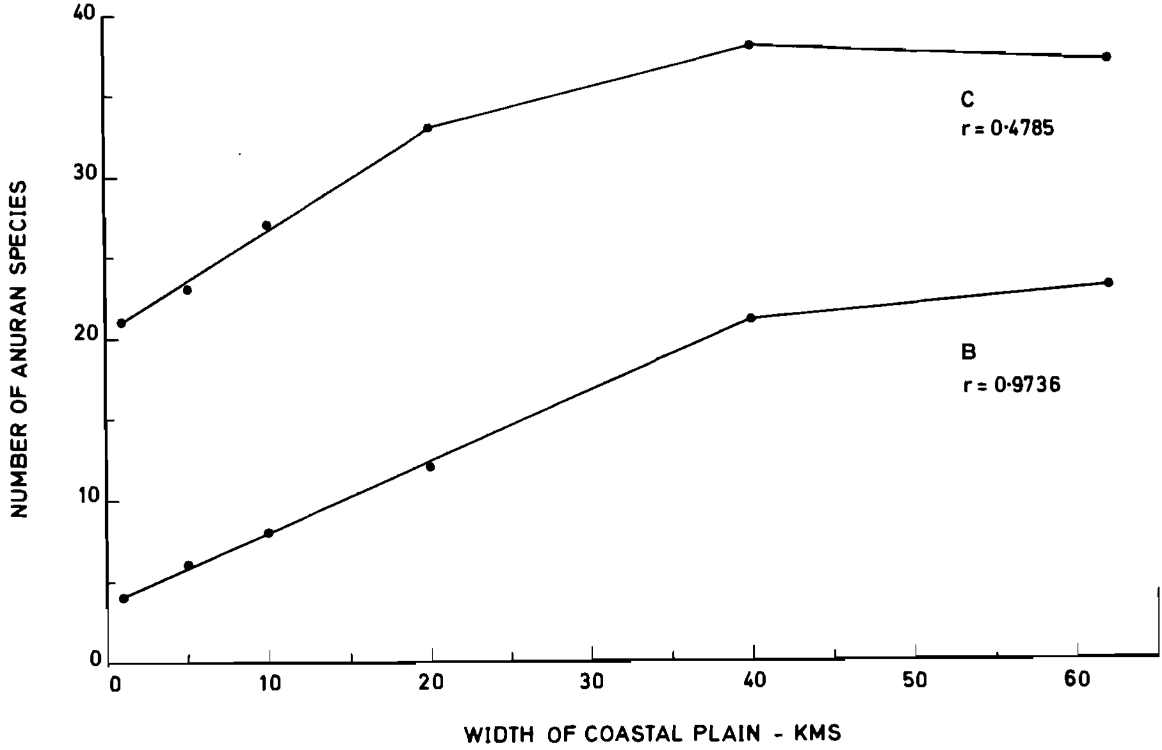

FIGURE 3
Diagram showing correlation between number of anuran species and width of coastal plain (see Fig. 2 and text).

similar shape and a correlation of sorts obviously exists. To examine this more closely, the number of species in lines B and C have been plotted in Fig. 3 against the width of the coastal plain. Line B shows a striking feature: five of the six points lie virtually on a straight line. Calculation of correlation coefficients in this case has some theoretical objection in that the X variate is not truly stochastic, but the results of such a calculation would not be materially different if coastal plain widths were selected at random instead of by the non-random variate of degrees of latitude. A regression line plotted for the points in line B has r = 0·9736, the significance probability of the null hypothesis being correct being only between ·001 and ·002, indicating a degree of correlation so high as almost to be suspect. This test shows that frog species restricted to the coastal plain show a marked fall in number correlated with the width (therefore the area) of that plain. However it should be noted that only a small number of species (in the statistical sense) is involved, and the results could easily be disturbed by new records from parts of Zululand and Natal that remain to be collected.

The decrease in the number of B species at each line of latitude is almost logarithmic over the first five points; in line C, which represents the total number of Zululand species, the decrease is almost exactly logarithmic over the first four points (Fig. 3). These results confirm in a rough way the tendency already referred to for a change in area to be matched by a logarithmic change in the number of species, but the number involved is too small for that correlation to be investigated with certainty.

Obviously the correlation demonstrated above is not in itself a causal explanation, but it has heuristic value in indicating where such an explanation might be sought. A decrease in extent of the acceptable territory of a set of species will influence those species in a number of ways: for example, fewer individuals can now be present and demes will, therefore, be smaller, the variety of habitats will be reduced, particular habitats may diminish in size and complexity and hence offer fewer microhabitats, interspecific competition may be intensified, predation may assume a new significance, and the availability of preferred food may be affected because of an unfavourable response by prey species to some of these changes. Until possibilities such as these have been investigated, Poynton's contention that the subtraction of "tropical" species in Zululand is due to thermal factors must be sceptically viewed. The thermal gradient southwards in Zululand is slight, indeed published evidence for it is somewhat contradictory, and his hypothesis would be difficult to sustain; in terms of mean July temperatures roughly corrected to sea-level (from WB 19)—Otobotini, 27° 25'S, 18·7°C—Dukuduku, 28° 21'S, 17·2°C—Empangeni, 28° 46'S, 17·5°C—Stanger, 29° 20'S, 18·6°C. For frogs the 18°C mean July isotherm has no proven significance.

EFFECTIVE TEMPERATURE

Effective Temperature and the biological significance of summer

Obviously the most direct influence which temperature will have in any region will occur at the time when its fauna is most exposed and susceptible to thermal factors. In this connection it is relevant to note that many animals have special adaptations to cope with or avoid winter conditions: they may avoid them directly by migration to more equable regions; they may hibernate, usually withdrawing from the environment to sheltered places; they may pass through the winter in a phase of the life history occupying a sheltered habitat, or in which development is inhibited and cold-hardiness is more pronounced; or animals may tolerate the winter environment with the aid of adaptations, morphological (such as increased thickness of pelage or plumage), physiological (adjustment of metabolic rates, increased food consumption) and ethological (huddling, nest-making), as many homeotherms do. From a broad biological point of view, the warm months of the year, when most animals are actively feeding, breeding and moving about, and when the bulk of plant life is growing and reproducing, seem of paramount importance. This must be especially true of southern Africa where winters (with the exception of the S.W. Cape) occupy the dry season of the year.

Such a concept, in which the biological importance of the summer months is stressed, is, of course, not new. Merriam, as long ago as 1894, based his division of North America into "life-zones" on isotherms obtained by summing mean daily temperatures. The extent to which such isotherms were alleged to coincide with the distribution of various animals and plants formed the basis for Merriam's two temperature laws, namely—

1. that the northward distribution of life is limited by the total quantity of heat available during the period of growth and reproduction (the summer), and
2. that the factor limiting the equatorward distribution of life was the mean temperature of a brief period in the hottest part of the year.

Errors and defects in Merriam's system were soon detected (eg. Kendeigh 1932, 1954; Shelford 1932), but despite these the concept of the importance of the summer period remains unaffected.

A recent study by Bailey (1960) develops the idea of summer as the biologically most significant time of the year. He points out that on the global scale the ebb and flow of life over the seasons are systematically related to the thermal environment. There is an awakening of life alternately in each hemisphere with the amelioration of winter weather and the onset of spring, extending progressively from the equatorial zone polewards, then retreating in the reverse direction at the end of the warm period of the year. To express this progression, Bailey has devised a numerical factor which he calls Effective Temperature* (abbreviated to ET for both singular and plural in the following text). Accepting the climatic classification of Köppen (1931), two limits were selected, namely a tropical climate limited by the 18°C mean for the coldest month of the year, and a polar climate limited by 10°C mean temperature for the warmest month of the year. With these as a basis Bailey has prepared a nomogram and equations from which ET can be obtained and his paper should be consulted for the full details. The only data required are mean annual temperature (T) and mean annual range of temperature (AR—the difference between the means of the warmest and coldest months). The equations are—

$$^{\circ}\mathrm{C} \qquad \mathrm{ET} = \frac{8\mathrm{T} + 14\mathrm{AR}}{\mathrm{AR} + 8}$$

$$^{\circ}\mathrm{F} \qquad \mathrm{ET} = \frac{14{\cdot}4\mathrm{T} + 57{\cdot}2\mathrm{AR}}{\mathrm{AR} + 14{\cdot}4}$$

Fig. 4 shows the nomogram and reveals on inspection the properties of ET which may be summarised as follows:—

1. ET is a temperature in °C or °F, covering a gradient from cold to warm climates.
2. A change from cold to warm climates is indicated by an ascending scale of ET; the emergence of a true summer marks the limit of polar conditions, a summer which increases in warmth and length until, at the tropical limits, a true winter disappears.

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[*] It is unfortunate that Bailey chose a term homonymous or nearly so with several others coined by different workers for various concepts which have in common the idea of expressing or representing the biological effectiveness of warmth. Bailey's ET should not be confused with: (1) *Effective Temperature*, a concept in medical climatology, developed to measure human comfort in various climates; as its numerical expression is based on factors of warmth, humidity and air movement in combination, it is not a temperature but an empirical index. (2) *Temperature Efficiency*, which attempts to measure the effectiveness of warmth in promoting plant growth, and is determined from the number of days with mean temperature above 40°F and the amount of rise above that limit.

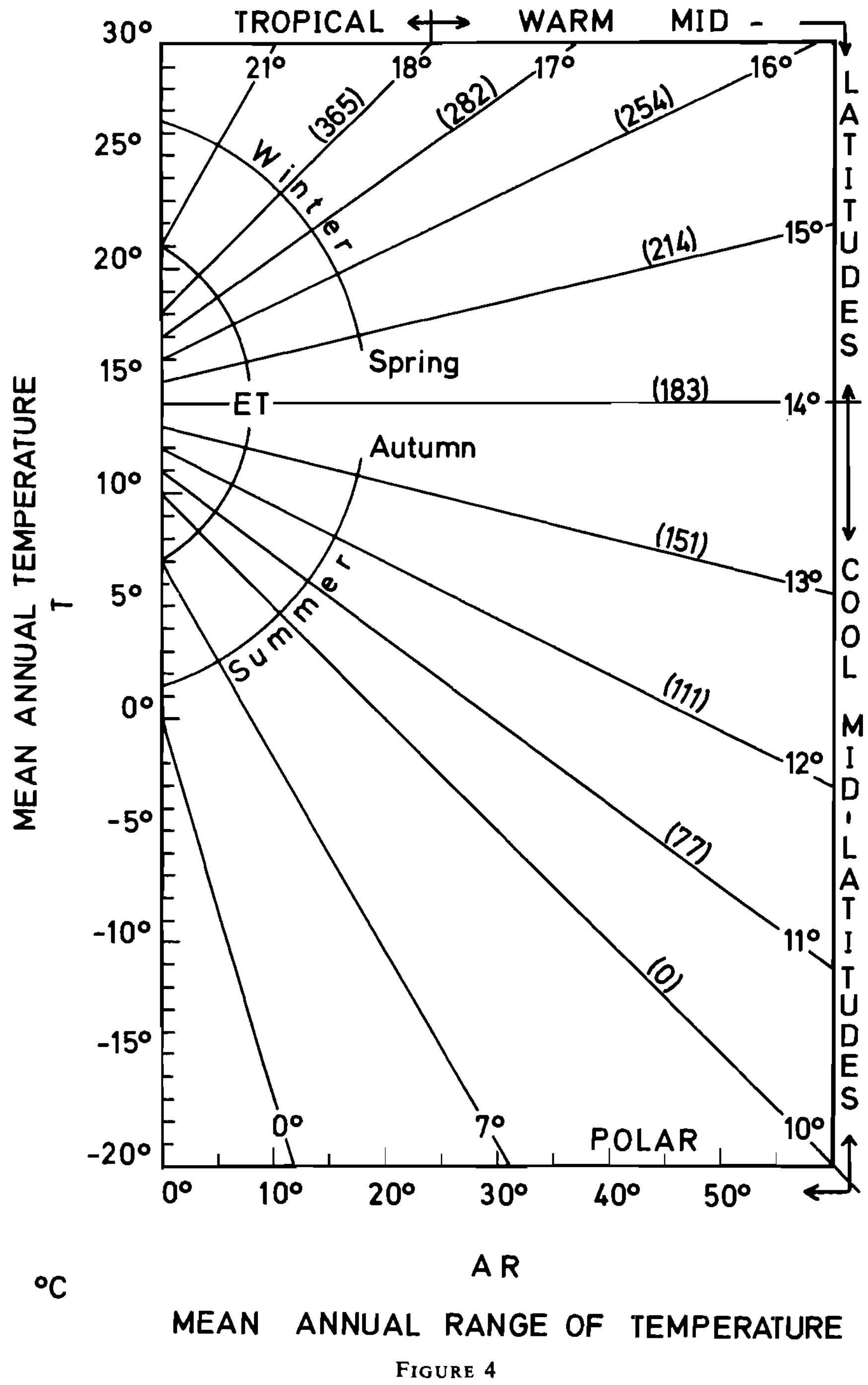


FIGURE 4

Nomogram for determination of Effective Temperature in °C. The two parameters are Mean Annual Temperature and Mean Annual Range of Temperature. Effective Temperature values are given at the ends of the radii, and on each radius in parenthesis is the theoretical number of days in a year on which mean temperature will exceed the Effective Temperature. A Tropical Climate has an Effective Temperature above 18°C and a Polar Climate one below 10°C, and the climates of intermediate latitudes are graded in between. (After Bailey, 1960, with small modifications.)

3. By the method of derivation, ET represents the temperature at the beginning and end of the warm season.
4. An important feature of ET is that it carries a strong presumption as to the duration of time over which the specified temperature applies. This arises from the progression in time with which ET occurs in the annual march of temperature, a progression which shifts ET from summer to winter as climates change from polar to tropical. Quantification of ET by application to the sine wave representing the annual march of temperature, furnishes not only the value of ET but also the duration of the period in which temperatures are warmer than ET. Thus both ET and the length of summer increase together.
5. To conclude, ET measures warmth by defining a sliding scale specifying temperatures at the beginning and end of the warm season, and implicating the duration of that period. An increase in ET can be associated with increase in the proportion of the year with temperatures warmer than ET.

An Effective Temperature map of southern Africa

Using the equations provided by Bailey, ET were calculated for stations south of the Zambesi and Cunene Rivers. These calculations are based on the following data:

1. Temperature statistics published by the South African Weather Bureau (1954) for stations in South Africa, South West Africa, Lesotho, Botswana and Swaziland.
2. Temperature statistics for some stations not recorded in the publication referred to above, provided by the Weather Bureau, Pretoria; these stations are in the Kruger National Park, Natal Drakensberg, Zululand and South West Africa.
3. Unpublished temperature recordings made by staff members of the Natal Parks Board in the Hluhluwe, Ndumu, Umfolosi, Charters Creek, Giant's Castle and Royal Natal National Park Reserves.
4. Rhodesian temperature statistics published by the Ministry of Mines and Transport (1952).
5. Moçambique temperature statistics derived from bulletins published by the *Servico Meteorologico de Mocambique*.

ET were calculated for all stations with complete records, the values obtained were plotted on a map, and isolines were drawn for ET values of 14° - 19°C. It was soon apparent that over much of the area a close positive correlation exists between ET and topography, a relationship not surprising in view of the correlation between mean annual temperature and altitude, and advantage was taken of this in plotting the isolines. The altitude of each station was considered in relation to the ET and latitude, and the probable lie of isolines between stations was estimated accordingly. In areas of low relief the position of isolines between stations was estimated by interpolation.

Despite the large number of stations used (about 644), the data for certain parts of southern Africa are inadequate; where that is the case, or where uncertainties exist because of anomalous results given by adjacent stations, the isolines are dashed. Areas of uncertainty are:

1. North-eastern Zululand (see p. 150).

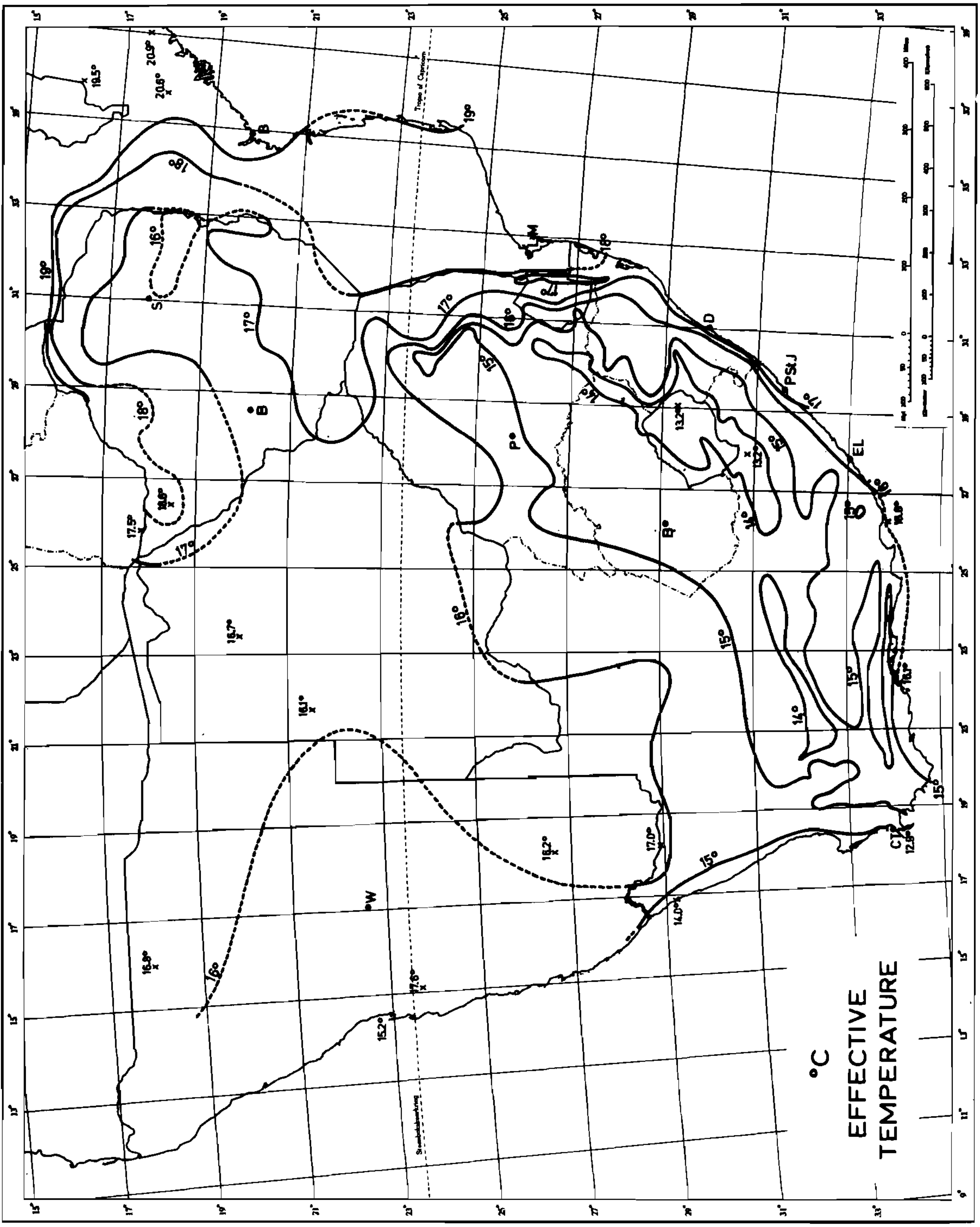


FIGURE 5

An Effective Temperature map of southern Africa in °C. The isolines are dashed where their course is uncertain because of inadequate data.

2. South West Africa and Botswana; this vast territory has very few stations and the isolines are based mainly on altitude correlations. ET values for various stations are given. The high figure of 17·6°C for Gobabeb in the Namib Desert should be noted as it contrasts with 15·2°C at Walvis Bay and 15·8°C at Windhoek; evidently there is a rapid temperature gradient inland from the coast, which is reversed when the highlands are reached.
3. Rhodesia; although the stations in this territory are quite well spaced, they are not sufficiently numerous. The Eastern Highlands are too complex to analyse in detail with existing information, and, by contrast, the topographic changes in the central part are sufficiently subtle for the lie of the 16·0°C isoline to be uncertain at present.

One further difficulty in the preparation of the map needs to be mentioned, that of scale. In topographically complex areas, such as the Southern Cape, Eastern Plateau Slopes and Middleveld, the lie of the isolines must be far more intricate than is shown. However exact correlation between topography and ET in such areas is obviously impossible to determine with certainty because of inadequate data, and even when the more general trends can be reasonably well inferred they cannot be shown on a map of the scale used.

The climate of southern Africa from the point of view of Effective Temperature

Fig. 5 shows the ET map of southern Africa. It has some resemblance in detail to mean annual temperature (real isotherm) maps, but otherwise is not especially like maps of other thermal parameters apart from occasional similarities due to topographic control. Values of ET range from over 20°C in the north-east part of Moçambique, to between 13°C and 14°C; the lowest ET calculated is 12·9°C for the summit of Table Mountain on the Cape Peninsula, rather a surprising result but one explicable on account of the windiness and cloudiness of weather over that mountain. No climate statistics are available for the higher parts of Lesotho and the Drakensberg Escarpment, those above 8,000 ft, but it is certain that ET below 13°C will be found there.

Bailey presents a scheme of classification of ET for the world, dividing the range into a ten-zone classification of warmth, as follows:—

TABLE 3

ET (°C)	*Category*
	Torrid
24·1	
	Hot
20·8	
	Very Warm
18·0	
	Warm
15·5	
	Mild
13·4	
	Cool
11·6	
	Very Cool
10·0	
	Cold
8·6	
	Very Cold
7·5	
	Glacial

Southern Africa has five categories, *Cool, Mild, Warm, Very Warm,* and *Hot;* a considerable part of the area is *Warm* or *Very Warm*, and the *Hot* and *Cool* parts are of limited extent. South Africa proper, largely contained by the 16°C isoline, is *Very Warm* only in N.E. Zululand, being otherwise *Warm* to *Cool.*

Bailey provides a small-scape map showing the approximate global distribution of ET and it is interesting to ascertain from this the relative situation of southern Africa. In the African context, to the north of southern Africa there is a fairly narrow belt of *Very Warm* ET, followed by a wide band of *Hot* ET extending higher across the continent and including the Horn of Africa and West Africa territories along the gulf of Guinea, but excluding the East African Highlands. This is succeeded by a narrower, Subsaharan, transverse zone of *Very Warm* ET, and most of the Sahara and North Africa, excepting Highlands, is in the *Warm* category. The Mediterranean countries of Europe and Asia Minor experience a *Mild* climate which is succeeded by *Cool* conditions over most of Europe and the British Isles apart from highland areas. Thus, although not reaching far south beyond the Tropic, southern Africa has a wide range of ET conditions.

Comparing southern Africa with Australia we have the following situation. Australia shows three latitudinally arranged zones, *Very Warm* occupying a little less than the upper third of the Continent, *Warm* occupying somewhat more than the middle third, and *Mild* in approximately the lower third, the influence of the highlands not being shown. Tasmania and New Zealand are *Cool.* Southern Africa thus is like Australia in terms of ET, but not as cool as Tasmania or New Zealand. This information may be used as a guide for a settlement of the confusion which exists over the use of the terms "temperate" and "warm temperate", which have both been applied to South Africa on many occasions. Thus, Darlington (1965: 108) says firmly that South Africa is "*warm*-temperate" when compared with other southern lands. If ET is a reliable guide, South Africa is directly comparable to Australia, being largely *Warm* to *Mild*, grading to *Very Warm* northwards, and having *Cool* areas localised in the highlands. If the term "Temperate" is reserved for the thermal environment of New Zealand and Tasmania, and "Cold Temperate" for that of southernmost South America, South Africa and Australia are "Warm Temperate". However, these absurd and contradictory terms are best abandoned in favour of some other scheme, such as ET or the completely new definition and classification of temperateness given by Bailey (1960, 1962).

The distribution of Effective Temperature over southern Africa

Taking the isolines in turn, starting with the warmest, we have:

20°C. In the region mapped only the two stations indicated on the Moçambique plain north of the Zambesi have ET higher than 20°C. Values for stations further north show that this isoline crosses the coast between Quelimane (19·7°C) and Pebane (20·2°C).

19°C. This isoline apparently includes a small, narrow part of the coast where it is intersected by the tropic, crosses the coast just south of Beira to include the Pungwe flats, then swings far inland along the Zambesi Valley to just beyond Chirundu (19·1°C).

18°C. At its southern end this isoline crosses the Zululand coastal plain and cuts across the coast near 27° 30'S (see pp. 150-151). It runs north along the eastern edge of the Lebombo and apparently skirts this range to its northern extremity. Five stations down the eastern half of the Kruger Park have ET values of 17·4°C, 17·6°C, 17·6°C, 17·4°C and 17·4°C, whereas all Moçambique stations have figures not far above 18°C on the western side of that territory below latitude 22°S. Over the remainder of its course the isoline avoids the rising country fringing the Rhodesian Highlands before shifting west along the Zambesi. In Rhodesia it presumably follows the contour of the rising country to the south, before crossing the Zambesi east of Livingstone (17·5°C). Thus practically all of Moçambique south of 21°S has ET above 18°C.

17°C. This isoline has a complex and interesting course. In the south it crosses the coast between Port St. Johns and Bashee River mouth; proceeding north until about 29°S lat. it encloses an elongate, very narrow coastal strip, after which it swings further inland to include the Zululand coastal plain and western Swaziland, up over the lowveld, turning west along the Limpopo and enclosing the eastern corner of Botswana; thereafter, following the contour of the land in Rhodesia, around the Eastern Highlands, re-entering at the northern end of the highlands, apparently following the contours again; its course in eastern Botswana is problematical before reaching Kasane (17·0°C) at the eastern end of the Caprivi Strip. The value of 17·6°C for Gobabeb in the Namib has already been mentioned. Note also the value of 17·0°C for Goodhouse, a localised hot area in the Orange River Valley.

16°C. Two isolated areas enclosed by this isoline require prior mention, namely, the elongate Lebombo range bordering Swaziland on the east and the higher parts of east-central Rhodesia, enclosing the eastern part of the highlands. Undoubtedly this isoline must be present in the Chimanimani area. In the south the isoline enters South Africa at the mouth of the Great Fish River (16·0°C), and runs a short way inland along the coast much like the 17°C isoline; Bird Island (16·6°C) and Cape St. Blaize (16·1°C) are isolated places with ET figures above this. Topographic control is evident in the Eastern Transvaal; after swinging to the west the course of the isoline is less clearly marked until it re-enters the northern Cape Province. The remainder of its course in South West Africa is speculative. Most of Botswana must have an exceedingly slowly changing temperature regime.

15°C. This isoline has a complex course in which topographic control is very obvious. Noteworthy features are the wide re-entrant areas in the Great and Little Karroos, the Kei River Valley, Tugela Basin, and Tankwa and Doring River Valleys. A narrow strip of the South African Atlantic Coast is also enclosed. The influence of the Transvaal Escarpment is clearly shown.

14°C. This isoline encloses the coldest and highest parts of the country in two areas which are only just separated by values of 14·2°C at Middelburg and 14·1°C at Steynsburg. The western portion lies over the Great Escarpment, including parts of the Sutherland and Fraserberg districts. The eastern portion includes much of Lesotho and the high country to the south and south-west, as well as all the Drakensberg escarpment, the higher foothill country extending into the Natal midlands, and an elongate, narrow strip along the watershed as far north as Jessievale (14·0°C). A marked re-entrant is caused by the Orange River Valley. Heights along or close to this isoline are Jessievale (1,733 m.), Nottingham Road (13·9°C, 1,438 m.) and Steynsburg (14·1°C, 1,478 m.). It is likely that small, isolated areas on the Cape folded mountain ranges have ET values below 14°C.

Characteristics of the thermal zones defined by Effective Temperature

It was mentioned above that an important feature of the ET scale is the implication of the duration of the warm season. According to Bailey (p. 4) the duration of time in a year in which mean temperatures are warmer than ET at any locality is given in days by the equation—

$$\mathrm{Td} = 182{\cdot}6 + 2{\cdot}032\alpha$$

where Td is the time period and α is an angle determined from the expression—

$$\sin \alpha = \frac{\mathrm{ET} - 14}{4} \quad (\mathrm{ET\ in\ ^\circ C})$$

$$\text{or } \sin \alpha = \frac{\mathrm{ET} - 57{\cdot}2}{7{\cdot}2} \quad (\mathrm{ET\ in\ ^\circ F})$$

For the isolines found within the region included in this study, the following calculated values of Td apply:

TABLE 4

ET °C	*Td (days)*	*ET °C*	*Td (days)*
18° and above	365	14°	183
17°	282	13°	151
16°	254	12°	111
15°	214		

By the method of derivation, any place with an ET of 18°C or higher should have mean daily temperatures throughout the year higher than 18°C. In practice, this is not entirely accurate; thus, Lourenço Marques in 1963 had 22 days with a mean temperature below 18°C, though ET for that year was 18·5°C, and in the same year the lowest mean daily temperature at Inhambane (ET 19·4°C) was 18·0°C (7 July).

In a tropical climate, without mean daily temperatures lower than 18°C, a true thermal winter can be said to be absent. On the other hand, at 13°C ET only about one-half of the year theoretically has mean daily temperatures above that value. In accordance with the proposition that cold spells are biologically significant in the tropics and warm spells of increasing significance with increasing distance from the tropics, ET shifts from winter to summer as the ET values diminish (Fig. 4). This is shown in the Table 5 in which the stations selected provide an approximately latitudinal transect covering almost the greatest ET range in South Africa.

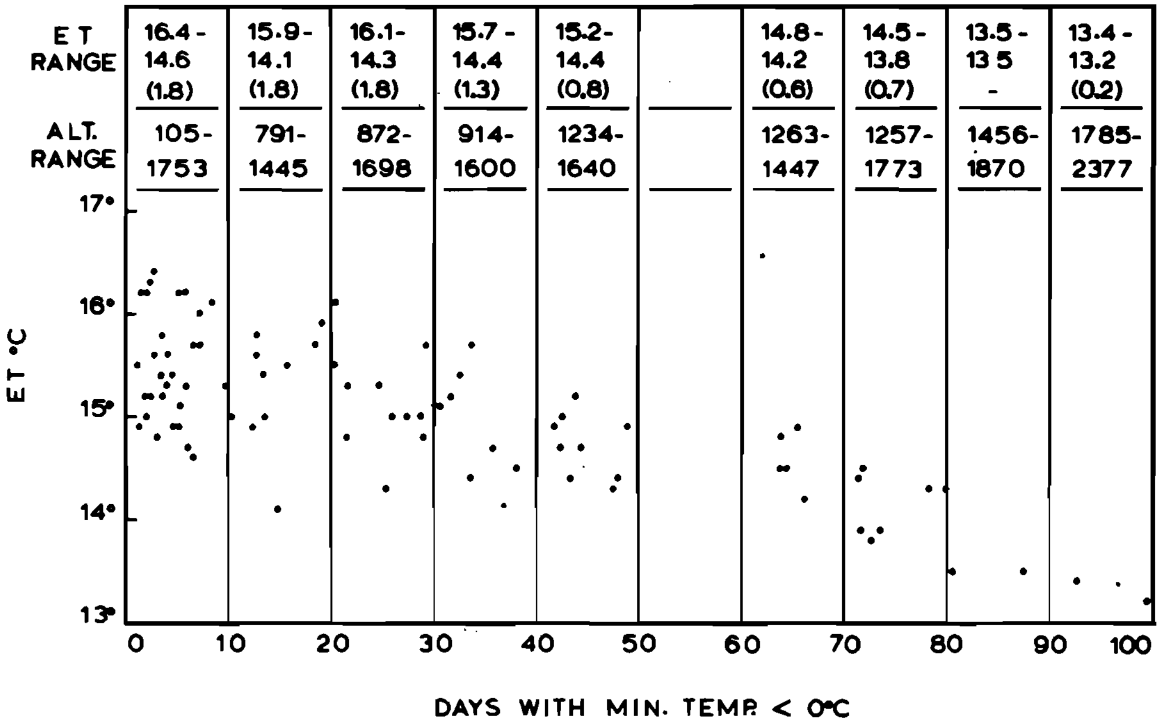


FIGURE 6

Diagram showing the relationship between frost incidence and Effective Temperature for 84 stations in South Africa. The stations are those in Table I of WB 19, which have at least one month with an average of at least one frost day. The Effective Temperature range and altitudinal range (in meters) are given for the stations in each column at intervals of ten frost days.

TABLE 5

Locality	*ET °C*	*Calculated days T > ET*
Durban	17·2	304
Pietermaritzburg	15·8	237
Cedara	14·9	211
Nottingham Road	13·9	180
Mokhotlong	13·2	158

Frost is probably an important ecological factor, directly for plants and directly or indirectly for animals. Bailey (1960: 9) points out that Köppen's choice of the 18°C mean for the coldest month as the limit of the tropical climate probably was guided by the likelihood of freedom from frost during winters with such relative warmth. Bailey states that, for midlatitude grades of warmth and areas of continental aspect, "the period of the year in which temperatures are warmer than ET will correspond rather well to the duration of the frost-free period". He found that this relation holds very well for the United States but poorly for Norway, and assumes that the latter result is due to the relatively maritime climate of that country.

In South Africa the correspondence between the frost-free period and ET is unlike that described for the United States, there being far fewer frost days than predicted, but that is not unexpected as South Africa borders the tropics and is subject to weather systems of maritime origin. Frost incidence is always a complex matter subject to a multitude of factors. Data and maps given in WB 28 (132-7) show it to be influenced by altitude and latitude; these factors partly determine ET, but the relation between frost and ET is nevertheless far from simple. Fig. 6 shows the incidence of frosty days plotted against ET for 84 South African stations. The points are widely scattered for places with up to 10 frost days, but thereafter the scattering narrows around the regression line as the number of frost days increases and ET decreases. Dividing the frost days into columns at each ten-day interval, the ET and altitudinal ranges covered by the stations in each column are given. The greatest ET range occurs in the first three columns (1·8°C), and the range becomes progressively narrower with increasing frostiness. The altitude range in each column is considerable but the lower altitudes together form a series rising almost continuously with increasing frostiness.

ET is thus a poor general guide to frostiness in South Africa. The sample shows that stations with more than 60 frost days have ET less than 15°C, and those with more than 80 have ET less than 14°C. Only the latter stations show a tendency towards a linear correlation between ET and frost incidence, and these seven stations are all relatively high (1,438-2,377 m.). This correlation probably is due to the continentality of the country enclosed by the 14°C isoline, in other words to relatively great altitude and relief, and distance from the sea, factors which in combination impose definite thermal characteristics and override maritime influences. By contrast, the highest ET of a station with regular frost, in the sample analysed, is 16·4°C, some way short of Köppen's limit for a tropical climate.

THE BIOLOGICAL SIGNIFICANCE OF EFFECTIVE TEMPERATURE IN SOUTHERN AFRICA

Snakes and Effective Temperature

To demonstrate that ET depicts the thermal environment in a way which is of biological significance in southern Africa, I propose to describe the correlation existing between the distribution of snakes and the ET pattern. At the outset it must be stressed that this method—to pass from an apparent cartographical correlation to a biological conclusion (*post hoc*, *ergo propter hoc*)—places many pitfalls in the path of the researcher. Apparent correlations observed on maps may be spurious or susceptible of other explanations, and any correlation should not be accepted without a consideration of as many aspects as possible of the biology of the species concerned. The method, however, is valid, especially if the taxa used are chosen on an appropriate basis. The sort of correlation to be looked for is a general one, indicating a *tendency* for dispersal to agree with the ET patterns. As the ET isolines represent integer values, they are arbitrary and may have no special importance: indeed some intermediate values of ET may be biologically important ones.

Snakes were chosen partly because they are poikilotherms and thus are subject to thermal features of the environment in a way and to a degree more significant than are the homeotherms. Like most other reptiles, the snakes are strongly heliothermic, being heavily dependent on the exogenous heat source of solar radiation which they utilise by behavioural adaptations. Although morphologically very specialised among reptiles, their physiological adaptations are relatively poorly developed; according to Cowles (1940), snakes are incapable of sustained activity at either such low or such high temperatures as the lizards, and they have a lower critical maximum temperature than other reptiles. Also, they have very limited ability for effective physiological temperature limitation; only the incubating Python is known to be able to raise its own temperature a little, and no snake is known to cool itself by panting as many lizards can. Furthermore, snakes are inactive in the winter over much of South Africa; they hibernate in sheltered places, and if they do occasionally emerge on warm winter days, they do not feed. Snakes, therefore, are likely to be exposed to the thermal conditions of summer. A decisive factor for the choice of snakes is also the recent monograph by FitzSimons (1962) on the species of southern Africa. The particular species whose ranges are mapped below are terrestrial and without dietary specialisations. In addition, for comparative purposes, some examples of anuran distribution are given, taken from Poynton (1964a).

Tropical Species

Snakes which should be especially affected by the ET pattern are the tropical species, those that have a wide range in the cartographical tropics of the Ethiopian Faunal Region and have entered South Africa from a northern centre of dispersal. The primary obstacle to dispersal which such species meet is increasing aridity to the west, south of about lat. 22°S. The general lie of this barrier is indicated roughly by the 400 mm. (16 inch) isohyet in Fig. 7. Aridity limitation in the west is apparent in the distribution of many of the species mapped by FitzSimons (1962), and is well shown by most of the ones discussed here. Those tropical species which occur on the western side seem mostly to have entered from the north, and many of them are represented in the west by subspecies. In the case of more or less continuous distribution via northern Botswana, the subspecific characters presumably are morphological expressions of physiological responses to the changing environment; there are also cases of apparent vicariant speciation which suggest interruption of gene flow in earlier times between eastern and western sectors. However, many tropical species do not extend into arid western parts but within the eastern half of South Africa range southward to varying degrees. Such species, in the course of extending their range south of the Limpopo, meet in the Transvaal progressively decreasing ET conditions in an area of increasing rainfall, as well as the marked ET gradient at the escarpment in the Eastern Transvaal and over the middleveld in Swaziland. In Natal the ET isolines tend to follow the coast and depict long, narrow tongues of relatively warm climate extending down the south-eastern coast into the Cape Province. The distribution of some tropical species will be examined against this background.

In his monograph FitzSimons maps the ranges of 90 species. If a "tropical" species is considered to be one which has the greater part of its range within the cartographical tropics, and if several species with a restricted distribution in the Limpopo Valley-Rhodesia area are included in that category, the total breaks down into 50 tropical species, 34 species confined to South Africa (including South West Africa) or with most of their range there, and six species of indefinite range not fitting well into either category. Of the tropical species, 10 seem to have acclimatised to much of the range of ET conditions in South Africa; for example, *Bitis arietans*, the puff-adder, is virtually ubiquitous (FitzSimons, map 73), and the mole-snake, *Pseudaspis cana* (FitzSimons, map 24), has a similarly wide range over nearly all of the subregion. A tropical species not found in the western half of South Africa but ranging over much of the eastern sector is *Aparallactus capensis* (FitzSimons, map 58). However, most tropical species have a more restricted distribution south of the Limpopo, like that of the following examples:

1. *Python sebae* (African Python). Fig. 7. The distribution of this species is shown with the 15°C ET isoline. This very large snake is strongly heliothermic and is unlikely to be excluded by rugged topography except of the most precipitous kind. FitzSimons refers to the Python's liking for water, and I am indebted to Dr. J. A. Pringle (pers. comm.) for the interesting observation that the females provide a moist microclimate for their eggs during early stages of incubation by wetting their bodies. Water seems to be an important factor in the ecology of this snake but must be adequate east of long. 27°E, and this makes the agreement with the isoline particularly interesting.
2. *Naja nigricollis nigricollis* (Black-necked Cobra). Fig. 8. Subspecies in South West Africa and the far western Cape are omitted from the map. Described as a savanna species by FitzSimons, this snake attains a large size and is catholic in diet. In the eastern half of South Africa it does not penetrate far within the 15°C isoline.
3. *Dendroaspis polylepis polylepis* (Black Mamba). Fig. 9. According to FitzSimons, this species prefers bush country at altitudes not exceeding 4,000 ft. It is a very active snake, fond of basking, and may attain a large size. Broken topography does not exclude it. In Natal it occurs mostly close to the coast, but has penetrated up certain river valleys with Acacia Bushveld. Very few localities fall within the 15°C isoline though some are close.
4. *Atractaspis bibronii* (Burrowing Adder). Fig. 10. A small viper, usually not exceeding 2 ft in length. According to FitzSimons, this is a burrowing species, usually active on the surface at night. It seems able to live in both arid and humid localities. If the locality records give a fair idea of the true range of this species, the correlation with the 15°C isoline is surprisingly good, and the influence of temperature factors on a species with such habits is a matter for investigation.

The four species considered above show a considerable measure of correlation between their distribution pattern and the 15°C isoline. That this correlation obtains in the southern Transvaal is especially interesting as that area has no pronounced topographic features. To the east of the Transvaal escarpment, topographic control of dispersal is possible but can hardly be operative in the middleveld area of Swaziland and the dissected country of midland Natal, rugged though it may be, in the cases of the Mamba and Python. A large proportion

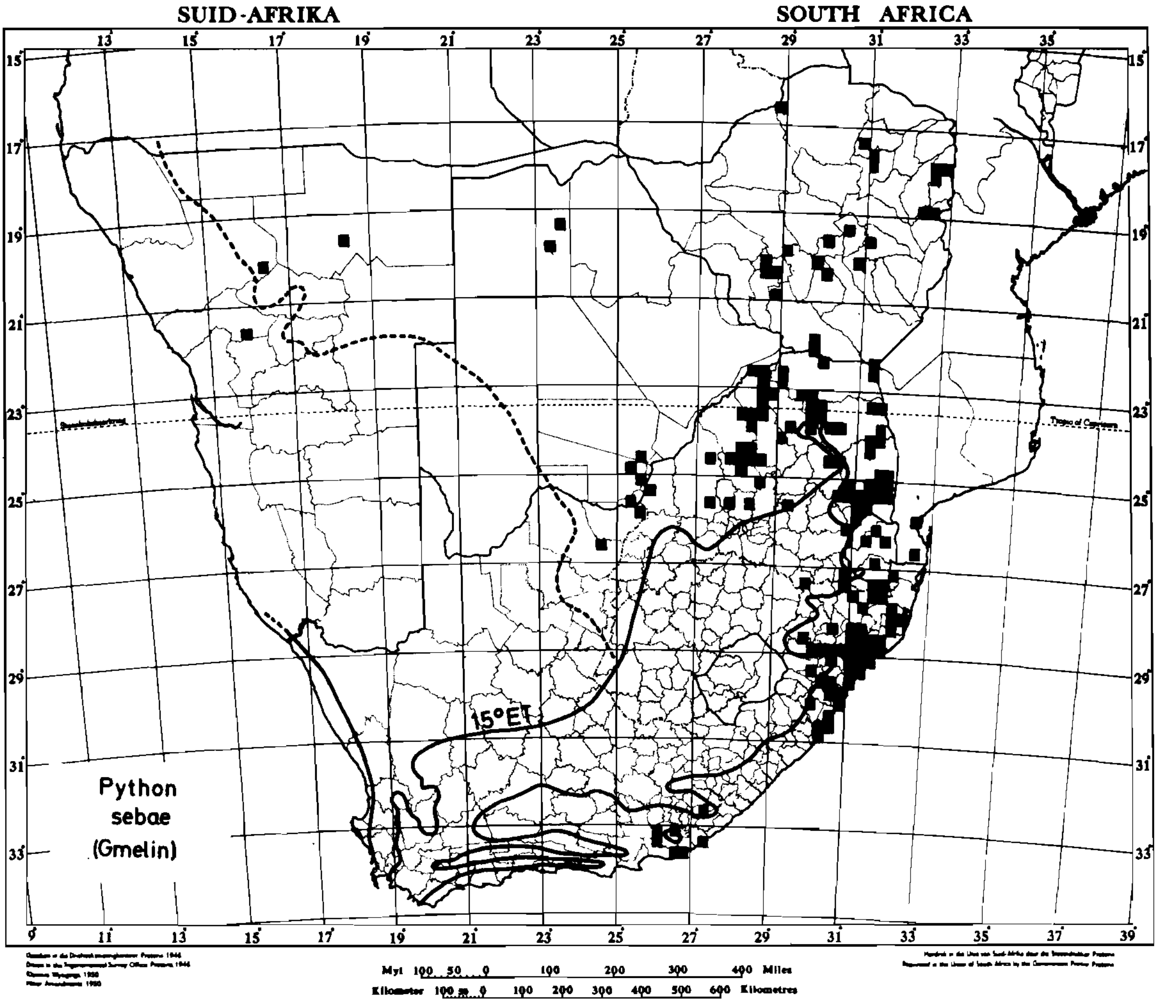


FIGURE 7
The southern distribution of the African Python, with the 15°C Effective Temperature isoline; the dashed line shows part of the 400 mm. isohyet (from WB 28). In this and the following maps the distribution of the species is plotted on a ¼° square grid, each block being about 16 miles (25·6 km.) square.

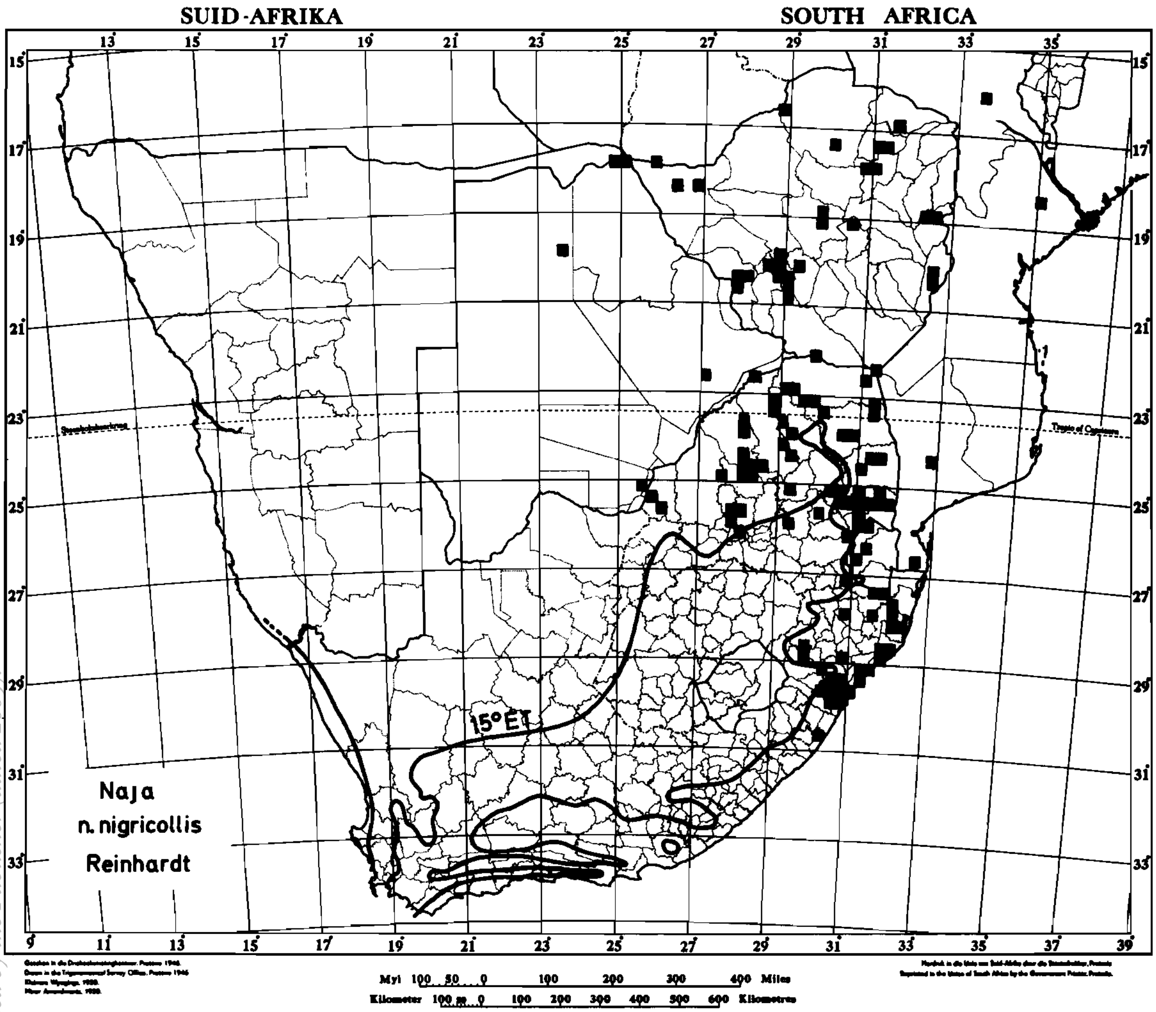


FIGURE 8
The southern distribution of the Black-Necked Cobra, with the 15°C Effective Temperature isoline. The range of two western subspecies is not mapped.

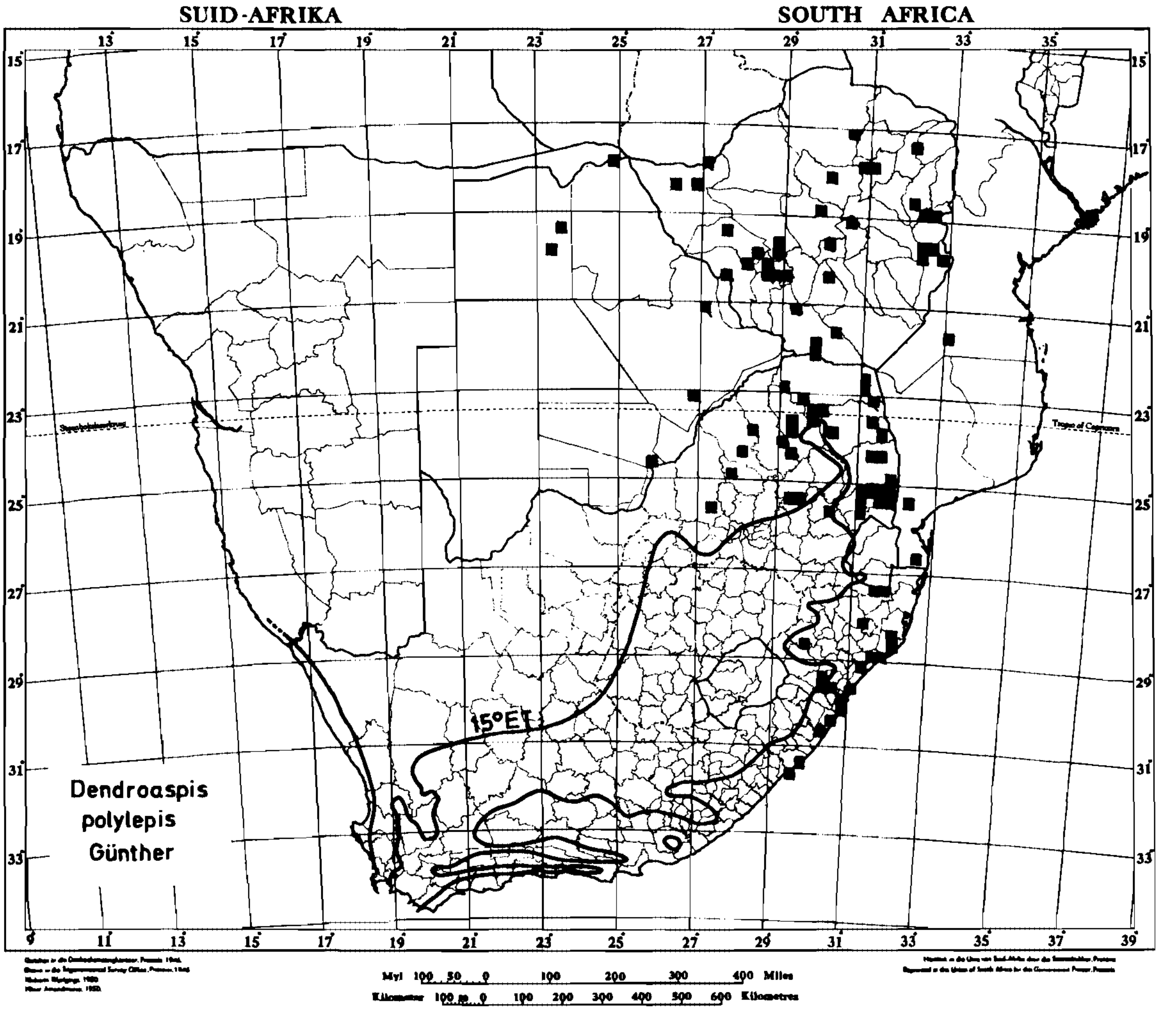


FIGURE 9
The southern distribution of the Black Mamba, with the 15°C Effective Temperature isoline.

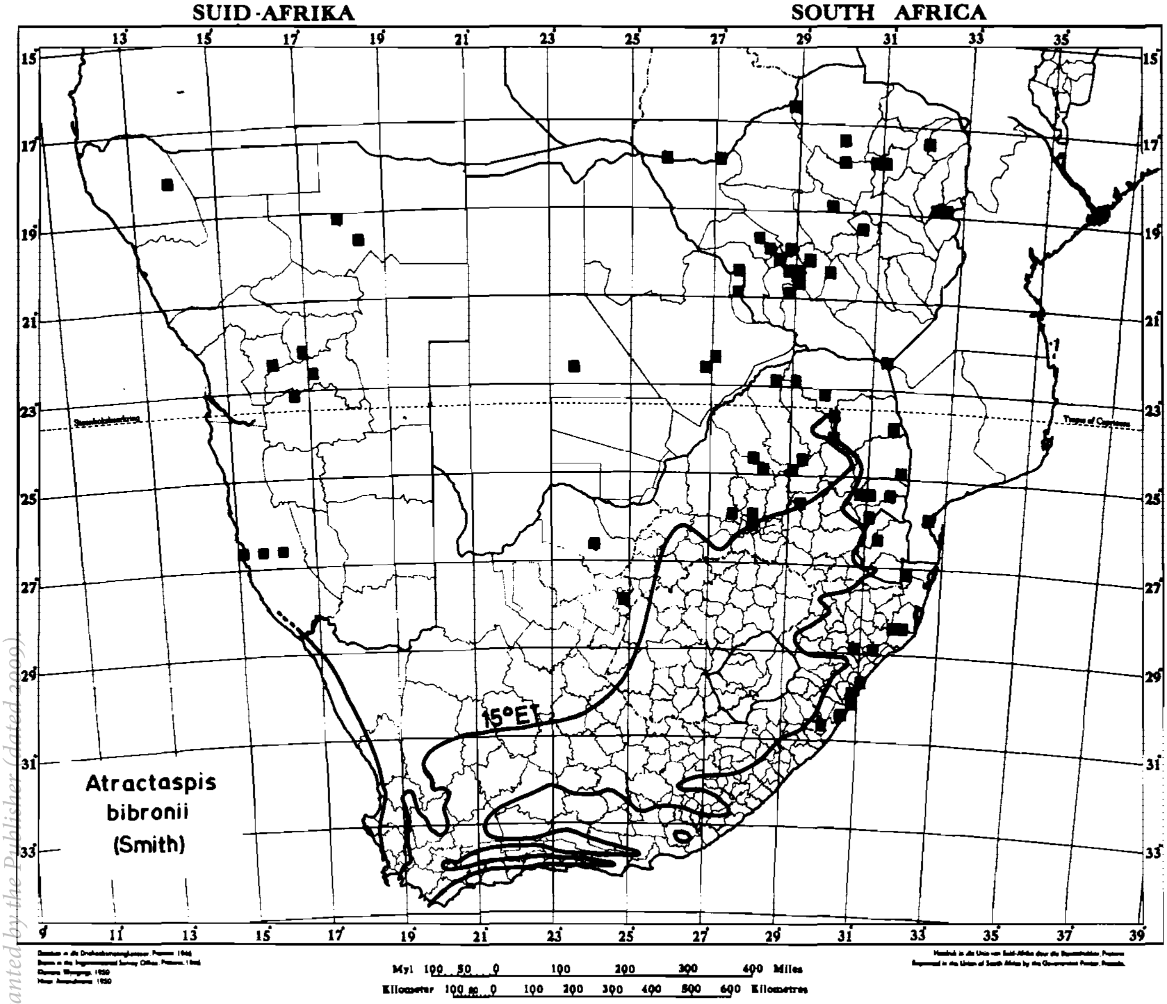


FIGURE 10
The southern distribution of the Burrowing Adder, with the 15°C Effective Temperature isoline.

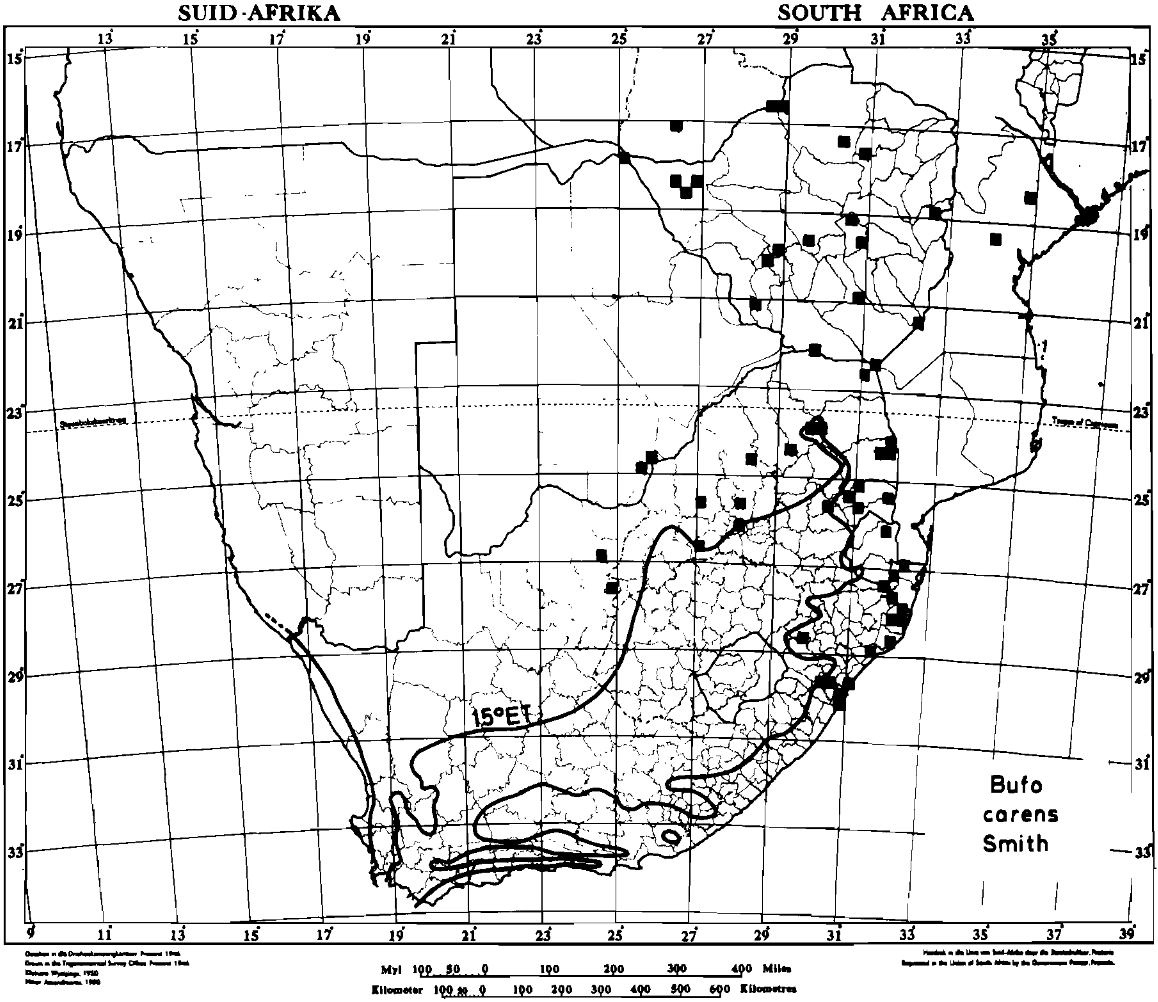


FIGURE 11
The southern distribution of the toad *Bufo carens* Smith, with the 15°C Effective Temperature isoline.

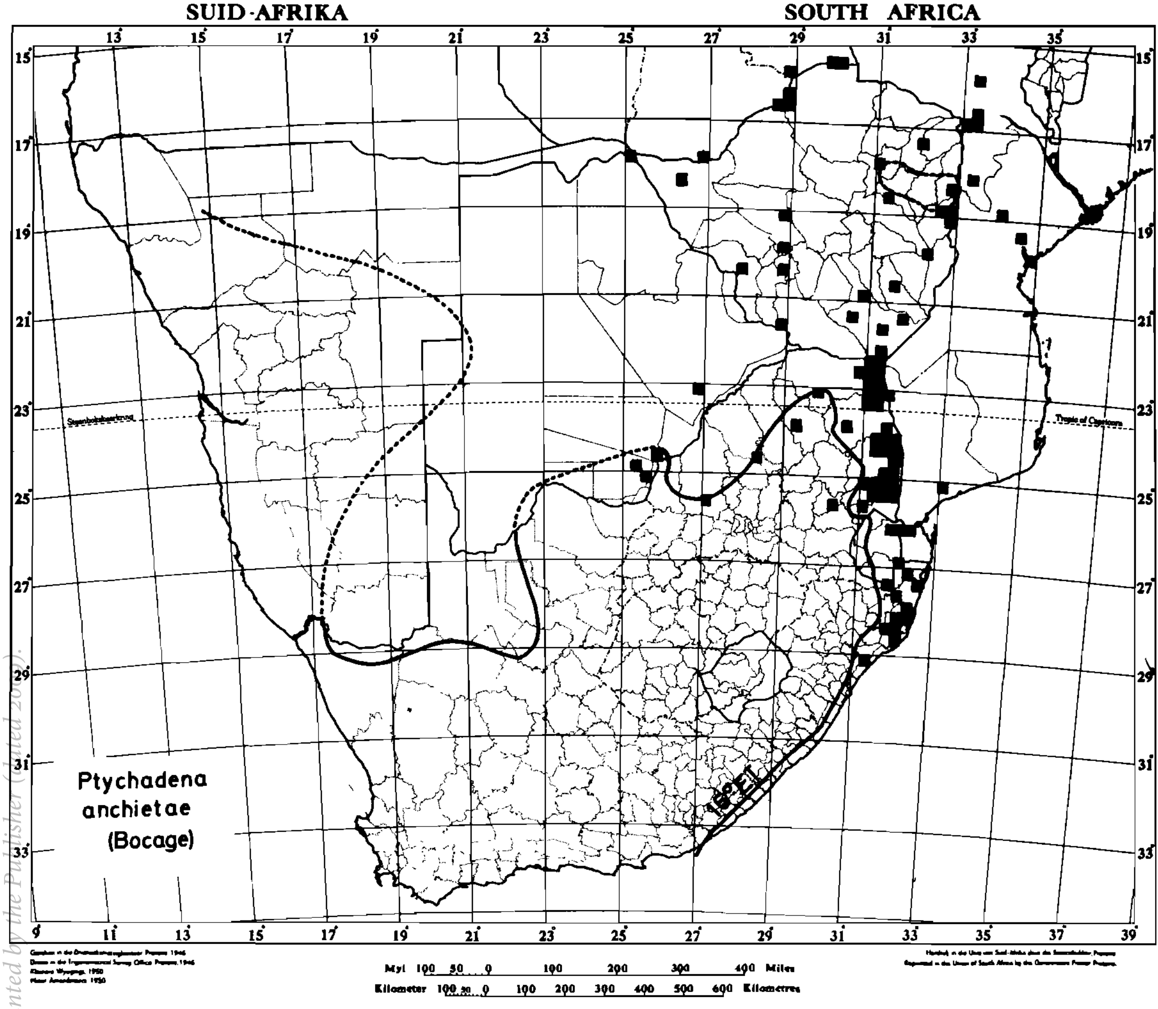
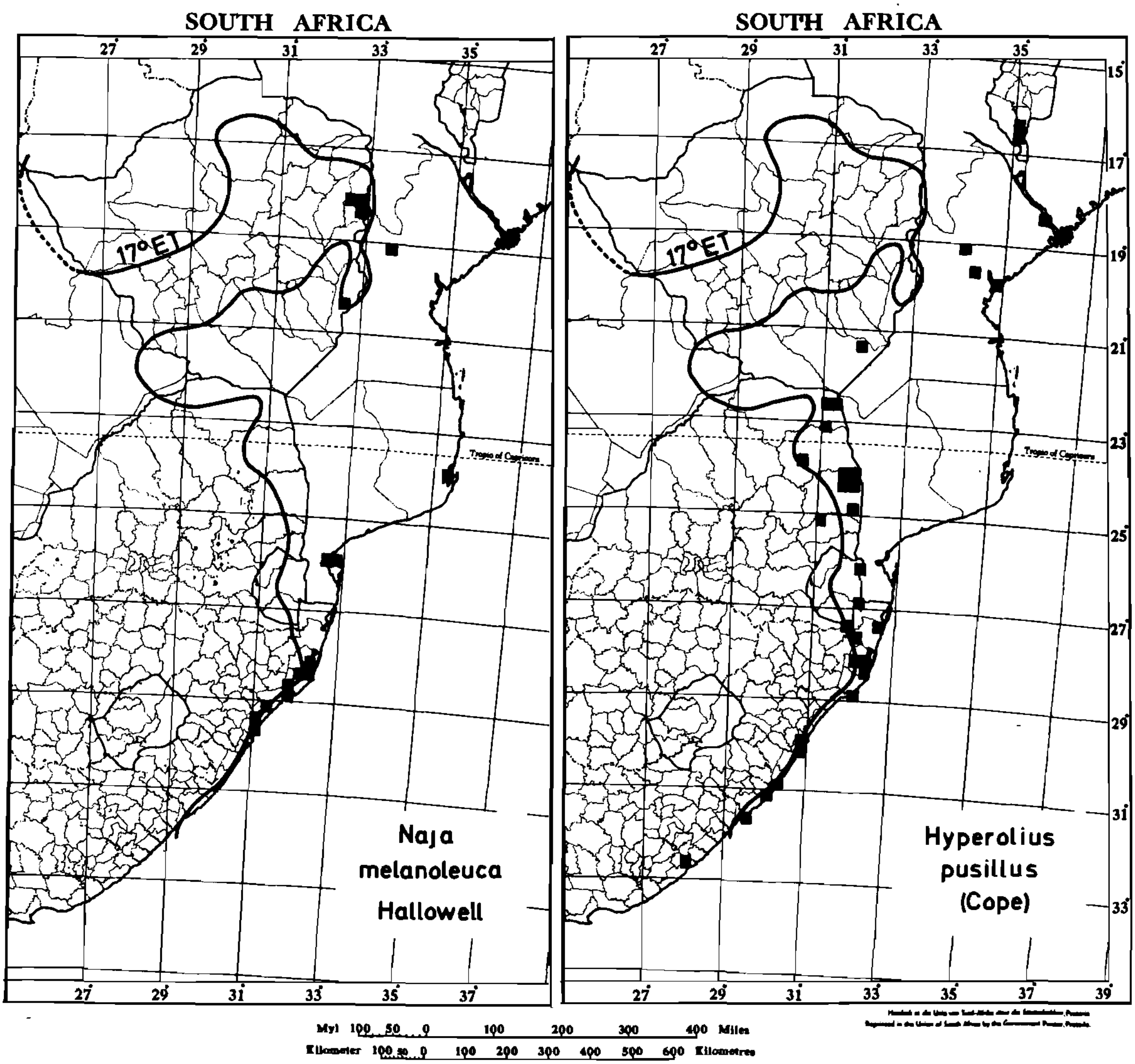


FIGURE 12
The southern distribution of the frog *Ptychadena anchietae* (Bocage), with the 16°C Effective Temperature isoline.



FIGURES 13, 14
The southern distribution of the Forest Cobra (Fig. 13) and a tree frog (Fig. 14), with the 17°C Effective Temperature isoline.

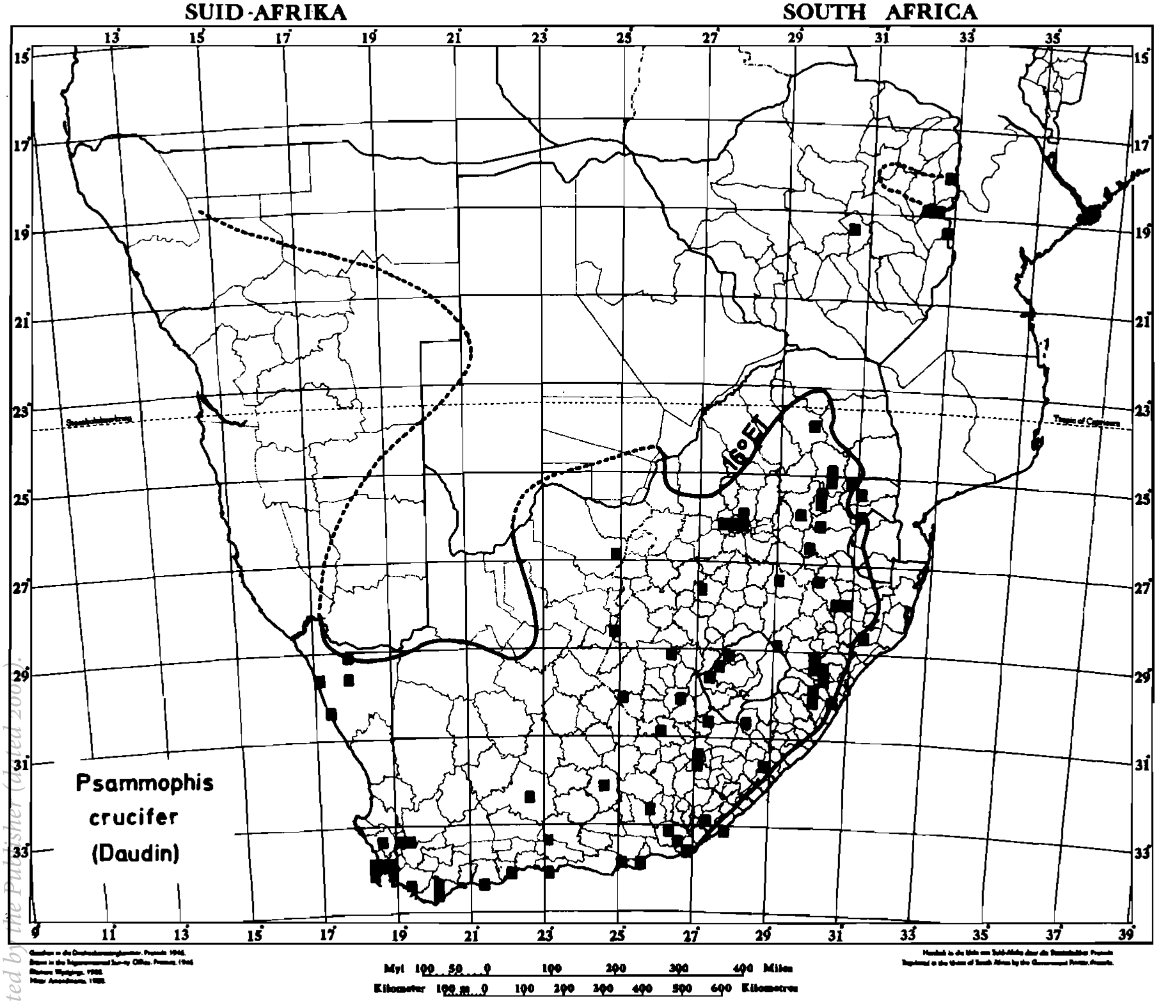


FIGURE 15
The distribution of a grass snake, with the 16°C Effective Temperature isoline in South Africa and Rhodesia.

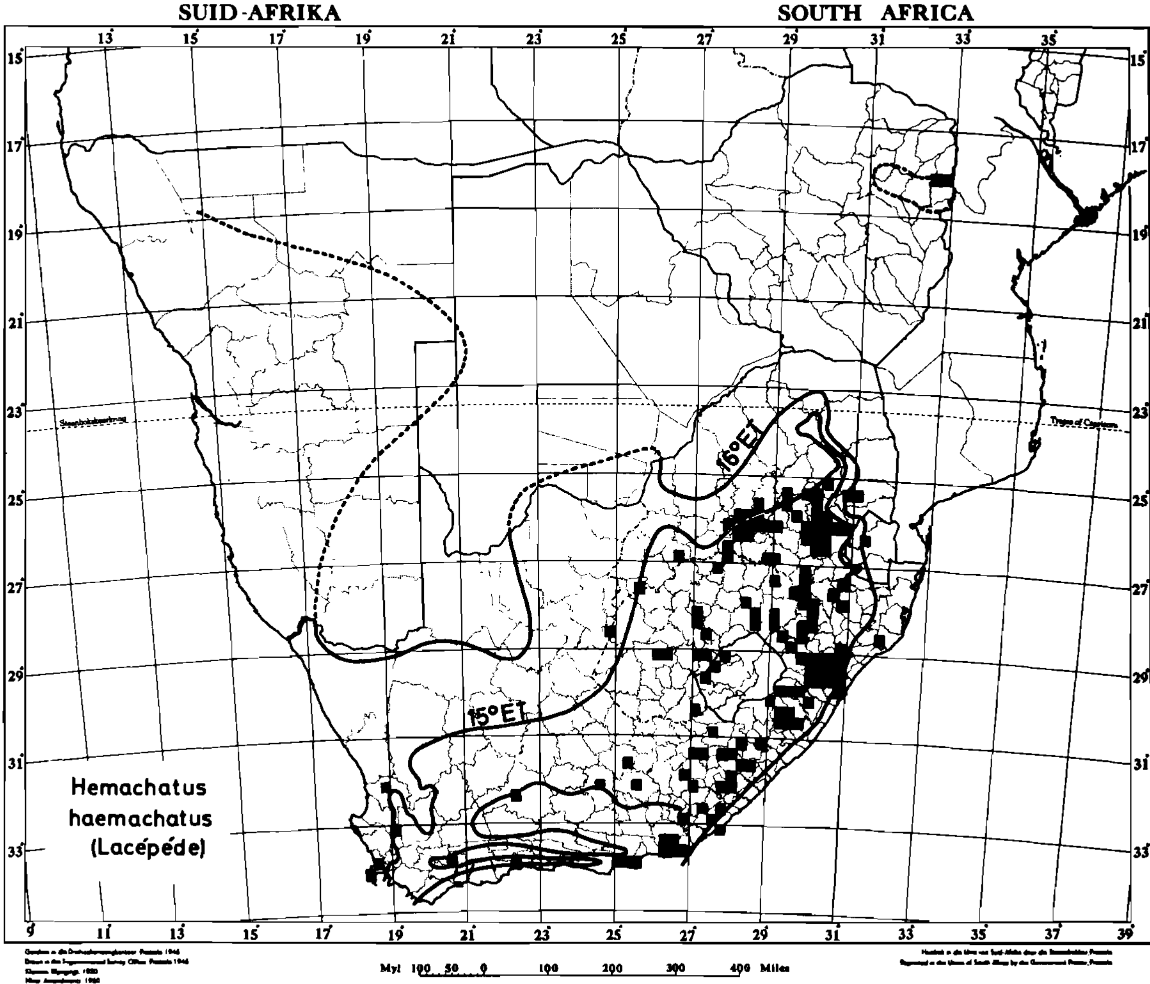


FIGURE 16
The distribution of a spitting cobra, with the 15° and 16°C isolines, the latter also in Rhodesia.

of those tropical species which have been recorded from a sufficient number of localities to make comparison possible, shows the same features in distribution: see the maps in FitzSimons (1962) for—*Lycophidion capense* (map 18), *Mehelya capensis* (map 20), *Philothamnus semivariegatus* (map 22), *Philothamnus hoplogaster* (map 24), *Telescopus semiannulatus* (map 33), *Dispholidus typus* (map 37), *Thelotornis kirtlandii capensis* (map 38), *Psammophis sibilans* (map 46), *Calamelaps unicolor miolepis* (map 52), *Elapsoidea sundevalli* (map 61), *Naja haje* (map 64). Some species seem associated more closely with the 16°C isoline—*Typhlops schlegelii* (map 4), *Psammophis subtaeniatus* (map 44), *Causus defilippi* (map 72). It is apparent from the distribution maps given by Poynton (1964a) that the range of many tropical species of frogs in South Africa is like that of these snakes. As examples, the ranges of *Bufo carens* (Fig. 11) and *Ptychadena anchietae* (Fig. 12) are given.

Certain tropical snake species seem to be limited in their distribution south of the Zambesi mainly to the eastern lowlands and fringing areas. Such a species is the Forest Cobra, *Naja melanoleuca* (Fig. 13); others are the Gaboon Adder, *Bitis gabonica* (FitzSimons, map 74) and the Green Mamba, *Dendroaspis angusticeps* (map 68). Several frogs also have this sort of distribution, especially tree-frogs such as *Hyperolius pusillus* (Fig. 14). Such species, therefore, occur mainly in those parts of the subregion with the highest ET values, and thermal factors may be limiting for them, but the matter requires investigation for each species individually. Their distribution in Zululand in particular may be influenced by other factors (see p. 157).

In the total of 40 tropical species which show only a limited penetration into South Africa, there are five species confined to the warmest eastern areas, on the whole excluded by the 17°C isoline, 19 species which are known to cross the 16°C isoline in a few places only except in the dry north-west, and 16 species which are largely excluded by the 15°C isoline.

Non-tropical Species

Considering now the non-tropical species, those endemic to South Africa and South West Africa, we find among the snakes a number with restricted distribution. There is an endem-centre in South West Africa and another in the Natal-Pondoland midlands and coastal parts; there are also species endemic to the Cape mountains, and some, such as *Naja nivea*, the Cape Cobra, which seem confined to a large, dry, western sector of South Africa. Two species whose ranges are mapped here are somewhat unusual in their wide distribution, and are known to occur in Rhodesia as well; these are a grass-snake, *Psammophis crucifer* (Fig. 15), whose range south of the Limpopo falls almost exactly within the 16°C isoline, and the spitting cobra, *Hemachatus haemachatus* (Fig. 16), which FitzSimons says "appears to be almost equally at home on the coastal plains as up towards the tops of fairly high mountains at altitudes between eight and nine thousand feet". In the northern and north-western parts of its range this species seems never to occur far from the 15°C isoline, though in the eastern part it is present on the coastal plain.

Of the 34 South African species, 28 either are not known to cross the 16°C isoline or range beyond it only narrowly in the south-eastern coastal area, two species are not known beyond the 15°C isoline, one species has a fairly extensive range beyond the 16°C isoline (*Naja nivea*), and three species are confined to the endem-centre in the Natal-Pondoland area, spanning an ET range of 15° - 17°C. Many of the species falling in the first category have a very restricted known distribution, especially those in the arid western parts and on the Cape Mountains, and it is doubtful whether ET is of ecological significance to them.

The distribution of palms

A botanical matter involving ET seems worthy of mention. The poleward limit of palms, a subject of enduring interest to paleaobotanists, is mentioned by Bailey (1962: 8) who finds that this limit fits the 15·5°C isoline better than any apparent isotherm. In South Africa the five species of palms present have a coastal distribution; all occur on the Moçambique plain but drop out one by one southwards (Wicht 1967), *Phoenix reclinata* reaching the furthest south, just beyond the Fish River mouth in the Bathurst District (Deyer 1937), in an area between ET 16·0° (Great Fish River Point) and 15·5°C (Port Elizabeth). Bailey's finding is therefore confirmed.

EFFECTIVE TEMPERATURE AND SOME FAUNAL DISCONTINUITIES

It can be expected on general principles, and is shown by the examples considered in the last section, that where the ET gradient is steep (i.e. where the isolines are close together) the thermal environment undergoes great and rapid relative change and a pronounced faunal discontinuity occurs. A steep gradient of that sort exists on the Moçambique side of the Eastern Highlands of Rhodesia, at the escarpment in the Eastern Transvaal,* over the Middleveld area of Swaziland and the "Low Berg" escarpment between Natal and the Orange Free State (see King, 1951, Chapter XX, for an explanation of these terms), at the Drakensberg escarpment of Natal and the Eastern Cape Province, and in paracoastal Natal roughly south of lat. 29°S. In each of these areas the steepness of the thermal gradient is due to an abrupt topographic change, and the topographic factor itself may be a contributory limiting factor for many animals, both in a positive and a negative sense: positive in the case of animals (e.g. montane forest species) whose habitat requires such topography (such as sea-facing, rain-catching slopes), and negative for species that avoid steep slopes or environmental conditions due to them. The seven physiographic provinces mentioned above are well known as sites of pronounced faunistic change. Another faunal area of great significance is within the 14°C ET isoline in Lesotho and the Drakensberg terrain, where the invertebrate fauna changes profoundly above about 7,600 ft in the east and 7,200 ft in the west, in favour of temperate and palaeogenic groups. This change seems to be due to the interaction of temperature, topography and the effects of high altitude (Stuckenberg 1962).

It is interesting to observe that the South-West Cape, biologically the most distinctive part of Subsaharan Africa, has no special ET features. Admittedly the ET patterns there

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* The escarpment and adjacent highveld of the Eastern Transvaal were found by Schulze (1947) to be so distinctive as to constitute a well-defined climatic "province" in South Africa.

must be far more complex than the present map scale and data reveal, but on the whole, from the thermal point of view, the South-West Cape has much in common with the upper Natal Midlands (ET 14° - 15°C), and does not deserve to be distinguished as "temperate", as some authors have done. It follows that much of the biological uniqueness of that region must be due to its winter rainfall. The disposition of the mountain ranges is also important because aspect has a direct influence on temperature and rainfall (Levyns 1962); the seaward-facing slopes are more mesic because of less insolation and a higher rainfall than the hotter, relatively dry and barren interior slopes. These factors, together with summer aridity, impose peculiar environmental stresses on fauna and flora alike (see Stuckenberg 1967).

Of special interest and importance is the extension of the ET 17° and 16°C isolines down the south-east coast. The origin of this southward extension of warm climate, aptly described by Poynton (1964b: 212) as a "tropical peninsula", lies in the presence of the Agulhas Current which, as is clearly shown in Fig. 17, flows like a vast, warm river along the south-eastern seaboard and has an important influence on the climate of the coastal strip at least as far as East London. This narrow, elongate zone of relatively warm climate enable many tropical species of plants and animals to extend their range southwards (see Poynton 1961); examples mentioned in the previous section are *Naja melanoleuca* (Fig. 13), *Dendroaspis angusticeps*, *Bitis gabonica* (FitzSimons 1962, maps 68, 74), and *Hyperolius pusillus* (Fig. 14). The decrease in width of these ET zones which starts roughly at lat. 29°S and becomes progressively more pronounced towards Durban (30°S), is a feature of great importance as it is a bottleneck through which many tropical species evidently do not pass. Faced with a narrowing coastal plain bounded by rapidly rising land, the tropical lowland fauna rapidly diminishes in taxonomic content south and west.

Southern Natal is an area of great zoogeographic interest. The thermal gradient from Durban on the Natal coast to Mokhotlong in Lesotho is the greatest in South Africa (table 5). Much of the same range of thermal conditions exists from sea-level to the summit of the Drakensberg between roughly lat. 29°S and 31°S, and is associated with the very rapid rise of land from the sea to the crest of the escarpment at 10,000-11,000 ft in little more than 100 miles, an average of about 100 ft a mile. A section of this region is shown in aerial oblique in Fig. 18. This view shows a landscape of great topographic diversity, in which several physiographic features of special concern can be observed.

1. In the background, the snow-covered face of the Drakensberg escarpment which rises precipitously over 4,000 ft in one grand sweep; together with the foothills whose accordant summits (6,000-7,000 ft) collectively form a landscape known locally as the "Little Berg", this escarpment has an ET range from about 14°C to less than 13°C.

2. Two prominent scarps or treppen, at about 2,000 ft and 4,000 ft, aligned roughly parallel to the coast, each step up the level of the land by more than 1,500 ft. Part of the upper one forms the face of the Karkloof range and mountainous country near Balgowan, where the 14°C isoline runs more or less along the crest of the scarp. The lower one is especially well defined and can be traced continuously from Zululand southward into Pondoland; it is responsible for the abrupt change in ET values from 15·8°C at Pietermaritzburg to 14·9°C at Cedara only a few miles to the west. These scarps are important as


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zones of speciation and dispersal, as well as being barriers. King (1942, 1954), and King and King (1959), discuss their mode of origin and age.

3. Inland from Durban the outcrop of Table Mountain Sandstone dipping to the east on the seaward side of the monocline axis (Fig. 1), forms an elevated, scarp-bound block overlooking the very narrow coastal plain. The ET decreases from 17·2°C at Durban to 15·7°C at Hillcrest, a distance of about 20 miles westward.

4. The country between the escarpment and the sea is deeply gashed roughly east-west by valleys whose rivers are responding to Plio-Pleistocene uplifts of land (King and King 1959). These valleys may be so deep and steep as to strongly influence local rainfall and thermal conditions towards hotness and dryness, and some tropical elements penetrate up the valleys though they cannot cross the high country between them.

EFFECTIVE TEMPERATURE IN THE LAST GLACIAL PHASE OF THE PLEISTOCENE

Reduction of Mean Annual Temperature

A reduction in mean annual temperature over Africa during the later Upper Pleistocene, probably synchronously with the last glacial episode (main phase of the Würm) in the northern hemisphere, is reasonably well established; this reduction is calculated to have been of the order of 4° - 7·2°C (there are many reviews of this subject, *inter alia* Flint 1959; Cook 1962, 1964; Van Zinderen Bakker 1962, 1963, 1964, 1966; Moreau 1963, 1966). It is by no means certain to what extent the whole continent was affected, and the evidence for South Africa in particular is meagre. Van Zinderen Bakker (1963: 338) noted that the temperature factor requires study as most of the attention in African Pleistocene work has focussed on changes in rainfall; later (1966: 129) he commented, "It has often been said that changes in temperature of the magnitude of only 5°C are of minor importance in a tropical continent such as Africa. These changes have, however, been of very great significance . . . Little but consistent changes of this nature can have an enormous influence on the distribution of plants and animals". As mean annual temperature is a datum used in the calculation of ET, an attempt to ascertain the effect of such a reduction on the ET range in South Africa seems worthwhile; for this purpose the temperature reduction is taken to have been 5°C.

Bailey (1960: 15) points out that a change in absolute warmth as might be judged by differences in mean annual temperature will affect maritime climates most of all. This is clear

FIGURE 17

A photograph taken by the American meteorological satellite Nimbus II on 5 October, 1966. The view shows South Africa and surrounding ocean. The Agulhas Current is very clearly apparent as the dark strip outlining the south-eastern coast. This image was recorded at night by measuring infrared radiation: the warmer the surface the darker the image. Banks of cloud over South West Africa and the northern Cape Province show as white masses. Compression of data has resulted in some distortion as revealed by the curves in the rows of superimposed dots. Nimbus II circled the earth in about 100 minutes in near polar orbit, at an altitude of about 1,100 kilometers. (Published with permission from the U.S. Naval Oceanographic Office.)

from an inspection of the nomogram (Fig. 4); in an ideal climate with no annual range in temperature, a change of 8°C in mean annual temperature covers the ET range from 10° to 18°C, whereas such a change in a climate with a mean annual range of 20°C alters the ET much less (12·9° - 15·1°C). In other words, maritime climates are more sensitive than continental ones. Bailey concludes that (1) "changes in the strength and nature of atmospheric circulation can significantly alter the warmth of climate as judged by effective temperature", and, "The floral evidence related to such alteration would be displayed only in climates quite warm or quite cold"; (2) ". . . substantial changes in climates of medium warmth, if detected by floral evidence throughout the midlatitudes, would require a control that could be general only by introducing significant changes in the heat budget of the earth as a whole". The considerable late Pleistocene changes which have occurred in the African flora usually are explained as a consequence of changing rainfall, though Van Zinderen Bakker (1962) has emphasized that the term *hypothermal* rather than *pluvial* is more appropriate for the period.

*South Africa during the Hypothermal**

Accepting a reduction in mean annual temperature of 5°C for the last phase of the Würm glaciation, a decision has to be taken on the extent to which mean annual range of temperature would have been affected by such a reduction. Because mean annual range is in effect a measure of the continentality of a climate, I am assuming (on the postulate that topography and the

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* In the period between the preparation and publication of this paper, two important articles have appeared which require mention here. Van Zinderen Bakker (*Background to Evolution in Africa*, Ed. Bishop and Clark, Univ. Chicago Press, 1967, pp. 125—147) has described possible climatic changes in Africa resulting from latitudinal expansion and contraction of climatic belts during hypothermal and hyperthermal periods. He reasons that the intertropical convergence would in a hypothermal be further south than at present, during the southern summer, resulting in moist air from the tropics reaching further south than at present; and that in the southern winter the polar front would be further north, nearer South Africa, causing cyclonic rains to reach further inland, particularly over the central plateau. Coetzee (*Palaeoecology of Africa*, 3, pp. xi + 146, 1967) reported on palynological studies of cores taken at Aliwal North and dated at a time span over about 3,000 years falling in the late part of the last Glacial in Europe. She found indications of cooler, moister climate alternating in three cycles with warmer, drier climate, the vegetation fluctuating between grassveld and karoo.

FIGURE 18

An aerial oblique view of part of southern Natal, from above the sea off Durban, looking westward, taken on infrared film early on 22 June, 1964, after a heavy fall of snow on the Drakensberg Escarpment and Lesotho. Durban is spread over the narrow coastal plain in the foreground, and just beyond the country rises rapidly owing to the presence of Table Mountain Sandstone. The Umgeni River is on the right; it passes through an area of intricate, rugged topography, the "Valley of a Thousand Hills", visible in the right middle distance and overlooked by the prominent, flat-topped "Table Mountain". In the centre and left middle distance a strip of fairly featureless country follows an outcrop of Ecca Shale, and beyond this the first scarp referred to in the text can be discerned. A second scarp further inland is most clearly apparent on the right of the picture where the Karkloof Range shows as a dark, narrow strip. In the background is the Drakensberg, about 100 miles (160 km.) away. Much of this escarpment is close to or exceeds 10,000 ft (c. 3,000 m.) in altitude, and at the time was snow-covered down to about 5,000 ft. The distance north-south covered by the photograph is about 100 miles. (Published with permission from the Editor of the "Natal Mercury".)

relation between land and sea during the late Pleistocene were not much different from what they are at present) that this range was unaffected. Confirmation of this view was expressed in a letter from the Weather Bureau, Pretoria, replying to my query on the subject. However, there can be little doubt that changes in the nature and strength of atmospheric circulation did occur (Krauss 1960), and these would have affected the climate of South Africa probably increasing the mean annual range of temperature, but at present no way of detecting or estimating such changes exists.

After reducing mean annual temperatures by 5°C, ET were calculated for three series of stations (Table 6):

TABLE 6

Locality	*Altitude M.*	*Present ET*	*Hypothermal ET*	*Percentage Difference*
1. Durban	s.l.	17·2	14·7	14·5%
Hillcrest	695	15·7	13·5	14·0%
Pietermaritzburg	684	15·8	13·8	12·7%
Cedara	1,079	14·9	12·9	13·4%
Nottingham Road	1,438	13·9	12·2	12·2%
Mokhotlong	2,377	13·2	11·5	12·9%
Maseru	1,571	14·4	12·6	12·5%
Prieska	933	15·7	14·1	10·2%
Okiep	927	15·3	13·5	11·1%
Port Nolloth	s.l.	14·0	11·6	17·1%
2. Kynsna	s.l.	15·3	13·1	14·4%
Deepwalls	519	14·7	12·4	15·6%
Willowmore	826	14·7	12·8	12·9%
Steynsburg	1,478	14·1	12·4	12·1%
Bloemfontein	1,422	14·7	13·0	11·6%
Johannesburg	1,753	14·9	12·9	13·4%
Louis Trichardt	961	15·9	14·0	11·9%
Messina	549	17·7	15·7	11·3%
3. Punda Maria	462	17·4	15·5	10·9%
Pusella	748	15·9	14·2	10·7%
Woodbush	1,528	14·4	12·2	15·3%
Pietersburg	1,283	15·1	13·3	11·9%

(1) a roughly latitudinal series across South Africa between 29° and 30°S, from Durban in the east to Port Nolloth in the west; (2) a roughly longitudinal series through the middle of

the country, from Knysna in the south to Messina in the Limpopo Valley; (3) a short traverse over the eastern Transvaal escarpment from Punda Maria on the lowveld to Pietersburg on the highveld. In the case of the first two series, sea-level would have been lower by a maximum of a little over 100 m., thereby increasing mean annual temperature at the coast by about 0·5°C, but this small change is ignored.

The effect of this reduction would have been considerable. The present ET range, from *Cool* to *Very Warm*, was shifted downwards by a whole grade (see Table 3), so that a *Very Cool* climate would have occurred in the highlands (above about 2,200 m.), which is the ET grade of present-day Canada and Northern Europe; *Cool* climate affected a large part of South Africa from the southern seaboard to beyond Johannesburg in the north, down to about 1,000 m. in Natal, and along the west coast (this is the present ET grade of Tasmania, New Zealand, Central Europe and much of the United States); *Mild* areas were in the northernmost Cape and Transvaal, and in Natal below 1,000 m. to sea-level; finally, *Warm* climate existed in the Transvaal lowveld and Limpopo Valley, and in Northern Zululand. On the basis of the accepted lapse rate of 0·6°C per 100 m. (a little too high on average for South Africa, according to WB 28, p. 98), a change of 5°C is equivalent to a lowering of thermal levels through a little more than 800 m. Over most of the latitudinal middle of South Africa the ET levels would have been depressed by 800-1,000 m., but by much more than that in the south of the Cape Province, and somewhat less in the warm lowlands of the Limpopo Valley and eastern lowveld. In accordance with deductions from the nomogram, mentioned above, the greatest relative differences are shown by coastal localities—ET values for Durban, Knysna and Port Nolloth were reduced by more than 14%. There is a considerable reduction of ET at the two montane forest stations of Woodbush and Deepwalls (over 15%), presumably also due to a relatively low mean annual range of temperature characteristic of the forest environment. Places in the northern interior with a warm climate and fair annual range of temperature show the least change in ET (10 - 11%), such as Punda Maria and Pusella.

Geological evidence of the Hypothermal

This speculative picture of ET during the hypothermal can be supplemented by information on the probable winter conditions in South Africa supplied by geological studies. Both du Toit (1948) and Kokot (1948) expressed the view that South Africa was too dry during the Pleistocene glacial periods for actual glaciation to have occurred. Alexandre (1962) described periglacial landforms in Lesotho down to 6,000 ft and Sparrow (1964) discussed the possibility of a periglacial climate in South Africa, citing examples of oversteepened slopes and the presence of cirque-like hollows in Lesotho and East Griqualand. Sparrow points out that a depression of the snowline in South Africa sufficient to cause glacial conditions could have happened; Flint (1957) had already suggested a possible snow line at 8,000 ft. Sparrow (1966) subsequently described apparent traces of periglacial phenomena in the south-east Drakensberg region. Cirques were found down to 8,000 ft. (2,440 m.) and other periglacial landforms occurred down to 6,000 ft (1,830 m.), the altitude-latitude diagram showing a progressive rise to the north as would be expected. Sparrow concludes, "It would appear that, during the Gamblian period of the Pleistocene, Southern Africa was cooler than at present with a snow line at about 8,000 ft (2,440 m.). Localised snow and ice patches were able to strip the terrain in a few areas and snow remained in sufficient quantity for cirques to form. Severe frost action took place at lower levels and localised permafrost assisted the movement of head by solifluction. At no time was the precipitation sufficient to permit any more than extremely localised ice formation".

Changes in the biotic pattern during the Hypothermal

Changes of this nature during the hypothermal would have had a direct influence on many animals. Poikilotherm vertebrates of tropical origin would have been especially sensitive to the colder, shorter summers. In a previous section, tropical snakes were shown to be at present largely excluded by the 15°C ET isoline; Fig. 19 shows the present position of that isoline and its presumed approximate position during the hypothermal. The movement of this isoline would have been less where it descended through a considerable altitudinal range, i.e., in Natal, Swaziland and the Eastern Transvaal, but over the central interior the isoline would have departed far from its present position owing to the general lack of relief on the relatively featureless Botswana landscape. A considerable portion of Rhodesia, excepting only the Limpopo and Zambesi lowlands, would have been enclosed by the 15°C isoline. Tropical snakes presumably would have had to retreat to the Limpopo Valley, eastern lowveld and Zululand coastal plain to obtain equivalent ET conditions; anuran species may have had to make similar movements. Conversely, South African species, many of which seem at present to occur only within the 15°C isoline, would have been able to spread into Rhodesia via eastern Botswana, though probably only those species not excluded by relatively arid conditions. Two species of snakes which apparently did that are *Hemachatus haemachatus* and *Psammophis crucifer* (see Figs. 15, 16). With the return of warmer conditions after the hypothermal, these species apparently had to restrict their Rhodesian range to the cooler, higher eastern and central areas from where they are known today.

During the hypothermal considerable areas of South Africa and Rhodesia would have been climatically favourable for the establishment of boreal insect species immigrating from North Africa where presumably they would have retreated from the glacial cold of Europe. Such species would have been able to take advantage of the more extensive "islands" of temperate climate that existed on the discontinuous series of highlands from Ethiopia to South Africa during the hypothermal. Today such species are mostly mountain dwellers in the eastern escarpment country and Lesotho, or occur in the southern and south-western Cape, seldom being present in both areas, but usually within the 15°C isoline. I have previously listed some examples of boreal elements in the Diptera (Stuckenberg 1963); the masarid wasps discussed by Gess (1965) are another example, and many others exist.

In addition to directly affecting the fauna, the hypothermal would also have had an indirect effect by altering the distribution and character of various vegetation types. In considering this, attention must first be given to the question of whether an increase in rainfall accompanied the decrease in temperature. The assumption is commonly made that these

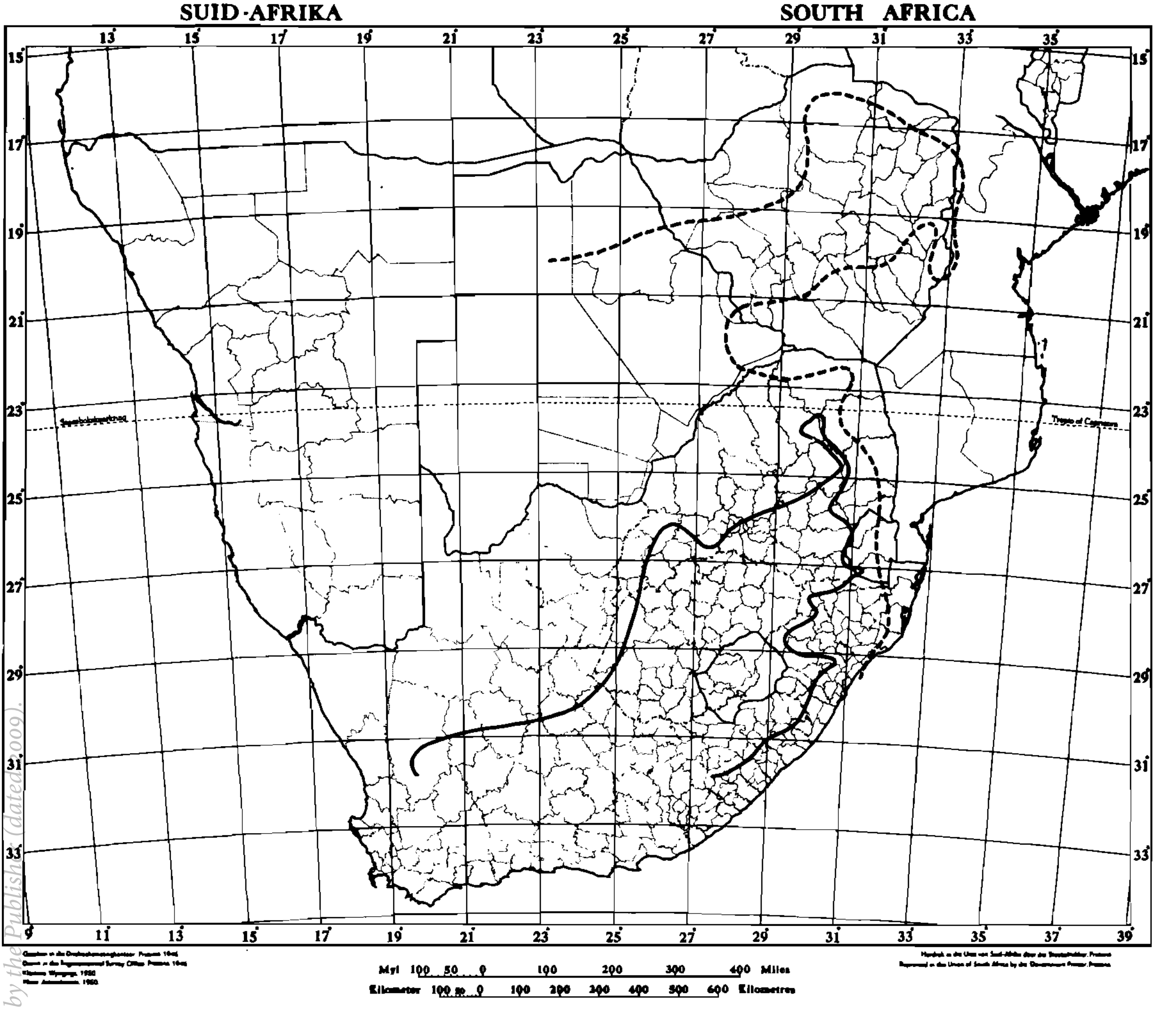

FIGURE 19
The 15°C Effective Temperature isoline in its present position (continuous line) and estimated position (dashed line) during a hypothermal period with mean annual temperatures 5°C below those of the present time.

changes were coeval, but there is much uncertainty. Flint (1959) commented that Pleistocene pluvials may not have coincided with glacials, but later (1963) said that they probably were synchronous. Bernard (1962) concluded that intertropical pluvials corresponded to interglacials in the high latitudes as a consequence of warmer tropical oceans. Van Zinderen Bakker (1962) considers the glacial period in Africa contemporaneous with the main phase of the Würm to have been more humid than at present owing largely to the lower temperatures. On the other hand, Galloway (1965) working in south-eastern Australia, found that during the last glacial period the climate there was windier and drier than at present, and concluded that the evidence indicated a lowering of atmospheric layers rather than a latitudinal movement of climatic belts (". . . the Ice Age is never more than a few kilometers above our heads".) This matter is important for an assessment of hypothetical vegetation maps of southern Africa published by Cooke (1962, 1964), in which he shows assumed effects of an increase to 140 - 150%, and a decrease to 50 - 60%, of the present rainfall. Cooke explicitly ignores possible temperature effects, but, in the case of his map showing hypothetical effects of increased rainfall, such effects cannot be disregarded if the pluvial is assumed to have coincided with a hypothermal period. The climate of South Africa probably was too cold for some of the changes he suggests to have occurred.

Cooke maps what he calls "Montane forest, evergreen forest and mountain communities" spreading far beyond the present patchy range in South Africa right up to the escarpment in the Eastern Cape and Natal, and over the highveld to the Zoutspansberg, thus over an area that would have been cooled to an ET of 13°C or less. I consider this distribution to have been unlikely. For one thing, forest tends to create its own climate to a moderate degree by promoting the formation of mist and creating conditions cooler and more humid beneath its canopy than exist in the surroundings. A reduced annual range in temperature is characteristic and this makes forest particularly susceptible to a change in mean annual temperature, as the results given above for Woodbush and Deepwalls show. The matter hinges on the ability of South African montane forest to withstand cold. Almost no investigations have been made on this subject, but it is discussed in some detail by Story (1952: 121-4); his main conclusion is that cold by itself is not a severely detrimental factor, at least for short periods (forests are known to survive freak falls of snow), but that cold winds have a very important effect. Such winds cause a great increase in transpiration at a time when trees cannot meet the demand, and physiological drought results. In winter this effect would be enhanced by the coldness of the ground water, because cold, wet soils cause physiological drought in direct proportion to their coldness. These influences increase in effect with altitude so that mountain slopes become progressively more unfavourable for forest with height. Another point is that the ET range on the plateau slopes may have been low enough to affect the ability of the trees to fruit or set seed in the concomitantly shorter, cooler summers.

If the pluvial coincided with the lowering of temperature discussed above, montane forest in Natal and the Eastern Cape would probably have been eliminated from the upper part of the range it now occupies (i.e., down to about 1,000 m.) except in isolated refugial areas, or would at least have been reduced in taxonomic spectrum by the disappearance of the more cold-sensitive species. In the intermediate zone of the plateau slopes this forest would show the same type of dispersal it has today, namely irregular distribution along scarps giving both wind shelter and a sea-facing aspect. In the milder paracoastal areas montane-type forest may have been more continuous than it is at present, but the vegetation called by Cooke "Forest-savannah mosaic", comprising many tropical species, would not have extended to the degree he shows but would have been detrimentally affected by the lower temperature. Thus, if palms are limited by the ET 15·5°C isoline, they would have disappeared from the South African coast almost completely. *Acacia* species such as *karroo* would probably have retreated to the northern and north-eastern lowlands; Story (1952: 39) concluded that dryness and cold each limit the spread of this species, and his map shows *karroo* to be at present outside the country bounded by the ET 14°C isoline.

Phillips (1931: 161-5) gives an interesting account of the subtraction of forest plant species (trees, woody shrubs, lianes) from Natal to the Knysna area, which may be summarised as follows:—

Distribution of forest flora

Knysna	*E. Cape*	*Transkei*	*Natal*	
←———	———	———	———	130 species
	←———	———	———	130 species
		←———	———	60 species
	>———	———<		9 species
>———<				25 species
TOTALS: 155	269	329	320	354 species

Phillips describes the Knysna forest flora as of tropical derivation, and considers the southward subtraction a consequence of the temperature gradient and possibly the relative ability of the different species to disperse. If this subtraction is a consequence of the present-day temperature range (say, Otobotini 17·9° - Knysna 15·3°C) the very much cooler conditions of the hypothermal (ET 15·5° and 13·1°C respectively) would surely have eliminated forest entirely from the southern Cape at least, and drastically reduced it in the Eastern Cape Province. In that case, the present distribution of forest would have been established in the 14,000 years since the recession of the hypothermal, a period marked by arid phases in southern Africa and probably a constantly increasing incidence of deliberate veld burning by indigenous tribes, therefore a period not especially favourable for the spread of forest. A better explanation of the subtraction described above would be to consider it as essentially the one established during the hypothermal, which has persisted owing in part to the post-hypothermal conditions already mentioned. An interesting point which seems to favour this view is that some species of forest trees which have reached the Knysna area from the north-east, have a very limited range in the Knysna area (only few specimens of some species were found), though these species seemed to be thriving there (Phillips 1931: 163-4); apparently these are recent arrivals, and they point to the possibility that other forest plants may not yet have attained their maximum range possible in present circumstances. Barriers established since the hypothermal may be hindering the southward spread of tropical forest plants; I am indebted to Prof. A. W. Bayer for pointing out that some tropical tree species stop on the northern side of what was until the era of modern agriculture a vast marshy area around the lower length of the Umfolosi River on the coastal plain just south of Lake St. Lucia.

Van Zinderen Bakker (1963) considered that vegetation levels in montane parts may have shifted downwards by 500-800 m.; his diagrams show a descent of forest and macchia, a westward extension of alpine grassland at the expense of the Karroo, a contraction of the bushveld, and the appearance of montane forest in some elevated areas where it does not occur today. This accords entirely with deductions which the modified ET picture suggests. Cooke's (1962, 1964) map showing macchia confined to the south-western Cape during a pluvial would be incorrect if the hypothermal phase coincided. Under such cooler conditions the macchia would have been at an advantage, being morphologically well adapted to conditions inducing physiological drought (see Story, 1952: 75-6), and probably achieved its maximum range then. Van Zinderen Bakker (1962: 29) states that "temperate forests" extended to the north-east of South Africa and merged with forested areas in Rhodesia and east-central Africa. However, many zoogeographical considerations are totally against a montane-forest type connection across the Limpopo Valley, at least during the last hypothermal (evidence for faunal movements in earlier Pleistocene hypothermals probably was blurred or eliminated by events during the most recent one). The montane forests and streams of the Rhodesian Eastern Highlands have little in common faunistically with those of South Africa (Stuckenberg 1962), apart from widespread, mainly tropical species of no zoogeographic significance, and in some groups the difference may be even at the family level (e.g. Opiliones; Dr. R. F. Lawrence, pers. comm.). Important indicator groups such as Blepharoceridae and Onychophora are absent in Rhodesia, and the flightless forest cryptofauna of Rhodesian escarpment forests is taxonomically quite different from, and relatively much poorer than, that of South African forests (Leleup 1965: 67). However, the Rhodesian highlands may have witnessed a climatic catastrophe in quite recent times. Moreau (1963: 414) refers to a dry phase 12,000 - 9,000 years ago in western Rhodesia where Kalahari sand was being redistributed, and this may have had a severe influence on the forest and stream environments of the eastern highlands where the faunal assemblages established during the hypothermal may have been eliminated and subsequently reconstituted by tropical elements. The poverty and tropical affinities of the Rhodesian forest cryptofauna certainly suggest this possibility.

To conclude, the influence of the hypothermal period on the South African fauna must have been greater than has generally been suspected. The present biotic pattern in fact must be relatively very recent, established in the 14,000 years since the recession of the last glacial, when the tropical fauna could extend back into territory from which it had previously retreated. Pleistocene changes of Effective Temperature may prove to be responsible for many details in the distribution and diversification of the South African fauna.

SUMMARY

Few studies have been made on temperature as a causal factor contributing to the formation of faunal assemblages in Africa. An early work by Bowan utilises various parameters of temperature and rainfall, on which he establishes a climatic classification of Subsaharan Africa allegedly relevant to bird distribution. There are deficiencies and defects in his scheme and inaccuracies in his mapping, and the value of Bowan's climatic classification is considered unproven. Later studies by Poynton are criticised on several counts, and his theses—that the biotic pattern of southern Africa is determined primarily by thermal rather than rainfall factors, that the 18°C mean July isotherm is a reliable climatic indicator, and that the southward subtraction of tropical anuran species in Zululand is a consequence of thermal factors—are rejected. Poynton's mapping of the 18°C July isotherm is shown to be inaccurate. A positive, highly significant correlation is demonstrated between the width of the coastal plain and number of tropical anuran species.

The biological importance of the summer months is stressed, and a description is given of a factor called Effective Temperature (ET) developed by Bailey to express the relative warmth and duration of the warm period of the year. ET measures warmth on a temperature scale, specifying temperatures at the beginning and end of the warm period, and implicating the duration of that period. An ET map of southern Africa is presented and its features discussed. A range from *Cool* to *Hot* on Bailey's scale is demonstrated, and southern Africa is shown to be similar to Australia in terms of ET. Characteristic of the ET zones are described and the period of the year with mean daily temperatures above ET is given for each zone. The relation between ET and frost in South Africa is discussed and ET shown to be a poor guide to frost incidence.

A close correlation is demonstrated between the distribution of snakes and the ET zones. A causal relationship is considered to exist because of physiological and behavioural adaptations of snakes to temperature factors. Most tropical species are excluded by the 15°C ET isoline, whereas most South African endemic species do not range beyond the 16°C isoline. Frogs show similar correlations. The distribution of palms shows a relation to ET.

Faunal discontinuities occur where the ET gradient is very steep; such a gradient is associated with pronounced topographic changes. The location of the more important gradients is given. The absence of thermal features peculiar to the South-West Cape is pointed out, and the assumption is made that the biological uniqueness of that area is due to its winter rainfall. The Agulhas Current is important for its effect on the south-eastern coastal strip; zones of warm climate are deflected down the coast and allow a southward extension of the tropical fauna and flora. The significance of the topography of southern Natal in limiting these zones is discussed.

Assuming a reduction in mean annual temperature of 5°C during the last glacial episode of the Pleistocene, the effect this would have had on the ET zones is calculated. The climate of South Africa would have been much colder, with ET grades of present-day Canada and Tasmania over much of the country. In accordance with predictions, relatively greatest changes in ET would have been suffered by coastal areas and forested localities. Places

in the northern interior with a warm climate and moderate annual range of temperature would have experienced smallest changes in ET. Winter conditions during the hypothermal period, as deduced from geological evidence, indicate peri-glacial conditions down to 6,000 ft. Changes in the biotic pattern during the hypothermal would have been marked; the tropical fauna would have had to retreat to northern and north-eastern lowlands, and some species now restricted to South Africa would have been able to range into Rhodesia. The vegetation of South Africa would also have been affected. Forest probably was restricted, and the present-day subtraction southward of the forest flora between Natal and Knysna possibly was established during the hypothermal. Tropical plant species, such as palms, would have been forced to withdraw northwards. Zoogeographic evidence is against a montane-forest connection across the Limpopo Valley during the hypothermal.

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