

PATTERNS IN THE DISTRIBUTION OF SOUTHERN AFRICAN TERRESTRIAL TORTOISES (CRYPTODIRA: TESTUDINIDAE)

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ABSTRACT

Distribution maps for the ten southern African species of land tortoise have been prepared using published sources and recent museum records. Three hundred and thirty-six new records have been added to these maps by a recent Cape Province tortoise survey, and a further 65 of the older records have been re-confirmed. A relatively clear picture of the range of each species is now available, although the records in South West Africa are not yet adequate enough to resolve the problems posed by the vague localities published at the beginning of the century. The Cape Province of South Africa clearly stands out as the world's richest area in terrestrial testudinids.

INTRODUCTION

In Africa, south of the seventeenth parallel of latitude (corresponding approximately to a line following the courses of the Zambezi and Cunene Rivers), there are ten species of terrestrial chelonians. Nine (and perhaps all ten) of these species occur in the Cape Province, South Africa, and six are endemic to the Cape and the adjacent portion of South West Africa. The Cape Province is, in fact, the richest area in the world as far as species of land tortoises are concerned. In one district of the eastern Cape Province, five species of land tortoise and one water tortoise are known to co-exist naturally.

The alleged decline in numbers of Cape tortoises over the past 40 years has caused concern in some quarters. This paper is a contribution towards the understanding of the geographical distribution of the tortoises of southern Africa in general, and the status of the Cape assemblage in particular.

MATERIALS AND METHODS

The taxonomic inter-relationships of the southern African species are still the subject of debate. For the purposes of this paper, however, the arrangement proposed by Loveridge & Williams (1957) has been adopted, giving five genera and ten species, two of the species being subdivided into subspecies.

The published sources of the localities cited by these authors were traced, each record was individually assessed, and occasional outright errors, or errors in transcription, were detected and discounted. Despite the vague nature of many of the localities, it was possible to obtain a reasonably accurate distribution picture for each species after plotting the acceptable localities

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the mouth is raised during breathing so that the glottis lies in the cup-shaped internal nares. During sniffing, when air is to be passed by the olfactory bulbs, the crocodilians drop and raise the pharyngeal floor (while the glottis remains closed); they also involve the pharyngeal chamber in vocalization.

The lungs are ventilated by changing the volume of the pleural space which is anteriorly defined by the rib cage. Two kinds of movements affect the pulmonary volume. The first is a change in the proportions of the rib cage, the second a shift in the posterior limit of the cage by anteroposterior movements of the liver.

These movements of the liver effect the basic ventilatory changes. A decrease in pulmonary volume, a rise in pressure and an outflow of gas is effected by contraction of the transverse muscles of the body-wall which thus push the liver anteriorly. An increase of the pulmonary volume, a fall in pressure, and an inflow of gas is effected by contraction of the diaphragmatic muscles that tie the liver to the pelvis; the liver is then moved caudad by muscles that lie parallel to and on its line of movement.

The position of the ribs determines the volume of the pleural cavity. However, the crocodilian rib cage is complex, as each rib is tripartite and the cartilaginous medial (intercostal) and ventral (sternocostal) segments bend as well as fold. Muscle activity is further complicated by the changing angle of the sheets of deep and superficial intercostals (and of course by the age-associated change in the level of intercostal fibres). Thus the deep fibres between the ventralmost costal segments fire antagonistically to those crossing the dorsalmost spaces. Similarly the superficial intercostals generally fire antagonistically to those deep intercostal fibres immediately adjacent to them, but may fire in parallel with the deep fibres crossing the intercostal spaces of another rib segment.

As the crocodilian body-wall is flexible rather than rigid, it can be deformed by externally applied pressures. When a caiman immerses itself, or even dives, the pressure of the pulmonary contents reflects the overburden as does the breathing cycle. The time for inhalation becomes reduced, the thorax moves less, the pulmonary pressure drops smoothly to subatmospheric during inhalation rather than showing a change of rate, and the pressure after each breath tends to overshoot rather than terminate at the intercycle level. Also the inspiratory muscles fire at a lower rate or become silent.

All of these symptoms reflect two basic shifts (Gans 1976). The first is that the animal compensates for the extra work required to inhale against an overburden by letting the overburden-induced pressure (rather than independent muscular action) power the exhalation. The second adaptation is that the resting position of the rib cage changes with imposed pressure. A diving caiman apparently keeps its rib cage close to collapsed. Only the mechanically most effective diaphragmatic muscles act in inhalations, and the costal apparatus serves mainly to stabilize and only slightly to increase the diameter of the rib cage.

This example then confirms that ventilation in *Caiman* very much reflects the need to breathe while partially submerged. Analysis of the system while the animal is resting on land will only tell half the story.

The final caution then suggests that the parameters of the biology of crocodilians need to be examined on specimens on land and then immersed in order to gain an understanding of the complex nature of crocodilian adaptation.

The second caution then suggests that we need to study the morphology of large animals and to ask questions of their physiology. When maximally sized animals may be too difficult to obtain and deal with, one should at least attempt to include a few sexually mature specimens. One might perhaps include a plea to museum curators or perhaps museum directors to install maxi-bathtubs as part of the standard equipment in herpetological collections.

THE AMPHIBIOUS NATURE OF CROCODILIANS

There should be little question that crocodilians have been selected for survival at the interface between water and land. They are not truly aquatic. Thus they emerge to bask and lay their eggs on land, and the young use the land for shelter during much of their first three years (Pooley 1962). They are not terrestrial; thus they will desiccate rapidly and will use the water both to escape from certain predators and to ambush terrestrial prey. The selective bradycardia documented above (cf. Gaunt & Gans 1969), may be considered a withdrawal response of animals hiding under water. Food caught on land will be drowned and dismembered in the water; fishes caught in the water will be flipped into the air to be moved and positioned inertially for head-first swallowing. A pair of transverse flaps completely subdivides the mouth into an anterior (buccal) and posterior (pharyngeal) chamber. The crocodile can then breathe while the open mouth is holding prey under water.

The mixture of adaptations is perhaps best seen by looking at the crocodilian breathing patterns, both structurally and functionally (Gans 1976; Gans & Clark 1976). All crocodilians have to pass their respiratory gases through the elongate narial canal closed off from the buccal chamber by the secondary palate, thus providing a direct connection between the external naris and the pharynx (Figure 2). The air never enters the pharynx proper, because the floor of

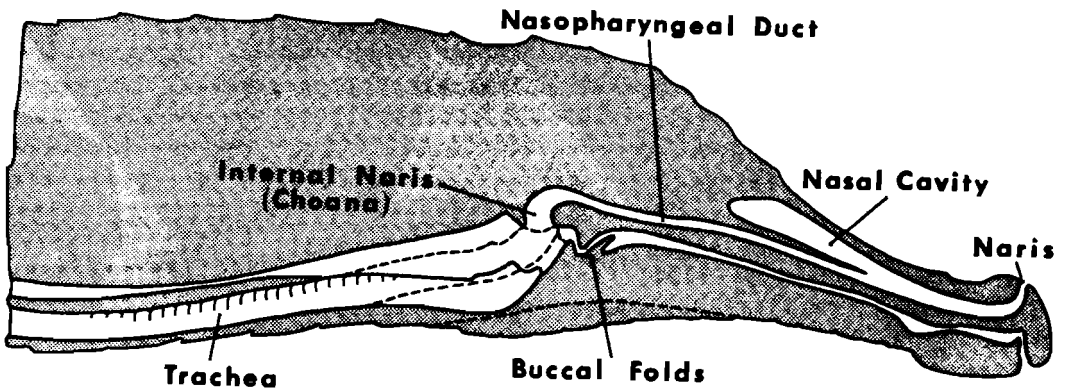


FIGURE 2

Diagram to show the position of the choana, trachea, and external nares as well as the chambers connecting them. The dashed line shows the position of the trachea during breathing, the solid line shows the position when the animal is drawing air into the pharyngeal cavity for sniffing.

by telemetry studies of different-sized animals in the wild. Our knowledge of such systems remains limited; for instance, these studies report no voluntary hyperthermia after feeding, although this has just been reported in an abstract (Lang 1975) for fully adult animals in the wild and of a different species.

Observations of ontogenetic change should, of course, not be attributed to some kind of intrinsic physiological drive. Rather, these observations might well reflect a transition of the ecological optimum. For instance, the capacity of juveniles to digest at slightly lower temperatures or to feed at slightly lower temperatures might be considered to be adaptive in terms of their more crepuscular habits (Pooley 1962). On the other hand, the comments on crepuscularity are based upon *Crocodylus niloticus* and the temperature observations on *Caiman crocodylus*, so that we lack exact equivalents.

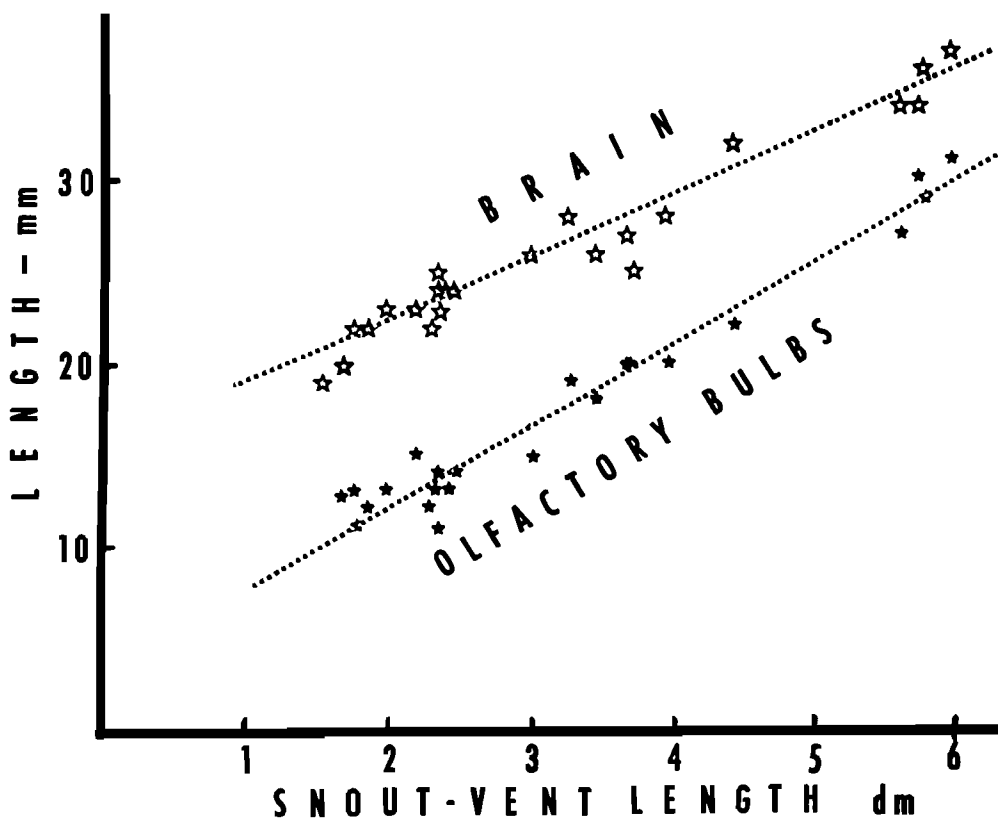


FIGURE 1

Length of olfactory bulb (solid stars) and remainder of brain (open stars) plotted versus snout-vent length for small to medium-sized specimens of the South American caiman *Caiman crocodylus*. Note the change in relative length. At 20 cm the olfactory bulb is only 50% as long as the rest of the brain; at 60 it is about 75% as long; it would presumably be equally as long as an adult. (Part of the data courtesy of Dr. R. G. Northcutt.)

a zone of higher rainfall than its congener *Psammobates tentorius*, i.e. usually over 300 mm per annum.

Only four of the 75 records shown have been obtained in the current Cape survey, two being previously unrecorded localities.

Psammobates tentorius (Bell, 1828) (Figure 7)

The three subspecies recognized by Loveridge & Williams (1957) are *tentorius*, *verroxii*, and *trimeni*. These authors, faced with a superabundance of names, and a paucity of adequately labelled material, chose the expedient course of 'lumping' the material into three groups based on one character, plastral pattern, which appeared to them to be also geographically well-differentiated.

- (i) *trimeni* (Boulenger, 1886) has a plastral pattern (dark-brown on yellow) which is sharply bounded but indented or broken through by a series of yellow rays.
- (ii) *tentorius* (Bell, 1828) has a sharply bounded plastral pattern which is very little indented or quite intact.
- (iii) *verroxii* (Smith, 1839) has a diffuse or indistinct plastral pattern often variable within one population.

Loveridge & Williams regard Matjesfontein (3320 BA) as being the approximate centre of a three-way intergrade zone, and suggest that there is little or no intergrading where *trimeni* and *verroxii* meet in Namaqualand, a case perhaps of 'circular overlap' (Mayr 1963), although in this case the suggestion is as yet unproven and the mechanism unknown. This concept of the *tentorius* complex is essentially the same as that proposed by Duerden (1907).

The large series available as a result of the recent Cape Province survey awaits detailed analysis, but the taxonomic situation appears to be further complicated rather than simplified. An attempt has been made in Figure 7 to indicate the extent of the intergrade zone between 'typical' populations of the three subspecies, and as this intergrade zone constitutes at least one-third of the range of the species, it is plain that much remains to be clarified.

One hundred and three of the 171 records shown have been obtained in the current Cape survey, 85 of these records being hitherto unrecorded localities.

Chersina angulata (Schweigger, 1812) (Figure 8)

The angulate tortoise (ploegskaarskilpad; rooipens; duineskilpad), has a curious distribution, parallel to the Cape coastline from East London (3327 BB) westwards to the Orange River Mouth (2816 CB). Thus it is found not only in coastal sandveld with a rainfall of under 100 mm per annum in Namaqualand, and in Karroid Broken Veld around Aberdeen (3224 AC) with a rainfall under 200 mm, but in sour grassveld associated with the coastal forest zone in the eastern Cape with a rainfall of between 600 and 700 mm. It appears not to occur above the 900 m contour.

South West African records are nearly all open to question, some specimens being 'buchu' pouches bought from natives, and none having been recently confirmed. Mertens (1955) recorded the species as having been found in Karibib in 1938 (2115 DD), a locality later quoted by Loveridge & Williams (1957), but Mertens (1971) stated that he had not seen any *Chersina* in the Karibib area. The 'Plateau' record has already been discussed. The Transvaal Museum has two apparently reliable records from the area in South West Africa opposite the Richtersveld.

The specimen recorded from Ndumu Game Reserve in Northern Zululand (Pooley 1965) was questioned by him at the time, and has since been found to have been a translocation (Pooley 1974 *in litt.*).

Eighty-six of the 122 records shown have been obtained in the current Cape survey, 70 of these being hitherto unrecorded localities.

Genus *Homopus* Duméril & Bibron, 1835 (Figure 9)

Homopus is, like *Chersina*, *Psammobates*, and *Kinixys*, a genus endemic to the Ethiopian Region, and four species are recognized. They are clearly divisible into two groups, which Hewitt (1937a) classed as separate genera, viz. *Homopus* (*areolatus* and *femoralis*) and *Chersobius* (*signatus* and *boulengeri*). Loveridge & Williams (1957) regarded this subdivision as unjustifiable, and assumed all four species to be allopatric, querying alleged sympatry between *areolatus* and *femoralis* at Cradock and Oudtshoorn.

The occurrence of sympatry in this genus is interesting and is important to the study of relationships between the four species.

areolatus/femoralis

The Oudtshoorn record of *H. femoralis* (from 'Welbedacht' farm: Fitzsimons 1946) was agreed by Fitzsimons to be an error (Haacke 1974 pers. comm.) although the corrected locality, between Uniondale and Willowmore, is equally questionable.

The problem in the Cradock area is that Loveridge & Williams (1957), assuming that *areolatus* cannot occur over 600 m altitude, could not reconcile the type locality of *femoralis* (Cradock) with Hewitt's (1937b) statement that he had the very closely related *areolatus* from the mountainous Cradock district. *H. areolatus* is not, however, confined to altitudes below 600 m (although over the greater part of its range it appears to be) and the 'Cradock Gap' in the Winterberg range permits it access to the 900–950 m altitude basin north of the mountain, where it is very rare. *H. femoralis* occurs on all of these mountains above and around Cradock. The two species probably do occur together in the less hilly parts north of Cradock, marginal to both species' range.

signatus/boulengeri

Another case of alleged sympatry is between the two '*Chersobius*' species (*signatus* and *boulengeri*) in South West Africa (Mertens 1955, 1971). For the reasons stated above in the section on *Psammobates*, it is difficult to accept both of these species from one locality. If either occurs, it would seem to be more likely to be *H. signatus*.

Again, both of these species are reported from the Piketberg area (3218 DC). The *boulengeri* was collected by Van Son in 1948 and is held by the Transvaal Museum. *H. signatus* has been collected several times in the current Cape Province survey from Graafwater, Clanwilliam, and Het Kruis, the latter locality being only 5 km north of the northern slopes of the Piketberg range; it might be reasonable to suggest, therefore, that the single Piketberg *boulengeri* is a translocation. However, as Van Son also collected a *H. areolatus* at Noupoort in 1948, which is quite extralimital for *areolatus* but not necessarily so for *boulengeri*, it may be that the two specimens from one collecting trip were accidentally transposed, Piketberg being within the range of *H. areolatus*. Alternatively, but less likely, the Piketberg record may be valid, as the Piketberg itself is an inselberg, separated from the foothills of the Olifantsrivierberg (known *signatus* country) by the strandveld of the Eendekuil/Het Kruis valley, and could conceivably maintain an outlying population of *Homopus boulengeri*.

femorialis/boulengeri

In this survey specimens of *H. femoralis* have been found together with *H. boulengeri* on three farms in three different parts of the mountainous area near Sutherland. This sympatry may be apparent rather than real, although the available evidence indicates that the populations do share the same habitat. Nevertheless, as *boulengeri* and *femorialis* appear to belong to different species groups, a suggestion of sympatry is not unreasonable, and Hewitt's subdivision of the genus *Homopus* is given added weight.

areolatus/boulengeri

Similarly we have found *areolatus* and *boulengeri* co-existing in similar habitats at the edges of their ranges in the eastern Cape.

In the Calvinia/Middelpos/Sutherland area (between 3119 BD, 3120 CC, and 3220 BC), a particularly interesting situation is apparent with all four *Homopus* species occurring within an 80 km radius of Middelpos. *H. signatus* occurs at Calvinia, *areolatus* at Middelpos (80 km SE of Calvinia), and *femorialis* and *boulengeri* at Sutherland (70 km SE of Middelpos).

Homopus signatus (Schoepff, 1792) (Figure 10)

This species appears to be confined to Little Namaqualand, from Kleinsee and Springbok in the north, to Graafwater and Clanwilliam in the south. The South West African records require confirmation. The rainfall within its range limits appears to be less than 250 mm per annum. One of its Afrikaans names is 'klipskilpadjie' – an apt description of the tortoise and its habitat. So far, the writers have not collected this species from areas without rocks or stones.

Seven of the 18 records shown in Figure 10 have been obtained in the current Cape survey, three of these being hitherto unrecorded localities.

Homopus boulengeri Duerden, 1906 (Figure 11)

This tortoise is also occasionally called the 'klipskilpad', although it is also called the 'rooi-skilpadjie' or 'donderweerskilpad'. It has similar habitat preferences to *H. signatus* and is very difficult to detect in its preferred habitat of ironstone ridges ('ysterkliprantjies'). Hewitt regarded it as rare and of restricted distribution, but recent findings indicate that its range is more than twice as extensive as had previously been thought, from Montagu, Prince Albert and Willowmore at the southern boundary of the Great Karroo, to Pearston in the east, Graaff-Reinet, Victoria West and Carnarvon in the north, and Sutherland in the west. Perhaps it has evaded more frequent sampling because it is extremely well camouflaged in its restricted habitat. At this stage, the possibility that it might occur in South West Africa is considered unlikely.

Thirty-three of the 43 records shown have been obtained in the current Cape survey, and of these 31 are previously unrecorded localities.

Homopus areolatus (Thunberg, 1787) (Figure 12)

The 'padlopertjie', as it is called, occurs along the southern coast of South Africa, and although there are one or two records of its occurrence in the Great Karroo, their validity is questionable. Included, however, are a Transvaal Museum record from 3221 DD and Van Son's record from Noupoort, as they may prove eventually to have been naturally occurring specimens from the limits of this species' range. In the eastern Cape, local climatic, topographical, and vegetation factors enable *areolatus* to extend inland to Cradock, and marginally through the 'Cradock Gap' into the basin north of the mountains known as the Cape Eastern Midlands. It is not yet known whether mountain ranges present an insurmountable physical barrier to the extension of range of *H. areolatus*, or whether they form an ecological barrier in that they effectively prevent rain from falling on the karroo areas further inland. *Homopus areolatus* is not apparently found in areas with less than 250 mm rainfall per annum. Although it is not normally found at altitudes above 900 m, there is a population in the Roggeveldberge around Middelpos (3120 CC) at an altitude of 1 300 m. This area has a rainfall exceeding 300 mm, considerably higher than in the surrounding karroo, from which *H. areolatus* is absent.

Fifty of the 70 records shown in Figure 12 have been obtained in the current Cape survey, and of these, 43 are previously unrecorded localities.

Homopus femoralis Boulenger, 1888 (Figure 13)

This, the largest of the four *Homopus* species, occurs at altitudes of over 900 m in the eastern Cape, the south-west Orange Free State, and perhaps the extreme south-west of the Transvaal. It almost certainly occurs (at over 1 800 m) in the mountains of south-west Lesotho, having been recorded from the Ben Macdhui area near Barkly East only 12 km from the Lesotho border (3027 DB). The presence of a hitherto unrecorded outlying population of this species was revealed in the Sutherland District in the western karroo mountains known as the Komsberge

in 1974. The records come from four separate quarter-degree squares, and there is no question as to their validity. The Komsberge, of course, attract a higher rainfall than the surrounding karroo, over 250 mm per annum, a relatively high rainfall being characteristic of the districts occupied by this species. It is not yet known whether linking populations exist along the Nuwveldberge and Onder-Sneeuberge between Sutherland and Graaff-Reinet (3224 BA).

Forty-eight out of the 63 records shown in Figure 13 have been obtained in the current Cape survey, and of these, 45 are previously unrecorded localities.

Kinixys belliana Gray, 1831 (Figure 14)

The hingeback tortoise (skarnierskilpad) in southern Africa occurs in Botswana, Caprivi, Transvaal, Natal, Swaziland, Rhodesia, Moçambique and possibly the extreme north-east Cape. It is a variable species, and although several specific and subspecific names have been applied to different populations in southern Africa (Hewitt 1931; Power 1927), Loveridge & Williams (1957) assign all to the nominate subspecies *Kinixys belliana belliana*.

Only one (2329 BB) of the 87 records shown was obtained in the course of the current Cape survey and one other was confirmed. The majority of the records are from specimens held by the Umtali Museum and the Transvaal Museum.

DISCUSSION

In view of the oft-repeated allegations of a decline in the numbers of tortoises in South Africa—an assessment of their present status in southern Africa might have some value. Do the distribution data suggest that there has been a recent range contraction or fragmentation in certain species? It would seem that if there is any threat to tortoises, it is likely to be in the more agriculturally developed, or environmentally abused, parts of the region in question, namely the four provinces of South Africa. In particular, the Cape Province, where endemism is concentrated, is likely to show signs of decline in tortoise populations.

In the Cape, the conservation of this rich assemblage of species is the responsibility of the provincial Department of Nature and Environmental Conservation. Land tortoises of the subfamily Testudininae are subject to commercial exploitation, particularly for the pet trade, and because of this, the Cape Provincial Administration has protected all species since 1950. The latest ordinance (1974) classes the endemic geometric tortoise, *Psammodon geometricus*, as an Endangered Wild Animal, and all other tortoises (together with the water terrapin *Pelomedusa subrufa*) as Protected Wild Animals. Hewitt (1933) regarded the geometric tortoise as 'almost extinct', and in 1938 he prepared a memorandum on behalf of the South African Museums Association unsuccessfully advocating the strict legal protection of this species together with *Geochelone pardalis* and *Homopus boulengeri*. Rau of the South African Museum successfully followed up reports that the geometric tortoise still survived (Eglis 1965), and, as a result, a reserve has since been created for its conservation (Rau 1969, 1971). It has also been shown to

survive in one or two areas outside the reserve.

Although Hewitt and others believed that *Homopus boulengeri* was endangered, the current survey suggests that this opinion is unjustified. It is simply difficult to find. The other three species of *Homopus* may still be found with little difficulty even around urban areas, as can *Chersina angulata*, and may thus be regarded as being satisfactorily numerous. *Chersina* is still regularly eaten by both white and coloured sections of the community but not by the Xhosa people of the eastern Cape. From discussions with over 200 farmers in different parts of the Cape, no tortoises other than *Psammobates geometricus* and *Geochelone pardalis* seem to be in any danger of total extinction but this does not exclude the possibility of local extinction. There is no doubt that general opinion holds that all species have been reduced in numbers in recent years. Veld fires, insecticides, drought, overgrazing, or an increase in mammalian predators have been suggested as possible causes. A combination of all these factors is perhaps more likely.

No natural population of *Geochelone pardalis* now exists in the western Cape coastal area, and there are indications that in certain eastern districts the species no longer occurs, for example at Rossouw (3127 AB), Dordrecht (3127 AC) and the Transkei. There are unfortunately no records of past abundance in these districts to provide a yardstick for the extent of the species' decline, nor, indeed, can one be sure that *Geochelone* was ever present. Loveridge & Williams (1957) expressed concern for the Cape population of *G. pardalis pardalis*, but as discussed earlier, the validity of this subspecies is questionable.

ACKNOWLEDGEMENTS

We would like to acknowledge the helpful criticism of Mr C. Jacot-Guillarmod, Director of the Albany Museum, who put the large collection of tortoises held by that institution at our disposal. Also Dr D. G. Broadley (Umtali Museum) and Mr W. D. Haacke (Transvaal Museum), both of whom were kind enough to send us photostats of the catalogue lists of the numerous tortoises held by their respective institutions. R. Rau provided us with details of the South African Museum collection and of his involvement with the geometric tortoise survey. Dr Nick Arnold (British Museum), N. Schaefer (Port Elizabeth Museum), N. Tietz (McGregor Museum, Kimberley), Dr B. R. Stuckenberg (Natal Museum), P. Swanepoel (Kaffrarian Museum), S. de Waal (Bloemfontein Museum), Dr R. G. Zweifel (American Museum of Natural History), Dr R. I. Crombie (The Smithsonian Institution), Dr E. E. Williams (Museum of Comparative Zoology, Harvard), are all thanked for sending details of the tortoises held by their museums. We are indebted to D. Bands and J. Verdoucq of the Department of Forestry, P. Skelton of the Albany Museum, J. Stegmann of the Department of Agricultural Technical Services, M. F. Nieuwoudt of the Hoërskool, Touwsrivier, P. J. Steenkamp of De Beers Consolidated Mines, and to many of our colleagues of the Department of Nature and Environmental Conservation, in particular H. Visser and R. Kannemeyer, for specimens. Approximately 150 farmers and friends in the Cape Province have responded generously to our appeal for tortoises. Mrs D. J. van Schoor and Mrs J. C. Greig typed numerous letters and drafts of this paper, and Mr Benjamin Mitani is thanked for laboratory assistance. Dr N. Fairall, Assistant Director, the Depart-

ment of Nature and Environmental Conservation, permitted the survey to be carried out, and provided assistance and suggestions.

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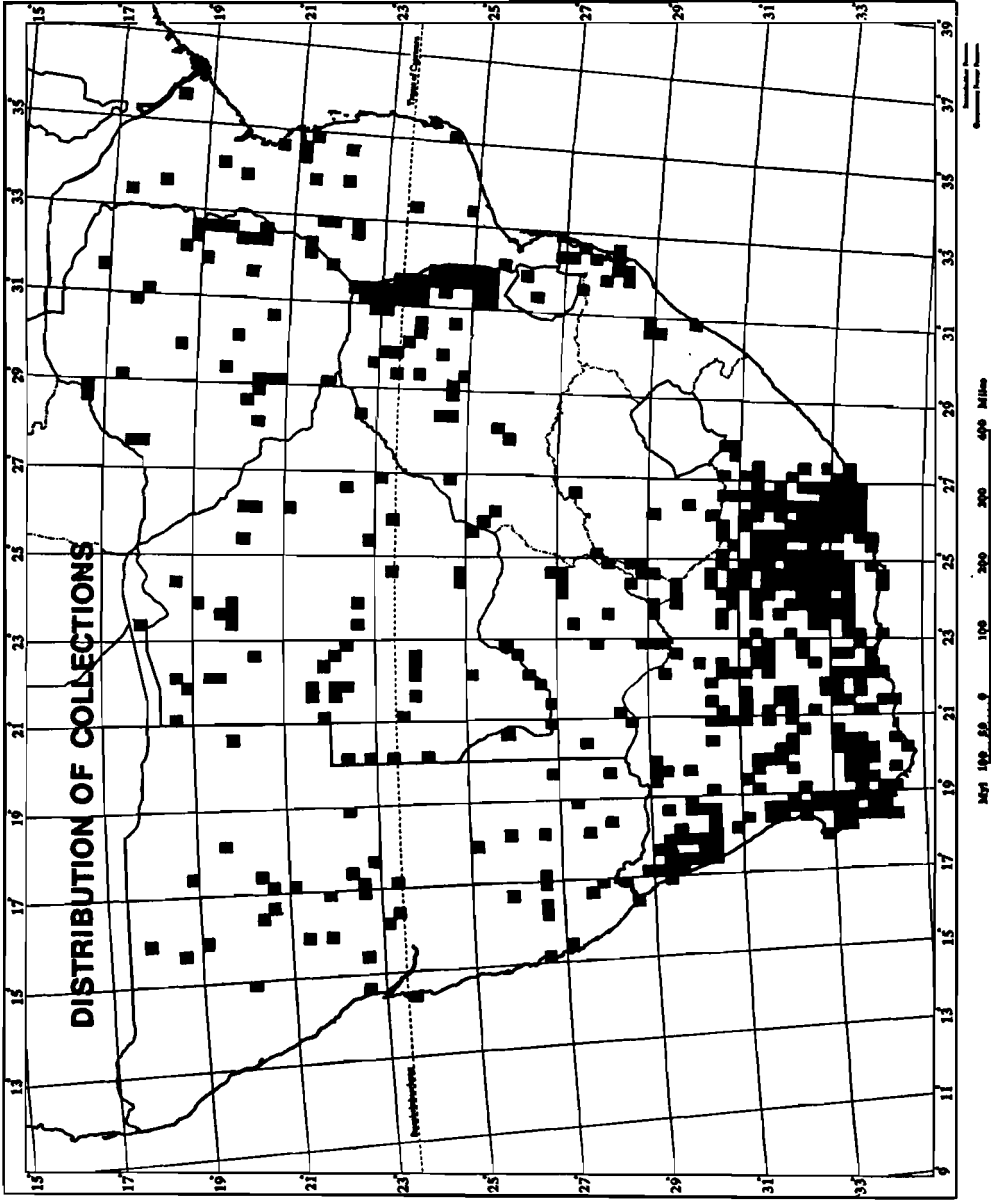


FIGURE 1

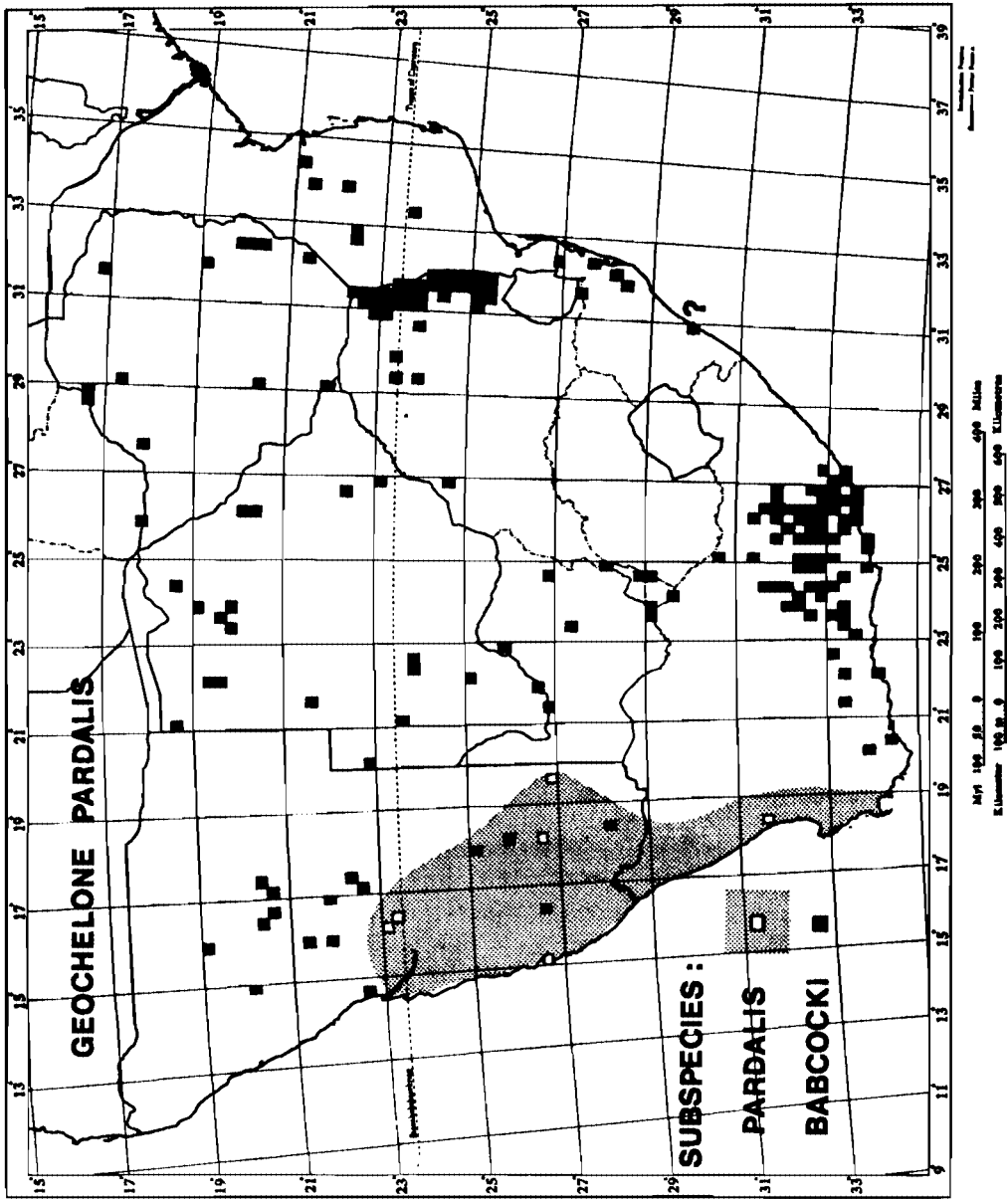


FIGURE 2

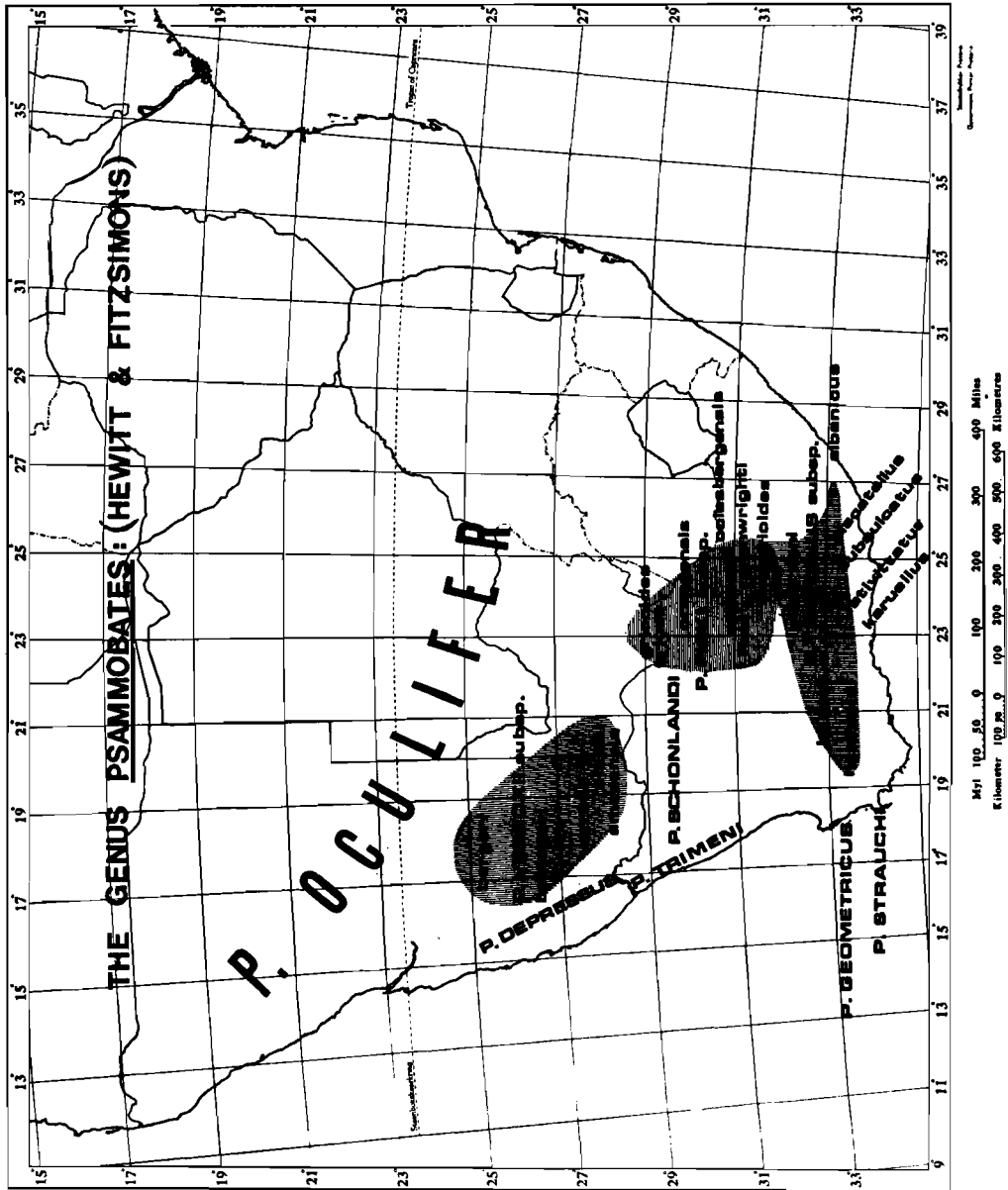


FIGURE 3

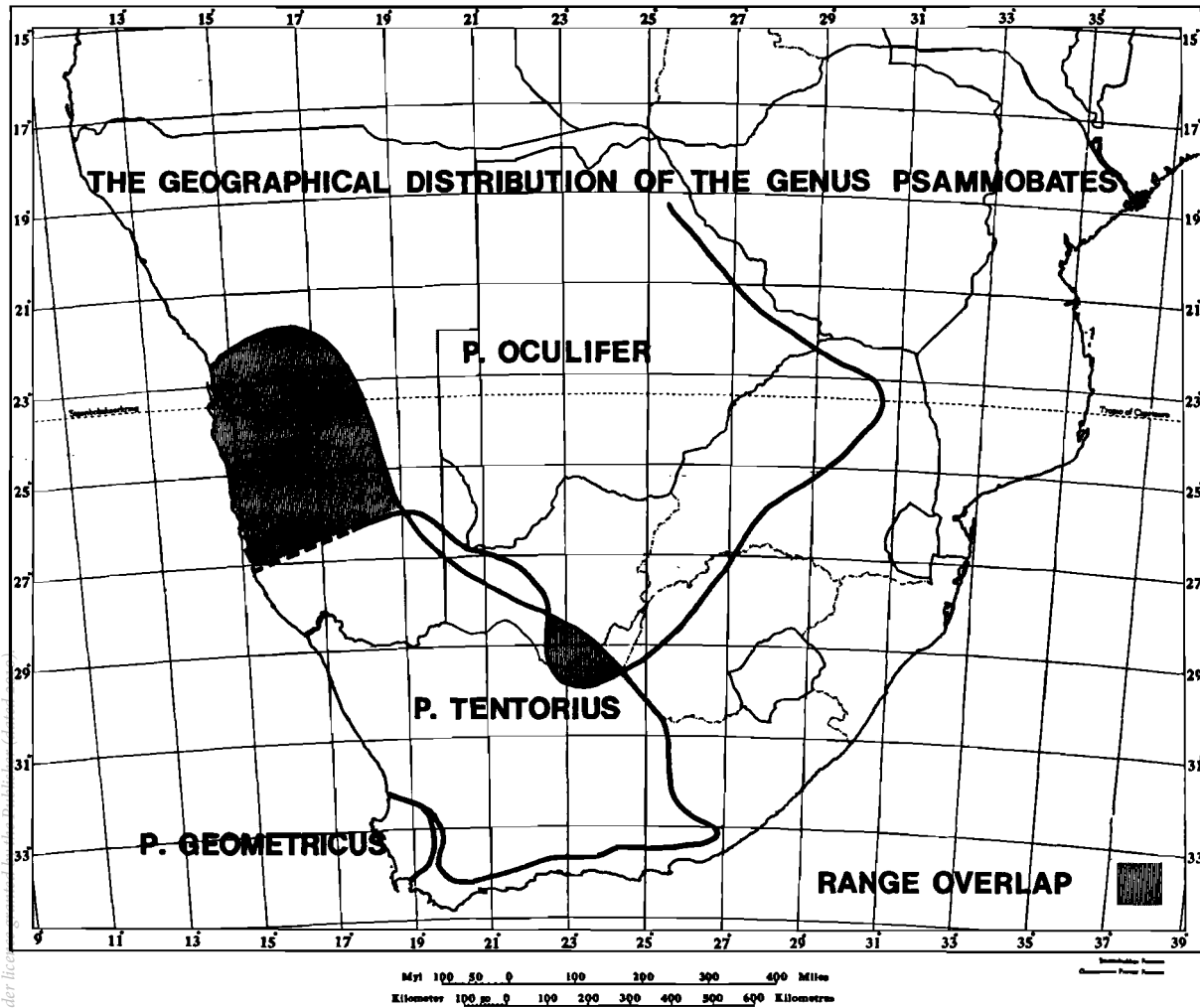


FIGURE 4

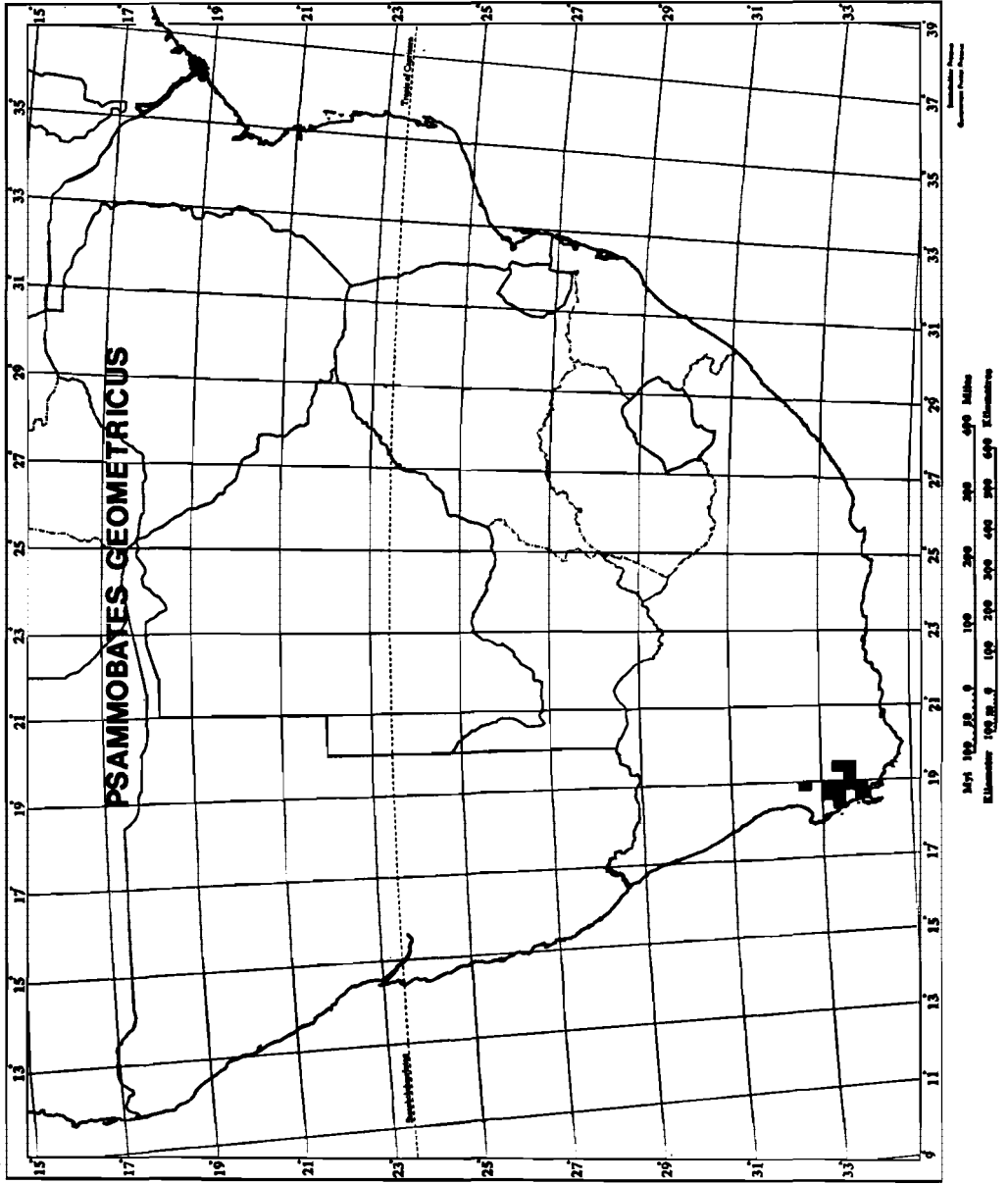


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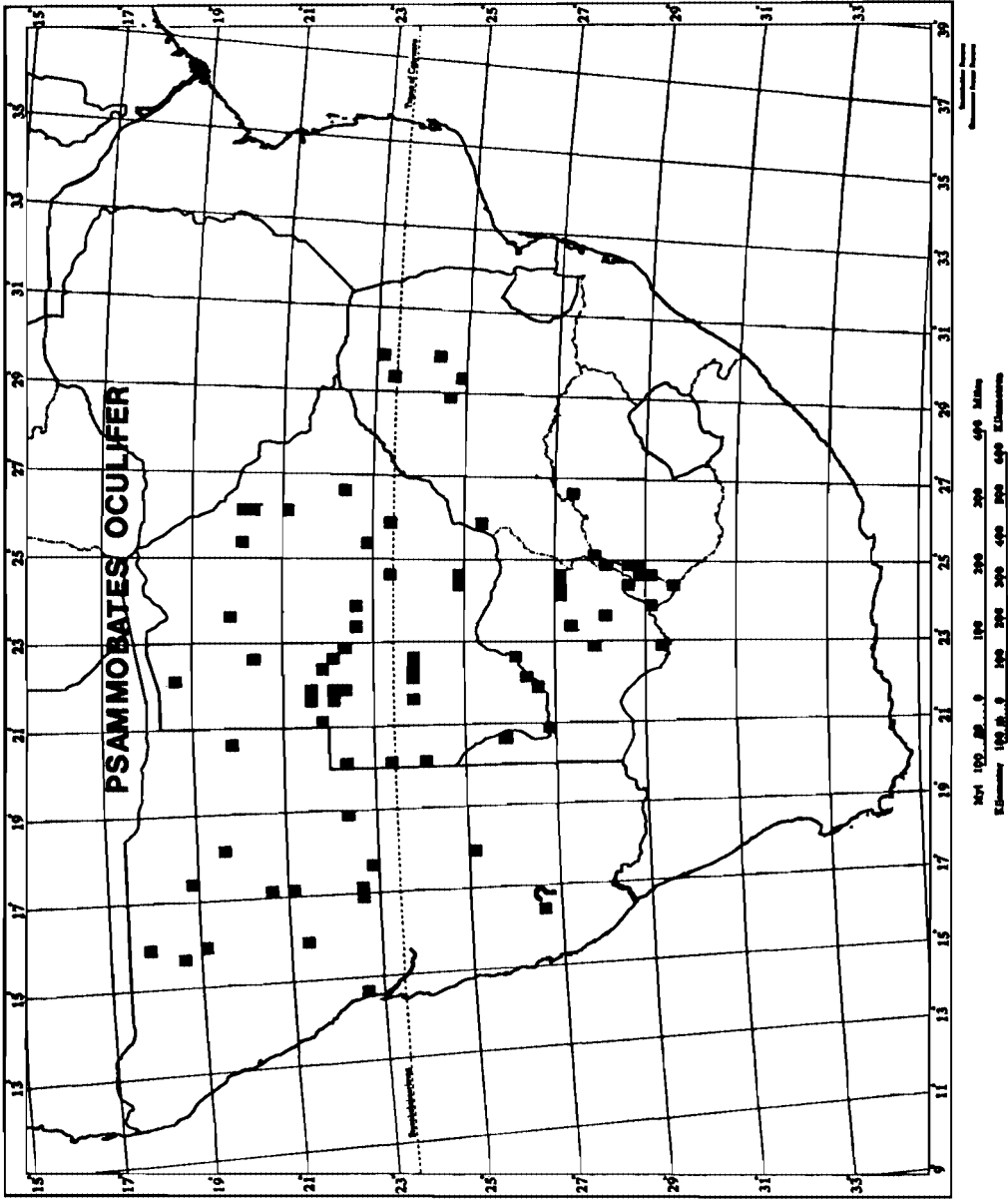


FIGURE 6

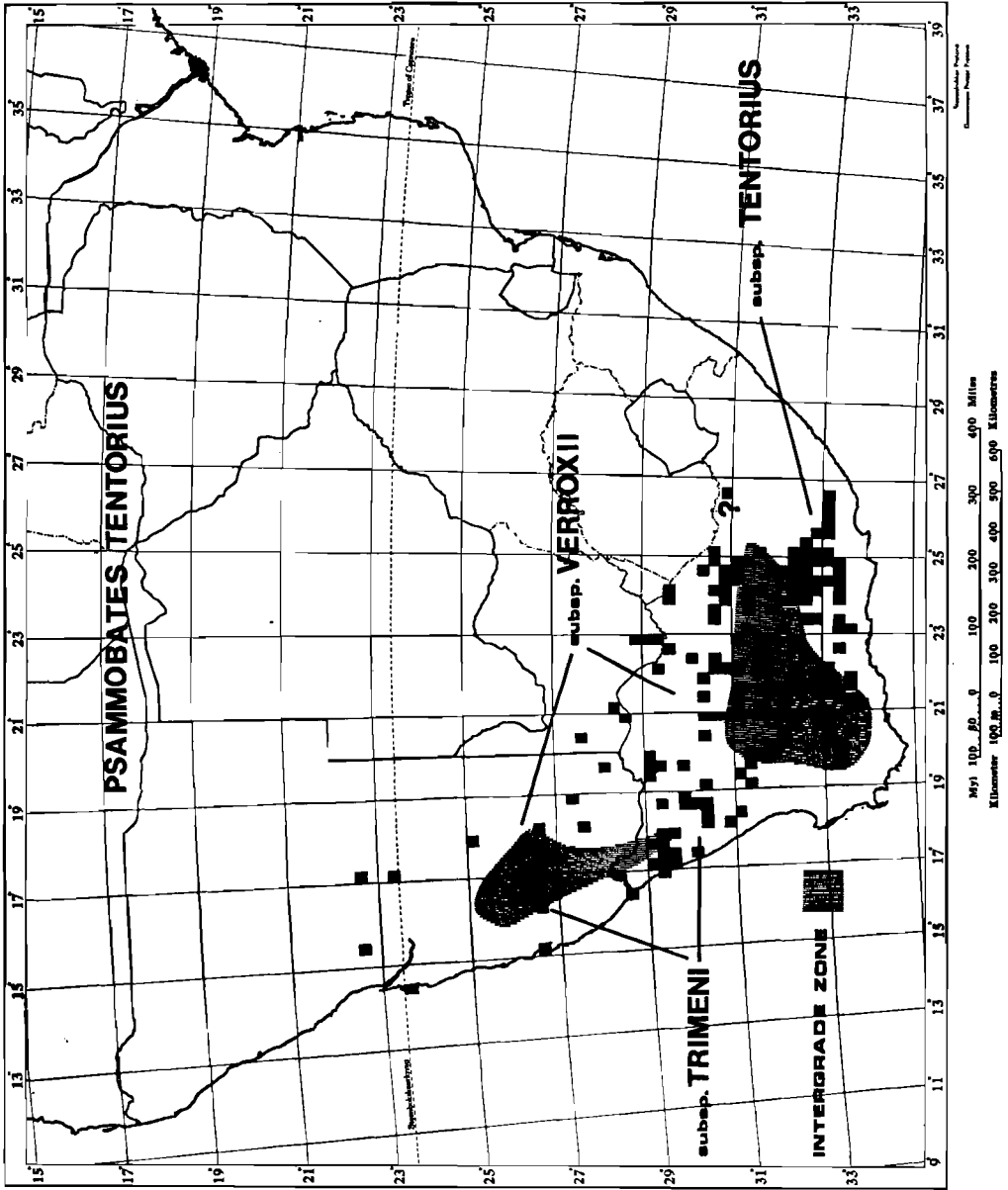


FIGURE 7

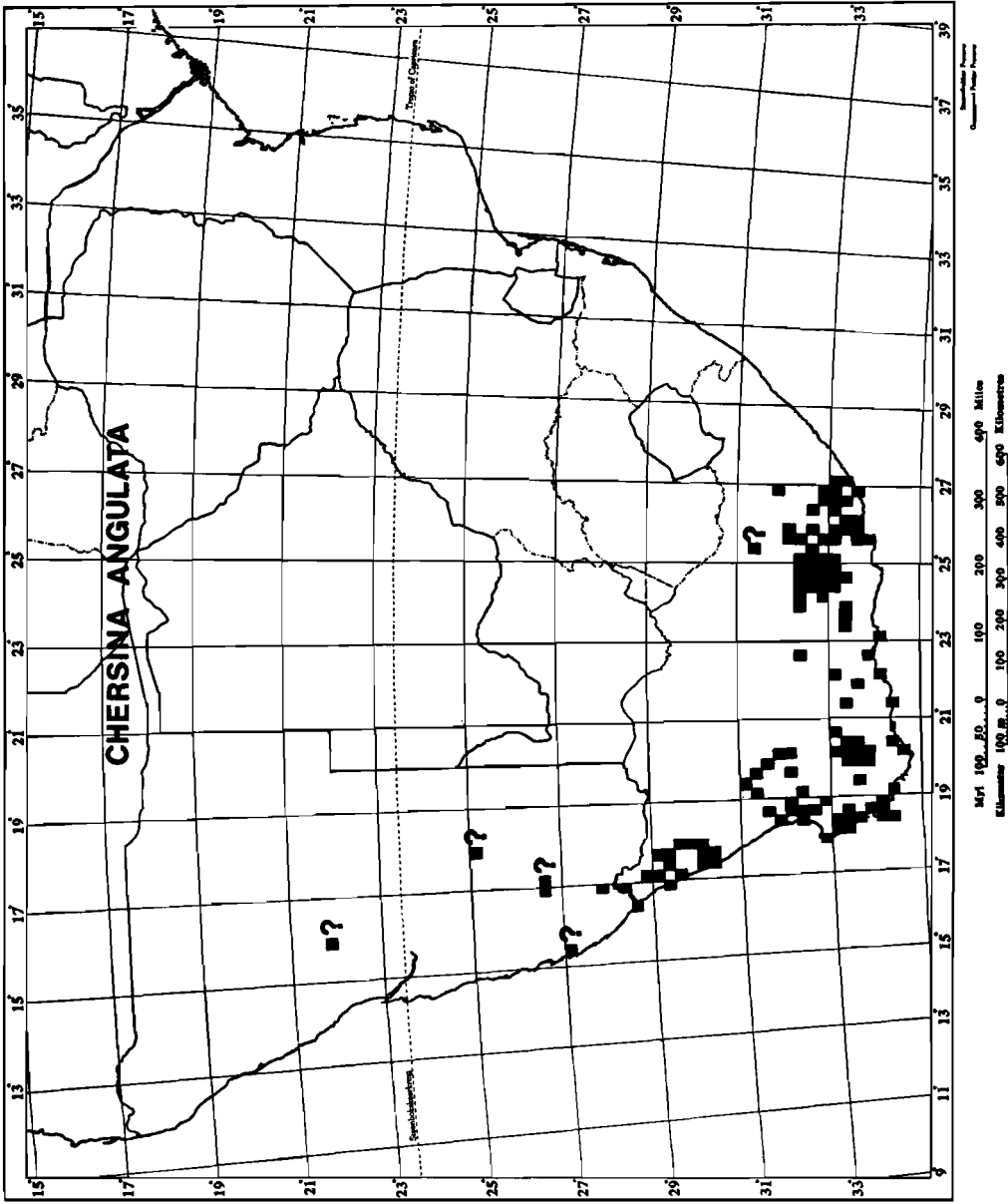


FIGURE 8

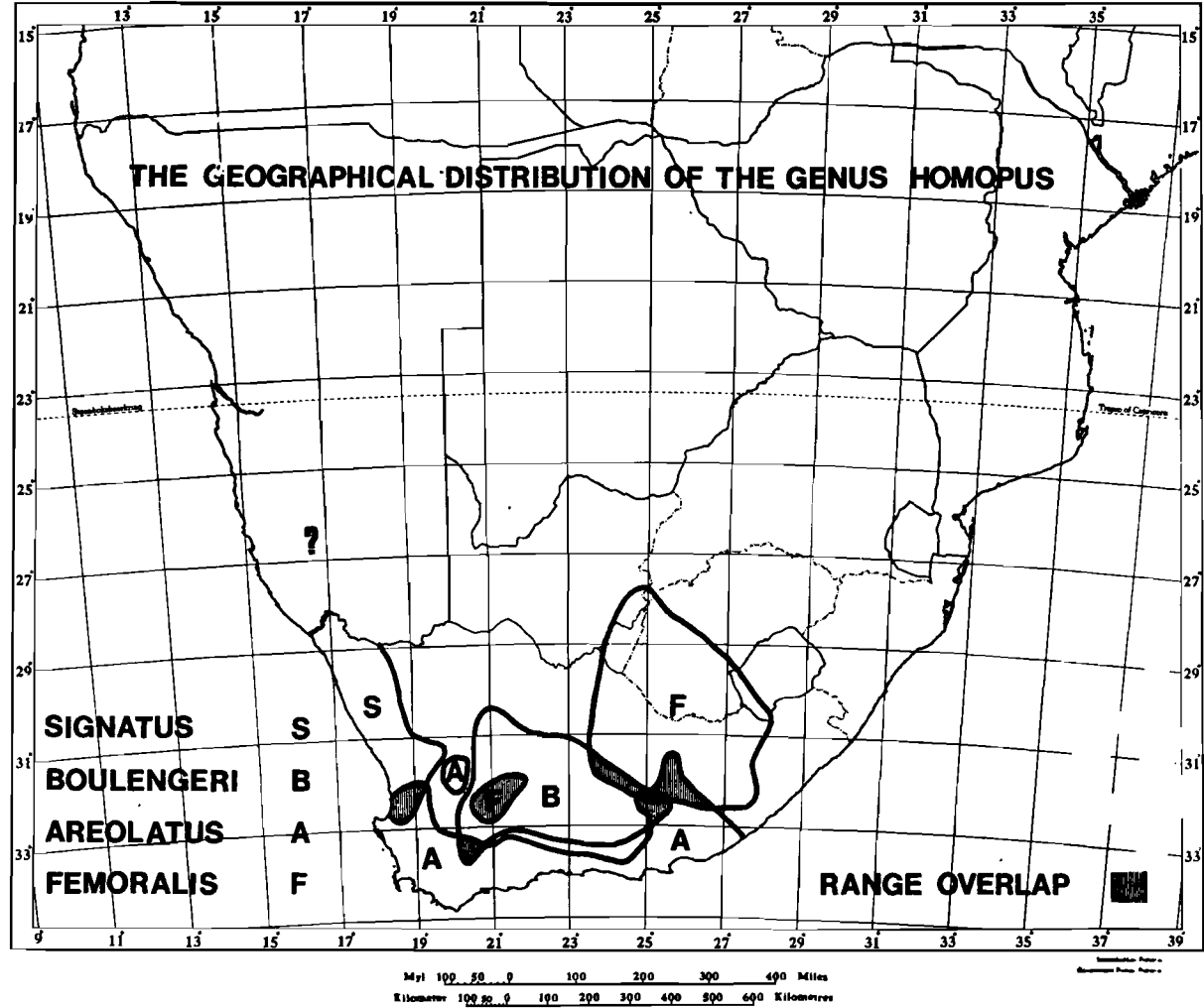


FIGURE 9

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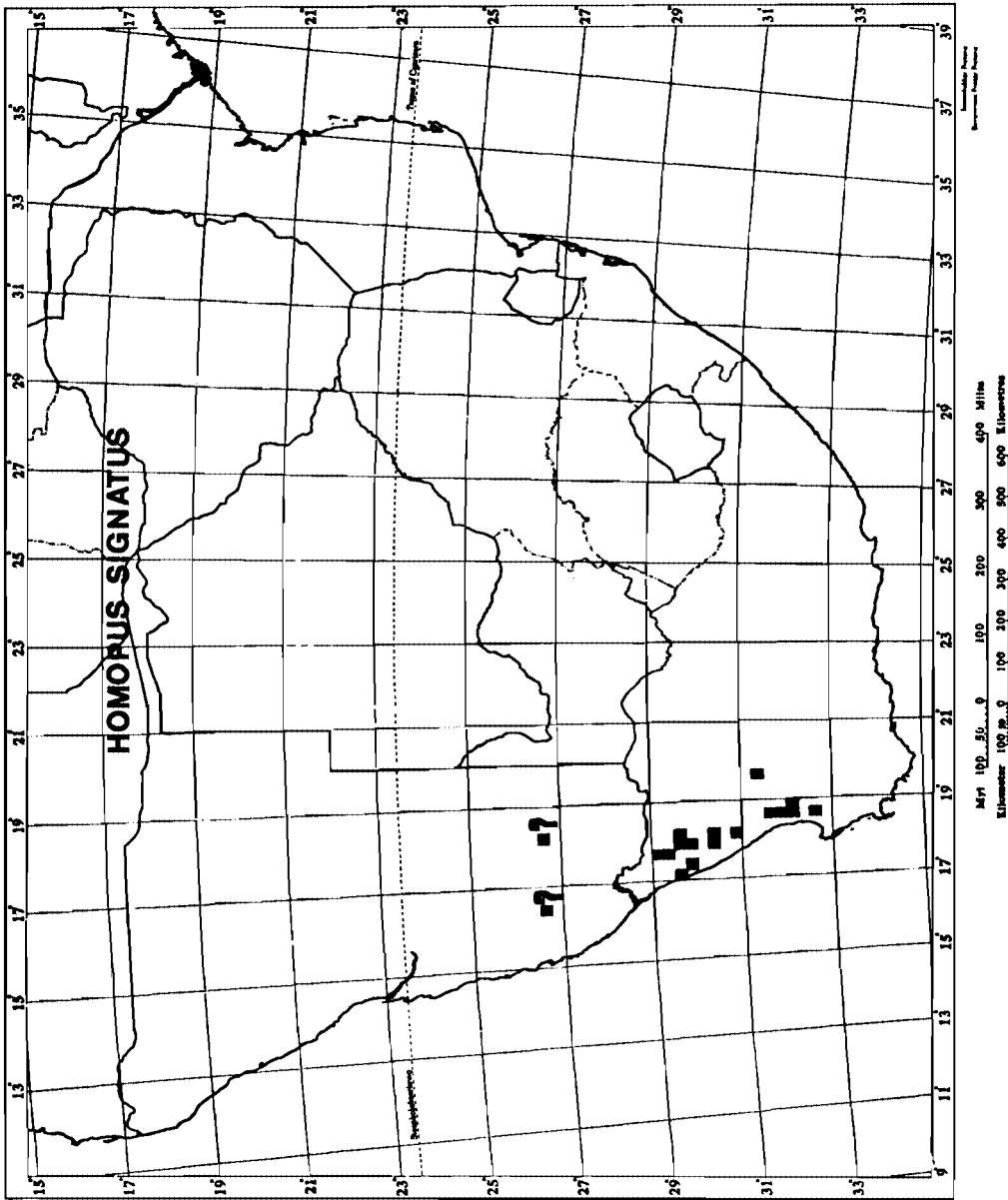


FIGURE 10

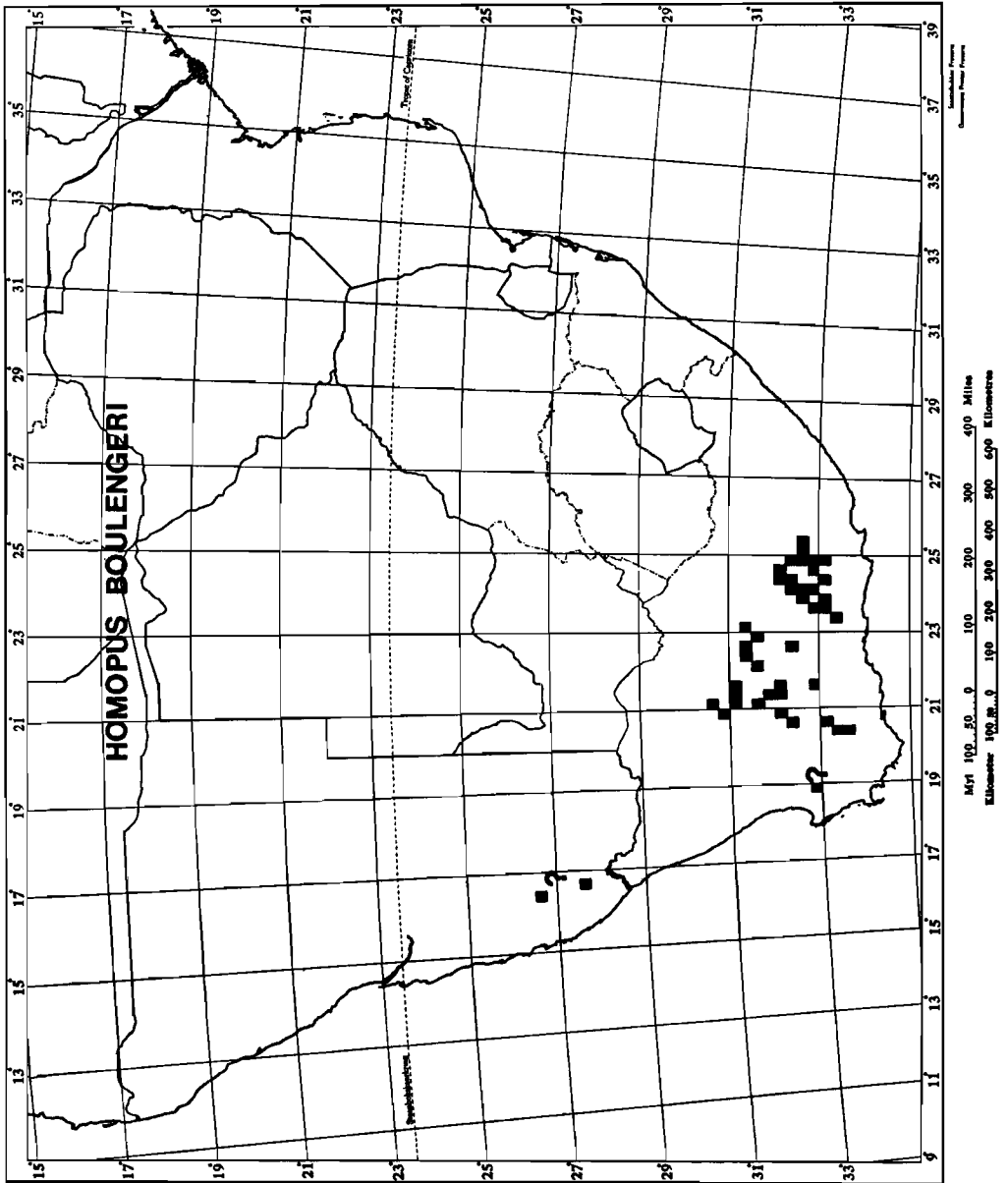


FIGURE 11.

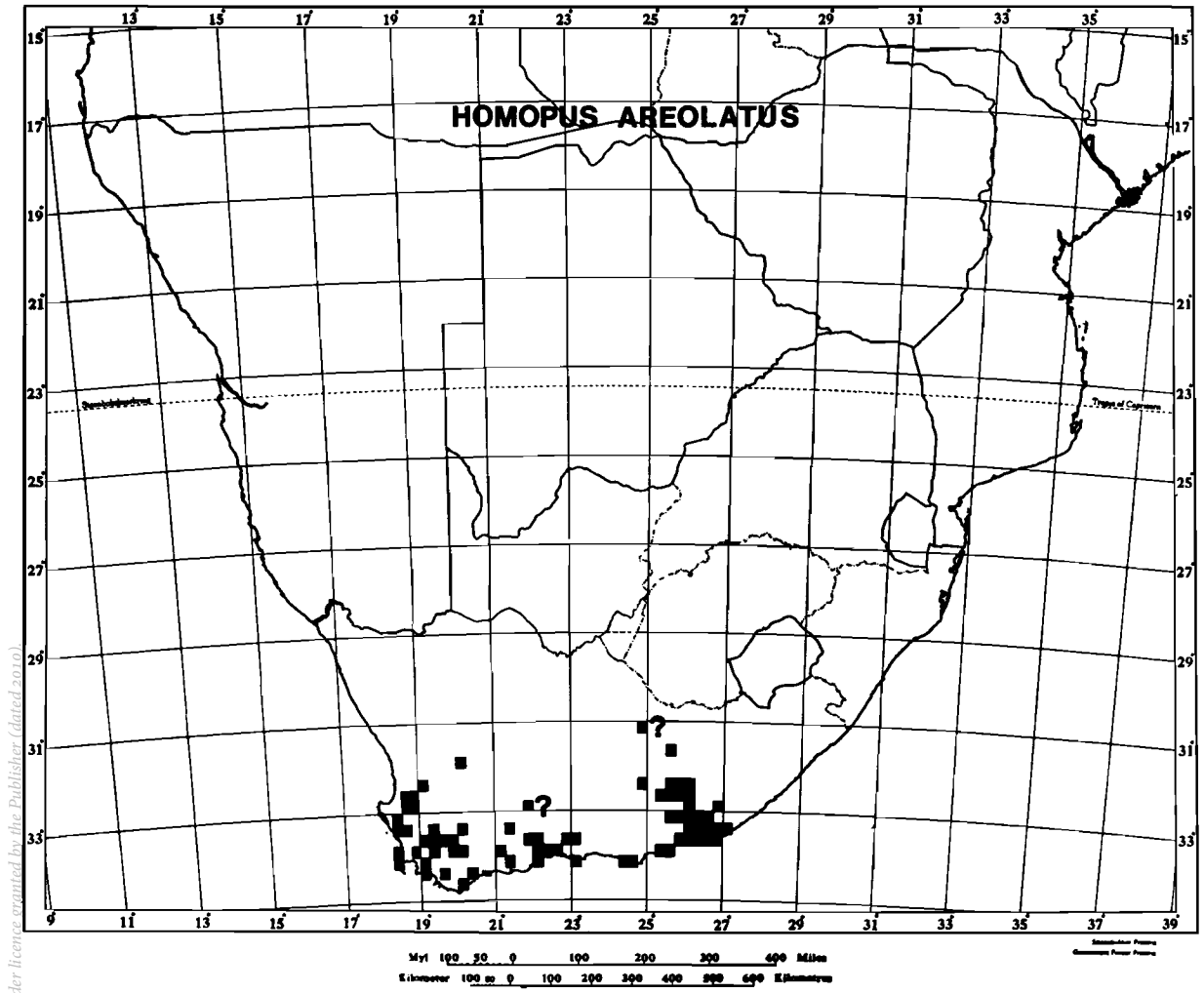


FIGURE 12

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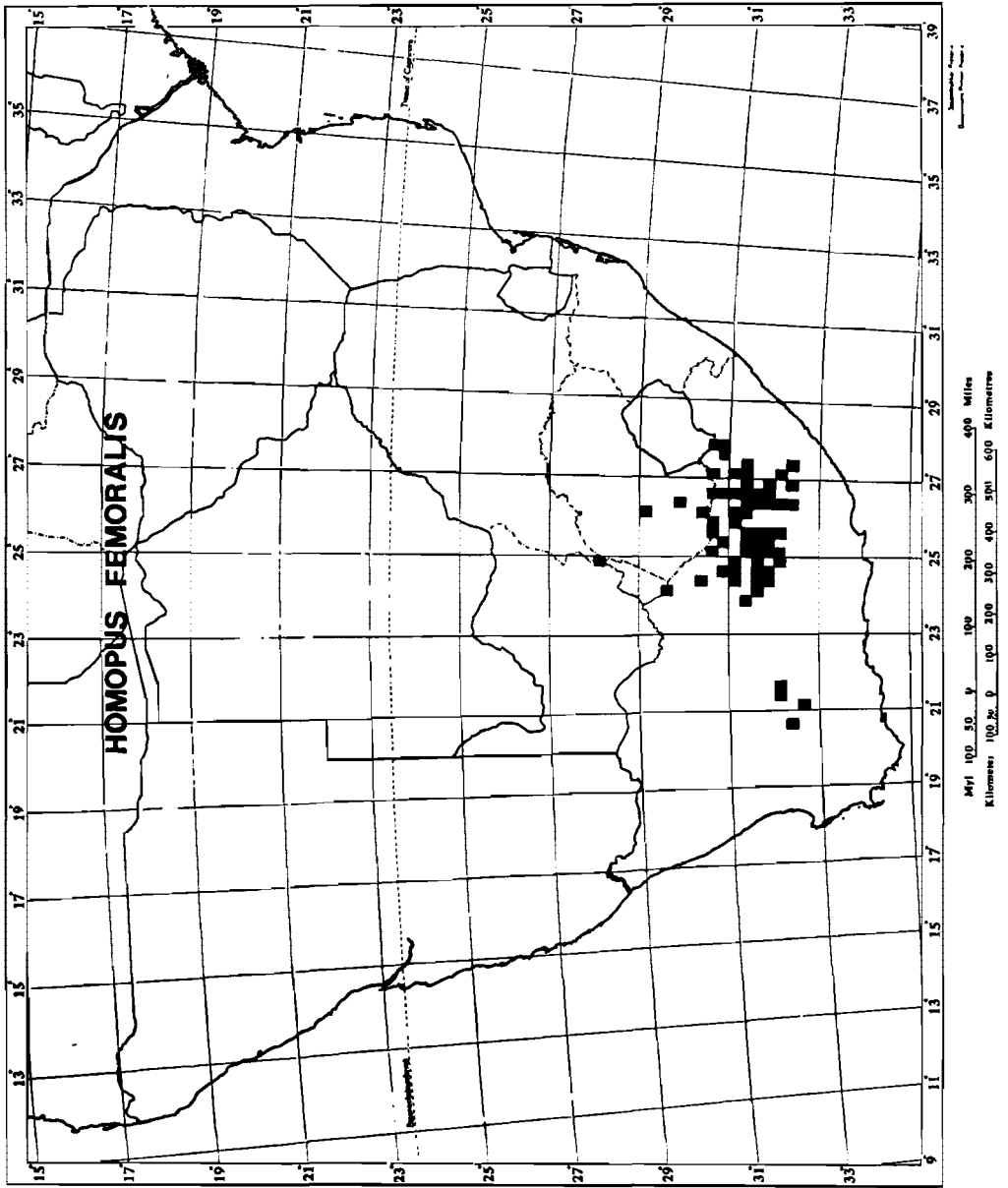


FIGURE 13

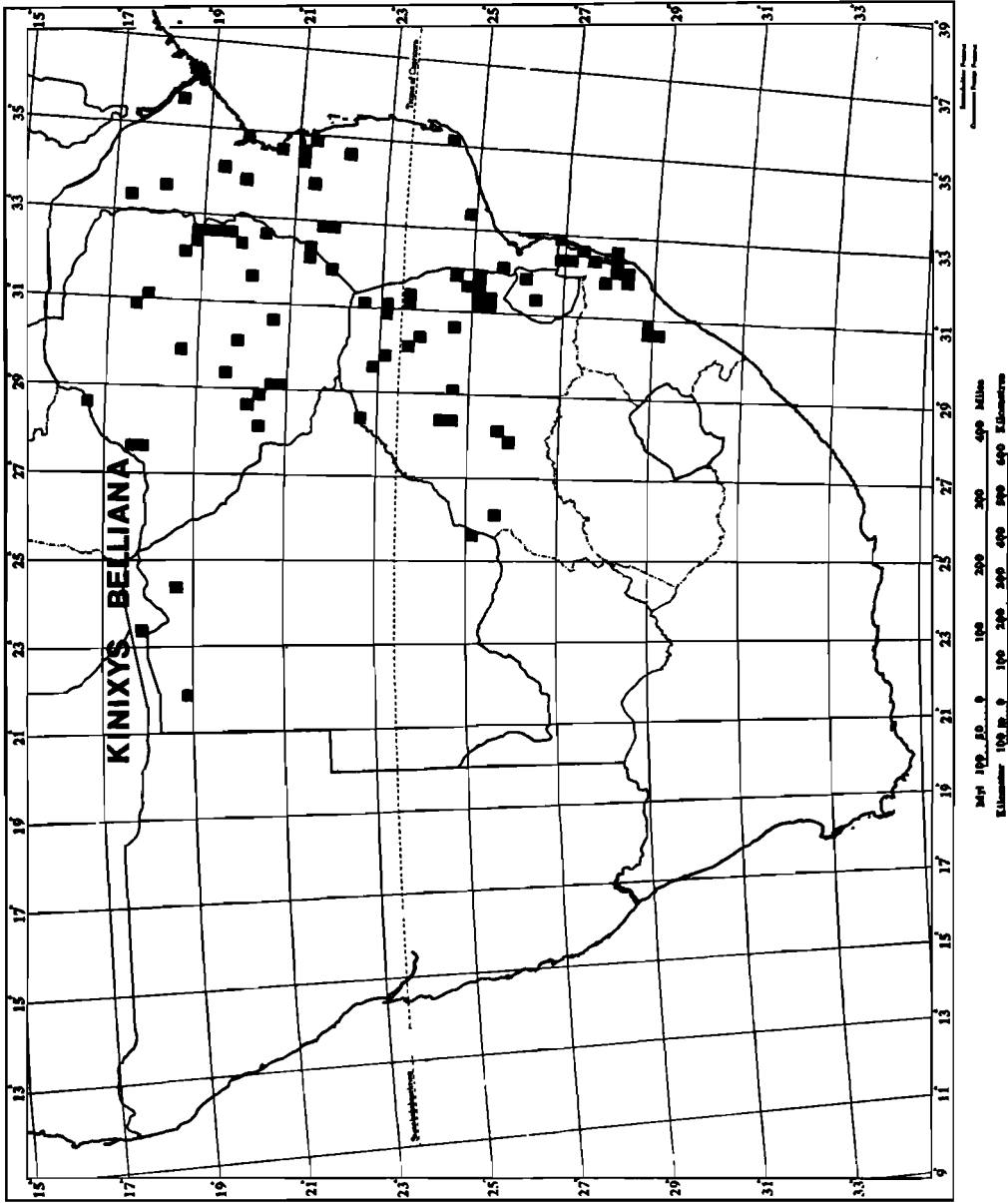


FIGURE 14

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