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SHORT NOTES

Intersexual dominance and differential mortality of Gemsbok *Oryx gazella* at Namib Desert waterholes

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ABSTRACT

Observations of gemsbok, *Oryx gazella*, were made in the Kuiseb River canyon of the Namib Desert. Adults individually contest one another for the right to drink from shallow water wells they dig in the sands of the dry river course. These waterholes are initiated at the dry bottom of open pools after seasonal flooding has passed and the open water dries up. Waterholes are not initiated *de novo* in riverbed sands. The number of open waterholes declines continuously throughout the dry season. A temporary linear hierarchy is established at each waterhole, allowing adult males to exclude adult females. A combination of flood and water shortage resulted in heavy mortality with a loss of all calves and a disproportionate mortality to adult females during one year of observations. No long term social organization could be detected, perhaps because of the extreme stress to the population at the time of these observations.

1 INTRODUCTION

Oryx are arid region mammals able to live indefinitely without free water (Taylor, 1969). We were surprised to observe aggressive struggles among adult gemsbok, *Oryx gazella*, for access to limited waterholes dug in the dry riverbed sands of the Kuiseb River, South West Africa. Typically, gemsbok obtain water in waterless regions from their food plants. There they select items with a high water content and feed upon grasses in the morning which by hygroscopic action have absorbed water during the dewy night and dawn (Taylor, 1969). Apparently the foods available in and surrounding the Kuiseb River canyon (Plate 1) do not offer adequate water supplies and reliance on free water is such that the lives of herd members depend upon successful competition for access to limited water supplies.

Here we report those competitive encounters and their effects on the condition and survival of different age and sex classes of gemsbok. Interspecific interactions with chacma baboons, *Papio ursinus*, are also discussed.

2 MATERIALS AND METHODS

Censuses were made whenever we drove through the canyon. The counts for 5 segments of the river are summarized in Table 1. Our census tract began at the abandoned Hottentot village of Homeb, 21,0 km upstream from Gobabeb. The first column of Table 1 records counts from there to the massive rocky valley wall on the north side of the river, 27,8 km upstream from Gobabeb. The next section upstream ran to a rock outcrop that juts into the northern edge of the riverbed, 34,0 km upstream from Gobabeb. The third census section continued on to 45,8 km where the canyon narrows. The next section terminated 59,3 km upstream, at a persistent pool, K, where the canyon narrows above Hudaob. Censuses ended 71,0 km upstream from Gobabeb.

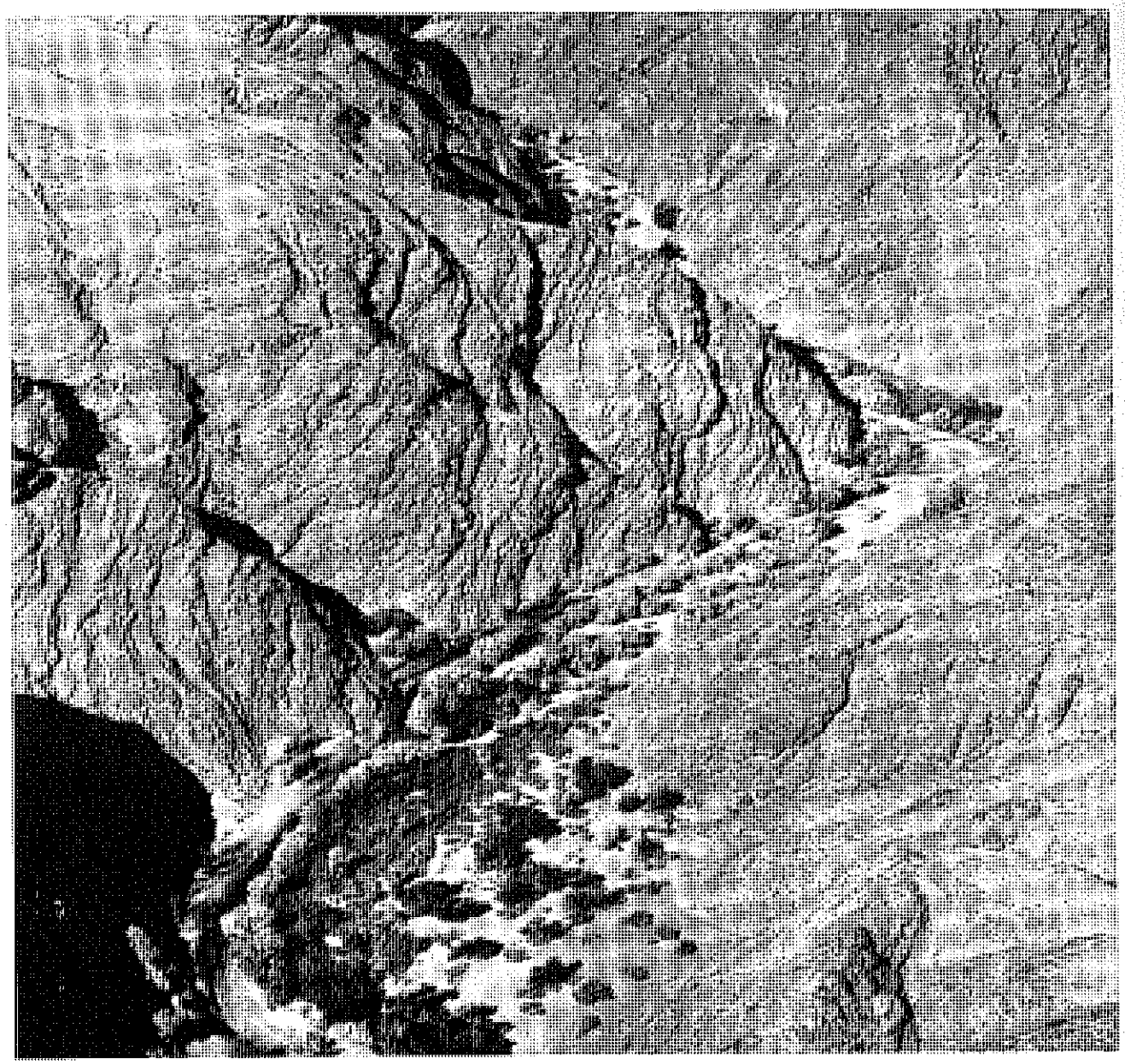

Plate 1. The Kuiseb River canyon in the vicinity of the C and D series waterholes (see text), about 45 km upriver from Homeb.

Our censuses (Table 1) are incomplete and offer only a general picture of populations in the canyon. We were unable to get a full count of the herd at any time because numerous individuals are bypassed by an observer on foot or traveling in a vehicle in the broader sections of the canyon. All figures in Table 1 are low estimates, but upriver from km 45,8 the values are more accurate since there the narrow canyon facilitates more complete censuses. Movement through the canyon without disturbing the gemsbok herd was difficult. Early in the study our movement on foot or by vehicle induced flight up the sandy southern side of the canyon. Later gemsbok seldom left the canyon and most movement was linear. By doubling back any herd member could easily avoid an observer on foot. However, in the narrower part of the canyon an observer may push the herd considerable distances. When we were in a vehicle we quickly passed the herd or, if this was not possible, we dropped back and waited until the group reached a point where avoidance was possible. After several weeks of continued exposure to our presence, the herd and certain individuals in particular became considerably more tolerant of our presence.

Most of the behavioural observations reported here were made from hides on the canyon walls. We found that hides at waterholes were satisfactory for observations of baboons (Hamilton *et al.*, 1975), but they proved unsatisfactory for gemsbok observations. Gemsbok, presumably responding to our scent, frequently fled and would not return. We then shifted to sites higher on the canyon wall, 50 to 120 m from the waterholes. At such sites we observed without apparent disturbance to the gemsbok. At night we sat in the open on the canyon walls at these sites without need for cover. Observations were made with binoculars and a tripod-mounted telescope. During

Table 1. Gemsbok counts in the Kuiseb River canyon. Five separate but contiguous segments of the canyon were censused. The census transect began at Homeb (Kilometre 21,0) and ran upstream 50 km. A dash indicates no census was taken in that segment of the riverbed. Totals are for the 21,0 to 45,8 km stretch of the river only. For identification of the landmarks relative to distance, see text.

	Distance upstream from Gobabeb (km)					
	21,0 to 27,8	27,8 to 34,0	34,0 to 45,8	45,8 to 59,3	59,3 to 71,0	Total
16 October 1972	10	0	—	—	—	10
17 October	0	4	—	—	—	4
20 October	9	7	22	—	—	38
22 October	6	5	—	—	—	11
25 October	19	7	12	—	—	38
27 October	13	1	8	—	—	22
7 December	24	58	30	—	—	112
15 December	24	62	34	—	—	120
25 December	—	—	71	99	—	71
28 December	—	—	—	67	51	—
1 January 1973	83	45	27	—	—	155
4 January	122	63	31	—	—	216
6 January	—	83	32	74	—	115
9 January	—	—	—	71	25	—
11 January	—	146	20	—	—	166
13 January	55	28	27	—	—	110
14 January	62	44	37	—	—	143
15 January	—	—	—	116	—	—
16 January	—	—	—	93	—	—
18 January	—	—	—	56	—	—
15 February	36	35	35	—	—	106
16 February	39	31	41	—	—	111
17 February	67	49	12	—	—	128
18 February	66	45	24	—	—	135
28 February	—	—	—	26	—	—
22 March	259	30	15	11	2	304
19 May	3	0	2	1	1	5
17 August	13	—	—	—	—	13
23 August	15	—	—	—	—	15
31 August	14	3	3	0	0	20
9 September	9	7	6	1	0	22
10 September	22	7	11	1	—	40

moonlit nights we could observe continuously. Field notes were recorded on tape for later transcription. We used a star scope during late December, 1972, and confirmed that activities were unaltered during the dark of the moon.

Some gemsbok could be recognized by distinctive pelage marks, scars, wounds, sex, horn and other characteristics. These criteria allowed us to individually identify any gemsbok present at a waterhole, but we were generally unsuccessful in determining their identity after they departed. However, some individuals with distinctive scars or broken horns were recognizable over a period of months.

When the condition of the herd declined in midsummer we devised a system to quantify the apparent relative physical condition of individuals:

1,0. Fully muscled or fat, no ribs show
2,0. Ribs show slightly, rump well rounded
3,0. Ribs well defined, rump well rounded
4,0. Ribs protrude, rump flat
5,0. Skeletal details well defined, rump concave

These conditions are demonstrated in the photographs accompanying this paper. Our intention was to define continuous grades in condition. Estimates were made to the nearest half-grade. In a test of comparability the three observers averaged less than 0,2 grades of difference for 50 individuals.

3 RESULTS

3.1 Gemsbok use of the Kuiseb River canyon

In the area of our investigation, the Kuiseb River canyon upriver from the Namib Desert Research Station at Gobabeb (23° 34′ S, 15° 03′ E), the pattern of movement of gemsbok populations is poorly known. Figure 1 schematically illustrates our limited knowledge of gemsbok movements relative to the linear riverine habitat of the canyon. Herds are in part nomadic, following the localized rainfall of the desert edge to areas of new grass. Gemsbok intrude deep into the massive sea of red sand dunes south of the Kuiseb River. There they graze on perennial grasses such as *Stipagrostis namaquensis* and other *Stipagrostis* species. The sometimes perennial *Asthenatherum glaucum* is a favoured food there. Movements may be localized (Figure 1, A) in the dunes under such conditions. For example, a herd of over 100 individuals worked fresh vegetation at Natab in the dunes, a few km upriver and into the dunes from Gobabeb during November and December of 1975. The extent to which such populations make lateral movements within the dunes is not known, but some shifting takes place (Figure 1, B).

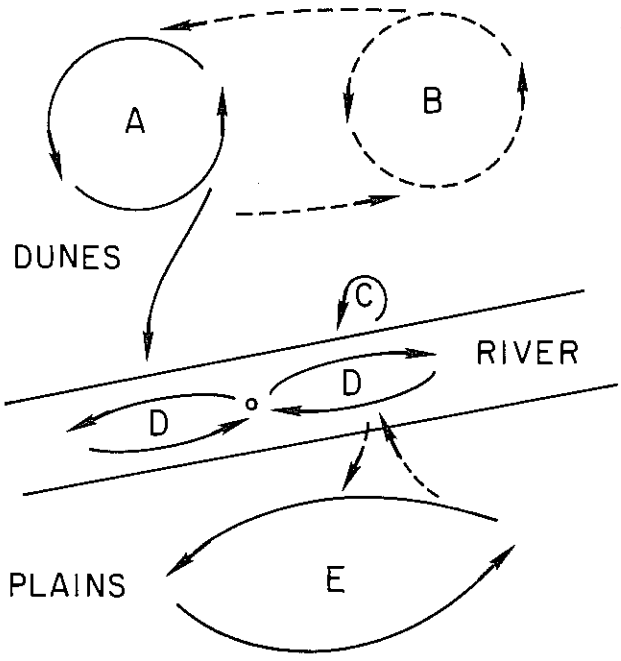

Figure 1. General patterns of gemsbok movement in the Namib Desert Park.

In 1972 less than 15 mm of rain fell anywhere in the dunes and a general movement of gemsbok from the dunes to the river began in September and continued for two months. At first movements were sporadic, involving short movements into and out of the canyon (Figure 1, C). From October

through December, 1972, the principal foods eaten by gemsbok were fallen *Acacia albida* pods in the canyon and *Stipagrostis namaquensis* vegetation in the dunes. Few animals moved along the riverbed or sought free water. In November, as ambient temperatures increased and these dune grasses became further depleted, the activity of the herd shifted exclusively to the canyon. There populations moved linearly between water sources and feeding areas within the narrow canyon (Figure 1, D).

Gemsbok from plains populations north of the river entered the canyon relatively infrequently (Figure 1, E). The plains populations utilized the artificial water source at Zebra Pan during the period of October 1972 through March 1973.

Populations in the canyon itself increased from mid-October through early January, then decreased in late January and remained low until mid-February when they began to increase (Table 1). This increase coincided with the bulldozing of watering ponds in the lower canyon by the South West Africa Conservation Department (Table 2). Populations peaked in late March just before local rains came and the river flooded. It was our impression that this second peak was the result of incursions of plains populations south into the canyon.

3.2 Social organization

Despite the limitations on individual identifiability we are confident that the individuals at waterholes maintained no persistent integrated groups. Individuals came to and departed from waterholes as individuals or irregular groups. Some easily recognized individuals were associated with one another on some occasions and not on others. Individuals which arrived in groups at waterholes often departed alone or with individuals already present at the waterhole. We tentatively conclude that the herds at waterholes were fortuitous collections of individuals. Early in the study brown calves were with their mothers, but as the environmental situation deteriorated at mid-summer many of these calves were abandoned. This suggests that the lack of persistent social groupings may be a reflection of the extreme environmental conditions and herd deterioration at the time of our study and may not reflect the highest level of social organization of this gemsbok population.

3.3 Water conditions

A critical component of the context of aggressive competition among gemsbok in the Kuiseb canyon is the spatial relationship of water and food. This relationship changes through time as the water table drops and available food is consumed.

The Kuiseb River floods almost annually following seasonal thunderstorms in the uplands to the east. Following flooding the water table drops and free flow is restricted to limited stretches of the riverbed (Table 2). As the water drops further, accessible water is confined to waterholes which dry up more rapidly in the downriver part of the canyon. As pools close and become fouled with algal blooms the gemsbok excavate wells with their forefeet. These excavations are deepened to clear water. As the water level drops further these excavations are deepened. Gemsbok and baboons eventually extend excavations to a depth of slightly over one metre. These deep excavations frequently fill with blowing sand. Once they are closed with dry sand, they are not reopened. Baboons also work these excavations and the maintenance of the gemsbok wells depends in part upon them. Gemsbok wells decrease in number as the dry season continues. They become restricted to the upstream, narrow sections of the canyon where the water table remains nearer the surface longer.

3.4 Food conditions

Gemsbok eat a variety of plant foods in the canyon. These include various grasses, several forbs, *Cyperus marginatus* leaves, and the leaves and stems of the woody shrub, *Euclea pseudebenus*. The leaves and smaller twigs of *Acacia albida* and *A. erioloba* are browsed to a height of about 1,5 m, the approximate limit of the reach of the gemsbok. Gemsbok do not abandon a four-footed stance while browsing. In the canyon their primary food is the seed pods of *Acacia albida*. These are picked up from the sandy ground and eaten entire, but the seeds are passed undigested. A smaller number of the pods of the less common *Acacia erioloba* are also taken. The pods of this tree do not fall continuously as do the pods of *A. albida*, and most of the gemsbok population have left the canyon before the pods of these trees drop in May and June. All *A. erioloba* pods within reach from a four-footed stance were eaten in the 1972-1973 season.

A small amount of some unpalatable plants is eaten by gemsbok during the period when more favoured foods have been exhausted. These foods include the leaves and stems of *Salvadora persica*, the smaller twigs and leaves of *Tamarisk usneoides*, and the leafy parts of the castor bean, *Ricinus communis*. The low value of *Salvadora* plants to gemsbok as forage is established by the surplus quantities of these relatively succulent (water content 71 % to 75 %) plants available at times of starvation and water stress.

The need for water and the contests for it reported here are probably related to the low water content of the *Acacia albida* pods which comprised the bulk of the diet after foliage was overbrowsed in the 1972-1973 season. The water content of *Acacia albida* pods ranges from an average of 5,2 % late in the day to as high as 13 % after heavy morning fog (Table 3). Most of the canyon range of gemsbok has heavy fog less than once per month and during the 1972-1973 study there were no fogs in the study area sufficient to significantly alter the water content of acacia pods. By comparison some of the common plant foods of the gemsbok in the dunes contain from 75 % to over 82 % water (Table 3). When the gemsbok population first descended into the canyon in October, 1972, there

Table 2. Location and characteristics of water sources along the Kuiseb River during the period of this study. An 0 indicates open water. An X indicates a gemsbok and baboon excavation. Blanks signify no available water. Locations of water sources are represented as distances (km) upstream from the Namib Desert Research Station at Gobabeb. Water sources above km 15,6 are signified by a letter identifying each site and number of each water source if more than one occur at a site.

Water Source		Homeb	Nature Cons.	Dig 2	Tree Hole	Nature Cons.	Dig 3	Bad Bend 1	A1	A2	B	C1	C2	C2.5	C3	C4	D1	D2	D3	D4	D5	D11	D12	E	F	G	H	I	J	K	L	M	N
		(21,0)						(30,3)	(36,6)	(36,6)	(44,1)	(44,7)	(44,7)	(44,7)	(44,7)	(44,7)	(45,2)	(45,2)	(45,2)	(45,2)	(45,2)	(45,2)	(45,2)	(51,7	(51,8)	(52,5)	(54,3)	(55,6)	(56,1)	(59,3)	(65,3)		
Oct.	15								×		0	0	0			0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
	22								×		0	0	0			0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
	29								×	×	0	×				0	0	0	0	0	0	0		0	0	0	0	0	0	0	0	0	0
Nov.	5								×		0	×	×			0	0	×	0	0	0	0		0	0	0	0	0	0	0	0	0	0
	12								×	×	0	×				0	0	×	0	×	0	×		0	0	0	0	0	0	0	0	0	0
	19								×		0	×				0	0	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	26								×	×	0	×				0	0	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
Dec.	3								×		0	×				0	0	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	10								×	×	×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	17								×		×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	24								×	×	×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	31								×		×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
Jan.	7								×	×	×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	14								×		×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	21								×	×	×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	28								×		×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
Feb.	4								×	×	×	×				0	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	11								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	18								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	25								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
Mar.	4								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	11								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	18								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	25								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
Apr.	1								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	8								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	15								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	22								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	29								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
May	6								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	13								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	20								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
	27								×	×	×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0
June	3								×		×	×				×	×	×	0	×	×	×		0	0	0	0	0	0	0	0	0	0

Table 3. Water content by weight of some gemsbok foods.

Plant Species	Per Cent Water
Dune Plains	
Trianthema hereroensis (vegetation)	82,1
Asthenatherum glaucum (leaves)	75,9
Monsonia ignorata (bulbs)	65,7
Stipagrostis sabulicola (leaves)	58,2
Hexacyrtis dickiana (bulbs)	57,0
River Canyon	
Acacia albida (sprout growth)	71,3
Cyperus marginatus (leaves)	68,9
Acacia erioloba (fresh pods)	52,7
Acacia erioloba (leaflets)	51,5
Acacia albida (ground dry pods during fog)	15,0
Acacia albida (ground dry pods during afternoon)	5,2

was an abundant supply of *Acacia albida* leaves and fresh growth with a high (71,3 % water) water content. As these sprigs were browsed away the shift to low water content *Acacia albida* pods took place. With that change in diet competition for water became intense.

The spatial relationship between water sources and food supplies further aggravated the stress on gemsbok in the canyon from December 1972 to mid-February 1973. Water sources became fewer and restricted to the upstream sections of the study area. These areas are not well vegetated due to the narrow nature of the canyon. Furthermore, foraging pressure by gemsbok and baboons on areas near water was extreme and food supplies, both browse and fallen acacia pods, were virtually eradicated above km 43 by mid-December 1972. Thereafter, gemsbok were forced to concentrate their feeding downstream at increasing distances from water. By early February significant numbers of fallen acacia pods were available only downstream from km 30 (Fig. 2) and water was available only upstream from km 44,1 (Table 2). The gemsbok were making significant up and down canyon treks between water and food. These movements were expensive in terms of energy and time expenditure as well as water loss.

Significant depletion of the downstream food sources did not occur until following the excavation of large ponds there in mid-February (Table 2) and the subsequent buildup in gemsbok population (Table 1). By late March, fallen acacia pods were virtually absent near these artificial excavations and complete loss of available browse had occurred.

3.5 Competition at water

Access to the limited waterholes depended upon the sex and body condition of the contestants and on the size and exposure of the waterhole. The single most striking pattern in aggressive interactions at water sources was male dominance of females. Males displaced females from waterholes in 149 of the 156 supplantings recorded between adults of different sexes (X^2 = 129,3, d.f. = 1, $p < ,001$). Between individuals of the same sex and age class, physical condition was an important determinant of success at gaining access to water.

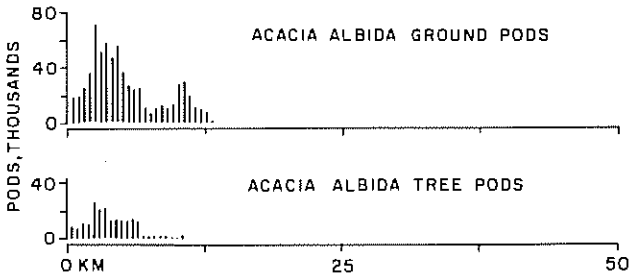

Figure 2. The distribution of *Acacia albida* pods on February 1, 1973. Acacia trees extend throughout the study area but pods have been eliminated from the ground and trees in the upstream areas by gemsbok and baboons.

In 35 of 40 recorded contests at waterholes in which the contestants were adults of the same sex and were of recognizably different physical condition and in which a clear-cut displacement from the drinking position of one individual by another occurred, the gemsbok gaining access to water was in better physical condition than the animal it evicted (X^2 = 22,5, d.f. = 1, $p < ,001$).

Overt aggression was rarely observed and never severe at open water sources. Open pools, such as waterholes I, J, K, M, and N, were present throughout the critical period of December 1972 through March 1973 (Table 2). But they were in the narrow, virtually vegetationless canyon far upstream from significant food sources. Hence they were not heavily used by gemsbok feeding below km 46. These animals watered primarily at the B, C, and D series gemsbok wells, each of which permitted only single-individual access. Our observations concentrated on the severe aggressive behaviour that developed at these sources.

The exposed nature of the D series waterholes (Plate 2) subjected gemsbok to extremely high midday temperatures and insolation, while at the C2,5 waterhole shade buffered climatic extremes throughout the day. Males dominated all waterholes at night and at the end of the day. Females had greater access towards the middle of the day at the exposed D series waterholes while males persisted in dominating the shaded C2,5 waterhole through the day.

The relationship of sunlight to access and the dominance order was complex. Frequently dominant males drank to temporary satiation but rested in the shade, returning from time to time to resume drinking. When males were present, especially late in the day, the sunlit waterholes frequently remained unoccupied in spite of the presence of unwatered females nearby.

Once we became familiar with the general situation at these waterholes we observed an orderly succession of behavioural events and spatial relationships. Adult males, when at wells or small open pools, take priority of access to water (Plate 3). Subordinate individuals stand by behind these watering individuals at about a body's length. Other individuals in the immediate vicinity also maintain a body length separation from other individuals. When supplanting takes place or new individuals move into the vicinity of waterholes, all individuals

Plate 2. Sixteen gemsbok assembled in the vicinity of the D series of waterholes. Note the regular spacing between individuals.

adjust their position to maintain this individual distance. This activity became particularly obvious to us when we viewed speeded up film of the activity at the D series waterholes where many individuals were present at the same time. The entire local herd may be stationary for an interval. Then, as a consequence of an interaction between two individuals, all individuals move, switching their conspicuous black tails as they do so. When a new equilibrium is established tail-switching ceases or becomes less frequent, and the individual spacing is maintained.

Individuals frequently challenge the drinking individual (Plate 4) which may either ignore the challenge, look up and make counter-threatening gestures, fight with the challenger, or voluntarily give way. In these interactions the most predictable result is that adult females give way to adult males. However, when we observed small groups of individuals whose identity could be determined for the duration of an interval of an hour or more of observation at a waterhole, it was possible to determine that a hierarchical order was established and maintained. This hierarchy appears to develop on an *ad hoc* basis at the watering point, but it is not determined entirely by physical encounters. Individuals in poor condition tend to be relatively low in rank order.

The position behind a watering individual may be vigorously contested (Plate 5). If an adult female is challenged by an adult male the female inevitably gives way. If two males or two females challenge in this posterior waiting position, one may give way to the other without a fight or there may be vigorous horn clashing. Females tend to fight with the tips of their horns (Plate 6) while males push against the bases of one another's horns. Injuries occurred occasionally during contests. These injuries usually involved a puncture wound or broken horn. Stabbings were rarely the result of head to head clashes but, instead, were inflicted by waiting individuals on the exposed flanks or rumps of drinking individuals. These occurred in two ways. First, when a relatively low ranking and apparently impatient individual attacked a more dominant one. And second, and less frequently, when a high ranking individual too vigorously prodded a subordinate that waited overly long to vacate a waterhole in response to the approach of the dominant. The conditions fostering these injuries were particularly prevalent at the peak of stress on the herd when many individuals were in desperate need of water. Under less stressful conditions the amenities of dominance-subordinance relationships occurred more frequently. In some instances these wounds were serious and probably lethal, especially when suffered by an individual already in poor physical condition.

In November and December there were a large number of one- to three-month-old calves in the canyon. These individuals occasionally visited the vicinity of waterholes (Plate 7). These youngsters

often approached water but were regularly rebuffed by adult males and females. At this time there was high juvenile mortality, the probable result of food and water shortages. Individuals were occasionally hounded by jackals *Canis mesomelas*, and both spotted hyaenas *Crocuta crocuta* and brown hyaenas *Hyaena brunnea*. Several juvenile calves died in the vicinity of the waterholes. During December carcasses were quickly devoured by hyaenas. A tuft of tail hair often was all that could be found of a known dead juvenile the day following its death.

The pattern of access to waterholes was generally predictable and obeyed the principles of access by the largest and best conditioned fighters. However, alternative tactics occurred infrequently. For example, one male, condition 4, was able to remain in the vicinity of the C2,5 waterhole by lying down next to it and adopting a submissive posture with horns held low over the back (Plate 8). Occasionally two individuals attempted to drink synchronously at the same waterhole (Plate 9).

One tactic used by a few females was to move directly to water when adult males showed any persistent sexual interest in them. These males, always large, good condition individuals, were well watered and showed no interest in drinking. The approach of these consorting males to the vicinity of water evicted smaller less dominant individuals (Plate 10). Such incidents did result in the followed females gaining access to water, but once they settled into the waterhole higher ranking individuals tended to challenge them and the courting male made no effort to defend the position of the female. On one occasion a female urinated while at the waiting position behind a waterhole. When the dominant male there left the waterhole to sniff the female and the urine spot, the female stepped into the waterhole and immediately began drinking. She was able to hold the hole less than two minutes before being supplanted by a third individual, a low ranking male.

M o r t a l i t y. During December and early January a marked decline in the condition of the herd occurred (Table 4) and considerable mortality followed. We found 43 adult carcasses and 3 grey phase juvenile individuals dead. No count was kept of brown infant mortality because these carcasses disappeared so rapidly that any count would be a large but uncertain underestimation. Of 34 adult carcasses which could be sexed, 26 (76 %) were females ($X^2 = 9{,}52$, d.f. = 1, $p < ,02$). The

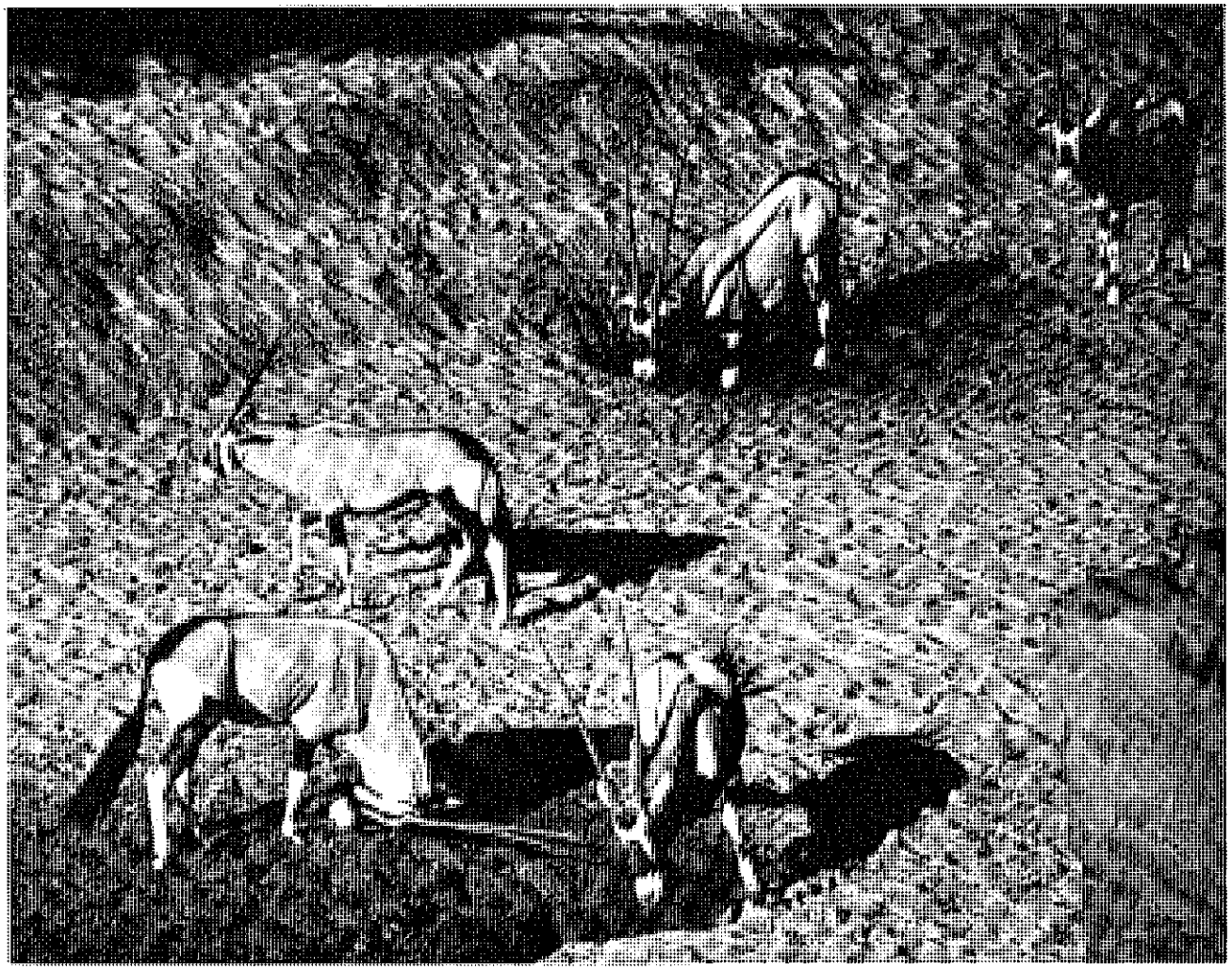

Plate 3. Action at the waterholes. In the foreground an adult male, condition 2,0, is evicting a female while another male, condition 1,5, walks by. In the background a male, condition 3,0, excavates a waterhole while a female, condition 4,0 waits.

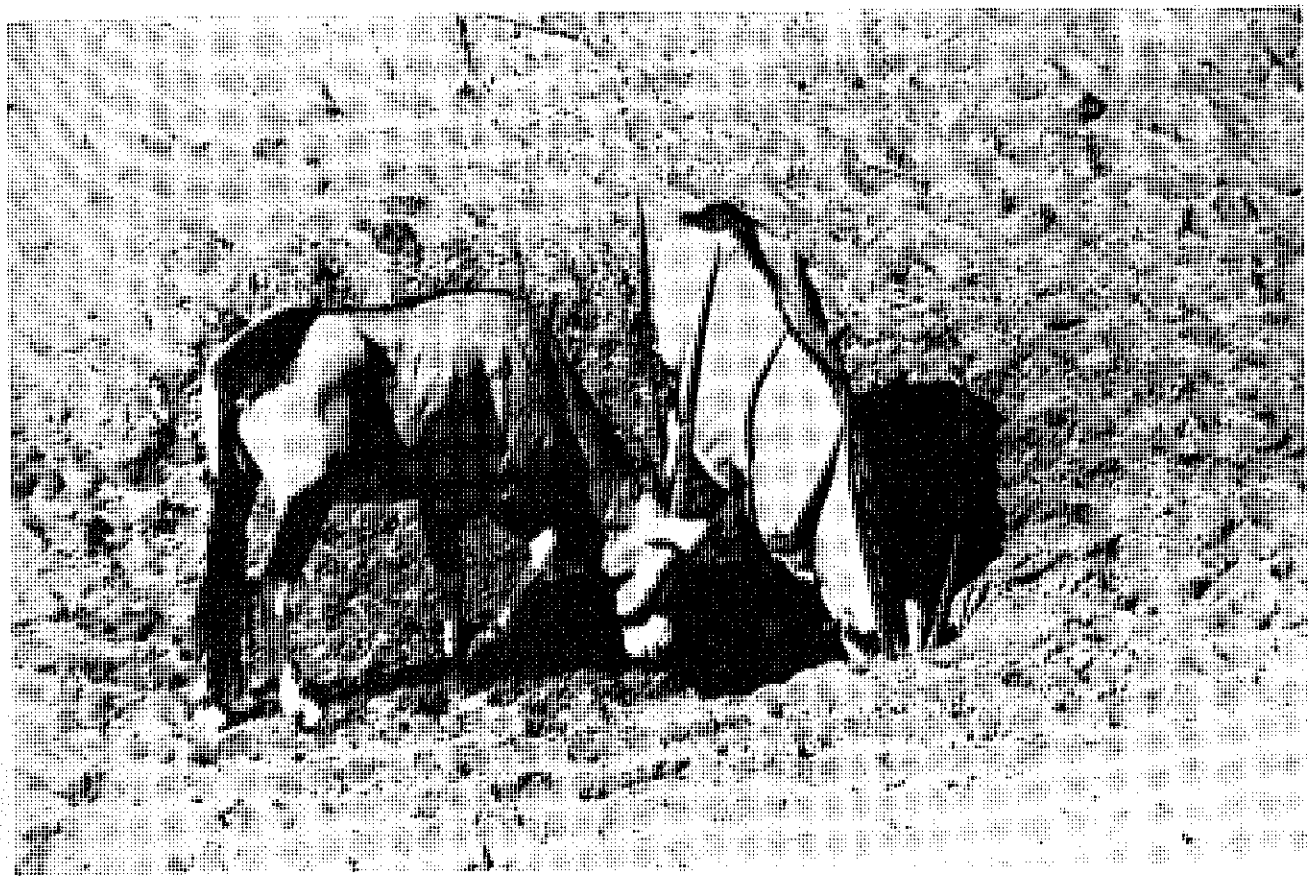

Plate 4. Challenging position at a waterhole.

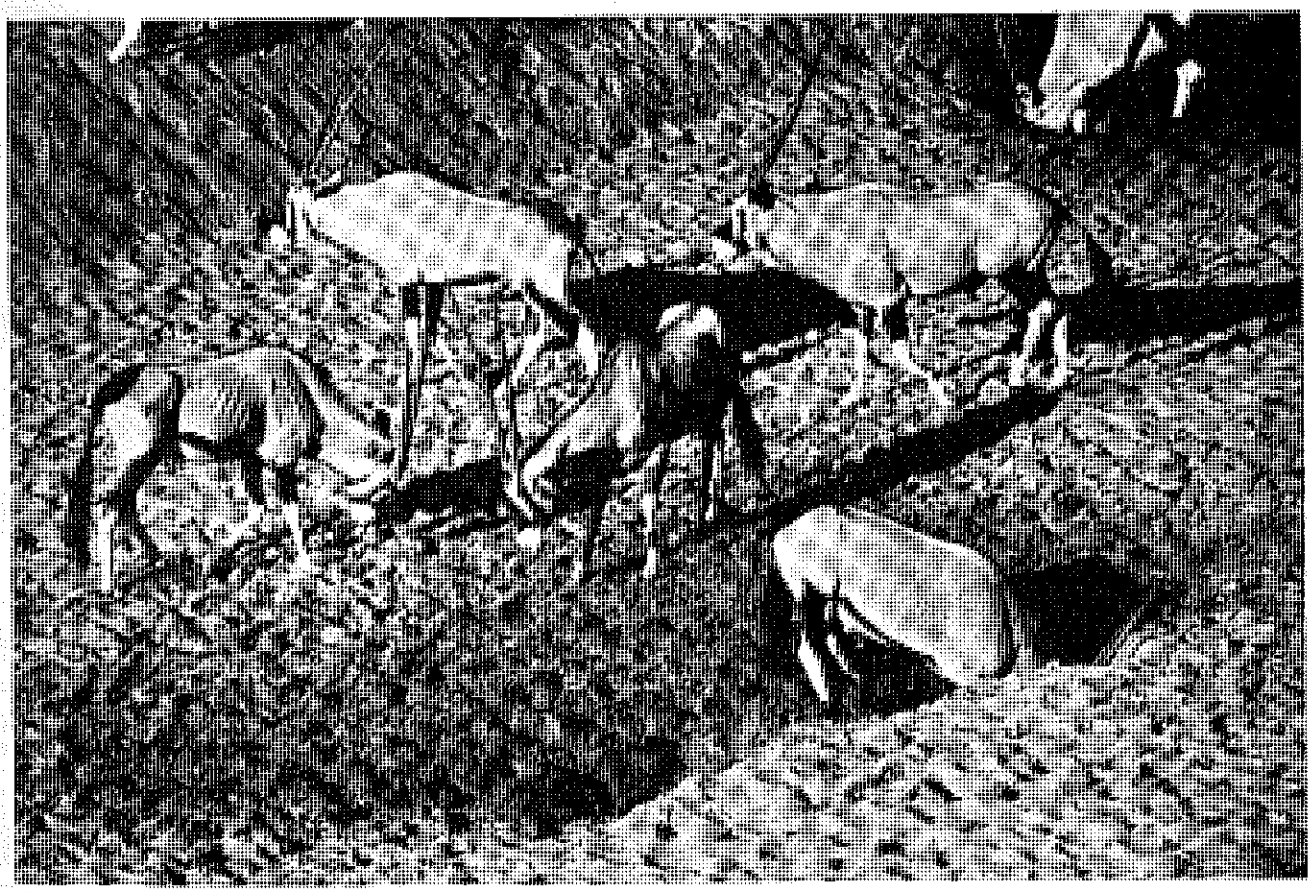

Plate 5. A male, condition 1, drinks. Two females, condition 4,0 and 3,5, spar for position behind the drinking male. In the background a male, condition 1, follows a female, condition 2,5.

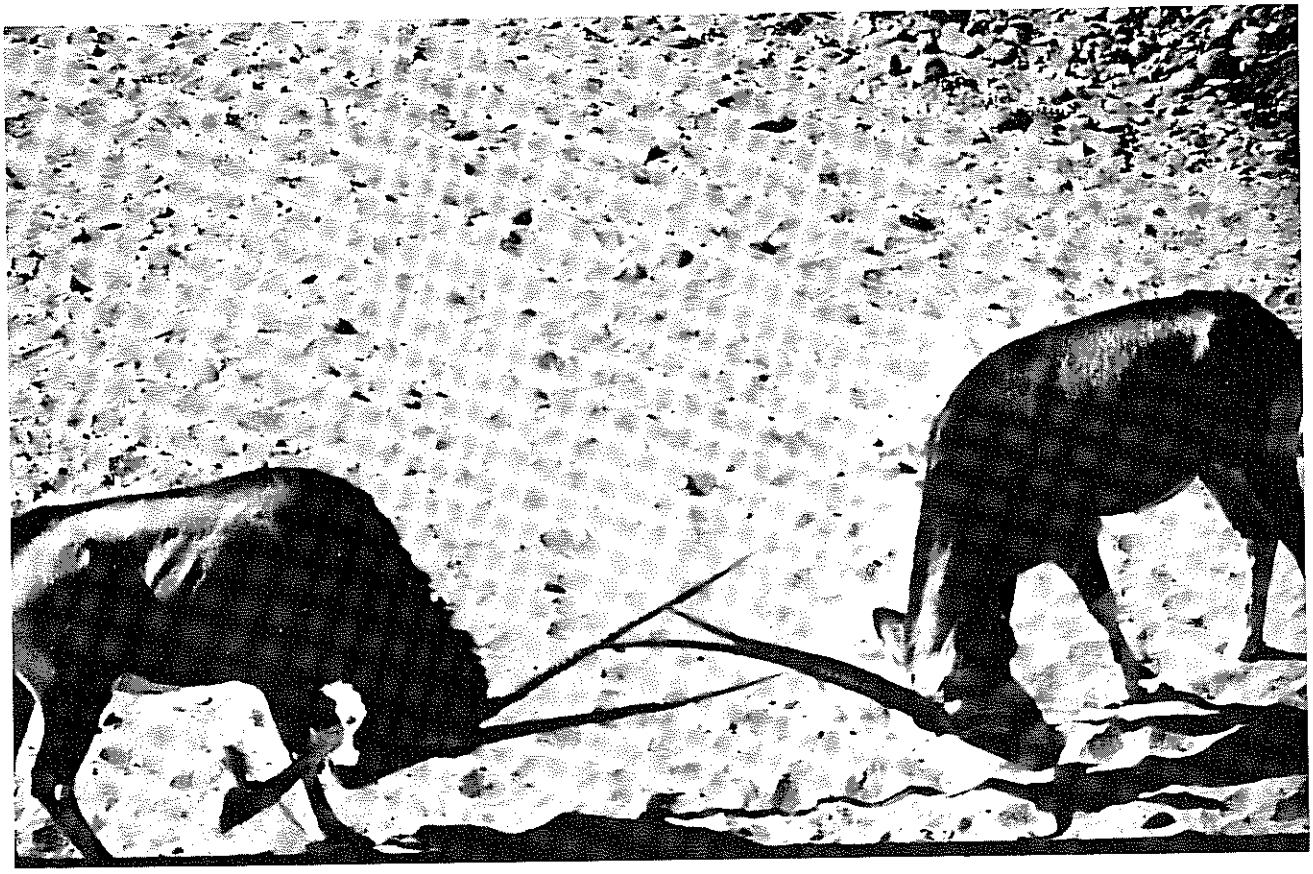

Plate 6. Females frequently fight with the tips of the horns.

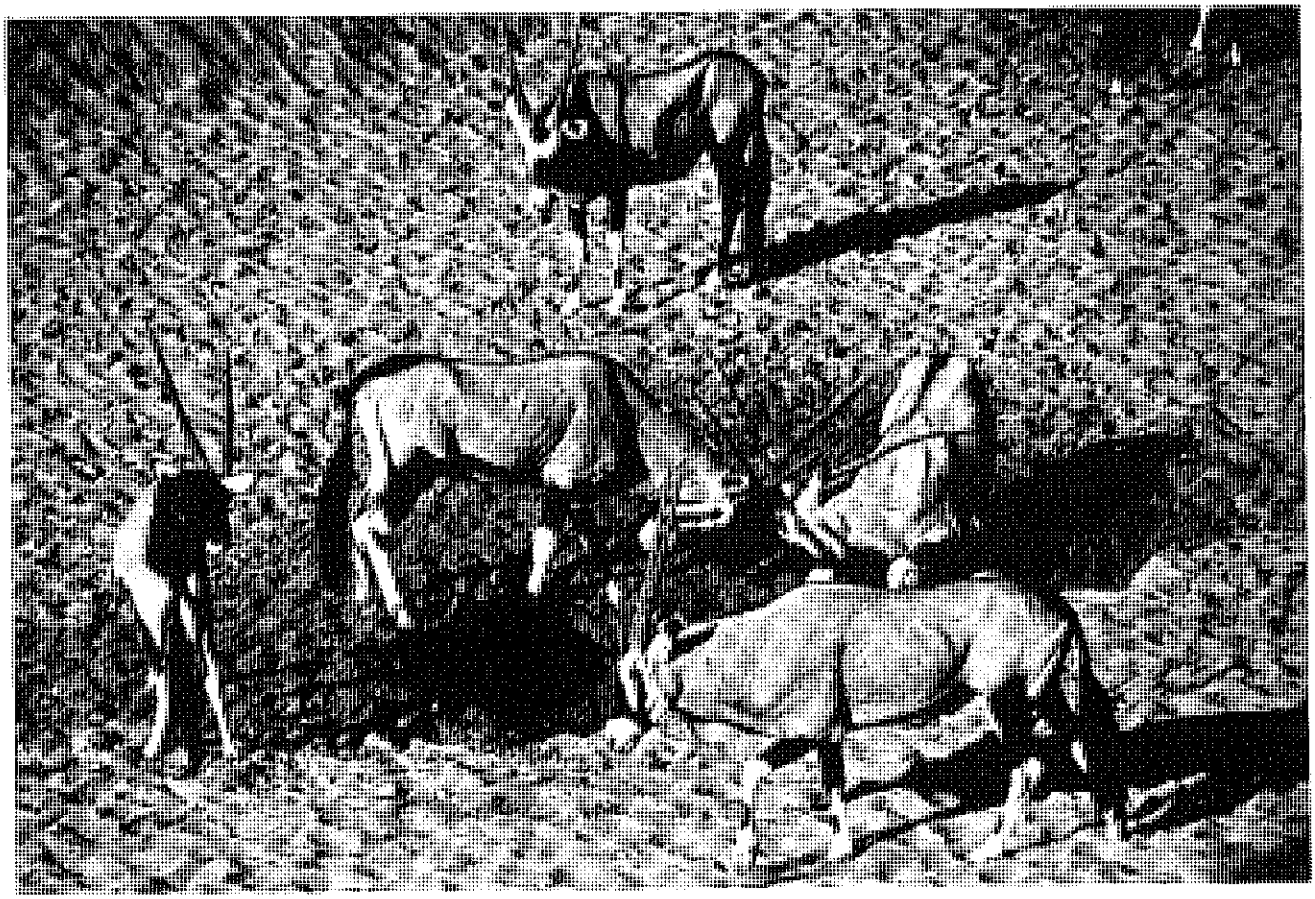

Plate 7. A young male watches, left, as two males at adjacent waterholes clash. The three foreground males are condition 1,5, the background individual is condition 3,5.

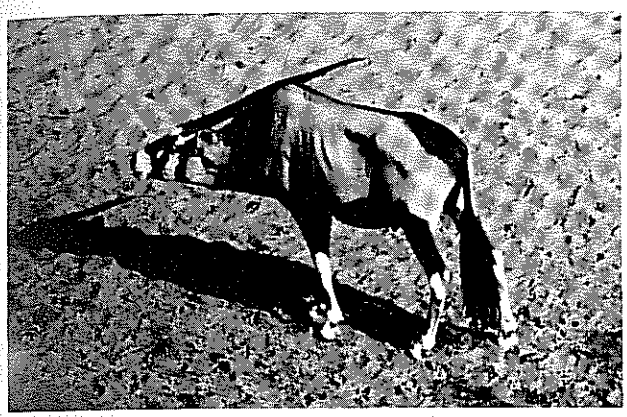

Plate 8. Extreme submissive posture, condition 4,0 male.

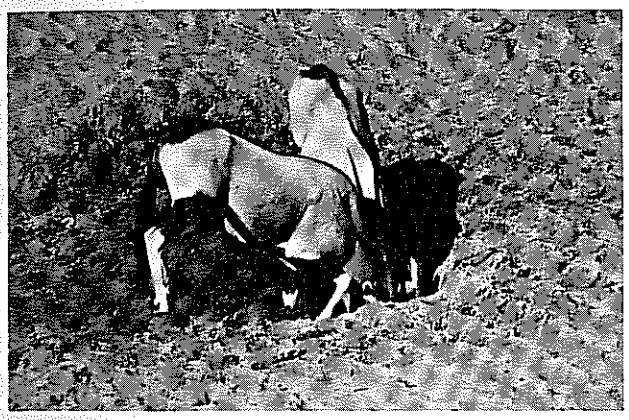

Plate 9. Two gemsbok, condition 2,0 and 3,0, share a waterhole. This is the only time we saw two oryx in the same waterhole at the same time.

34 carcasses represented less than half of the actual adult mortality which occurred. Often we observed emaciated and presumably doomed individuals (Plate 11), but we could not locate the carcass in the ensuing days. The greatest mortality occurred between 25 January and 13 February.

Perhaps one of the most interesting observations of this study was the apparent beginning of recovery of condition by the herd in late February and March, 1973 (Table 4), well in advance of flooding and the departure of the herd from the canyon. Our sample size for that interval is small, only 15 individuals, and no definitive conclusion can be made. But it appeared that the extensive mortality in January and early February may have reduced competition for food and water to levels where recovery of survivors became possible.

The situation reported here, involving the loss of most of the juveniles and a significant proportion

Table 4. Decline in the physical condition of the Kuiseb River canyon gemsbok herd in the summer of 1972-1973. The significance values are t-test comparisons of the means of males and females for the sample date. Physical condition is ranked from 1 (good) to 5 (poor). See text and figures for details.

Dates of Sample	Male Condition	Female Condition	Sig.
December 25-29	1,2 (30)	1,8 (40)	$< .01$
January 26	1,6 (26)	2,1 (22)	$< .01$
February 12	2,7 (37)	3,7 (30)	$< .01$
February 27, 28, March 17	1,9 (5)	2,6 (10)	N.S.

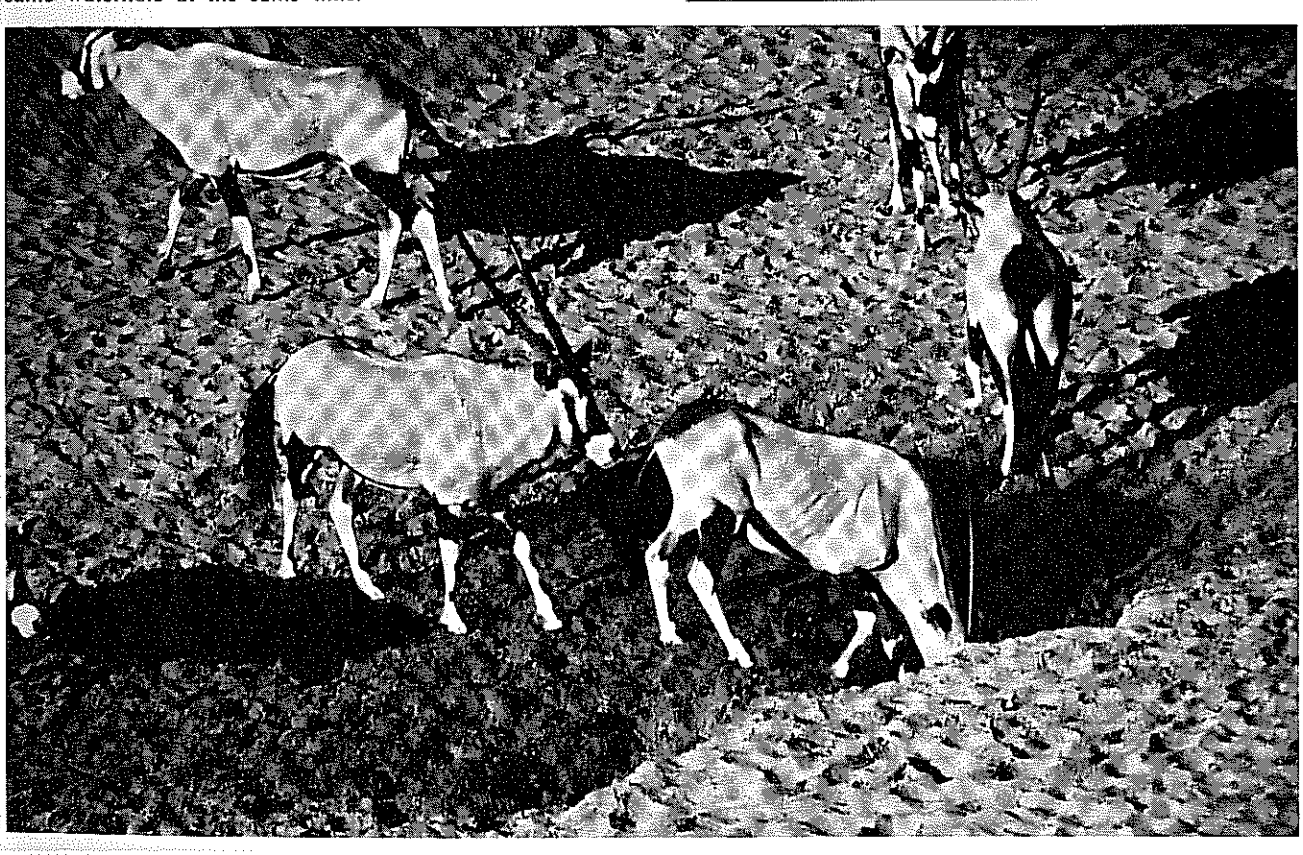

Plate 10. A female, condition 3,5, leads a following male, condition 1,0, to water, displacing a male, also condition 1,0. Female, background left, condition 3,0.

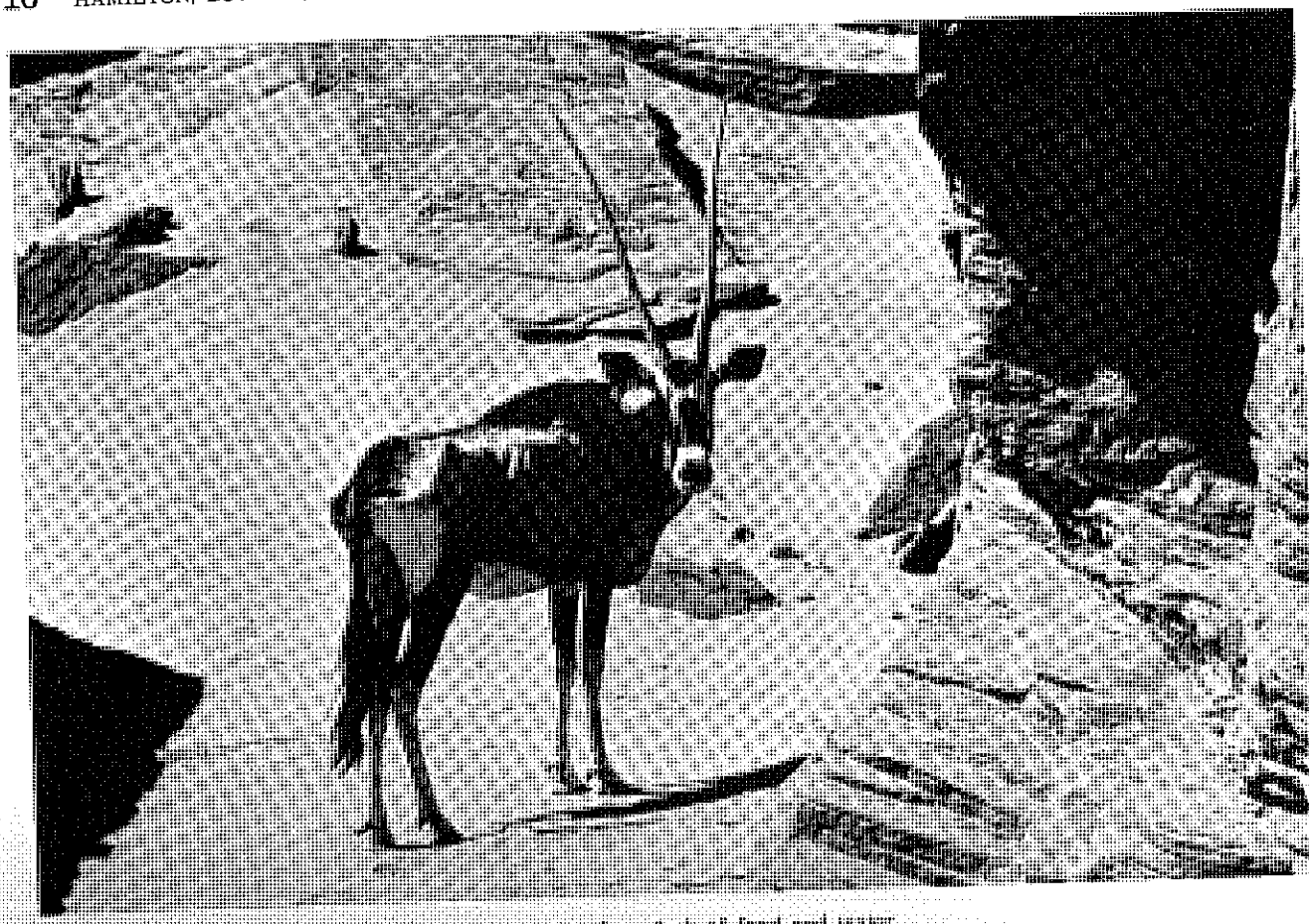

PLATE 11. A female tegu, condition 5 (see text), dying from lack of food and water.

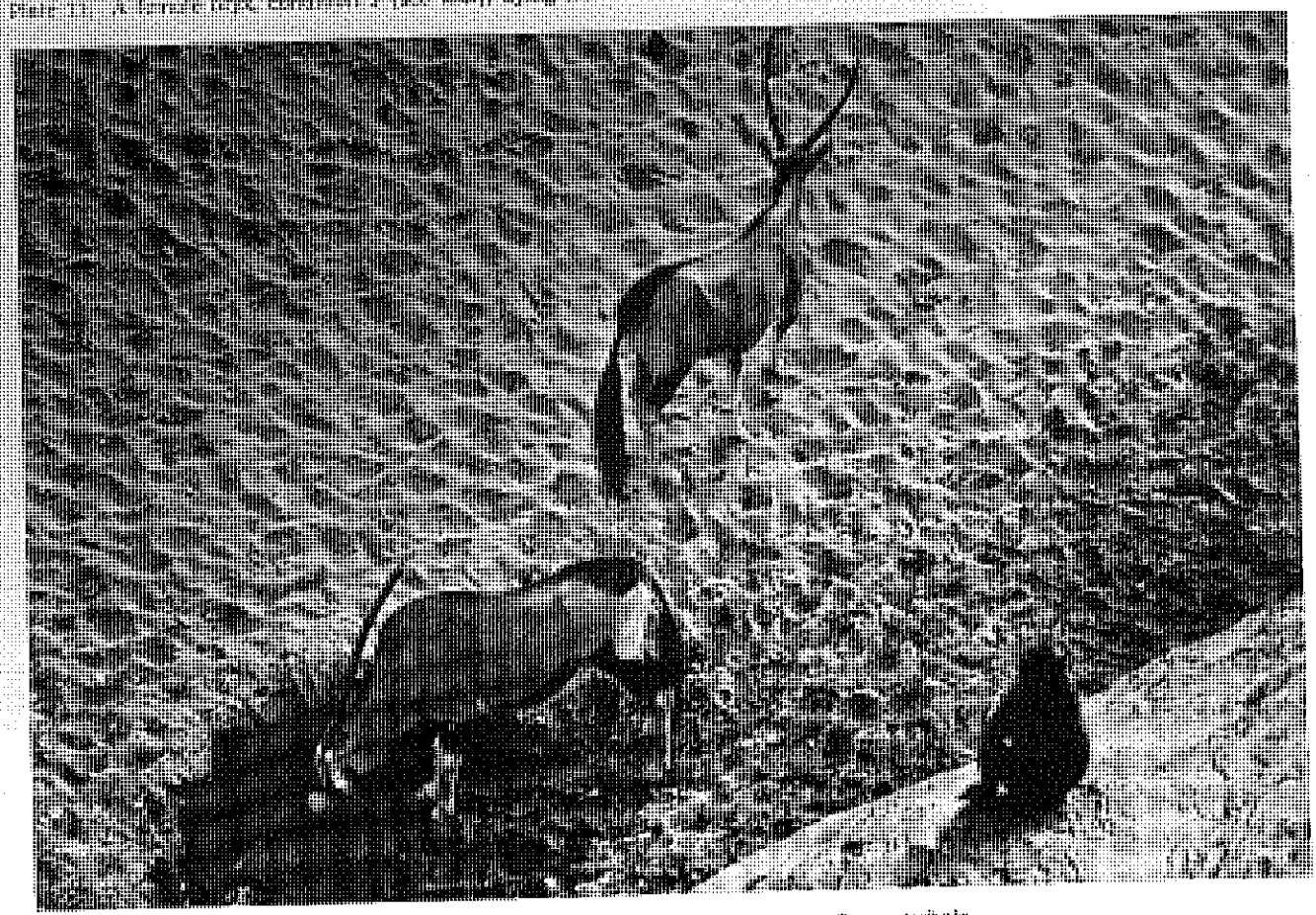

PLATE 12. A chacma baboon waits while gumsbok (condition 2,0 and 3,0) use the waterhole.

of the adults in a gemsbok population, obviously is not an annual event. In years of higher rainfall, grasses on the plains to the north and south of the Kuiseb River canyon maintain the herd in better condition and only small numbers of gemsbok come to the canyon to calve. This was the case in December, 1975, when less than 20 gemsbok were observed on each of three trips through our study area. All these individuals were in good condition, i.e. 2,0 or better. In some places shallow digs to water had been opened, but nothing resembling the intense competitive activities such as those we observed at the C and D waterholes in the 1972—1973 season was taking place. Nowhere was there significant depletion of ground *Acacia albida* pods. These pods were available throughout the study area.

Green grasses *Astenatherum glaucum* and *Stipagrostis goutostachyi* in the sand dunes south of the Kuiseb in November and December, 1975 and in the same months of 1976 were not completely exhausted. This contrasts with the depletion of these grasses in the dunes during the 1972-1973 study reported here.

3.6 Interspecific interactions with baboons.

Three troops of baboons reside in the Kuiseb River canyon (Hamilton *et al.*, 1975). Like the gemsbok, baboons move up and down the course of the Kuiseb River canyon, seeking preferred foods and water. Members of one of these troops were away from water as long as five days but in general the troops visited some watering site every day. As the water table dropped and the number of open waterholes declined in number (Table 2) the baboons were forced to excavate waterholes to maintain access to favourable foraging areas. These excavations were invariably sited in the bottom of wells initiated by gemsbok. Baboons move sand slowly by comparison with gemsbok but can excavate a narrow shaft with their hands. In the wet sand in the bottom of these digs, they may establish an additional 30 cm deep shaft to water that is little larger than the head and shoulders of a baboon.

As water conditions deteriorated gemsbok and baboons were thrust into increasing proximity to one another. Baboons often had to wait for long intervals before the waterholes were free from gemsbok activity (Plate 12). Baboons seldom threatened gemsbok and baboons gave way to any gemsbok that came within horn range of them. Baboons were not as reluctant as gemsbok to obtain water from wells during the heat of the day and at these times they gained access to the sunny, D series waterholes.

Gemsbok-baboon interactions were not limited to encounters at water. Baboons and gemsbok compete indirectly for some foods, particularly *Acacia* pods. The gemsbok do not digest the dried seeds of *Acacia albida* which were abundant in fallen pods during November throughout the canyon. The dried seeds are passed by the gemsbok which digest only the pod matrix. By comparison, baboons open dry pods and eat only the seeds, leaving the pods which may later be consumed by gemsbok. Nevertheless, the actions of the gemsbok make this resource increasingly unavailable. Baboons spend little effort opening individual gemsbok droppings to obtain the passed seeds. In the Kuiseb River canyon, unlike the situation we observed in other more mesic environments in Africa, antelope droppings are covered by sand quickly and dry hard so that baboons cannot rapidly process them for their acacia seed contents.

In the case of *Acacia erioloba* the entire green pod, seeds and all, is eaten by gemsbok from branches within their reach (1,5 m). After all pods at this level are removed this resource becomes virtually unavailable to gemsbok. Baboons, however, forage upon *Acacia erioloba* seeds. They climb into these trees and spend long hours opening pods and eating the seeds. Pods with seeds removed are dropped. Some are dropped before the seeds are removed.

As the food situation deteriorated in January and February the upper part of the study area, where the water situation was favourable (Table 2), was entirely stripped of available gemsbok foods . The few gemsbok remaining there often followed the baboons that occupied this area and ate the processed and unprocessed pods they dropped. At this time an unusual form of territoriality developed. Individual male gemsbok established themselves under the canopy of an *Acacia erioloba* tree being worked by a group of baboons. These individual gemsbok defended the space against conspecific intruders. Another male gemsbok might establish himself outside the edge of the drooping canopy and defend that space where some pods also fell. Thus there were established in effect two temporary concentric gemsbok territories.

This baboon-provided resource was not sufficient to maintain many gemsbok in the upper reaches of the canyon and at this season (Table 1) there was general movement of gemsbok to the downriver portions of the canyon where a more favourable food situation prevailed (Figure 2).

4 DISCUSSION

In some years such as the 1972-1973 summer a part of the Namib Desert Park gemsbok herd depends upon the Kuiseb River canyon oasis as a seasonal refuge for breeding and calving. Like other ungulates, gemsbok are migratory, and management schemes must consider the condition of all parts of the range.

The plains and dunes are the principal range for the Namib Desert Park gemsbok herd from March through August, when they graze upon the spotty grasses which emerge after seasonal rains. That part of the herd retreating to the Kuiseb River canyon shifts to browsing and scavenging the fallen pods of *Acacia albida*. With this shift in diet the need for free water increases and the free water re-

source becomes critical. Here we have shown a probable relationship between density and access to water, a relationship quite familiar to cattle herdsmen throughout the world. Expansion of the water resource by excavation, especially in the food rich 31 km stretch of the Kuiseb River above Gobabeb, will probably enhance survival of gemsbok when they live along the river. But such artificial expansion of the herd may put pressure on the alternate range as well as jeopardize recovery of riverine browse production. Any manipulation of the herd is therefore probably best accomplished in connection with a capture scheme and removal of females and juveniles. There is no management reason to expand the herd unless it is utilized. In a desert park it does not seem reasonable to encourage the expansion of herds of grazing animals beyond the limits of naturally occurring food supplies.

The establishment of a game fence along the eastern and northern boundaries of the Namib Desert Park to prevent encroachment by grazing domestic herds has protected the alternate range of the gemsbok. But at the same time it limits the extent of the alternate range. In the absence of early studies of gemsbok in this area it is not possible to know how far local populations of gemsbok ranged. The movements of gemsbok elsewhere in Africa suggest that movements may have been extensive following localized desert rainfall. Since Namib rainfall is spotty and therefore grass growth is patchy it follows that an expanded gravel and sand plains foraging area would reduce annual variance in food supply for the herd. This would enhance the herd's long-term survival potential as well as serve the interests of game viewers.

The establishment of open waterholes for gemsbok can be expected to localize their movements, inducing local overgrazing and possibly diminishing the utilization of dune and plain grasses when these items are fresh and have a high water content.

Our observations of the considerable impact we had upon the herd when we moved through the canyon in a vehicle, especially at the time of extreme water stress, emphasizes the need to carefully regulate visitor traffic in the Kuiseb River canyon and in other linear environments.

The interest of the Namib gemsbok population to man is its mobility and its ability to utilize marginal and unusual environments. Anyone who has observed a gemsbok high on a vegetationless red sand dune, resting at midday and catching the breezes that move through these dunes, or watched a line of gemsbok move along a trail in the interdune valleys will realize that such encounters are vastly more exciting than observing a herd of gemsbok at a man-made waterhole.

5 SUMMARY

During the unusually dry summer of 1972-1973 gemsbok in the Namib Desert Park left the dunes and gravel plains and assembled in the linear oasis of riverine habitat formed by the Kuiseb River. Contracting water and food supplies through the summer due to a dropping water table and overgrazing produced a severe limit on gemsbok population in the river canyon. This situation was aggravated by a progressive restriction of water supplies to narrow upstream portions of the river canyon and of food resources to the wide, dry downstream parts of the valley. Gemsbok-made excavations to water, localized points of access to a critical resource, became the objects of intense competition.

Access of individuals to waterholes was correlated with the sex and physical condition of contenders and the exposure of the waterhole to direct sunlight. Males dominated females and easily supplanted them from waterholes. Animals in better physical condition supplanted those in poorer condition. At sunlit waterholes males drank at dawn and dusk and throughout the night. Females were more likely to use exposed locations at midday. At shaded excavations males retained principal access as long as they were shaded. Thus females were less likely to reach water and when they did it was often under marginal environmental conditions.

The physical condition of the herd deteriorated through the summer and significant mortality occurred in the assembled herd of about 400 gemsbok during late January and early February 1973. The condition of females declined more rapidly than that of males and female mortality was greater. Virtually all calves perished.

The dependence of gemsbok on water is unexpected as this species is able to obtain water from natural food. The movement of gemsbok into the canyon resulted in a change of diet with a greater use of foods with lower water content.

No persistent social groups were observed and gemsbok moving to waterholes did not leave in the same groups in which they arrived. Contests at waterholes were sometimes vigorous and included fighting and sometimes resulted in serious and probably lethal injuries.

The Kuiseb River canyon appears to be a vital part of the environment of the Namib Desert Park gemsbok herd, serving as an oasis in certain stressful years. Resources there are limiting and fluctuations in water availability induced by natural forces and human perturbation will probably induce population changes in the gemsbok herd.

The social organization of the herd will result in the survival of some individuals even under extreme conditions.

6 ACKNOWLEDGEMENTS

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Welwitschia mirabilis: structural and functional anomalies

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CONTENTS

ABSTRACT

Welwitschia mirabilis displays certain morphological and physiological features that may be regarded as either gymnospermous or angiospermous. It appears to be a C3/CAM plant, the CAM pathway of photosynthetic CO_2 fixation probably having evolved in order to adapt to the extremes of the Namib Desert habitat. The apparent ability to switch from C3 to CAM suggests that *Welwitschia* originated during a time when more favourable climatic conditions prevailed. And this raises a question: is the Namib Desert not a comparatively young desert? Seen *in toto*, the many anomalies (eg. gymnospermlike sieve cells, megastrobili, naked-seededness; angiospermlike vessel elements, microstrobili, CAM, mode of chlorophyll formation) confirm the viewpoint that *Welwitschia* represents an extremely specialized endpoint in plant evolution and that it is not closely related to any extant gymnosperm or angiosperm.

1. INTRODUCTION

Welwitschia mirabilis, monogeneric, monospecific Namib Desert endemic, is considered to be a gymnosperm (Foster and Gifford, 1959) although the patristic relationship with other taxa in this classis is not clear. Even the degree — if any — of cladistic relationship with *Ephedra* and *Gnetum* with which it is grouped in the Gnetales, is obscure. There is a lack of fossil evidence to clarify the latter relationship. The position of *Welwitschia* in the hierarchy of the plant kingdom therefore remains tenuous (Benson, 1971) and recent morphological, anatomical, physiological and biochemical investigations (Bornman *et al.*, 1972, 1973, 1974, 1976; Dittrich and Huber, 1974; Evert *et al.*, 1973; Schulze *et al.*, 1976; Senger and Bornman, 1976; Whatley, 1975) have revealed further anomalous features without really contributing to a clarification of its taxonomic status.

In a part of the central Namib, *Welwitschia* can be found growing over at least an 150 km west-east transect ranging from coastal lichen desert through full desert and grassland scrub-desert to grassland-savanna. A community comprising numerous, large, presumably old and visually vigorous specimens, occurs in the full desert of the Welwitschia Flats at the confluence of the Khan and Swakop rivers, within the ambit of the coastal fog. This remarkable long-lived, large-leaved plant lacks many of the xeromorphic features that characterize most of the species with which it shares its biome. The range of *Welwitschia's* phenotypic plasticity must be regarded as narrow; the geographically-confined desert habitat probably limits the effects that environmental factors otherwise might be expected to have.

This brief review notes and considers those features,

primitive, advanced and unusual, that accord this aberrant member of Africa's flora its degree of anomalousness.

2 MATERIALS AND METHODS

Leaf and cotyledonary material were collected from field- and greenhouse-grown plants and prepared for light and electron microscopy as reported earlier (Evert *et al.*, 1973).

3 OBSERVATIONS AND DISCUSSION

3.1 Morphological anomalies

Welwitschia mirabilis is an acephalous plant, its shoot apex becoming overgrown and obliterated by tissue of the developing stem shortly after germination, resulting in the closed system of its growth.

The leaf is the longest-lived in the plant kingdom. It possesses a basal or intercalary meristem and is parallelveined, features common also to the Monocotyledoneae; it is isolateral and amphistomatic. The origin of the stomata is syndetochelic (the subsidiary cells deriving from the same protodermal cell as the guard-cell mother cell), whereas commonly in the gymnosperms the stomatal type is haplochelic (the subsidiary cells are not related to the guard cells). For a desert — or any — species, the number of stomata, which occur in about equal numbers ab- and adaxially, is exceedingly great (Bornman *et al.*, 1972). The cotyledons live and remain photosynthetic for approximately one to two years.

Transfusion tracheids abound in the leaf, ensheathing each vascular bundle and, joined end to end, running the length of it. This specialized conducting tissue also occurs in the stem and root.

Like other Gymnospermae the phloem tissue comprises sieve cells, albuminous cells and parenchyma (Evert *et al.*, 1973). However, unlike other Gymnospermae, *Welwitschia* (as well as *Ephedra* and *Gnetum*) has xylem tissue typical of the Angiospermae.

3.2 Reproductive anomalies

The seeds are borne naked on scales, deriving from a single terminal ovule on a megastrobilus or cone, in other words they are gymnosperm-like. The embryo is embedded in a nutritive gametophytic tissue (Bornman *et al.*, 1976). The male reproductive structure is a pseudo-hermaphroditic flower consisting of six stamens each with a trilocular anther and an aborted pistil, in other words angiosperm-like. Unlike any other known plant, fertilization occurs in the pollen tube rather than in the embryo sac or archegonium. The embryo, upon germination, develops a non-vascularized foot-like protuberance reminiscent of that of the pteridophyte *Selaginella*. This protuberance has been shown to have an haustorial function (Butler, 1976). A similar structure, but vascularized, also occurs in *Gnetum*.

3.3 Physiological and biochemical anomalies

3.3.1 Photosynthetic pathways

There probably are a number of pathways by which photosynthetic carbon dioxide (CO_2) fixation is accomplished but three of them are becoming better understood. Firstly, in most plants the first stable product of CO_2-fixation is 3-phosphoglycerate (3-PGA); and since it is a 3C-compound, the plants in which this form of fixation occurs, are known as C3-plants. In many tropical species, especially in the panicoid grasses, the primary fixation product is the 4C-organic acid oxalacetate (OAA). Plants with this type of fixation are termed C4-plants. In the third case, many succulent species, particularly those belonging to the Crassulaceae, Cactaceae and Euphorbiaceae, and plants that occupy an arid biome, open their stomata during the night, take in CO_2 and fix it into OAA which is subsequently converted to malate, isocitrate and other organic acids. During the day when these plants close their stomata, CO_2 is released from the oxidation of these acids and used immediately for photosynthetic carbon reduction. Such plants are said to have a Crassulacean acid metabolism and are referred to simply as CAM-plants.

3.3.2 Ecological adaptations

The CAM type of photosynthetic carbon metabolism is an adaptation that allows efficient utilization of water. Cool night conditions, as often occur in the Namib, are not conducive to transpiration; and during hot day conditions the stomata of CAM-plants remain closed. As a consequence, the ratio of transpiration to photosynthesis is low and such plants can photosynthesize and conserve over long periods the water they store in their fleshy leaves and stems (Ray, 1972). This would appear to be the kind of adaptation that would suit perennial, drought-tolerant desert species (possibly *Hoodia* and *Sarcocaulon* — Schulze and Schulze, 1976) very well. However, neither in aspect nor in internal structure does *Welwitschia* even remotely resemble the typical succulent. Also, *Welwitschia* may open its stomata during the day, but only during the early and mid-morning periods when this coincides with the incident fog (Bornman *et al.*, 1972).

The leaves of C4-plants usually have the so-called Kranz anatomy, that is, a distinct bundle sheath

parenchyma surrounding the vascular tissue, the chloroplasts of which differ in size and structure from those of the adjoining mesophyll parenchyma. C4-plants furthermore have a very low CO_2 compensation point, which means a larger potential for CO_2 uptake. Under conditions of stress a C4-plant uses water more efficiently relative to its photosynthetic capacity than does a C3-plant with its high CO_2 compensation point. Also, in contrast to C3-plants, C4-plants lack (or have a greatly diminished) photorespiration, which means that photosynthetically-fixed CO_2 is not released and wasted. The latter are much more efficient in production of photosynthate than C3-plants at high light intensities and high temperatures or at low CO_2 concentrations. In fact, their photosynthetic temperature optimum is above 30°C, a temperature at which C3-plants are completely inactive photosynthetically. A C4-type of photosynthetic metabolism would thus appear to be an advantage in a desert environment with its high temperatures and light intensities, especially to annual, rapidly-growing, drought-escaping grasses such as for example *Stipagrostis namibensis*.

The vascular bundles in the leaf of *Welwitschia* are not surrounded by a bundle sheath of parenchyma as is the case for example in the C4-grass *Setaria* (Figure 1), but instead by well-developed transfusion tracheids (Figure 2). The cotyledonary leaves — which have a short life expectancy — also do not possess a distinct bundle sheath (Figure 3). Whatley (1975) recently reported the occurrence of a peripheral reticulum in chloroplasts of *Welwitschia*, a feature once thought to be confined to C4-plants but which, it appears, also occurs in certain CAM-plants as well as in C3-plants. A peripheral reticulum therefore does not seem to be the sole prerogative of a C4-plants's plastid. Whatley makes the interesting suggestion that the peripheral reticulum in *Welwitschia's* chloroplasts presupposes that this feature was available to chloroplasts prior to angiosperm evolution (and by implication prior to C4 and CAM evolution). It is a pity that because of a lack of material, Whatley's observations were based only on the cotyledon which, in relation to this plant's life-span, hardly has any relevance at all as a photosynthetic organ.

Figures 4 and 5 are electron micrographs showing details of mesophyll parenchyma cells approximately midway between two vascular bundles and adjacent to a vascular bundle, respectively. In the latter case, the mesophyll cell adjoins a differentiating transfusion tracheid. Obviously, a much more detailed study is required to ascertain with certainty whether qualitative and quantitative differences exist between the cellular inclusions of the mesophyll cells relative to the position of the latter in the leaf. However, Figures 4 and 5 would suggest that the chloroplasts (Ch) possess morphological similarity. Even chloroplasts in *Welwitschia* callus cultures appear similar in size and shape to those shown here.

C3-plants that are found in the Namib Desert habitat (see Schulze *et al.*, 1976) are either ephemeral or have developed drought-evading morphological and anatomical features. The latter include the ability to reduce surface area either by the folding or abscising of leaves. In addition, such plants usually have thick cuticles and few, deeply-sunken, abaxially-occurring stomata. Some species are aphyllous or possess greatly reduced leaves.

3.3.3 ^{13}C: ^{12}C Ratios

It is to be expected that C3-, C4- and CAM-plants would reflect in their biochemical activities the diversity that is characteristic of their form, structure and other functions. For example C3-plants should have a preponderance of RuDP-carboxylase, the enzyme that fixes CO_2 to ribulose-diphosphate in the Calvin (C3) cycle. Likewise, PEP-carboxylase, Malic enzyme, NADP-malate dehydrogenase and NAD-Malate dehydrogenase could be expected to occur in C4- and CAM-plants in various amounts and proportions.

Dittrich and Huber (1974), ruling out the possibility of C4 metabolism because of the lack of Kranz anatomy, investigated CO_2-fixation in the three genera of the Gnetales and found that *Welwitschia mirabilis* contained substantial activities of PEP-carboxylase, malic enzyme and NADP-malate dehydrogenase. In contrast *Ephedra gerardiana* and *Gnetum gnemon* apparently do not possess the necessary set of enzymes for CAM. They concluded that *Welwitschia* "clearly exhibited" Crassulacean acid metabolism and is therefore the most primitive CAM-plant known.

The CO_2 fixed in photosynthesis can incorporate in photosynthates either the radioactive isotope ^{14}C (used experimentally) or the stable isotopes ^{12}C and ^{13}C, the latter which occur in atmospheric CO_2 in the ratio of 98,89%^{12}C: 1,11%^{13}C, respectively. As explained simply and elegantly by Osmund and Ziegler (1975), some plants incorporate a slightly higher proportion of ^{13}C than ^{12}C into sugars during photosynthesis. These are so-called *heavy* plants; others that incorporate a lower proportion are *light* plants. A value, the $\delta^{13}C$ value*, has been established to measure the amount of ^{13}C taken up relative to ^{12}C during photosynthesis. Smith and Epstein (1971) determined $\delta^{13}C$ values for plant tissue from 104 species (60 families) and *inter alia* grouped them into two categories: those with low $\delta^{13}C$ values (−24 to −34‰) and those with high $\delta^{13}C$ values (−6 to 19‰). *Welwitschia* was the only gymnosperm with a high $\delta^{13}C$ value, namely — 14,4‰ (see Table I).

Carbon isotopic ratio determinations have an important predictive significance. It appears, as a general rule, that plants with enriched $\delta^{13}C$ values are C4-Plants and those with low values are C3-plants. CAM plants occupy a more or less intermediate range. The value for *Welwitschia* quoted above (−14,4‰) would immediately suggest that this plant's photosynthetic metabolism is that of a C4-plant. However, Schulze *et al.* (1976) recorded in the Namib a range of values for *Welwitschia* from −17,39 to −23,31‰ (Table 1). Interestingly, they found no variation in $\delta^{13}C$ values over the

length of the leaf, but a considerable variation in the leaves of plants depending upon their habitat.

$$* \delta^{13}C^{0}/_{00} = \frac{^{13}C/\ ^{12}C \text{ Sample}}{^{13}C/\ ^{12}C \text{ Reference}} - 1 \quad \times 1000$$

(See Smith and Epstein, 1971, for explanation.)

Plants on the coastal gravel plain yielded higher values than those growing in the grassland-savanna. Schulze *et al.* concluded that *Welwitschia* with a less negative $\delta^{13}C$ value than C3-species and a more negative $\delta^{13}C$ value than C4-species, assimilates CO_2 partially via the CAM pathway. At least, *Welwitschia* appears to have the ability to alternate between CAM- and C3-metabolism depending upon environmental conditions.

3.3.4 Chlorophyll formation and distribution

Senger and Bornman (1976) recently ascertained that the mode of light-dependent chlorophyll formation in *Welwitschia* is typical of that in the Angiospermae and not of that in the Gymnospermae which, except for *Cycas* and *Gingko*, form chlorophyll in the dark. Ratios of chlorophylls a:b are much lower in desert-growing plants than in greenhouse-grown seedlings and plants. However, no significant differences in the *in vivo* spectra of chlorophylls between *Welwitschia* and other plants were detected and on this basis no taxonomic inferences could be drawn.

3.3.5 Uptake and movement of tritiated water

Bornman *et al.* (1973) reported that *Welwitschia* could absorb and transport the water which condensed on its leaves during the fog. They compared rates of uptake of tritiated water under conditions of fog and föhn and suggested that the stomata might be the path of entry. It appeared, too, that water taken up by the leaf was transported preferentially in a proximal direction (away from the point of application in this case) towards the basal meristem. The mode of entry of at least some of the condensed fog is by no means clear. Dr W. Barthlott (Heidelberg, Germany) in a personal communication (1976) produced scanning electron microscopical evidence of adaxial cuticular depressions containing numerous micropores in the leaf of *Welwitschia*. Might water be absorbed through the cuticle? However, if water is able to enter the leaf via these cuticular interruptions there seems to be no reason why it should not also be lost similarly.

4 CONCLUSION

It has come to be assumed that C3— or Calvin cycle photosynthesis is the ancestral condition and therefore associated with primitive plants. Such plants typically lack the Kranz syndrome. Likewise, the C4— or Hatch-Slack type of photosynthetic carbon dioxide fixation appears to be an evolved condition, associated in particular with members of the grass family. Such plants typically possess the Kranz syndrome and respond well to environmental conditions of high temperatures and light intensities. CAM photosynthesis appears to be the prerogative of succulent plants, many of which inhabit arid areas. It is regarded as a derived or advanced condition, although it has not been found in the grasses.

Welwitschia mirabilis, a non-Kranz plant, with both primitive and advanced morphological, anatomical and reproductive features, seems to reflect an equal physiological diversity: chlorophyll formation is light-dependent as is the case in the angiosperms; of all the gymnosperms it appears to have the least negative $T^{13}C$ value; and to date it is the most primitive plant in which CAM has been detected. Furthermore, it is not a typical succulent.

Further studies (CO_2 compensation point, post-illumination burst, oxygen effect on photosynthesis, etc.) are required to establish with certainty this plant's ability to switch from C3 to CAM, but it seems that *Welwitschia* evolved the CAM syndrome as a secondary physiological phenomenon in order to adapt to the climatic upheaval of progressively developing conditions of aridity. In this connection two questions can be raised: firstly, did *Welwitschia* not originate under more moderate temperate or tropical conditions; and, if this indeed was the case, is the Namib Desert, in contrast to the popularly held view, not a comparatively young desert?

The degree of anomalousness (summarized in Fig. 6) which is emerging in respect of *Welwitschia mirabilis* appears to underscore its defiance of being categorized as either gymnosperm or angiosperm, and places new emphasis on Foster's and Gifford's (1959) view that it be regarded rather as an extremely specialized endpoint in evolution which is not closely related to any extant gymnosperm or angiosperm.

5 ACKNOWLEDGEMENT

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Table 1. Isotope discrimination of some selected species.

Family	Plant	Photosynthesis	$T^{13}C^0/_{00}$	Reference
Gymnospermae	*Welwitschia mirabilis*	CAM/C3	—14,4	Smith, Epstein (1971)
Gymnospermae	*W. mirabilis* (coastal desert)	CAM/C3	—18,3 —21,2	to Schulze *et al* (1976)
Gymnospermae	*W. mirabilis* (grassland desert)	CAM/C3	—20,3 —23,2	to Schulze *et al* (1976)
Gymnospermae	*W. mirabilis* (grassland-savanna)	CAM/C3	—20,7 —22,9	to Schulze *et al* (1976)
Gymnospermae	*Gingko biloba*	C3	—25,6	Smith, Epstein (1971)
Gymnospermae	*Podocarpus elata*	C3	—26,6	Smith, Epstein (1971)
Gymnospermae	*Cycas revoluta*	C3	—27,0	Smith, Epstein (1971)
Gymnospermae	*Gnetum africanum*	C3	—30,2	Smith, Epstein (1971)
Gymnospermae	*Pinus halepensis*	C3	—30,8	Smith, Epstein (1971)
Gramineae	*Eragrostis nindensis*	C4	—12,6	Schulze *et al* (1976)
Gramineae	*Stipagrostis namibensis*	C4	—13,9	Schulze *et al* (1976)
Gramineae	*Saccharum sp.*	C4	—13,9	Smith, Epstein (1971)
Gramineae	*Zea mays*	C4	—14,0	Smith, Epstein (1971)
Asclepiadaceae	*Hoodia currori*	Succulent*	—11,7	Schulze *et al* (1976)
Zygophyllaceae	*Zygophyllum simplex*	Succulent*	—14,0	Schulze *et al* (1976)
Euphorbiaceae	*Euphorbia transvaalensis*	Succulent*	—15,4	Schulze *et al* (1976)
Amaranthaceae	*Arthraerua leubnitziae*	Aphyllous	—22,0	Schulze *et al* (1976)
Euphorbiaceae	*Euphorbia phylloclada*	Succulent*	—22,1	Schulze *et al* (1976)
Amaranthaceae	*Celosia spathulifolia*	C3	—22,3	Schulze *et al* (1976)
Zygophyllaceae	*Zygophyllum stapfii*	Succulent*	—22,3	Schulze *et al* (1976)
		*CAM?		

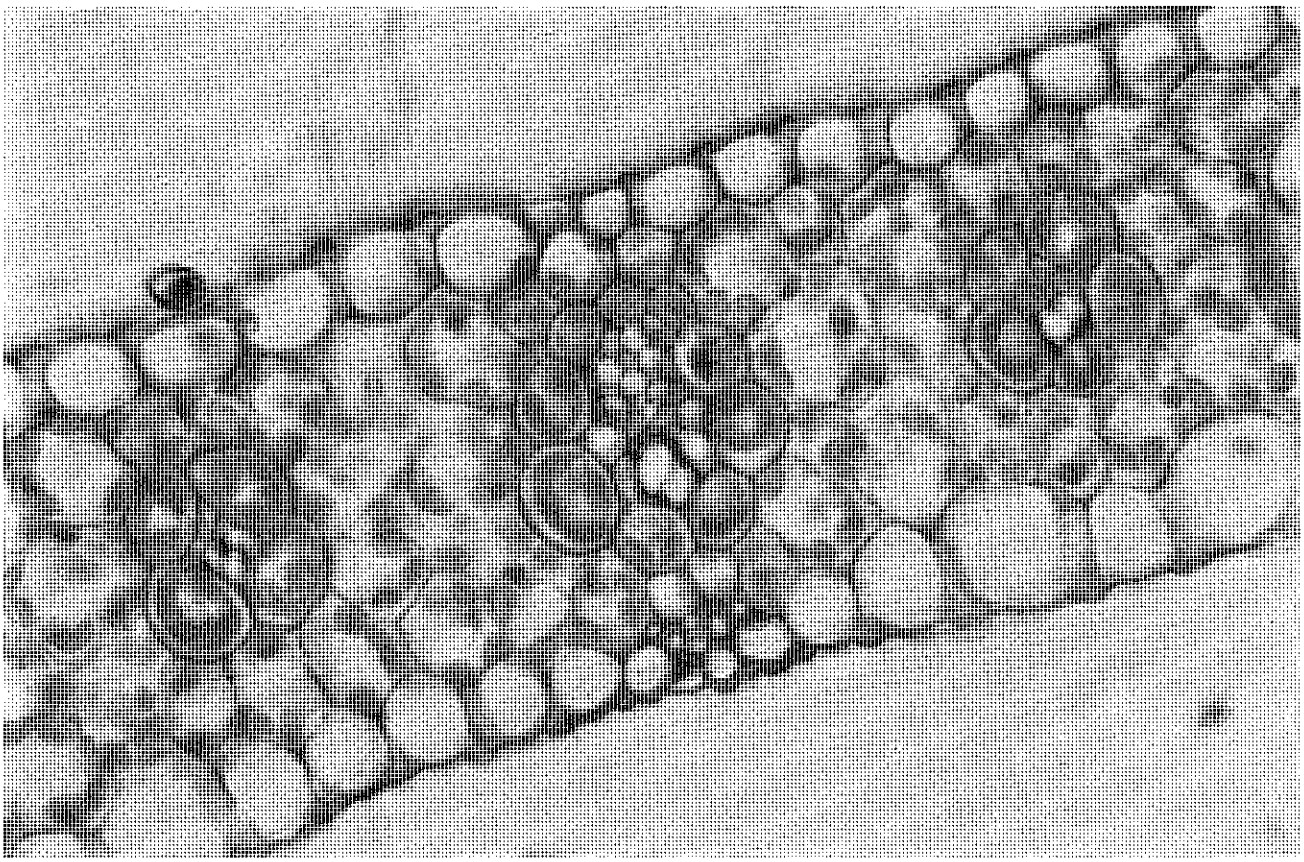

Plate 1. Transverse section of leaf of *Setaria* sp. showing three vascular bundles each surrounded by a distinct bundle sheath of large parenchyma cells, displaying the so-called Kranz syndrome. *Setaria* is a C4-plant.
X200.

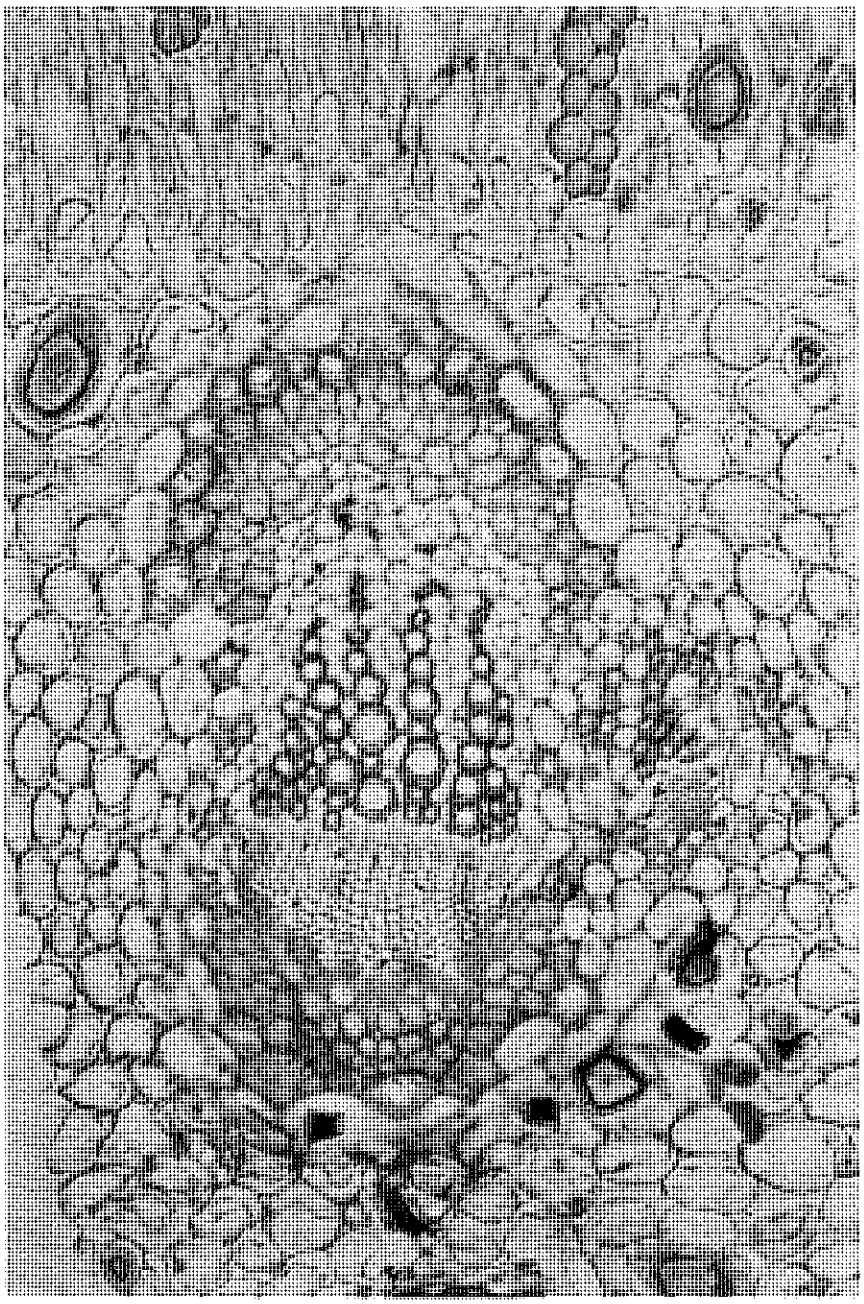

Plate 2. Vascular bundle of a 3-year-old leaf of a desert-growing *Welwitschia* plant. Note nearly complete ring of transfusion tracheids (red-staining, perforated cells) surrounding bundle that is capped ad- and abaxially with fibres. There is no bundle sheath.
X 50

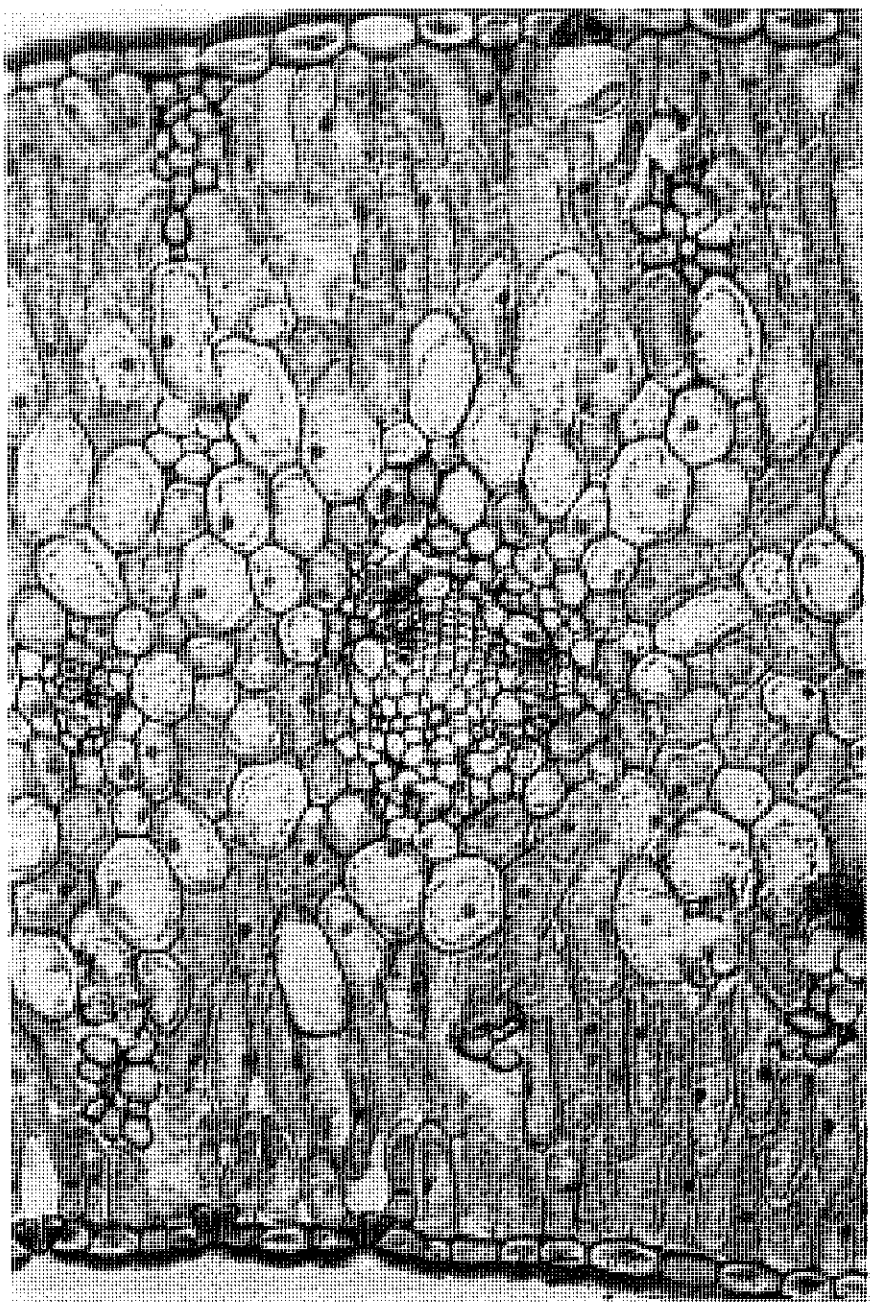

Plate 3. Vascular bundle of a 1-year-old cotyledon of a desert-growing *Welwitschia* seedling. Note that the cotyledon is isobilateral and that spherical mesophyll cells vary in size, contrasting with elongated palisade parenchyma. There is no distinct bundle sheath. Differentiation of transfusion tracheids is already occurring.
X 50

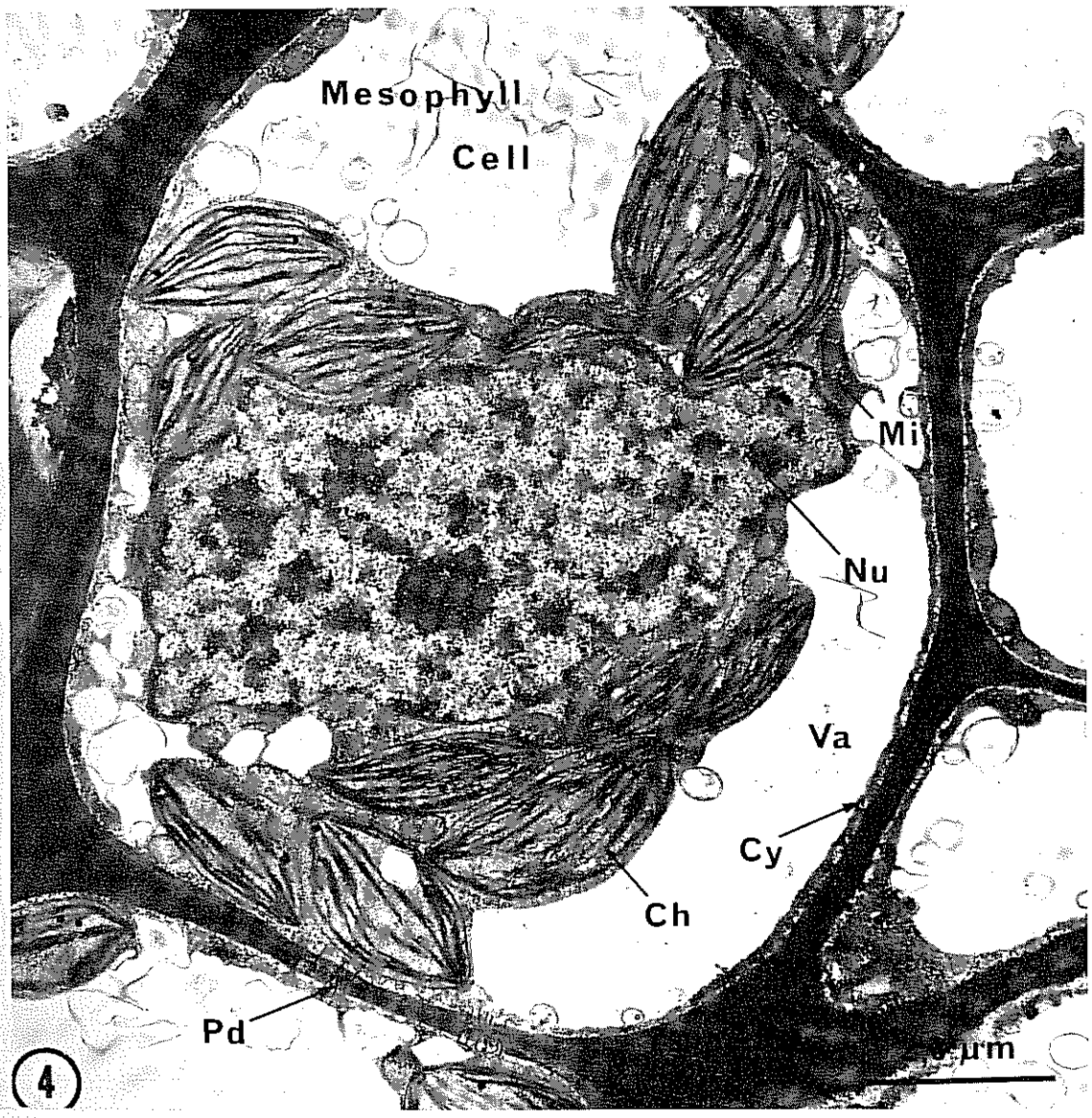

Plate 4. Mesophyll cell, approximately midway between two vascular bundles, in a three-year-old leaf of a desert-growing *Welwitschia* plant. Ch, chloroplast; Cy, cytoplasm; Mi, mitochondrion; Nu, nucleus; Pd, plasmodesmata; Va, vacuole.

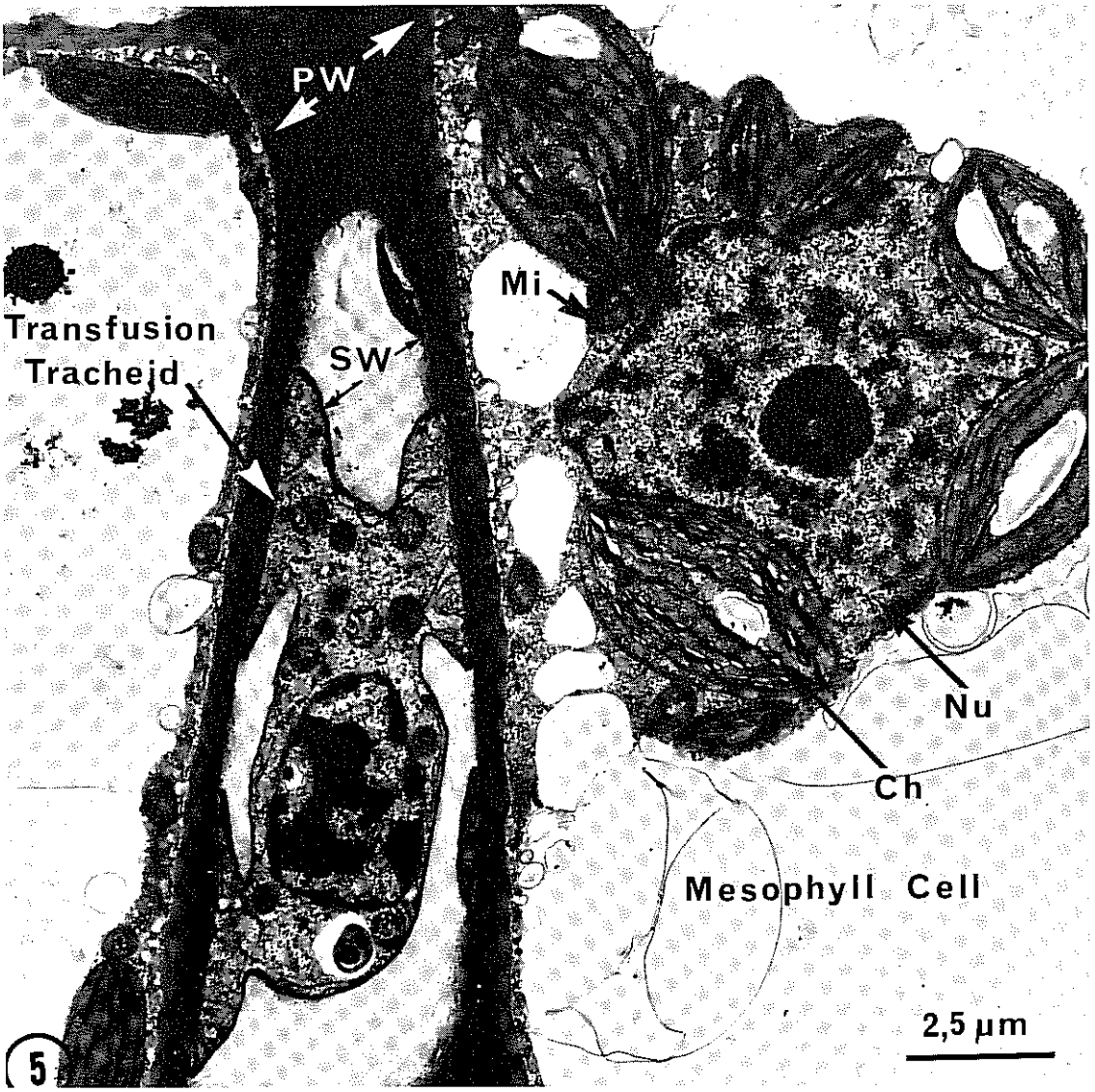

Plate 5. Detail same as in Figure 4, except that the mesophyll cell adjoins a differentiating transfusion tracheid to the inside of which (left) is a xylem parenchyma cell. Ch, chloroplast; Mi, mitochondrion; Nu, nucleus; PW, primary wall; SW, secondary wall.

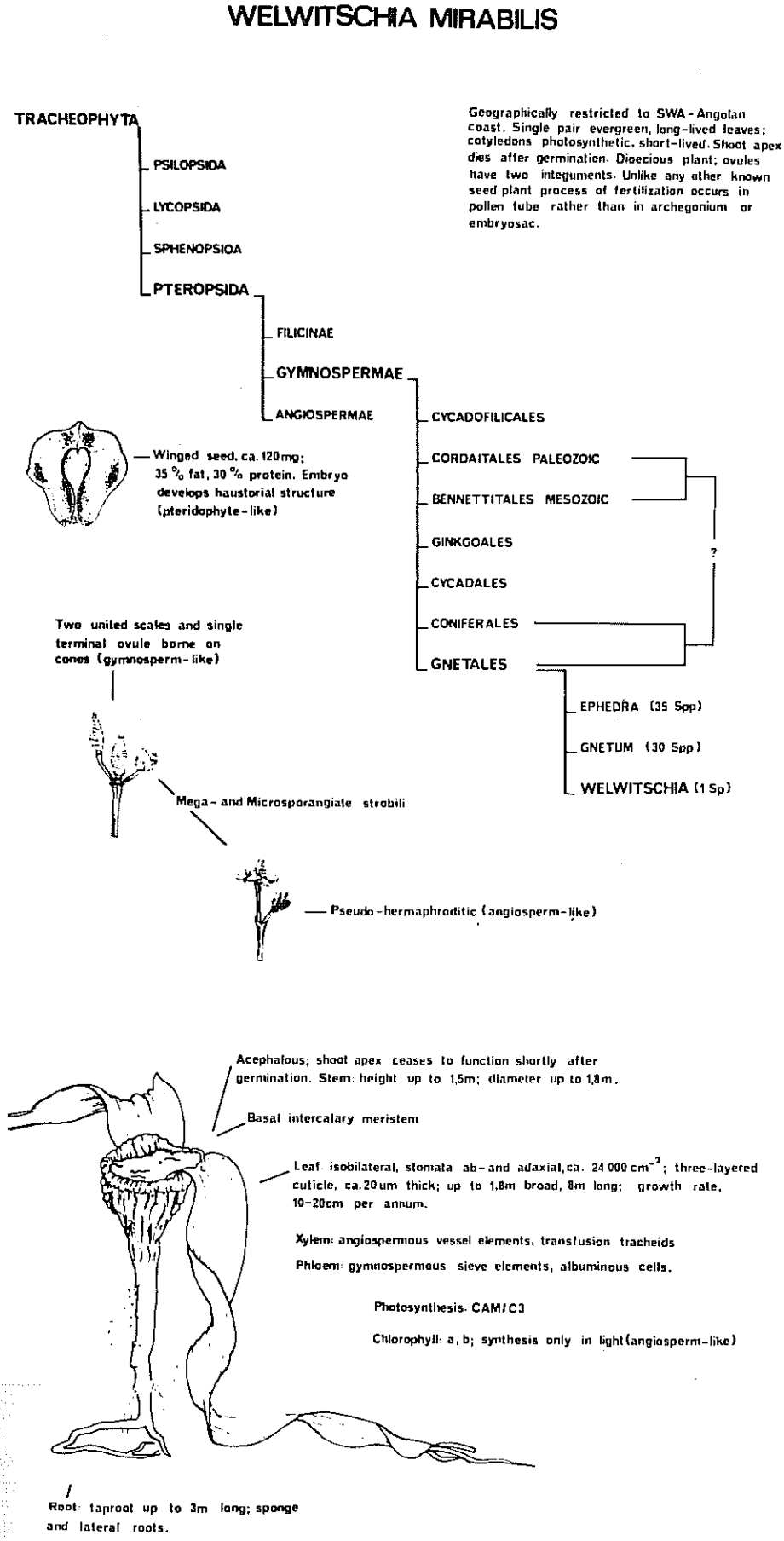

Figure 1. Diagram summarising some of the salient features of *Welwitschia mirabilis*.

The distribution of the genus Aloe in the districts Bethanien, Lüderitz and Warmbad, South West Africa

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CONTENTS

ABSTRACT

The purpose of this study was to do a (preliminary) survey of the distribution of the species of the genus Aloe in the south of South West Africa. All available physical and biotic data were collected to compile the distribution map of the various species. The relative density of each of the different species was also determined. A complete background study was made to search for additional information which may help to explain the distribution patterns. It is clear that certain aloes are associated with the winter rainfall such as *Aloe pearsonii, A. pillansii, A. ramosissima* and *A. erinacea.* Others for instance *A. littoralis, A. hereroensis* and *A. claviflora* grow mainly in summer rainfall areas. *A. pachygaster* showed a marked preferance for soils of limestone or dolomite origin. However, the distribution pattern of certain species such as *A. variegata, A. karasbergensis* and *A. dichotoma,* was very difficult to explain.

1 INTRODUCTION

The larger part of southern Africa can be classified as arid to semi-arid, with periodical droughts occurring over most of the region. Owing to this and the cost of water for irrigation the succulent and drought resistant plants have become more and more sought after as garden plants. During the last decade aloes have become so popular that they probably top the list. Apart from this they have also become a collectors item. Aloe fans are known to travel long distances to collect rare species. The southern parts of South West Africa, with its great variety of succulents and relatively high densities, has become a veritable 'collectors paradise'. With the paving of the roads this area was opened up and an ever increasing number of collectors were attracted. When furniture removal vans, filled with aloes, started leaving the territory the authorities became alarmed. During 1970 a study was launched to determine the distribution of the various species of the genus Aloe, especially in the southern parts of South West Africa. Although the thrust of this study was aimed at the genus Aloe, other succulents occurring in the study area also received attention. The results of this study were used to formulate departmental policy and legislation to protect this particularly interesting heritage in South West Africa.

The genus Aloe shows a wide distribution in South West Africa. It was decided, however, to concentrate on the magisterial districts of Bethanien, Lüderitz and Warmbad in the south-western corner of the territory. This area has, as already mentioned, a big variety and high density of aloes and other succulents The study area covered a surface area of 66 892 sq. km — excluding state land and home land areas — between Latitudes 20° 30′ S and 28° 57′ S and Longitudes 16° E and 20° E.

2 METHODOLOGY

The large extent of the study area raised all sorts of practical problems, the least not being to develop a relatively accurate and quick way of determining status and measuring other factors in the field, which could have some influence on the distribution and status of aloes. It was decided to consider each farm in the study area as a sampling unit. On each sampling unit small plots, 1/16 ha in extent, was set out at random in each locality where aloes occurred. In these plots all available physical and biotic data were collected and the relative density of each of the different aloe species determined. To facilitate this, a table was compiled and completed for each small plot.

Aspects covered in the table was a short topographical description of the immediate vicinity, the direction and degree of slope — the latter measured with an Abney level. Loxton's (1966) method was followed to describe the soil with emphasis on the parent material; colour, number, shape and size of stones. With the aid of the geological map of South West Africa (1964) notes on the geological formations were taken down.

The second important aspect considered, was the associated vegetation in the plot. The most prominent plants were annotated and using Acocks (1955) method, a five point scale reading from poor to very good, the relative density for the associated vegetation was classified. A slightly different method was applied to determine the relative density of aloes. If possible, all the aloes in the plot were counted. The average distance between the aloes was determined and classified according to a five point scale reading from very rare to very common. Very rare, represented a relative density of less than two per sample plot. All these details were later used on the distribution maps. The condition of the aloes was also quantified on a five point scale. The classification was based on phenomena such as: general condition of the aloes; the presence of parasites and/or signs of disease; whether the population was well-balanced for example, was there any evidence of seedlings, young plants etc., and whether the plants were damaged by animals or man.

In conclusion, a small uncontrolled contour map as well as a profile of the sample plot was drawn. Any interesting features were photographed. All the data mentioned as well as the rainfall were statistically tested using the wellknown X^2-test and the binomial test for the purpose of testing relationships between factors which were suspected of having an effect on distribution. These in fact did prove valuable in explaining some of the distribution patterns.

As mentioned earlier, a major problem was the large study area. The results should therefore be regarded as preliminary and not a totally accurate representation of the distributions. Furthermore, during the course of the survey the study area was in the grip of a severe drought and large parts of it were uninhabited.

3 PHYSICAL CHARACTERISTICS OF THE STUDY AREA

3.1 Geomorphology

The study area can be divided into six geomorphological regions (mainly after Barnard, 1964). The Karasberg flats cover the whole of the Warmbad districts except for the Karasberg mountains and South Kalahari in the north, and the mountains of the Orange river trough in the south. Several dry tributories of the Orange river originate in the Karasberg mountains and meander across the plains. The most important rivers are the Gamkab, the Haib, the Hom and the Ham. The geological systems Nama, Karoo and the Granite-Gneiss complex form the basis of the flats. The landscape is dominated by soft sloping granite hills. *Aloe hereroensis* can be found on these hills. On the shale plains the circular and semi-circular patterns formed by *A. claviflora* can be observed.

The Karasberg mountains form a geomorphological region of its own and is an excellent example of fault topography. These mountains are built up by the erosion-resisting Kuibis quartzites and old granite gneiss rocks. A landscape of narrow gorges, irregular gneiss ridges and broad sand valleys is found in this region. Along the mountain slopes *A. dichotoma* is a common sight. *A. karasbergensis* also occur in these mountains.

Immediately west of the Karasberg mountains a small part of the Southern Kalahari region is found. A landscape of sand dunes, "streets" and dry pans typifies this region. No aloes were observed in the dune area, however quite a few *A. hereroensis* were found on the shale ridges which originate from the underlaying Karroo System.

The whole of the Bethanien district can be classified as the hilly region of the Swartrand. These hills are mostly flat-topped with extremely broken and rocky slopes. The region can be subdivided into the Swartrand escarpment (2 000 m) to the east and the lower mountains and ridges (1 000—1 500 m) of the locally known Rooirante, to the west. These two regions are drained by the Konkiep River southwards to join the Fish River. An aloe common to this area is *Aloe pachygaster* which is confined to the dolomite and limestones of the Nama System.

A. littoralis and *A. hereroensis* occur along the slopes of the Swartrand escarpment and the ridge of the Rooirante.

To the west of this region, stretching from north to south, lies the Western escarpment. For the greater part the escarpment is not clearly defined and near Aus and Witputs wide valleys intersect the mountains. The escarpment rises to a height of 1 500 to 1 800 m and is built up by the old granite gneiss rocks which are sometimes covered by the Nama System. *A. pachygaster* is readily found on the dolomite and limestones of the Schwarzrand series (Nama System). Furthermore *A. dichotoma*, *A. pillansii, A. ramosissima, A. pearsonii* and several other species also occur in these mountains. A few rivers originate in the mountains, continuing westwards to disappear in the Namib desert.

To the west of the escarpment the landscape is dominated by the sandflats and insel mountains of the southern Namib. On these mountains a few hardy *A. dichotoma* and *A. ramosissima* struggle to survive in the desert conditions.

3.2 Soils of the study area

Van der Merwe (1962) classified the soils of the study area into two main groups namely: the Sands of the Kalahari and the Soils of the Desert and Semi-desert areas. Basically, the geology and the soils are closely related because the low rainfall prohibits chemical weathering to a large extent.

3.3 Climate

The climate proved to be the most important factor in explaining the distribution patterns of genus Aloe. The cold Benquela current, the St. Helena anticyclone, the relatively high humidity (80%) caused by the cold sea, and the prevailing west and southwesterly winds, are the main factors responsible for the mist conditions along the western escarpment and in the Orange River trough. The small amount of winter rainfall is caused by the northerly movement of the cold fronts normally responsible for rains in the Western Cape. It must however be stressed that a certain amount of summer rainfall reach this area. This means that the area gets a small amount of rain throughout the year, as illustrated by the following table.

	Tsirub (13) *(Lüderitz district)*	Witputz-Süd *(Lüderitz district)*
January	6,9	5,5
February	4,3	10,3
March	19,0	13,4
April	7,3	10,9
May	3,8	7,6
June	10,8	9,5
July	9,5	7,1
August	8,4	6,1
September	3,0	3,5
October	1,4	2,0
November	1,4	5,5
December	2,5	5,3

These mountains contain a unique variety of aloes in this so-called winter rainfall area.

In the summer humid air enters the study area from the north and east and the rare showers are convection storms. The isohyets follow the contour lines, the rainfall decreasing as the landscape falls away in a westerly direction. The rainfall fluctuates between 50 mm and 200 mm per year. The high intensity of the storms, their irregularity, high evaporation and high drainage limit the efficiency of the summer rainfall to a large extent.

Rainfall however plays a very important part in the distribution of certain aloes and is one of the main factors used to clarify the distribution patterns of the different species.

4 BIOTIC BACKGROUND

4.1 Vegetation

The basic classification of the vegetation is based on the work of Giess (1971).

4.1.1 Dwarf shrub savanna

Approximately 80 per cent of the Warmbad and Bethanien districts are covered by this vegetation type. The trees, such as *Acacia karroo, Ziziphus mucronata, Euclea pseudebenus* and *Rhus lancea,* are mostly confined to the dry washes. The only trees adapted to the extremes outside the rivers are *Boscia foetida, Pappea capensis, Ozoroa namaensis, Parkinsonia africana* and a rare *Acacia erioloba.* The tree layer varies from two to six meters. The shrub layer could be divided into large shrubs up to 1,5 to 2 meters, such as *Cataphractes alexanderi, Phaeoptilum spinosum, Rhigozum trichotomum, Acacia nebrownii.* A second layer varies from 20 cm to approximately 1 meter. The following species are dominant:

Petalidium linifolium, Aizoon schellenbergii, Barleria lancifolia, Salsola tuberculata, Zygophyllum ssp., Eriocepholus ssp., Pteronia luciliodes

The grasses common to this area are perennials such as:

Stipagrostis ciliata, S. obtusa, S. uniplumis, Antephora pubescens

and annuals such as:

Schmidtia kalahariensis, Enneapogon brachystachyus, Eragrostis nindensis.

In conclusion great grass plains broken by dry washes with shrubs and a lonely tree typify this vegetation type.

4.1.2 Desert and succulent steppe

This vegetation type occurs in the southern half of Lüderitz district and follows the Orange River westwards, from approximately the middle of the Karasburg district. The vegetation is closely related to the influence of the winter rainfall. The effectivity of the precipitation is responsible for an exceptionally rich species-composition. The landscape is dominated by a dense succulent shrub layer which varies from 30 cm to 1 m +. In dry years grasses are rare. Trees are confined to the drainage systems except tree-aloes such as *Aloe pillansii* and *A. dichotoma.*

Trees such as:

Acacia erioloba, Boscia foetida, Euclea pseudebenus, Ozoroa namaensis, Schotia afra

are confined to the dry rivers.

Aloe ramosissima dominates the higher shrub layer and can grow up to a height of 4 metres. Other shrubs that should be mentioned are:

Ceraria fruticulosa, Ceraria namaquensis, Zygophyllum namaquensis, Hermannia grandiflora and *Euphorbia* ssp.

The succulent layer consists mainly of the following families:

Mesembryanthemaceae, Zygophyllaceae, Portulacaceae, Crassulaceae, Euphorbiaceae and Asclepiadaceae.

To the north perennial grasses such as *Stipagrostis ciliata* and *Stipagrostis obtusa* occur.

The strange and interesting cactus-like *Pachypodium namaquanum* also known as elephant's trunk, could be used as an indicator or character species for this vegetation type. The greatest variation of aloe species was found in this region.

4.1.3 Mixed tree and shrub savanna

This vegetation type is also known as the Southern Kalahari savanna. It occurs only in the north-western corner of the Karasburg district. *Aloe hereroensis* was the only aloe observed in this region.

The trees occur mainly on the slopes of the dunes and *Acacia haematoxylon* is very typical for this vegetation type.

The shrub layer is quite often well developed and varies in heigh from 0,6 m to 3 m on the average. The most common species are:

Grewia flava, G. deserticola, Acacia mellifera ssp. *detinens, Rhigozum trichotomum, Phaeoptilum spinosum* and *Acacia hebaclada.*

They occur mostly in the washes and dune streets. The grasses are mainly:

Stipagrostis ciliata, S. uniplumis, S. ambilis, Eragrostis lehmanniana and the annual *Schmidtia kalahariensis* is a common pioneer in over-grazed area.

4.1.4 The semi-desert and savanna transition (Escarpment Zone)

The vegetation in the mountainous areas of the escarpment in the north of Lüderitz and Bethanien districts is representative of the above-mentioned vegetation type.

The trees are mostly confined to the well-watered narrow kloofs. The most common species being:

Ficus ssp. mainly *Ficus cordata, Acacia karroo, Ziziphus mucronata* and *Rhus lancea.*

In the mountains *Aloe dichotoma* is very often quite prominent. An interesting feature is the adaptations of *Boscia foetida* which varies its growth form from a tree to a low-growing or even a creeping type of shrub.

The shrub layer is well-developed and is on the average seldom more than 2 meters in height. Species such as:

Eberlanzia spinosa, Cadaba aphylla, Zygophyllum ssp., *Rhigozum trichotomum, R. obovatum* and *Phaeoptilum spinosum.*

The grass layer consists of the following species: *Digitaria dinteri, Anthephora pubescens, Stipagrostis ciliata* and *S. obtusa.*

4.1.5 Riverine woodlands

The alluvial soils and greater water supply in the riverbeds are responsible for this vegetation type. The tree layer do not exceed 10 meters. The most common species are:

Euclea pseudebenus, Acacia karroo, Acacia erioloba, Ziziphus mucronata and *Rhus lancea.*

The shrub layer is usually also well developed and is on the average approximately 2 to 3 meters high. Most common species are:

Tamarix usneoides, Rhus viminalis, Grewia flava, Phaeoptilum spinosum and *Rhigozum trichotomum*, etc.

Sometimes *Juncus* sp. and *Phragmites* sp. grow in the riverbeds especially near fountains. The Orange River is the only perennial river in the south of South West Africa.

4.2 The infuence of man and his activities

People influence the local distribution of aloes in the way of farming and collecting. Sheep had evidently grazed *Aloe karasbergensis* and *A. claviflora.* However grazing does not seem to be as great an influence as trampling. To a certain extent proof of this was found on the farm Oas (29), in the Warmbad district where a camp was not utilized for a certain period. *A. hereroensis* was found to occur in and around the camp, but a very marked difference was the amount of young plants and seedlings in the camp.

People collecting aloes is another factor endangering this genus. Even though the South West Africa Administration has enforced laws to protect these plants, it is still a known fact that great numbers of them are removed from their natural habitat.

4.3 The influence of parasites

The well-known *Loranthus* sp. found on *Aloe ramosissima,* is so far the only plant parasite observed. Although it may influence the growth of the plant, it is rather improbable that it will influence the distribution pattern of the species to any noticeable extent. Aloes are however rather susceptible to different species of the parasite, Coccidae. On the farm Schwarzeck (130) in the Warmbad district, it was found that the pest-scale influenced the status of the aloes, by killing large numbers of the plants. This scale is especially effective in times of drought. Two species were identified as *Separaspis capensis* Walker and *Duplachinaspis brevipora.*

Other pests are *Eriophys aloinis* an aloe cancer and the well-known "vrot" caused by an insect which is a member of the genus Brachycerus. The last two mentioned pests are rather seldom encountered, so it is not likely that they are responsible for any great loss of plants.

4.4 The influence of wild animals

The following plant-eating animals are known to live in the study area. Springbok *Antidorcas marsupialis,* steenbok *Raphicerus campestris,* gemsbok *Oryx*

gazella, klipspringer *Oreotragus oreotragus*, mountain zebra *Equus zebra hartmannae*, kudu *Tragelaphus strepsiceros*, baboon *Papeo ursinus*, and dassies *Procavia capensis*. Of all these animals, it was observed that the last three definitely feed on the aloes. Baboons are perhaps the only ones that cause great damage to the plants, because it was found that they often destroy the whole plant. There were several occasions where the author observed that *A. hereroensis*, *A. gariepensis* and *A. dichotoma* were severly damaged. Kudus and dassies definitely eat aloes as observed respectively by Van der Schijf (1959) and Swart (1970), but unfortunately the actual amount of damage could not be determined.

5 THE DISTRIBUTION PATTERN OF THE DIFFERENT SPECIES

The distribution of certain aloes is definitely associated with climatic conditions and for the purpose of this study they are grouped together.

5.1 Aloes associated with winter rainfall

These aloes occur in the Desert and Succulent steppe vegetation type (Giess 1971). Their distribution is accordingly related. Although all the other environmental factors were tested the winter rainfall and mist conditions proved to be the only satisfactory explanation for their distribution. The fact that in some cases, for example *Aloe pearsonii*, the plants are mainly confined to the south and south-western aspects, emphasize the important role of the prevailing rains from the west.

5.1.1 *Aloe pearsonii* Schonl

In South West Africa *Aloe pearsonii* (plate 1) is limited to three farms in the south of the Lüderitz district (map 1) and it is also known to occur in some of the mountains in Diamond Area No. 1 and state land. It is however a quite common aloe in the neighbouring Richtersveld across the Orange River to the south. Locally the plants cover whole mountain slopes and there is a definite preference for rather steep south-western slopes ($\pm$ 15—20°). Although the aloe is very limited in its distribution the fact that it occurs in such large numbers sometimes many thousands, is to some extent, reassuring.

5.1.2 *Aloe pillansii* L. Guth

This tall aloe (plate 2) quite often over 10 m high, is one of the rarest aloes in South West Africa. This species is confined to three farms (map 2) and is known to occur in the stateland to the south and west of these farms. The aloes occur from the Orange River northwards for approximately 50 km. Similarly to *A. pearsonii*, they prefer the mountains and are protected from man in that they mostly occur in relatively inaccessable localities in the mountains of the western escarpment. They sometimes do occur on the sandy plains between the mountains.

5.1.3 *Aloe ramosissima* Pillans

The most northern locality of the species is approximately 100 km north of the Orange River, on the farm Pockenbank no. 68 in the Lüderitz district (map 3). The plants grow as shrubs (plate 3) and although their distribution is related to climate there is however no preference for mountains or plains. Very often large numbers were observed near or at the foot of a slope. The occurrence of a plant parasite on this species was a very interesting feature, as already mentioned.

5.1.4 *Aloe microstigma* Salm Dyck

This aloe (plate 4) occurs only in the southern and central parts of the Lüderitz district. Its distribution extends northwards from the farm Witputz-Süd (31) northwards to the farm Kubub (18) and Plateau (38) in the north (map 4). The local distribution is interesting as it grows on rocky outcrops as well as on the level plains in clusters or as individuals. Another interesting feature is that the species is quite common in the Western Cape, there being a very wide gap in its distribution in the Republic and in South West Africa.

5.1.5 *Aloe erinacea* Hardy

One of the rarest aloes (plate 5) in the world, it is endangered by the fact that it is not only very limited in its numbers, but also in its distribution (map 5). The plants occur mainly on the warmer north-western and north-eastern aspects. This is to some extent a paradox, considering the fact that it is the western side of the mountains which is under the influence of the mist and winter rainfall conditions. The only apparent explanation for this deviation must be in the intrinsic properties of the plant. Efforts to transplant the species into the summer rainfall area met with limited success which strengthens the fact that it is a winter rainfall aloe of the first order.

5.1.6 *Aloe gariepensis* Pillans

This aloe (plate 6) occurs in and along the southern sides of all three districts in the study area (map 6). In Warmbad district it forms a girdle which runs more or less parallel with the Orange River, with the most northern point not further than 50 km from the river. After testing the information statistically one can conclude that these aloes normally do not occur in areas with more than 100 mm of rain per annum. When correlated with the associated vegetation a significant relation was found with the succulent vegetation related to the winter rainfall. Although perhaps not so outstanding there is definite indications that the aloe could rather be classified as a winter rainfall aloe than a summer rainfall aloe. In most cases it prefers a slope of more than 10 degrees and considering the already low rainfall there is an apparent preference to well drained soils.

On the farm Schwarzeck (130) Warmbad district the author observed how the detrimental influence of scale in combination with drought conditions were responsible for the dying out of nearly 200 plants of this species. On several occasions baboons were not only responsible for eating the inflorescence, but also for the destruction of whole plants by removing the apices and eating only the juicy parts. Parasites and animals may thus play a role in the local status of the species.

5.2 Aloes associated with summer rainfall

5.2.1 *Aloe littoralis* Bak (A. rubrolutea Schinz)

This aloe (plate 7) is very common in the central and northern parts of South West Africa. In the study area however it occurs widely in the Bethanien district with two isolated occurrences, one each in the Warmbad and Lüderitz districts (map 7). Some interesting features about this aloe is that it is a wellknown host to scale. Sometimes the parasites cover the leaves to such an extent that they appear to be white. The flowering time of the species in the south differs completely from the same species in the central and northern parts of the country. In the north the plant flowers from March to May and in the south during November.

5.2.2 *Aloe hereroensis* Engler

These aloes (plate 8) occur on nearly every farm in the northern parts of the Bethanien, Lüderitz, as well as in the northern and eastern parts of the Warmbad districts. The most southern locality was on the farm Graswater (150) which is approximately 60 km south-east of Warmbad (map 8). The adaptability of the aloe is excellent because it will grow on nearly any terrain from sandy plains to rocky outcrops. However it has a preference for the higher rainfall area, especially between 100 and 150 mm per annum in the study area. An interesting observation was made on the farm Oas 29, Warmbad district, where the owner of the farm did not utilize a certain camp for several years. The total number of *Aloe hereroensis* counted in a 1/16 ha unit was 47, mostly young plants and numerous seedlings. Sheep farming obviously limited the growth of young plants. Furthermore, it was observed that baboons destroyed the plants so that it could be stated that man and animals constitute a limiting factor to the natural distribution of the species.

5.2.3 *Aloe claviflora* Burchell

In the study area *A. claviflora* (plate 9) was found only in the Warmbad district (map 9). It is however a very common species in the northern and Central Cape Province and western Orange Free State.

A. claviflora occurs in nearly the whole of the district, but its numbers are very limited in the Karas Mountains and in the Orange River trough. Except for two observations, they were not found to occur below the 50 mm isohyet and they did not occur north of the 150 mm isohyet. Rainfall would thus be a limiting factor. The plants occur mostly on level ground, having no aspect preference; the soils are sandy, quite often of shale origin and rather alkaline. Only one record could be obtained of this plant being utilized by sheep.

5.3 Aloes associated with soils

5.3.1 *Aloe pachygaster* Dinter

This aloe (plate 10) is limited to Lüderitz and Bethanien districts. It is commonly found in the whole southern half of Lüderitz district, stretching northwards from the Orange River to Aus vicinity. In Bethanien district the most northern locality is in the vicinity of Helmeringhausen (12). To the south numerous small colonies could be found, where Vergelee (169) and Moedhou (182) are the most southern localities (map 10). An interesting fact is that the Fish River forms apparently a natural eastern boundary for the species.

Of all the ecological factors measured the most outstanding feature was the association of this aloe with dolomite and limestone soils. The interesting phenomenon is that soils derived from limestone or dolomite are clayey and are wellknown for their bad drainage ability and this is of cause in conflict with the acceptance that aloes prefer well-drained soil. Nevertheless there is no doubt whatsoever that *Aloe pachygaster* is associated with dolomite and limestone soils.

Similar to *A. claviflora* there is a preference for rather level ground with no affinity for any aspect. This could perhaps be explained that if the slopes were too steep all the water would have run away before getting the opportunity to wet the clayey soil. Furthermore in contrast to other aloes it is apparently adapted to badly drained soils and will not rot or drown under its natural low rainfall conditions.

5.4 Aloes associated with both winter and summer rainfall and no preference for any ecological feature

5.4.1 *Aloe variegata* L.

Aloe variegata (plate 11) known as kanniedood, typifies this small aloe's ability to adapt itself to nearly any environment. The aloe is difficult to observe because it seldom grows higher than 20 cm and tends to grown in or under bushes and rock-crevices. Bearing this in mind the author would not like to bind himself to the given distribution map (map 11) because there may still be numerous localities which were overlooked. In conclusion it can be stated that it does occur in both summer and winter rainfall areas and no definite association with any of the measured environmental factors could be proved.

5.4.2 *Aloe karasbergensis* Pillans

This species (plate 11) is represented in all three districts forming the study area (map 12). Basically one can localize their occurrence into three main zones namely: The western escarpment, the northern part of the Karas mountains and a narrow strip between the Fish River and Grunau. *A. karasbergensis*

displays two growth forms and the author classified them into a "mountain type" and a "sandveld type". The latter tends to form clusters while the mountainous type mostly occurs individually. Similar to *A. claviflora*, *A. karasbergensis* was also observed to be eaten by sheep apparently to restore some or other mineral shortage probably potassium. Although all the possible environmental factors were tested no definite reason could be found for the specie's strange distribution pattern.

5.4.3 *Aloe dichotoma* Masson

Aloe dichotoma (plate 13) occurs in nearly the whole study area except in the north-eastern corner of Bethanien, the western section of the district Lüderitz and the north-eastern corner of the district Warmbad (map 13). It is apparent that *A. dichotoma* is well adapted to its environment with no particular preference for parent soil, aspect, etc. An interesting feature observed however, is the tendency to change its growth form, in more arid regions. It will for instance grow to three or four meters before branching. The author even observed plants growing up to 8 m with no branching at all. Furthermore it is associated with both summer and winter rainfall vegetation. There is also a slight preference for rather steep slopes considering the dense populations which often occur against mountains. In conclusion it was observed that baboons are very fond of the inflorescence of the plants. By feeding on it the flowers are destroyed and eventually very few seeds are left to promote the reproduction of the plants.

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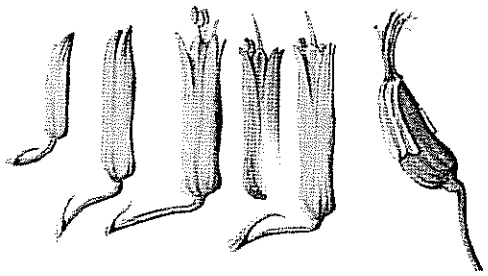


Plate 1. *Aloe pearsonii* Schonl

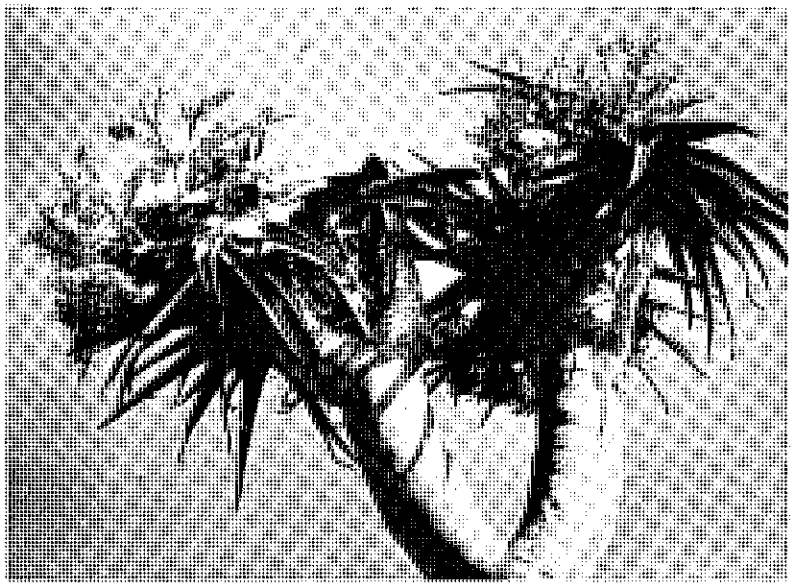
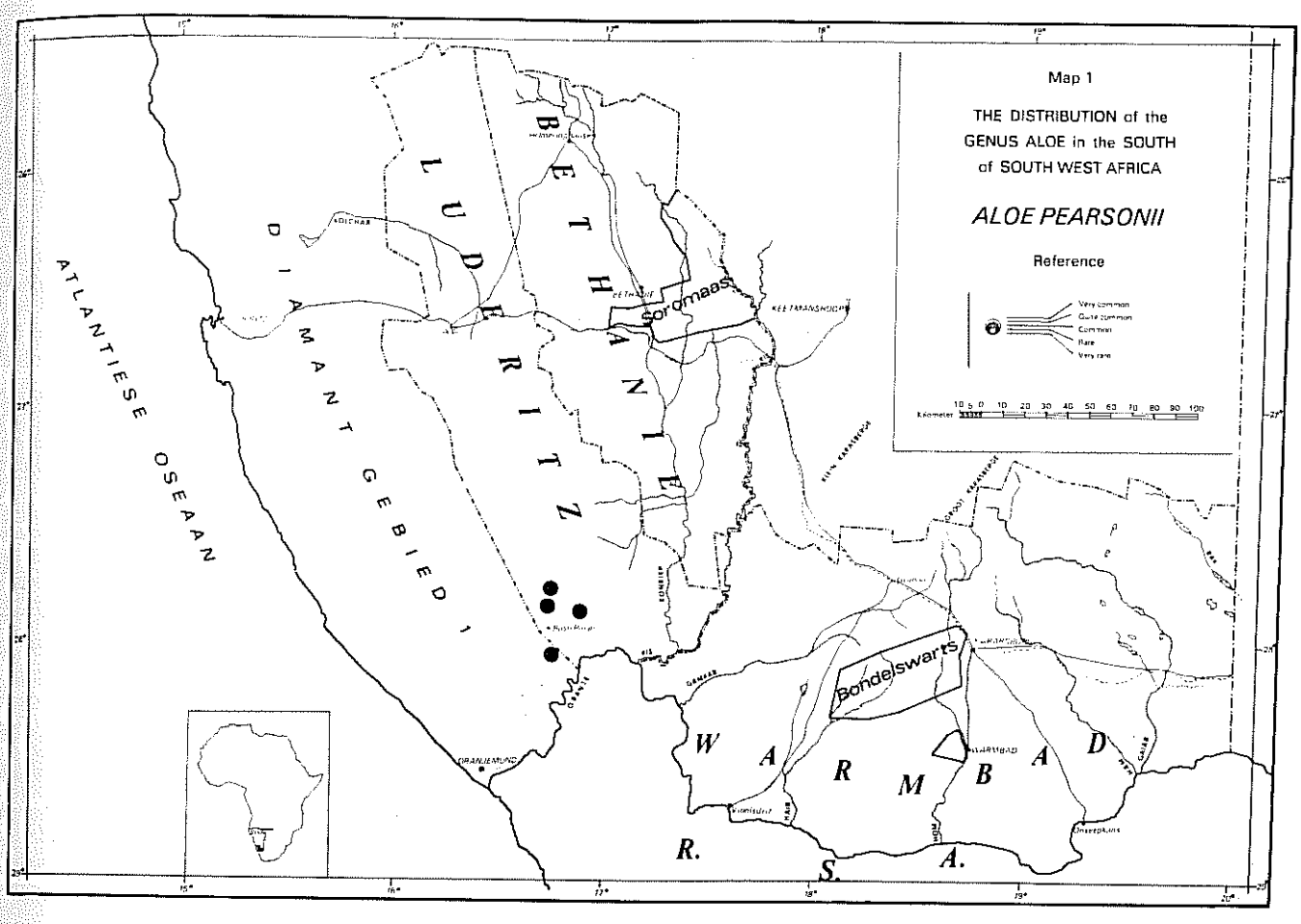
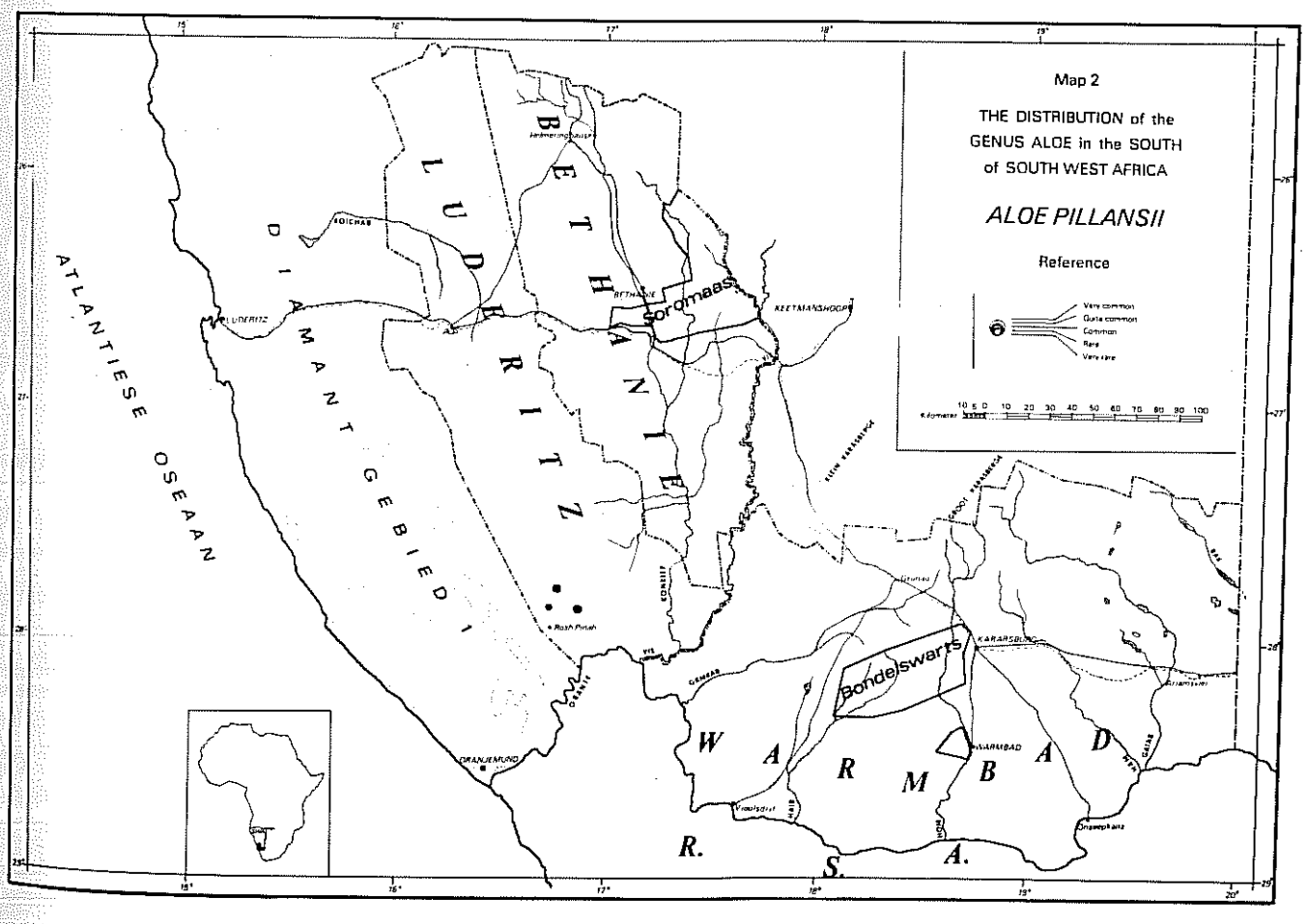


Plate 2. *Aloe Pillansii* L. Guth


Map 1
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE PEARSONII
Reference
Very common
Quite common
Common
Rare
Very rare
Kilometer
ATLANTIESE OSEAAN
DIAMANT GEBIED 1
LUDERITZ
BETHANIE
Sorgmaas
KEETMANSHOOP
Bondelswarts
KARASBURG
WARMBAD
GRANIET
ORANJEMUND
R. S. A.


Map 2
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE PILLANSII
Reference
Very common
Quite common
Common
Rare
Very rare
Kilometer
ATLANTIESE OSEAAN
DIAMANT GEBIED 1
LUDERITZ
BETHANIE
Sorgmaas
KEETMANSHOOP
Bondelswarts
KARASBURG
WARMBAD
GRANIET
ORANJEMUND
R. S. A.

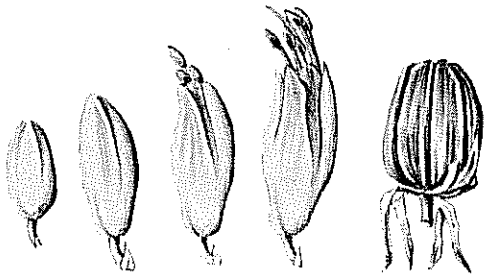
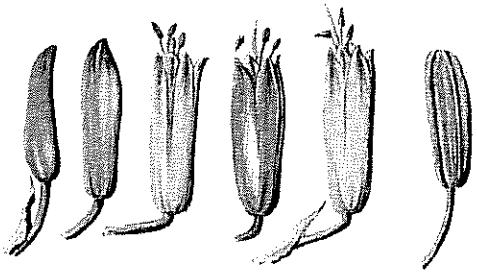


Plate 3. *Aloe ramosissima* Pillans



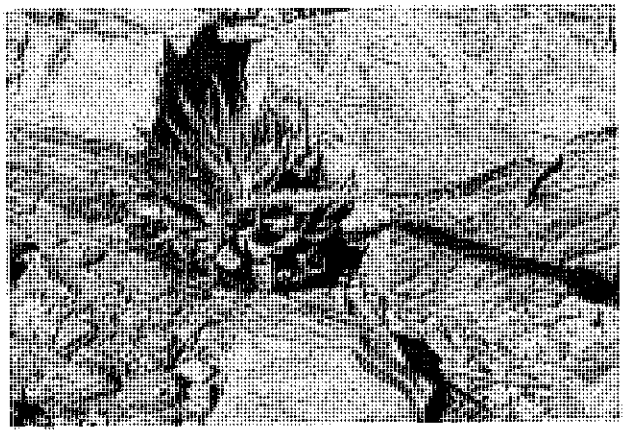
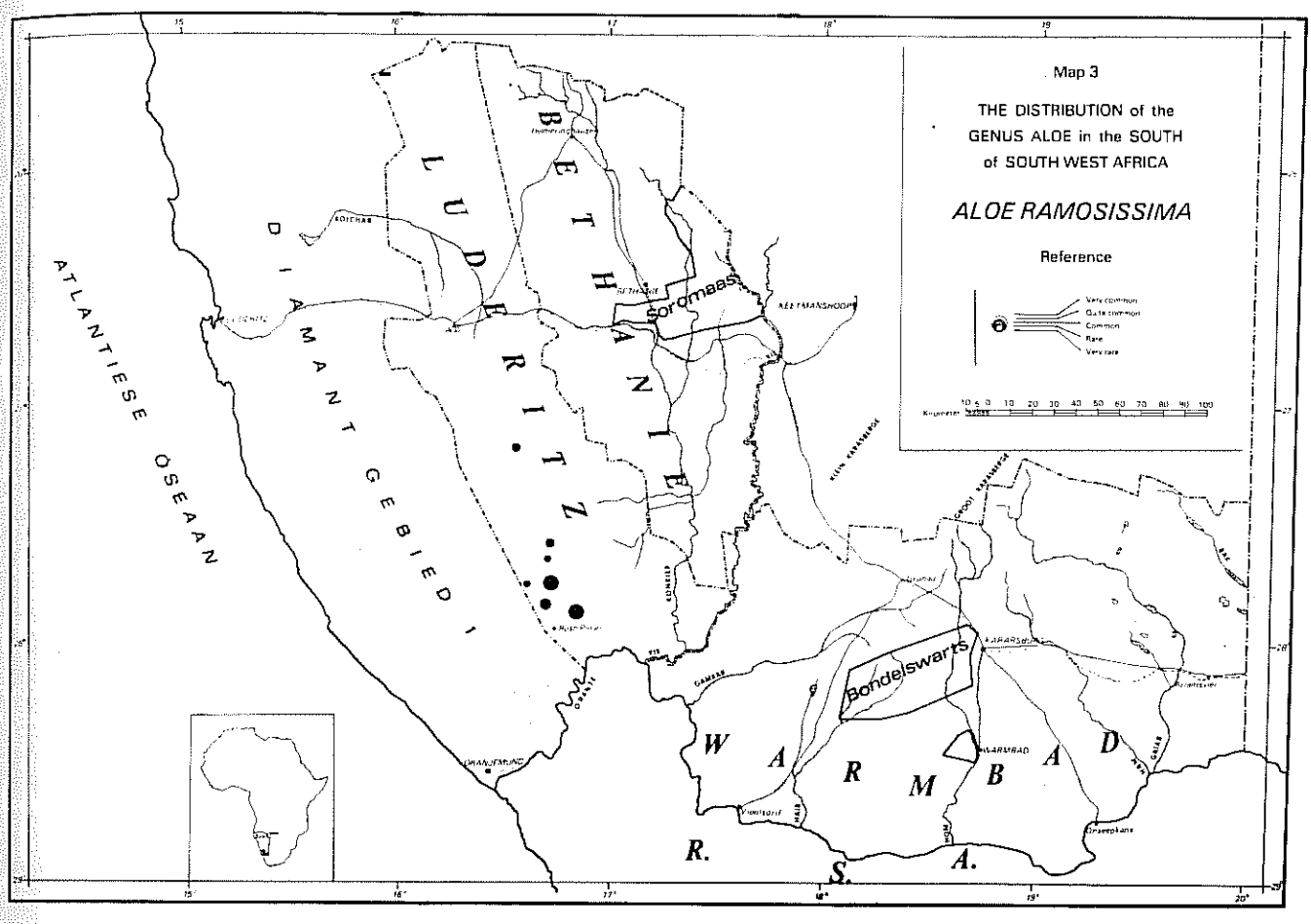
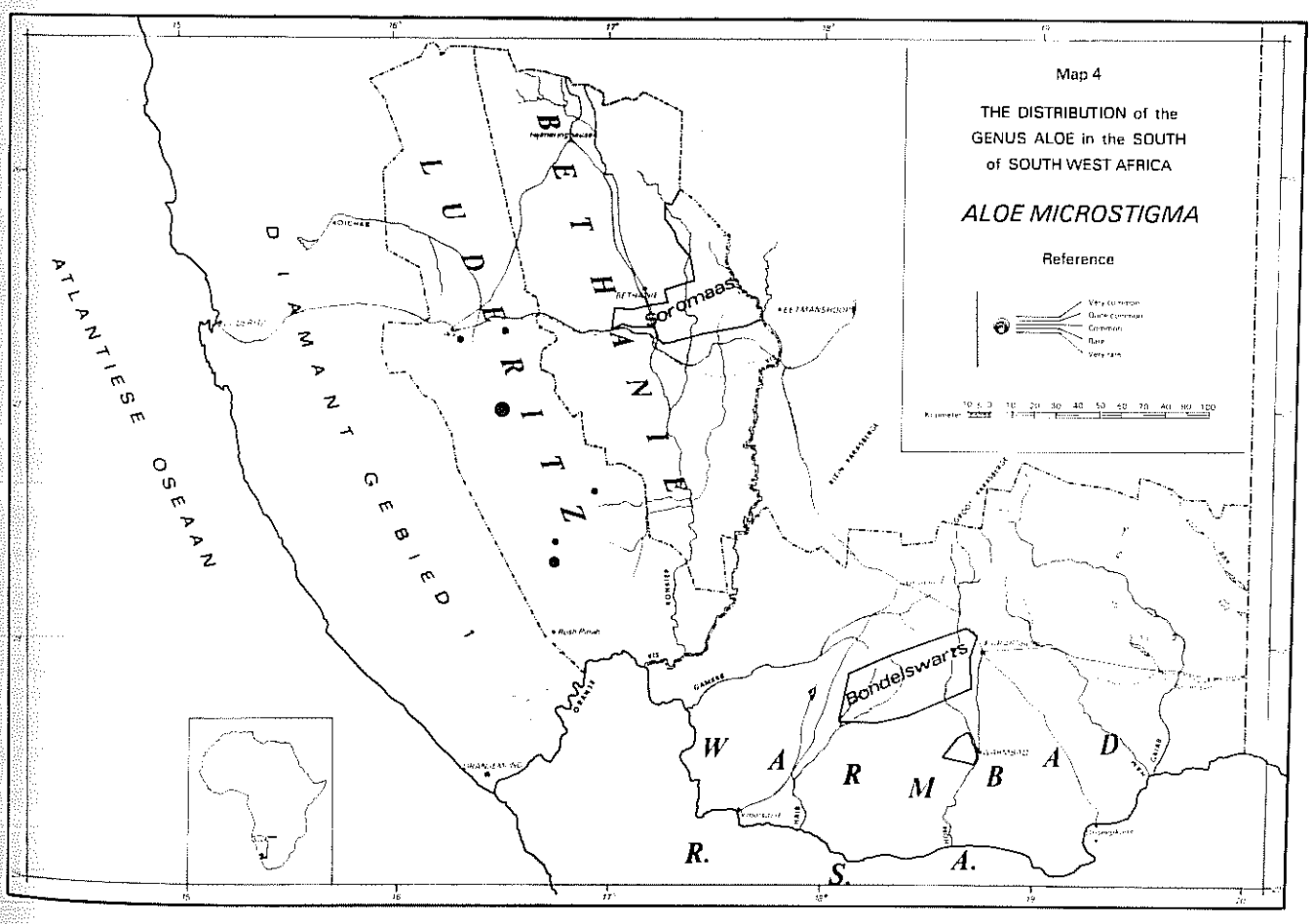
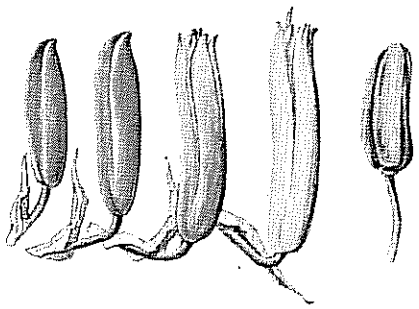


Plate 4. *Aloe microstigma* Salm Dyck


Map 3
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE RAMOSISSIMA
Reference
Very common
Quite common
Common
Rare
Very rare
ATLANTIESE OSEAAN
DIAMANT GEBIED
LÜDERITZ
BETHANIE
Sorgmaas
Bondelswarts
WARMBAD
R. S. A.


Map 4
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE MICROSTIGMA
Reference
Very common
Quite common
Common
Rare
Very rare
ATLANTIESE OSEAAN
DIAMANT GEBIED
LÜDERITZ
BETHANIE
Sorgmaas
Bondelswarts
WARMBAD
R. S. A.



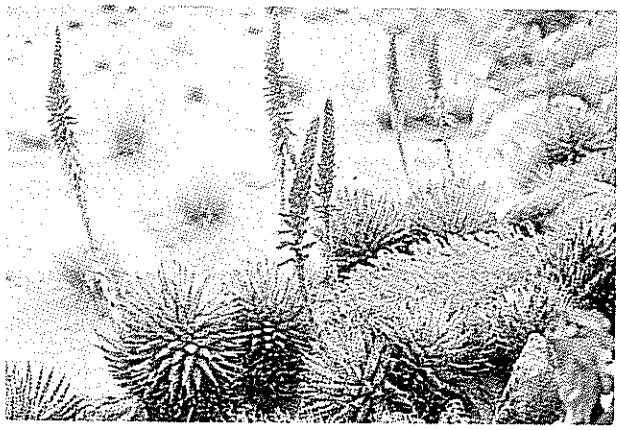


Plate 5. *Aloe erinacea* Hardy

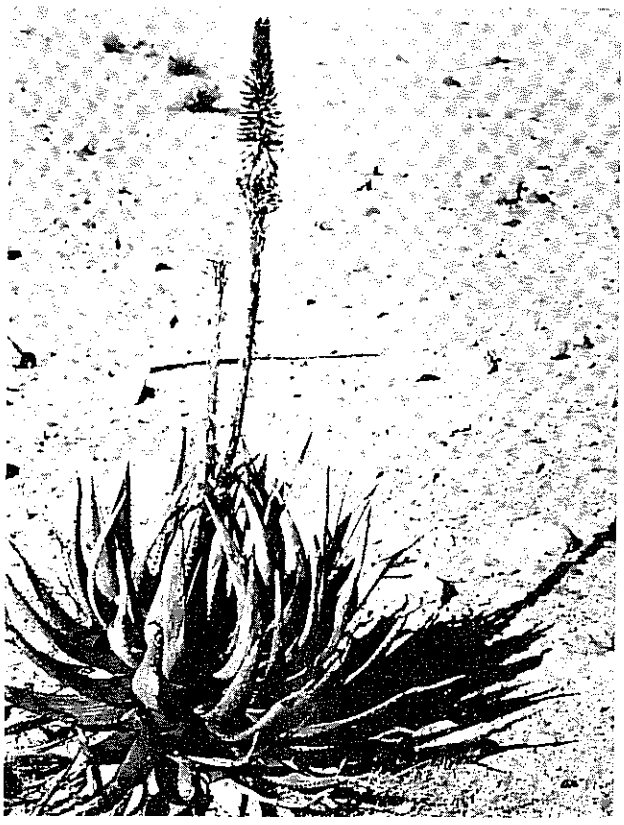
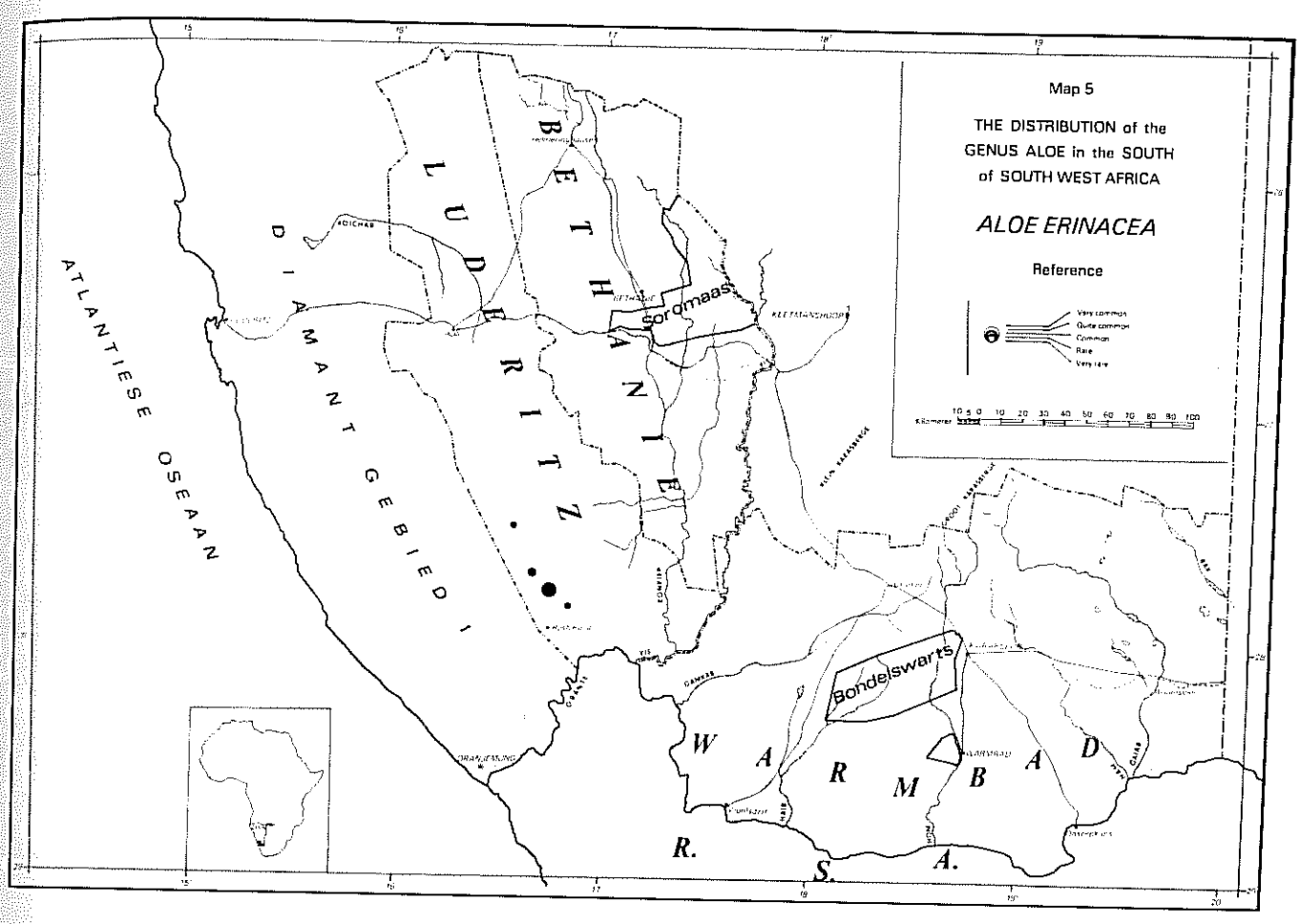
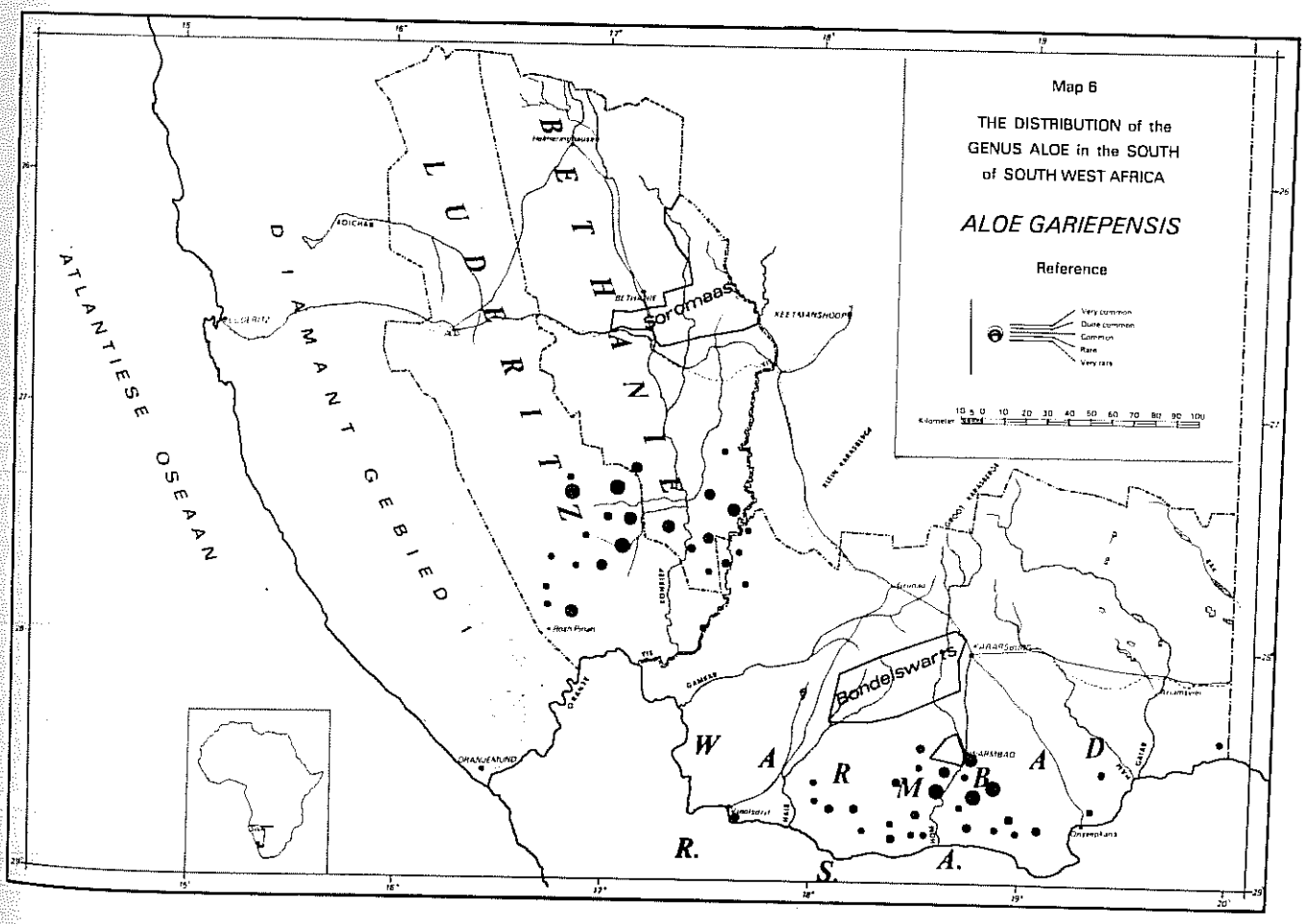
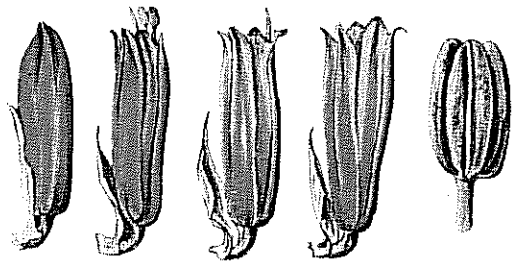


Plate 6. *Aloe gariepensis* Pillans


Map 5
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE ERINACEA
Reference
Very common
Quite common
Common
Rare
Very rare
Kilometer
ATLANTIESE OSEAAN
DIAMANT GEBIED
LUDERITZ
BETHANIE
Sorgmaas
Bondelswarts
WARMBAD
R.
S.A.


Map 6
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE GARIEPENSIS
Reference
Very common
Quite common
Common
Rare
Very rare
Kilometer
ATLANTIESE OSEAAN
DIAMANT GEBIED
LUDERITZ
BETHANIE
Sorgmaas
Bondelswarts
WARMBAD
R.
S.A.



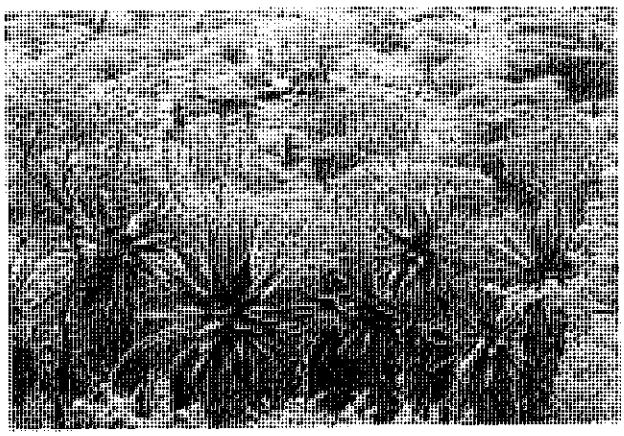


Plate 7. *Aloe littoralis* Bak (A. rubrolutea Schinz)

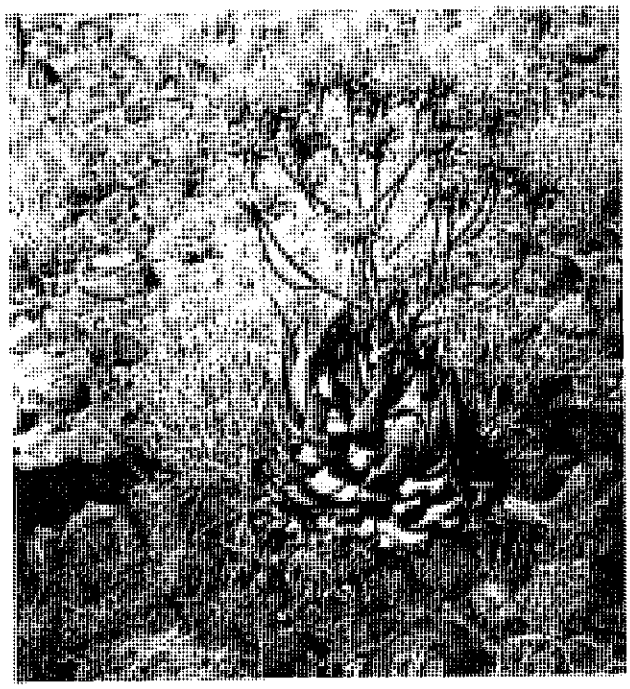
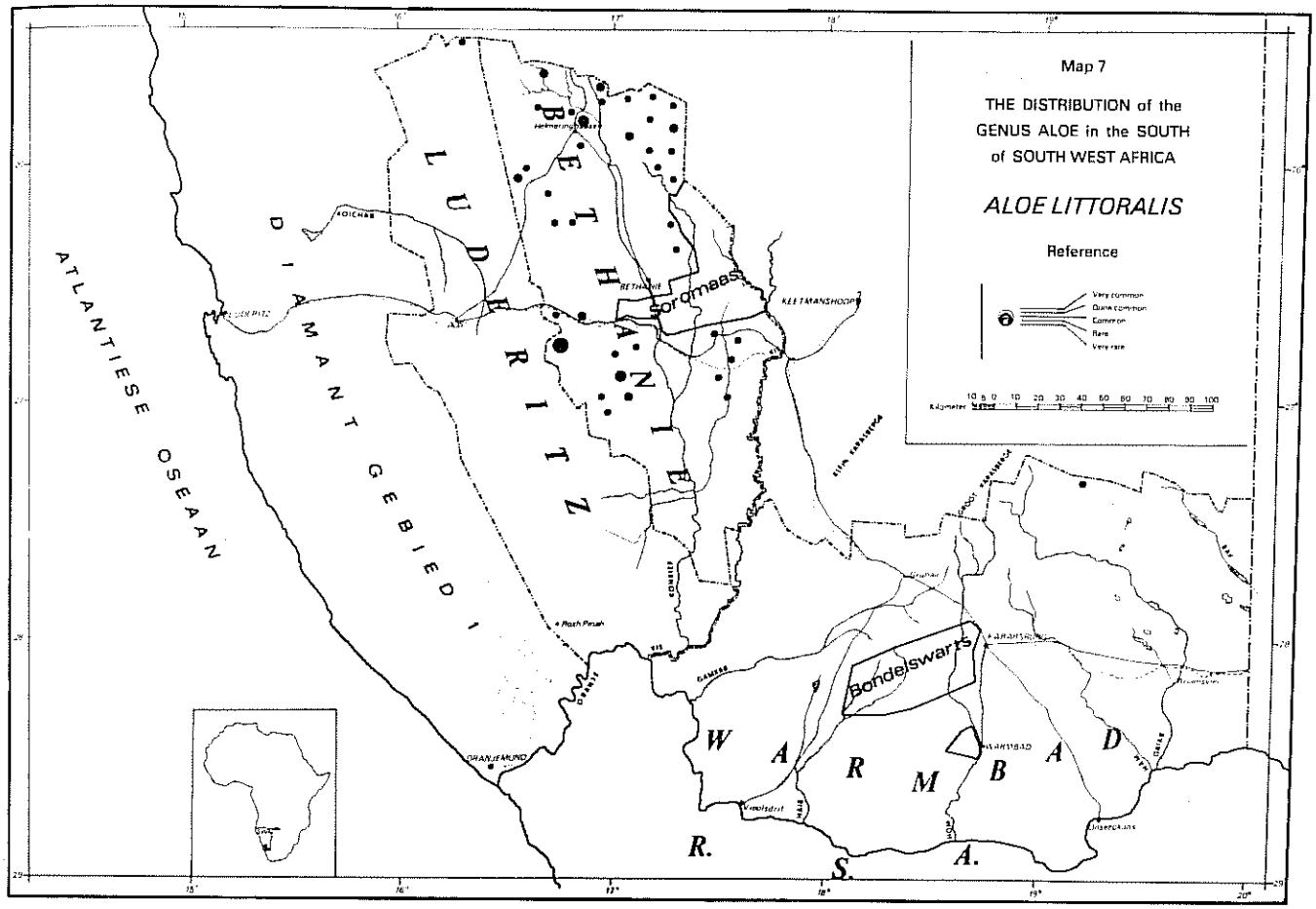
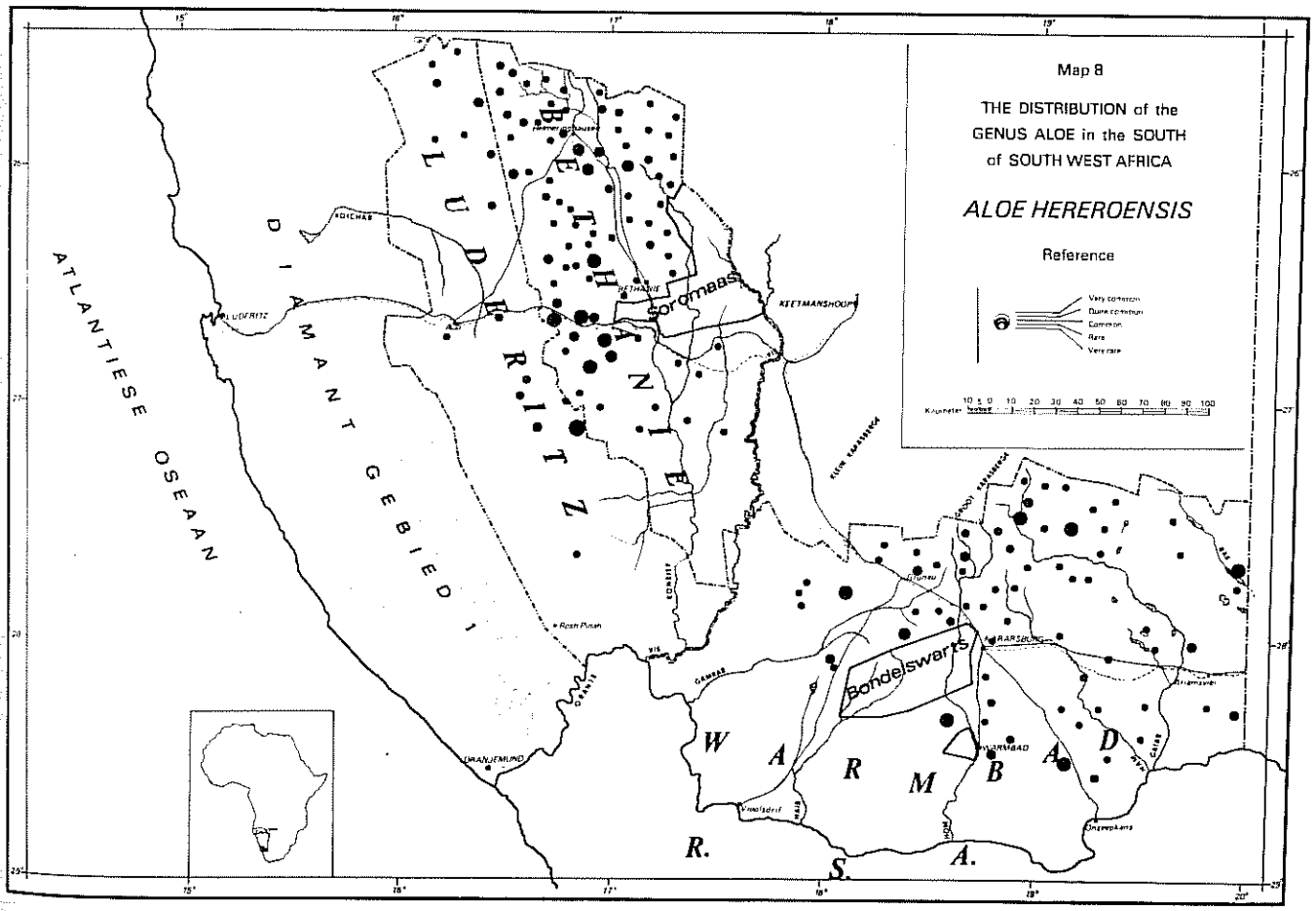
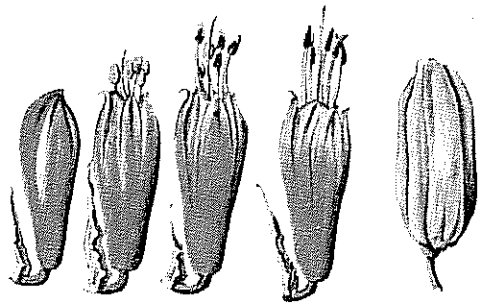


Plate 8. *Aloe hereroensis* Engler


Map 7
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE LITTORALIS
Reference
Very common
Quite common
Common
Rare
Very rare
ATLANTIESE OSEAAN
DIAMANT GEBIED 1
LUDERITZ
BETHANIE
HANIES
ZORITZ
Soromaas
KEETMANSHOOP
Bondelswarts
KARASBURG
KARIGIBAD
ORANJEMUND
Rosh Pinah
W A R M B A D
R. S. A.


Map 8
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE HEREROENSIS
Reference
Very common
Quite common
Common
Rare
Very rare
ATLANTIESE OSEAAN
DIAMANT GEBIED 1
LUDERITZ
BETHANIE
HANIES
ZORITZ
Soromaas
KEETMANSHOOP
Bondelswarts
KARASBURG
KARIGIBAD
ORANJEMUND
Rosh Pinah
W A R M B A D
R. S. A.



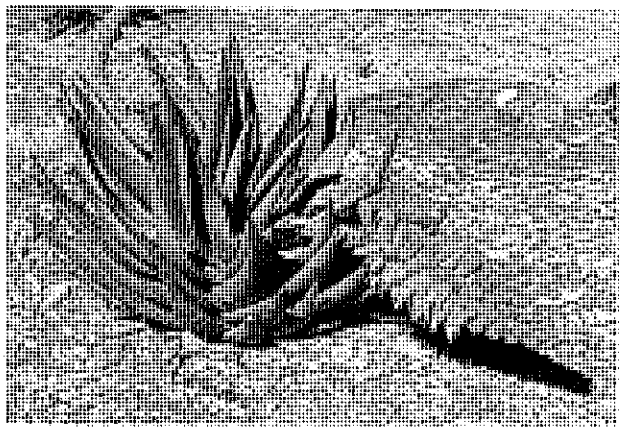
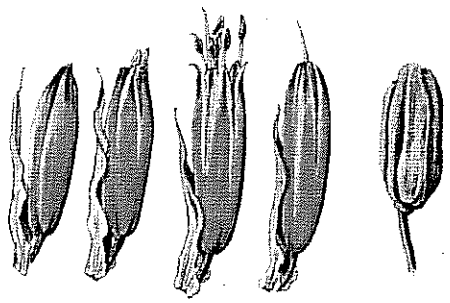


Plate 9. *Aloe claviflora* Burchell



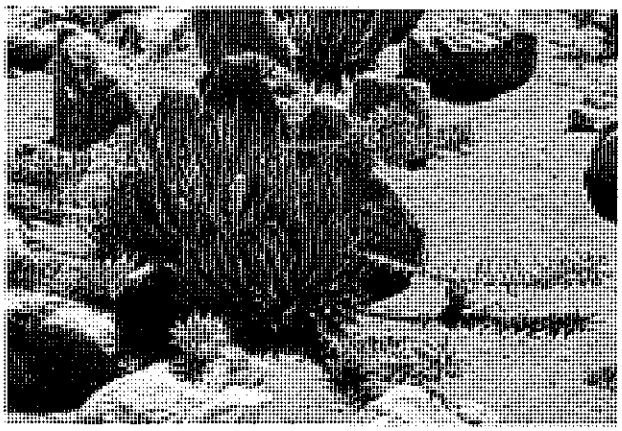
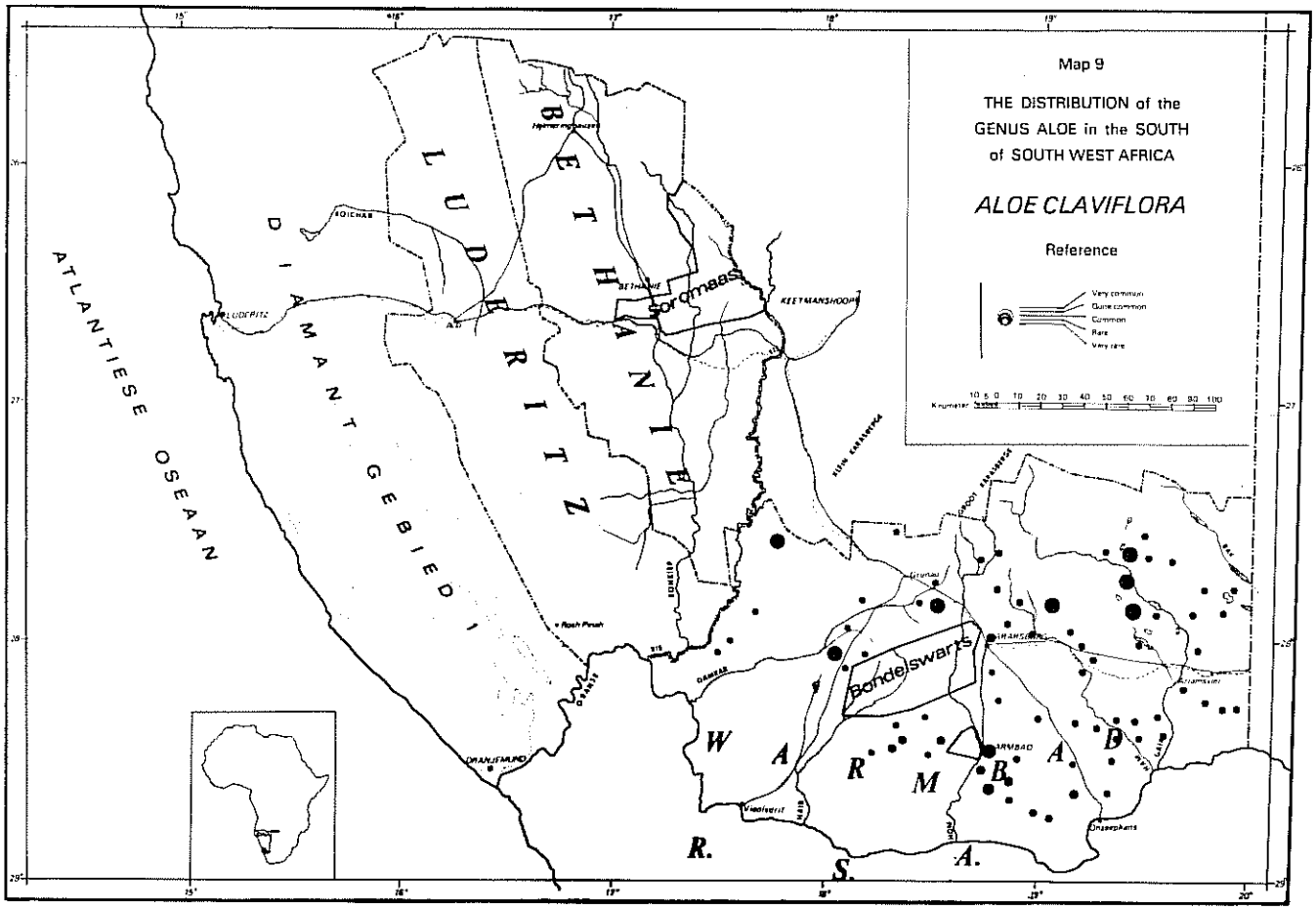
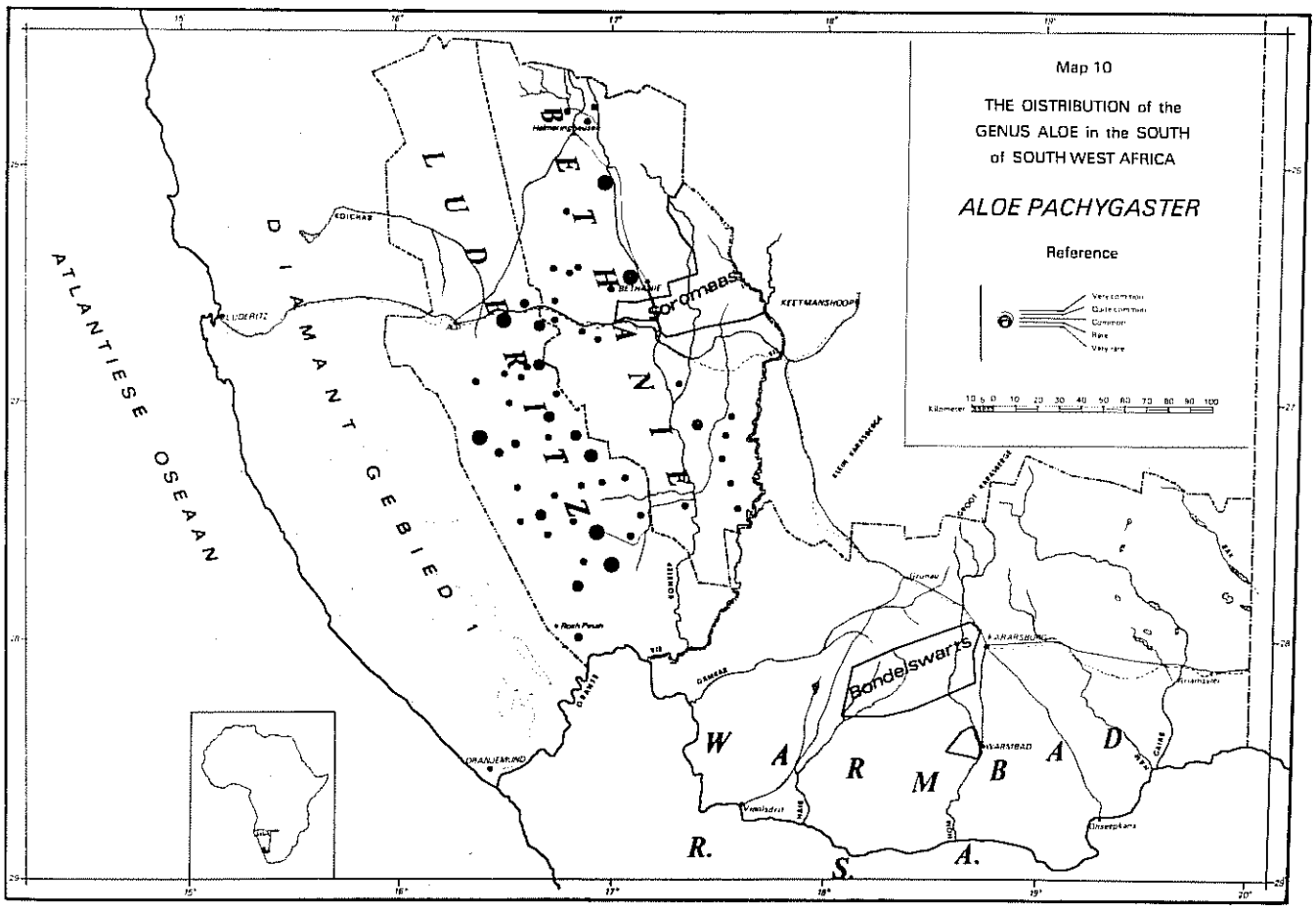
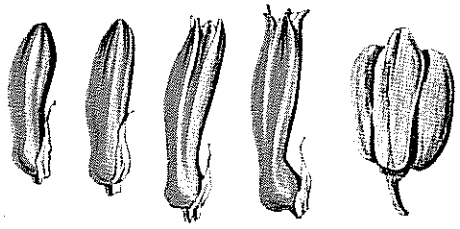


Plate 10. *Aloe pachygaster* Dinter


Map 9
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE CLAVIFLORA
Reference
Very common
Quite common
Common
Rare
Very rare
Kilometer
ATLANTIESE OSEAAN
DIAMANT GEBIED
LUDERITZ
BETHANIE
Keetmanshoop
Karasburg
Bondelswarts
WARMBAD
ORANJEMUND
Rosh Pinah
Grunau
R. S. A.


Map 10
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE PACHYGASTER
Reference
Very common
Quite common
Common
Rare
Very rare
Kilometer
ATLANTIESE OSEAAN
DIAMANT GEBIED
LUDERITZ
BETHANIE
Keetmanshoop
Karasburg
Bondelswarts
WARMBAD
ORANJEMUND
Rosh Pinah
Grunau
R. S. A.



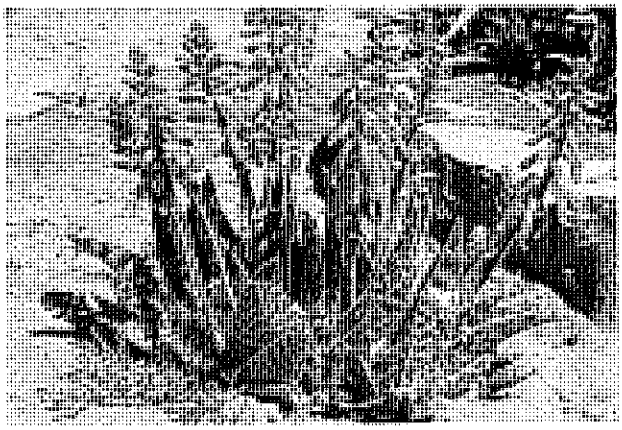


Plate 11. *Aloe variegata* L.

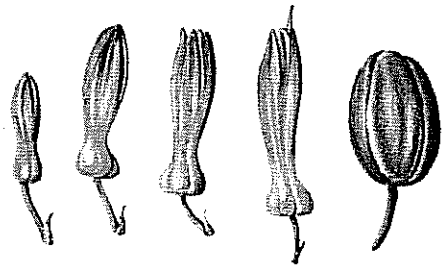
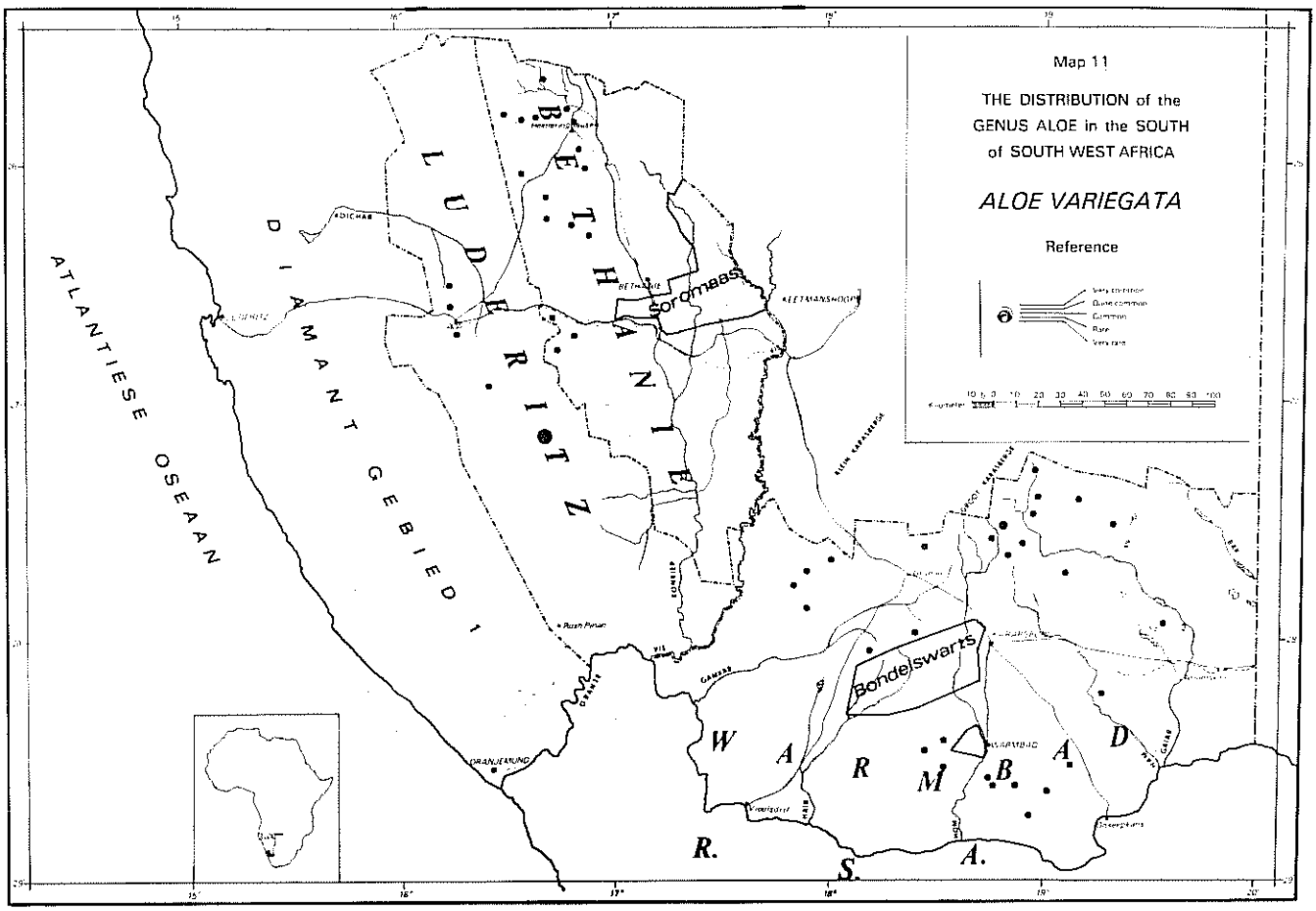
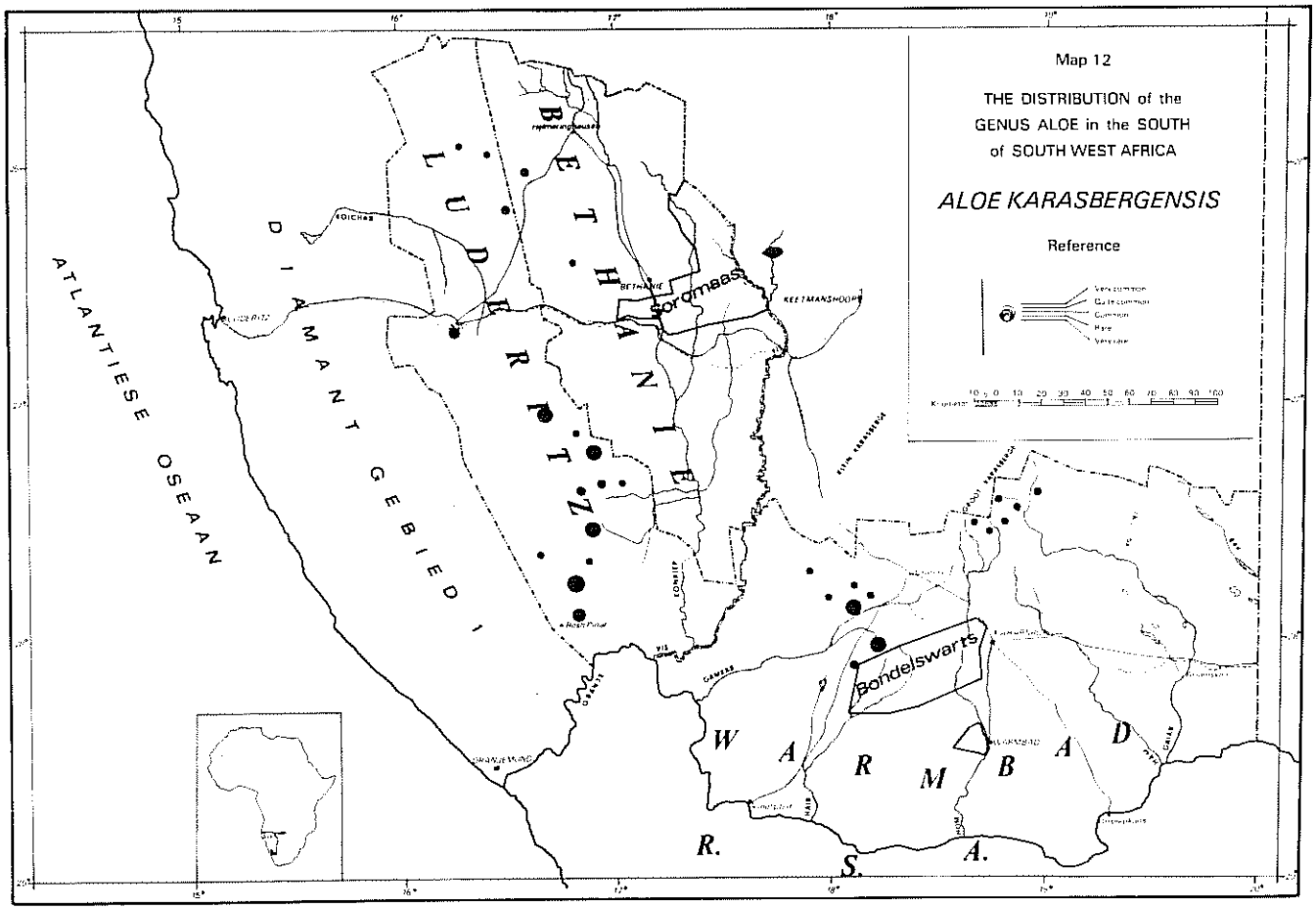


Plate 12. *Aloe karasbergensis* Pillans


Map 11
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE VARIEGATA
Reference
ATLANTIESE OSEAAN
DIAMANT GEBIED 1
LUDERITZ
BETHANIE
Soromaas
KEETMANSHOOP
Bondelswarts
WARMBAD
GIBEON
GROOTFONTEIN
ORANJEMUND
R. S. A.


Map 12
THE DISTRIBUTION of the
GENUS ALOE in the SOUTH
of SOUTH WEST AFRICA
ALOE KARASBERGENSIS
Reference
ATLANTIESE OSEAAN
DIAMANT GEBIED 1
LUDERITZ
BETHANIE
Soromaas
KEETMANSHOOP
Bondelswarts
WARMBAD
GIBEON
GROOTFONTEIN
ORANJEMUND
R. S. A.

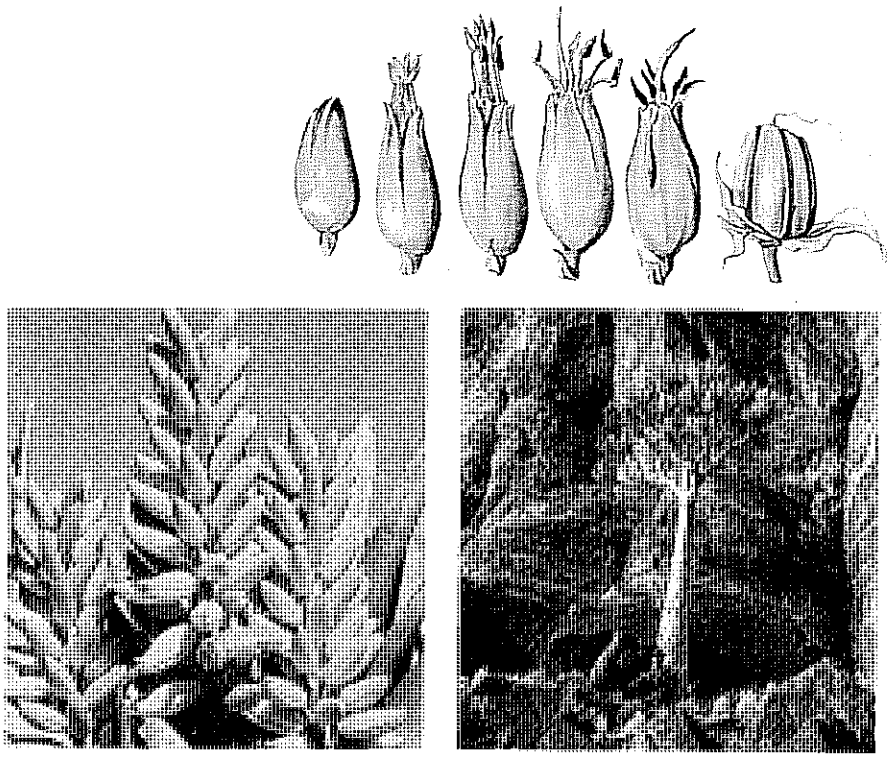
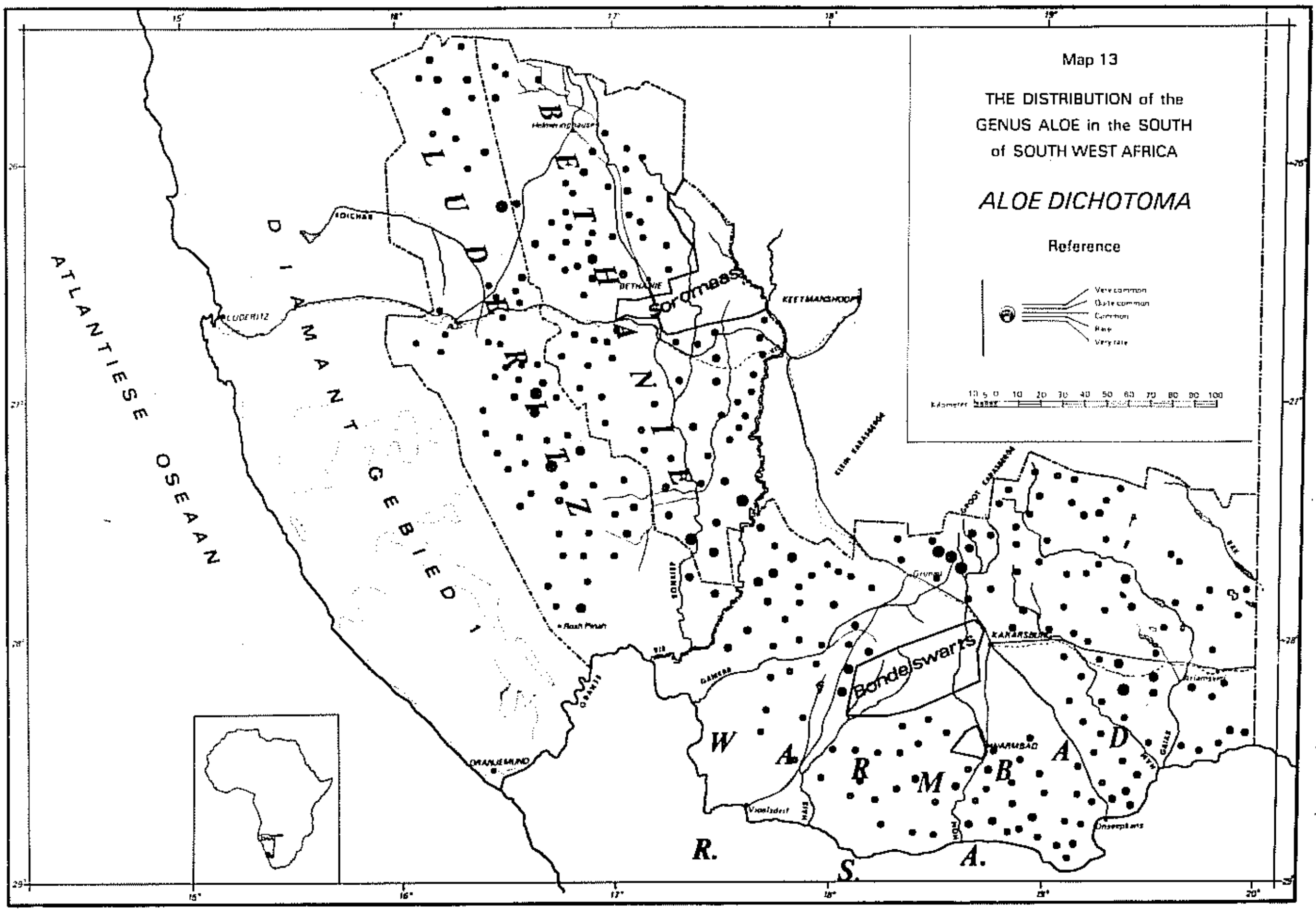


Plate 13. *Aloe dichotoma* Masson


Map 13
THE DISTRIBUTION of the GENUS ALOE in the SOUTH of SOUTH WEST AFRICA
ALOE DICHOTOMA
Reference
ATLANTIESE OSEAAN
DIAMANT GEBIED 1
LUDERITZ
BETHANIE
Soromaas
Bondelswarts
WARMBAD
R.S.A.

Reproduction of the catfish *(Clarias gariepinus)* in the Hardap Dam, South West Africa

by

I. G. GAIGHER

Department of Nature and Environmental Conservation, Cape Provincial Administration

CONTENTS

ABSTRACT

Clarias gariepinus which is an important angling and commercial fish in South West Africa was studied over a period of ten months. This species grows to a larger average size in the Hardap Dam than in most other waters studied. The sex ratio changed from 1:1 in fishes less than 80 cm in length to 7 males: 3 females in fishes over 100 cm in length. Females became sexually mature between 65 and 70 cm and males between 65 and 75 cm in length. Gonads were fully developed at the end of November but spawning only took place after the dam filled in March. There was an inverse relationship between the weight of intestinal fat reserves and the liver on the one hand and gonadal weight on the other hand. Fecundity increased with increase in length. They fed throughout the year and were generally heavily infested with intestinal parasites.

1 INTRODUCTION

The Hardap Dam is situated near Mariental in the upper reaches of the Fish River, a northern tributary of the Orange River system. It is the most important freshwater angling site in South West Africa (Gaigher, 1975 (b)) and has a potential for commercial utilization. Its larger indigenous fish fauna is basically similar to that of the Orange River, except that it contains only one species of yellowfish. The carp, *Cyprinus carpio* and the tilapia *Sarotherodon mossambicus* have been introduced and are well established in the dam.

C. gariepinus is an important angling fish in the dam. It is easily caught and grows to a large size. The flesh of this fish is highly prized by the local Africans and is in fact preferred to that of any other fish species. Although it is widely distributed in Africa and is of potentially great commercial importance in Southern Africa, surprisingly little has been published on its reproduction (Greenwood, 1955; 1956; Holl, 1968; van der Waal, 1974). Important information is given in unpublished reports and theses by Göldner (1967, 1968), Groenewald (1957), Meyer (1974), Mulder (1971) and Pott (1969).

Except for length-weight relationships (Bloemhoff 1974) no work has previously been done on the ecology of this fish in the Hardap Dam.

2 MATERIALS AND METHODS

Specimens were collected with the aid of gill nets, seine nets, longlines and by angling from September 1974 to February 1975 and also in April and June 1975. Poor results were obtained with gill nets. Seine nets were successful for a limited period when the fish congregated in the upper reaches of the dam for spawning. Longlines were only used during April and June and proved to be highly successful. Floats with hooks on 45 cm of line were spaced 2 m apart on a nylon rope. *Labeo* flesh was used as bait.

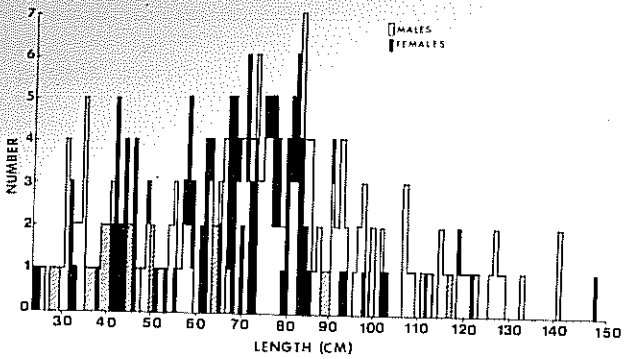


Figure 1. Length frequency distribution of male and female *Clarias gariepinus* collected from the Hardap Dam, September, 1974—June, 1975.

All specimens collected were measured, weighed, sexed and the weight of the gonads, liver, "intestinal fat" and viscera determined. The "intestinal fat" consists of a mass of fat loosely attached to the gut, excluding fat around the stomach. The fullness of stomach and gut and degree of infestation with abdominal parasites were recorded as well.

Maturity coefficients, liver and fat indexes were calculated as follows:

$$\text{M.C.} = \frac{\text{Gonad weight (grams)}}{L^3} \times 10^4$$

$$\text{Liver index} = \frac{\text{Liver weight (grams)}}{L^3} \times 10^4$$

$$\text{Intestinal fat index} = \frac{\text{Weight of intestinal fat (grams)}}{L^3} \times 10^4$$

3 RESULTS

3.1 Sex ratio and length-frequencies

Figure 1 shows the length-frequency distribution of 337 specimens collected during the survey. Because the specimens were collected with various gear, no conclusions could be drawn regarding the actual size composition of the population. Although females became less abundant than males in larger fishes, the largest specimen collected was a female with a length of 148 cm. In comparison with the results of Gaigher (1975 (a)), Göldner (1967), Mulder (1971) and van der Waal (1972), *C. gariepinus* seems to grow to a larger average size in the Hardap Dam than in most other waters where it has been studied.

Forty-six per cent of specimens under 80 cm in length collected (N = 230) were males. The percentage males increased with increase in length to 62 per cent in fishes between 80 and 100 cm (N = 73) and 71 per cent in fishes over 100 cm in length (N = 24). Both Hamman (1974) and van der Waal and Schoonbee (1975) found that male *C. gariepinus* had a faster growth rate than females. This explains in part why males are more abundant in larger size groups.

In this respect *C. gariepinus* differs from most South African silurids and cyprinids where the females normally grow faster and have a larger average size than males (Gaigher 1976; Hamman 1974; Mulder 1971). As in the cichlids, this fish has a breeding behaviour where individual males compete for females (van der Waal, 1972) and where bigger males therefore have a better chance of fertilizing females, a process which selects for fast-growing males.

3.2 Length at sexual maturity

Figure 2 shows that females became sexually mature when they are between 65 and 70 cm in length while males reach maturity at a length of between 65 and 75 cm. The smallest mature male and female collected were 65 and 67 cm in length respectively. The length at sexual maturity varies greatly from site to site. For example, van der Waal (1972) found that male and female *C. gariepinus* from the Olifants River near Marble Hall, Transvaal, reached maturity at lengths of 23—41 (mean 40) and 30—40 (mean 38) cm respectively. In the Vaal River males reach sexual maturity at lengths of 43—45 and females at lengths of 45—48 cm (Göldner 1967, Groenewald 1957, Mulder 1971).
Length at maturity seems to be correlated with growth rate so that a larger size at maturity points towards better environmental conditions. In the Hardap Dam and Olifants River populations males reach sexual maturity at a slightly bigger size than females while the opposite seems to be true for the Vaal River.

3.3 Breeding season and site

The breeding habits of *C. gariepinus* have been well described and discussed by van der Waal (1974).

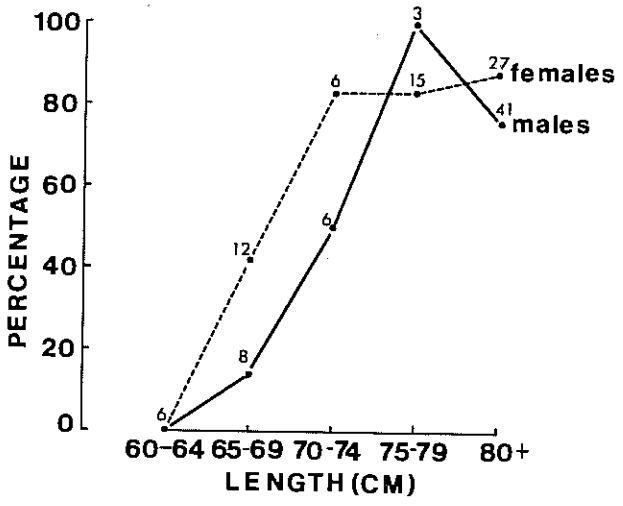


Figure 2. The percentage females with macroscopically visible eggs in the ovaries and males with maturity coefficients over 0,2 of different length groups of *Clarias gariepinus* collected from the Hardap Dam during the period December, 1974 to February, 1975.

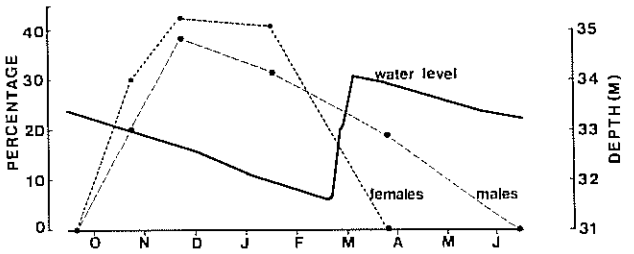


Figure 3. The percentage mature females with macroscopically visible eggs in the ovaries and mature males with maturity coefficients over 0,2 of *Clarias gariepinus* collected from the Hardap Dam, October, 1974 to June, 1975. The solid line represents the water depth at the wall during the same period.

The act of spawning is stimulated by runoff water and they spawn on vegetation submerged during flood periods.

In the Hardap Dam the gonads were already fully developed towards the end of November (Figure 3). However, although large concentrations of catfish were observed in the upper reaches of the dam during December and January, spawning took place only when the dam filled in March. All females collected in April were spent. Only two small fish of this spawn, with lengths of 72 and 54 mm were found in April. They were then approximately one month old.

The first part of the 1974/75 rainy season was exceptionally dry. It normally rains from December to April with a peak in January, February and March. Greenwood (1957), Holl (1968), Jackson (1961), Van der Waal (1974), etc., have all found that *C. gariepinus* breeds during the peak rainy season.

It is most interesting that *C. gariepinus* in the Hardap Dam moved upstream to congregate in the upper reaches in the absence of inflowing water. The movement must therefore have been triggered by an internal stimulus. It is possibly coincidental that the most suitable breeding sites are situated along the shores of the silt-laden upper reaches of the dam. As the water level drops during the dry season, the exposed silt becomes overgrown with various herbs which form ideal spawning beds when inundated.

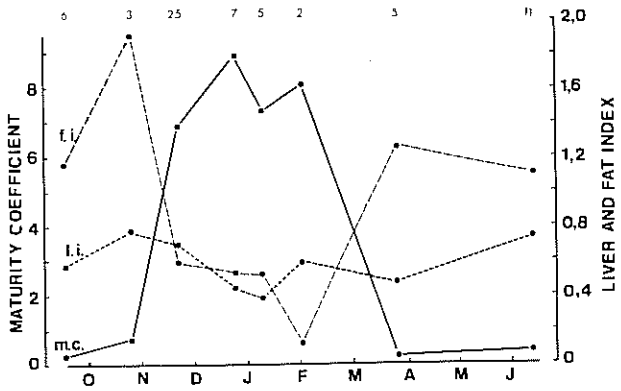


Figure 4. The relationship between average maturity coefficient, liver index and intestinal fat index of mature female *Clarias gariepinus* with developed gonads from the Hardap Dam, October, 1974 to June, 1975.

Meyer (1974) found that sexually mature *C. gariepinus* migrated upstream in the Elands River, a tributary of the Olifants River, Transvaal, from September to December, but most movement took place in October and November when the river was in flood. Through tagging he determined that the same fishes returned downstream in the period December to May with a peak in April. The population density of the Hardap Dam *Clarias* remained high in the uppermost reaches during December and January but by February they had apparently dispersed again without breeding because it became difficult to obtain specimens with the seine nets.

3.4 The relationship between gonadal development and intestinal fat and liver indices

In the past this aspect received no attention in work on South African freshwater fishes with the result that many questions on life cycles still remain unanswered. According to Shul'man (1974) fat is the main form of accumulation of reserve energy utilized for metabolic processes in fishes in periods of the annual cycle when ingestion of food is reduced or ceases. Fish, unlike other vertebrates, produce large numbers of eggs within restricted time periods which calls for especially intense energy expenditures. Fat may be deposited at several sites in the body and the sequence of its utilization depends on the functional state and nature of the processes demanding reserve energy. In this study it was impossible to do biochemical analysis, which would have been preferable. However, the results obtained by weighing intestinal fat give a basic indication of part of the energy cycle in this fish.

The liver index is of more doubtful value because the liver serves for the accumulation of both fat and glycogen reserves. According to Shul'man (1974) glycogen is of less importance as an energy reserve in fish but can constitute up to 10% of the weight of the organ. Black *et al.* (1961) found that glycogen diminished most markedly when fish were starving. Figure 4 shows a clear inverse relationship between the degree of gonadal development and the intestinal fat index in females. Energy is rapidly stored in the form of fat accumulation after the breeding season which reaches a peak just before the ovaries start to develop. The fat supplies energy for the synthesis of large numbers of eggs within a short time period and the weight of intestinal fat rapidly drops as the ovaries develop.

It seems as if less fat energy is utilized for gonadal development in males (Fig. 5) than in females, because the average intestinal fat index never dropped below 0,78. However, there was an inverse relationship between gonad weight and intestinal fat index of fishes collected after November and an increase in the amount of intestinal fat directly after spawning took place.

In both sexes there was generally an inverse relationship between maturity coëfficients and liver indices. Most of the changes in liver weight were probably

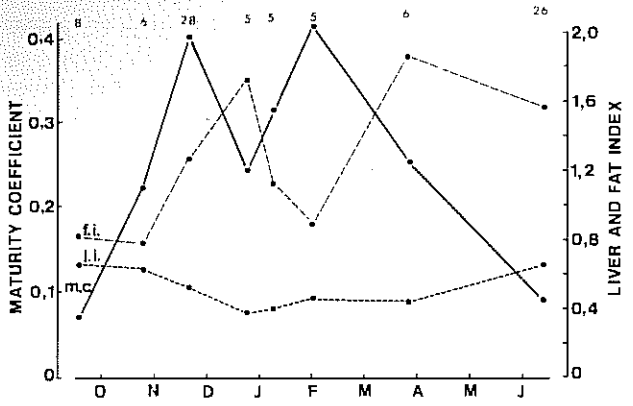


Figure 5. The relationship between average maturity coefficient, liver index and intestinal fat index of mature male *Clarias gariepinus* with developed gonads from the Hardap Dam, October, 1974 to June, 1975.

due to changes in fat content but this will have to be substantiated by biochemical analysis in future studies.

3.5 Fecundity

The fecundity increases exponentially with increase in length from about 70 000 in fishes with a length of 65 cm to more than 1 100 000 in fishes with a length of 120 cm (Figure 6). An exponential curve fitted to the data by the method of least squares is described by the equation:

$$\text{Fecundity} = 7923{,}5\ e^{0{,}04\ L\ (cm)}$$

The correlation coëfficient (r) for this line is 0,73. The results obtained by van der Waal (1972) on fishes which were mainly smaller than 65 cm are also indicated on the graph showing that his data fit well into the general picture. A line fitted to all the data combined is described by the equation:

$$\text{Fecundity} = 2787{,}75\ e^{0{,}05\ L\ (cm)}$$
$$r = 0{,}88$$

3.6 Food and parasites

The catfish were feeding during all surveys and every specimen, except one collected in June, contained food either in the stomach or in the gut. The stomach contents of 69 specimens were examined macroscopically. In 38 of these fish was the dominant food item, 29 contained mainly zooplankton and two were filled with detritus. A specimen with a length of 33 cm collected on the second October had consumed a small *C. gariepinus* with a length of 8,5 cm, once more illustrating the canibalistic nature of this fish.

Various parasites were collected from *C. gariepinus* during the survey, including the leech *Batrocobdella tricarinata* and the trematode *Diplostomum mashonense* from the brain cavity. However, most striking were infestation of the viscera, mainly with nematodes. Of 294 specimens examined for these abdominal parasites, 21 per cent were heavily, 18 per cent moderately and 60 per cent lightly infested. Only 1 per cent of the specimens contained no abdominal parasites. The high degree of infection was probably due to the presence of large numbers of fish-eating birds, mainly cormorants and darters on the dam.

4 DISCUSSION

Generally the study confirmed what had been known of the reproductive biology of this fish in other waters. However, certain interesting differences due to environmental conditions came to light. Firstly, as in the case of *Barbus cf kimberleyensis* (Gaigher, 1976), spawning coincided with the peak rainy season, and therefore took place later in the year than in the Transvaal. Owing to better environmental conditions *C. gariepinus* grew to a larger average size than in the Olifants River, Transvaal where the same species was studied by van der Waal (1972). They probably have a faster growth rate in the Hardap Dam and therefore reach sexual maturity at a much larger size. Fecundity increases with increase in length and a large fish can produce over a million eggs. Production of such masses of reproductive products within a short time period calls for large energy expenditures. Studies of changes in the amount of abdominal fat showed that the catfish provided for this by accumulating energy in the form of fat, especially during autumn and early spring. Similar studies in other areas may show whether this process has priority above

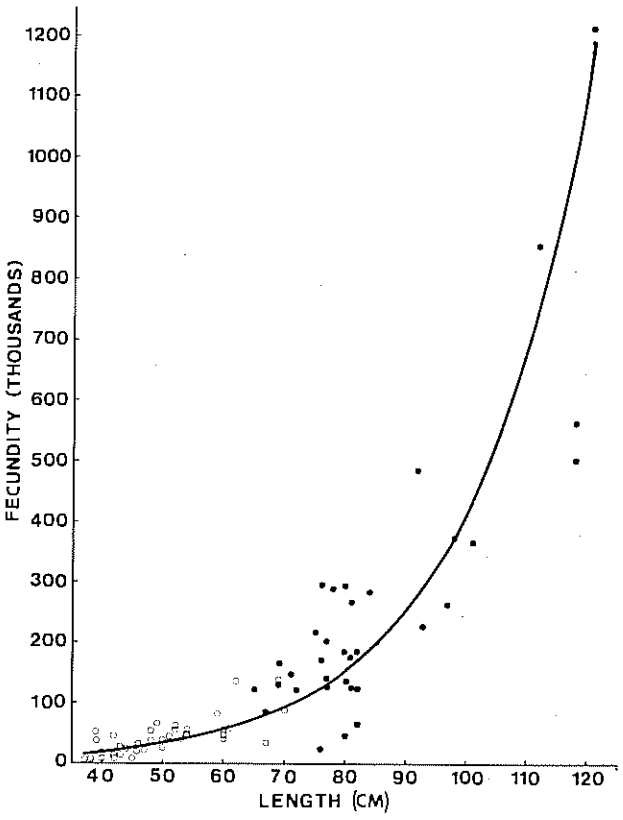


Figure 6. The relationship between fish length and fecundity of *Clarias gariepinus* from the Hardap Dam (dots) and the Olifants River (circles). The regression line was fitted to all the data combined.

growth rate. If so, it will explain why the growth rate of catfish in the Olifants River decreases rapidly after they have reached sexual maturity (van der Waal and Schoonbee, 1975). Males utilize less fat for the production of sperms and this to a certain extent probably explains their faster growth rate in comparison to females.

Observations and netting results indicated that catfish migrated towards the upper reaches of the dam when the ovaries were ripe, where they concentrated in anticipation of floods. They failed to spawn before the floods. It therefore seems as if the act of migration is triggered, at least in part, by an internal stimulus associated with the gonads, while the act of spawning is triggered by an external stimulus associated with runoff water.

Feeding took place throughout the year despite the low winter temperatures. Although the catfish were heavily infested with parasites, this did not seem to have any influence on their well-being.

5 ACKNOWLEDGEMENTS

The author is greatly indebted to the following: The Council of the University of Fort Hare for permission to do the survey during study leave.

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My wife for her help with the collection of fish and recording of data.

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Drinking times and behaviour at waterholes of some game species in the Etosha National Park

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CONTENTS

ABSTRACT

In the Etosha National Park some 33 000 observations on drinking patterns and behaviour were made on rhinoceros *Diceros bicornis*, zebra *Equus burchelli*, wildebeest *Connochaetus taurinus*, hartebeest *Alcelaphus buselaphus*, gemsbok *Oryx gazella*, kudu *Tragelaphus strepsiceros*, eland *Taurotragus oryx*, giraffe *Giraffa camelopardalis*, warthog *Phacochoerus aethiopicus*, springbok *Antidorcas marsupialis*, elephant *Loxodonta africana*, lion *Panthera leo*, jackal *Canis mesomelas*, hyaena *Crocuta crocuta* and ostrich *Struthio camelus*. Results were analysed and compared with similar studies elsewhere and suggest that variations may occur regionally.

1 INTRODUCTION

In the Etosha National Park perennial water is found only in fountains and in drinking-troughs supplied by boreholes. Rivers and water-courses are dependent upon rainfall and as such cannot be regarded as important sources. Rain-water pools are much sought after during the rainy season (December—April). Because of the general availability of water during the rainy season animals have no difficulties in obtaining water. This condition is, however of short duration and soon after the last rains have fallen the animals return to the perennial sources, often concentrating in large numbers around such sources. During the rains most ungulates concentrate in large herds on the favoured grazing areas (open flats, often far removed from the nearest perennial water source). When they are forced to return to their perennial sources, these sources become the centre of the animals' "orbit" and together with food, determines range and population units (Leopold, 1933). High density congregations of herds at waterholes have often been reported (Grzimek and Grzimek, 1960, Shortridge, 1934 and others) but the behaviour and ecological consequences thereof had not been investigated prior to the work of Weir and Davidson (1965). They, however, could not determine whether there is any competition for water or, if there is, which species would be involved. They suspected there might also be competition for time and opportunity to drink as distinct from competition for water itself.

2 METHOD

The data presented here were obtained from 19 censuses, each lasting 24 hours and over a full-moon period. Of these 19 censuses, six were conducted between the beginning of August, 1971, and the end of January 1972 at Chudop, a fountain near the Namutoni rest camp. This fountain may be visited by tourists in cars and therefor presents a possible source of disturbance. The other 13 censuses were conducted during the period August 1971 to February 1973 at Gobaub. Here an attempt was made to conduct a census for every month

of the year but this was not always possible as rains often made the access roads impassable. Gobaub is situated approximately 25 km south of the rest camp Halali and is inaccessible to tourists, hence no disturbance exists here. Over 32 000 animals were counted during these censusses. Numerous visits were made to these waterholes for behavioural studies.

An unrelated project on lions, during the course of which a pride of lions was followed day and night for continuous periods of up to ten days, provided further data on predation and drinking habits of these animals.

3 RESULTS

During the 19 censusses held in the Etosha National Park between August 1971 and February 1973, the following number of observations were made:

Rhinoceros (*Diceros bicornis Linn.*)	36
Zebra (*Equus burchelli* Gray)	22 358
Wildebeest (*Connochaetes taurinus* Burchell)	1 426
Hartebeest (*Alcelaphus buselaphus* Pallas)	941
Gemsbok (*Oryx gazella* Linn.)	905
Kudu (*Tragelaphus strepsiceros* Pallas)	1 937
Eland (*Taurotragus oryx* Pallas)	376
Giraffe (*Giraffa camelopardalis* Linn.)	407
Warthog (*Phacochoerus aethiopicus* Pallas)	203
Springbkok (*Antidorcas marsupialis* Zimmermann)	2 501
Elephant (*Loxodonta africana* Blumenbach)	436
Lion (*Panthera leo* Linn.)	133
Jackal (*Canis mesomelas Schreber*)	676
Hyaena (*Crocuta crocuta* Erxleben)	115
Ostrich (*Struthio camelus*)	221
Total	32 892

Peak drinking times

Figure 1 shows the drinking times of 32 671 animals of 15 species as observed at both localities. Ungulates, especially zebra, being the most numerous species, have influenced the histogram to show a peak between 12h00 and 13h00.

Figure 2 to 16 show the drinking times of 15 species.

Zebra (Figure 2) have a peak drinking time between 12h00 and 13h00 but have been observed to drink during every hour. Wildebeest (Figure 3) have a peak drinking time between 12h00 and 13h00. There is, however, a lesser peak between 10h00 and 11h00. They do not drink during all hours, especially from 20h00 to 24h00. Springbok (Figure 4) have two peak drinking times: between 09h00 and 10h00 and again between 12h00 and 13h00. They have been observed to drink during all hours. Gemsbok (Figure 5) have a peak drinking time between 12h00 and 13h00 and do not drink during all hours. Hartebeest (Figure 6) have a peak drinking time between 11h00 and 12h00 and show a decided preference to drink between 08h00 and 16h00. They do not drink during all hours. Kudu (Fig. 7) are essentially daylight drinkers with a peak between 09h00 and 10h00. They do not drink after sunset. Eland (Figure 8) have a peak drinking time between 09h00 and 10h00. Although they do not drink during all hours, they do not appear to be adverse to drink at night.

The small sample of black rhinoceros (Fig. 9) indicates that these animals prefer drinking from late afternoon to late evening, with a peak between 20h00 and 21h00. Giraffe (Figure 11) do not show a very definite peak but seem to prefer drinking between 18h00 and 19h00. They may drink during all hours. Warthog (Fig 12) are strict day drinkers with a peak drinking time between 14h00 and 15h00. Ostrich (Figure 13) are also strict day drinkers with a peak drinking time between 11h00 and 12h00. From the small lion sample (Figure 14) it appears that they do not drink during all hours and appear to prefer drinking between 17h00 and 23h00. Jackal (Figure 15) have two peak drinking times: at sunrise and sunset, with a preference to drink at night. They do not like drinking during the heat of day. The small sample of hyaena (Figure 16) shows a peak drinking time between 00h00 and 01h00. They seldom drink during the day.

The preferential drinking time (day or night) of all 15 species are shown in Figure 17. According to this the animals have been divided into five preference classes as follows:

Class	Preference	Species
A	Exclusively daylight drinkers	Ostrich. (Warthog and kudu intermediate with next class)
B	Predominantly daylight drinkers	Zebra, wildebeest, springbok, gemsbok, hartebeest, kudu, warthog and eland.
C	Day and night drinkers	Giraffe. (Jackal are intermediate between classes C and D)
D	Predominantly night drinkers	Lion, jackal, elephant, rhinoceros.
E	Exclusively night drinkers	None.

Fig. 18 shows the numbers counted at a waterhole (Gobaub) fluctuate through the year.

4 DISCUSSION

4.1 Peak drinking times

Comparing drinking times of species common to both Etosha and Wankie (Rhodesia) produces interesting differences. Weir and Davison (1965), with regards to drinking times, have divided the animals into four groups as follows:

Evening and night drinkers:
buffalo, zebra and giraffe with a pronounced evening peak between 16.00 and 20.00.

Night and morning drinkers:
wildebeest and eland with a peak in the morning between 05.00 and 09.00.

Daytime drinkers:
kudu, sable, roan and warthog which is particularly well marked in the case of warthog, which show a pronounced afternoon peak (between 14.00 and 17.00), are not recorded at all between 18.00 and 05.00 and then show a period of morning avtivity at the pan from 05.00 at 10.00 with decreased avtivity during the middle of the day (10.00 to 14.00).

Elephant show a pronounced peak in numbers between 16.00 and 02.00.

Buffalo and sable do not occur in Etosha and roan have only recently been re-introduced, hence no comparative data exist. The other species do occur and can be compared (Figure 17). Because of sunrise and sunset differences only the average times of sunrise and sunset have been shown in all the figures and this accounts for the fact that kudu appear to drink in the pre-dawn darkness while warthog again appear to drink shortly after sunset. If this were to be corrected, Figures 7 and 12 would indicate these animals to be exclusively daylight drinkers.

While Weir and Davison (1962) have recorded zebra and giraffe to be evening and night drinkers, data presented in Figure 2 shows that roughly 94% of all the zebra observed drink during the hours of daylight, with a peak drinking time at sunset. This agrees with the findings of Weir and Davison (1965) and Young (1970). This places zebra in the class of predominantly daylight drinkers (Table 2). Giraffe, according to the classification qualify for class C, the day and night drinkers as some 57 % of them have been observed drinking during daylight. However they fall just short of class B, the predominantly daylight drinkers. Their peak drinking time of just before sundown agrees with the data presented by Weir and Davison (1965).
Weir and Davison (1965) classified wildebeest and eland as night and morning drinkers. Figure 17 shows that nearly 95 % wildebeest and eland 83% eland drink by day. Wildebeest and eland fall in class B. Figures 3 and 8 confirm that both species here are predominantly day drinkers with clear peaks during daylight. Young (1970) also found wildebeest to be mainly daylight drinkers with a peak during midday.

Allowing for daylight corrections (different seasonal sunrise and sunset times) both kudu and warthog would be classified as exclusively daylight drinkers. Weir and Davison (1965) have shown clearly that kudu drink at night as well while warthog are more confined to daylight but may drink shortly before sunrise and shortly after dark.

Weir and Davison (1965) have placed elephant in a separate category but according to the data presented here they are mainly night drinkers which agrees with the findings of Young (1970).

Hamilton (pers com.), studying waterhole activities in the Kuiseb river, Namib Desert, noted that gemsbok were exclusive night drinkers (an adaptation to the arid conditions) whereas those of Etosha were found to be mainly day drinkers.

The foregoing has shown that differences in drinking times of the same species exists from place to place. Often major differences can be found in populations of the same species which are only a 100 km or more apart. Thus, for example, the senior author has shown that on farms outside the Etosha National Park, kudu tend to drink at sunrise and sunset, even during the night, but seldom during the day. With the data available it has become possible not only to determine whether the animals are nocturnal or diurnal drinkers, but to indicate which 6-hour period of a day is preferred (Table 4).

Table 4. Preferred six-hour drinking period as shown by percentage of total number of observations during these periods.

Species	00h00 to 06h00	06h00 to 12h00	12h00 to 18h00	18h00 to 24h00	Peferred period
	%	%	%	%	
Zebra	2,5	39,4	53,7	4,5	Afternoon
Warthog	0,0	25,1	73,4	1,5	Afternoon
Wildebeest	2,9	47,1	48,5	1,5	Daylight
Springbok	3,1	46,1	45,0	5,6	Daylight
Ostrich	0,0	46,6	49,8	3,6	Daylight
Gemsbok	1,9	43,2	51,8	3,1	Afternoon
Hartebeest	0,9	57,2	40,6	1,6	Morning
Kudu	0,0	71,1	27,7	1,2	Morning
Eland	6,7	57,2	25,0	11,2	Morning
Rhinoceros	22,2	0,0	11,1	66,7	Evening
Elephant	25,7	2,5	0,9	70,9	Evening
Lion	30,1	6,0	18,8	45,1	Evening
Jackal	26,3	24,2	9,5	40,2	Evening
Hyaena	66,1	7,0	0,0	27,0	Pre-dawn
Giraffe	23,6	26,8	21,1	28,5	—

4.2 Behaviour at Waterholes

4.2.1 Daylight drinkers

Daylight drinkers such as wildebeest, springbok, ostrich are all prey species of lion, leopard and cheetah and drinking over a 12 hour daylight period has obvious survival value in so far as predatores are easier avoided at waterholes. The peak drinking time is also spread over a greater time, thus assuring that all members have a better opportunity of obtaining water.

Wildebeest and springbok prefer drinking as a group after approaching the water with a fair amount of caution. The presence or absence of other species at the water influences this approach: greater caution is displayed if no other species are present at the water. Both species appear to prefer drinking away from the main "crush" of animals when possible, otherwise wildebeest will form a wedge to get to the water and spread out sideways at the water's edge. They rarely move into the water or show interspecific aggressiveness. Even intra-specific aggression is limited and usually limited to horn presentations. Springbok, being much smaller animals, cannot force their way to the water's edge and have to await an opportunity. Thus it often happens that many

hours may be spent in trying to get to the water. Springbok have been observed to drink at all times of the day and it is suspected by Bigalke (1972) that this activity also proceeds at night. Springbok approach water with extreme caution, moving slowly and with frequent pauses. During this approach displacement activities such as the lowering of the head as if in search of grazing denote tension, as does tail-wagging. They soon depart after slaking their thirst. Similar behaviour has been recorded from the Nossob River by Child *et al.* (1971) and by Bigalke (1972). A marked springbok was observed to drink every day during a four-day observation period.

Ostrich seldom make a direct approach to the water but prefer to appear at the clearing's edge, survey the area and then make a slow and devious approach. Drinking takes place when the opportunity presents itself.

All three species may spend some time near the water, engaged in resting activities before moving off.

4.2.2 Afternoon drinkers

Zebra, gemsbok and warthog are also prey species and the survival value of drinking during daylight is the same. All three species display a determined initial approach to the water but usually halt some distance away to make a short survey of the area. Again, should other animals be drinking this cautionary halt is dispensed with and they will often only stop at the water.

Gemsbok and zebra often walk some distance into the water before drinking. Should drinking space be limited they will stand shoulder to shoulder in the water. Warthog actively seek a space to drink and take care not to approach the larger animals too closely but rarely display any sign of caution when approaching a waterhole, as was also noted by Young (1970).

Both zebra and gemsbok, but especially zebra, are aggressive when drinking and this has great survival value in areas where water is limited. Aggressiveness, as exhibited by these two species, is usually to be found at small waterholes where they are crushed together in order to reach the water. At the large waterholes a minimum distance of about one metre is maintained between individuals and drinking proceeds without aggression. A shortage of water or of drinking space serves to intensify competition at a waterhole and this important point should always be borne in mind when artificial drinking places are created.

When crowded zebra will kick out wildly in an effort to maintain their drinking space. Gemsbok attain the same results by presenting their horns. This warning is often enough to keep females and sub-dominant males at a distance but zebra often misinterpret or ignore this warning and as a result fatal or serious wounds are often inflicted on them.

Upon completion of their drinking activities these species soon depart.

4.2.3 Morning drinkers

Hartebeest, kudu and eland are also prey species subject to the same survival values. When in large herds, eland drink together and, as with the other two species, show a great deal of caution when approaching water. Hartebeest and kudu often form large but temporary aggregations at waterholes. Eland drink and move off soon after drinking and kudu will also move off immediately but very often only as far as the nearest bush where they may spend some time resting. Hartebeest often rest next to the water where they may also engage in mock fights. These three species seldom show serious inter- or intra-specific aggression. On numerous occasions kudu have been observed drinking only some hours after they had arrived: their non-aggressive natures prevent them from competing with other species such as zebra or gemsbok. Because of this lack of aggressive tendencies it is to their advantage to drink earlier than the aggressive species. Direct competition for the water is thus avoided.

4.2.4 Evening drinkers

Evening drinkers are rhinoceros, elephant, lion and jackal. Rhino and elephant cannot be regarded as normal prey animals and their bulk allows them to ignore lions under most circumstances. Both these species are highly aggressive towards other species at waterholes of small dimensions and by drinking in the evening interspecific competition with the numerically larger other game species, confrontations are avoided. Whereas both Young (1970) and Mitchell (1963) noted that elephant approach water with much caution, the same cannot be said to be true for the elephants of the Etosha National Park. Here elephant have often been seen to approach water at a fast walk or run, completely ignoring tourist vehicles near the waterhole. This may be the result of these elephants having been completely undisturbed for many years within the reserve. It has, however, been seen that the elephants in the western area of the reserve are more prone to leave a waterhole at the approach of a vehicle, but these elephants are not as accustomed to vehicles as those in the eastern part of the reserve as this part of the reserve is at present not open to tourists. It has also been seen that when faced with a choice of drinking from cement troughs or muddy pools, elephant show a preference for drinking from the troughs.Young (1970) showed that elephant preferred cement dams to earthen dams and avoided cement troughs. Confrontations often occur when elephant and rhino arrive at the water at the same time. On one occasion a rhino was observed to chase away a few elephant; on another occasion elephant were seen to chase a rhino away.

Lion, which spend most of the day resting, only become active towards sunset and their first action is to drink. They show no caution when elephant or rhino are drinking and in fact, have often been seen to be chased away from water by these pachyderms. Jackal follow roughly the same pattern as

lions but have to show a certain amount of caution when any of the other animals are drinking. Of these species, lions are the most likely to rest for long periods next to the water.

It would be expected that waterholes would be of great importance to lion in obtaining prey. Predation does take place at waterholes but it more often occurs away from the immediate vicinity as most prey animals do not approach waterholes at night.

The presence of lions at a waterhole may cause a congestion in the normal flow of animals, as was also noted by Young (1970).

Little seems to be known about the drinking habits of lions. Hunters claim that lions invariably drink after feeding and this is often the case if they are feeding close to water. In Etosha, however, kills are usually some distance from water with the result that the lions cannot easily slake their thirst. Schaller (1972) found it difficult to determine the frequency with which lions drank water was easily obtained. Moreover, he found only two cases out of 25 where lions drank within an hour of feeding. He could not determine a specific drinking time.

4.2.5 Pre-dawn drinkers

Hyaenas becomes active at sunset and drinking is one of their last activities after having searched for food. After drinking they quickly disappear from the waterhole.

4.2.6 Indiscriminate drinkers

Giraffe show no clear period during which they drink, hence they often become the prey of lions when they drink during the night. Young (1970) also noted the cautionary habit of giraffe when approaching water: a great deal of time is spent browsing in the vicinity of the water during which time they make a careful reconnaissance of the area. Before actually drinking, a few false attempts may be made and any sudden disturbance, such as birds flying off, may be sufficient to abort the drinking attempt for some time. Being so cautious is of high survival value as they are extremely vulnerable while drinking.

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Fig 1 Drinking times of 32671 animals, comprised of 15 species, in the E.N.P.

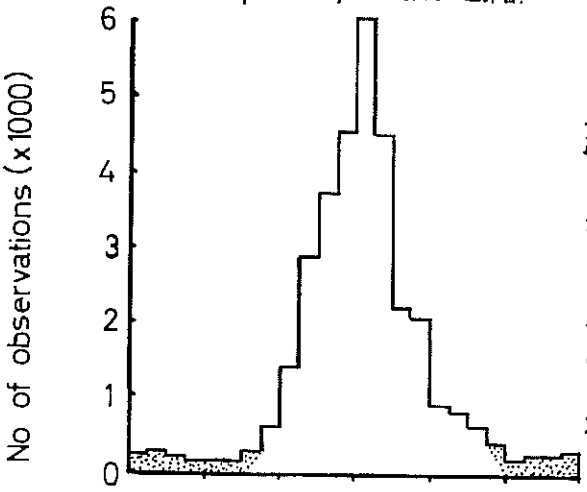


Fig 2 – 16 Drinking times

Fig 2 ZEBRA (n = 22358)

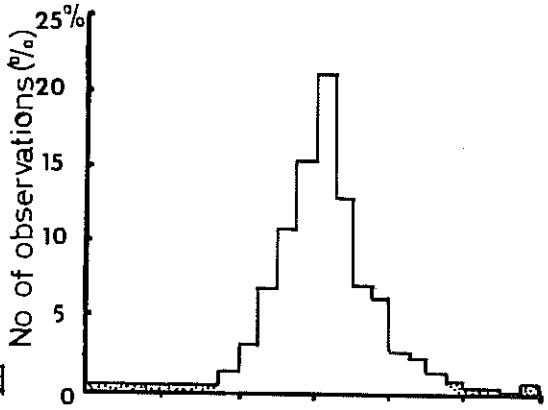


Fig 3 WILDEBEEST (n = 1426)

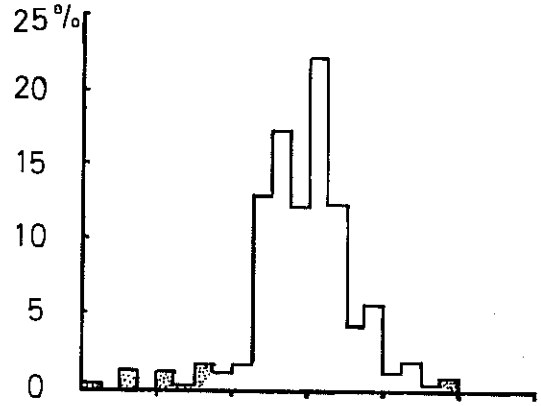
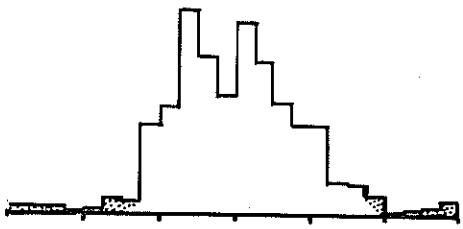


Fig 4 SPRINGBOK (n = 2501)



No. of observations (%)

Fig 5 GEMSBOK (n = 905)

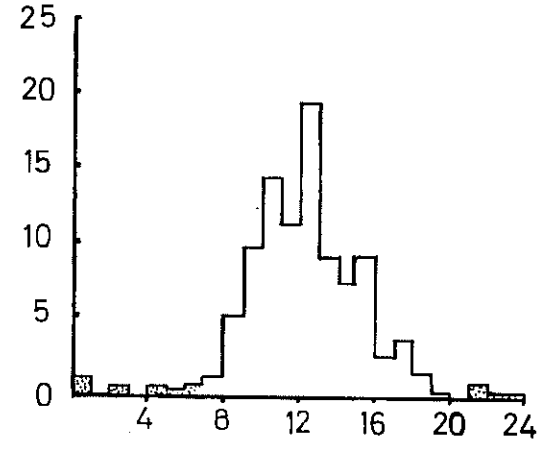
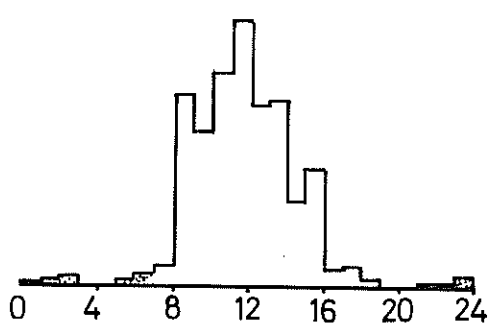


Fig 6 HARTEBEEST (n = 941)



TIME

Drinking times (cont.)

Fig 7 KUDU (n=1937)

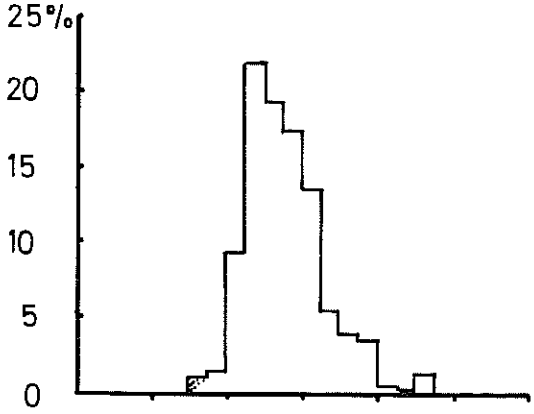


Fig 8 ELAND (n=376)

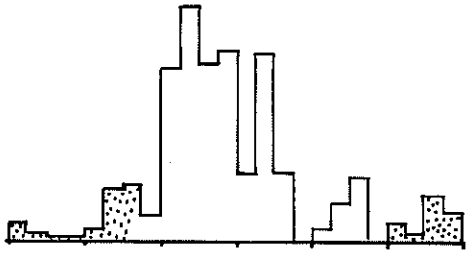


Fig 9 BLACK RHINOCEROS (n=36)

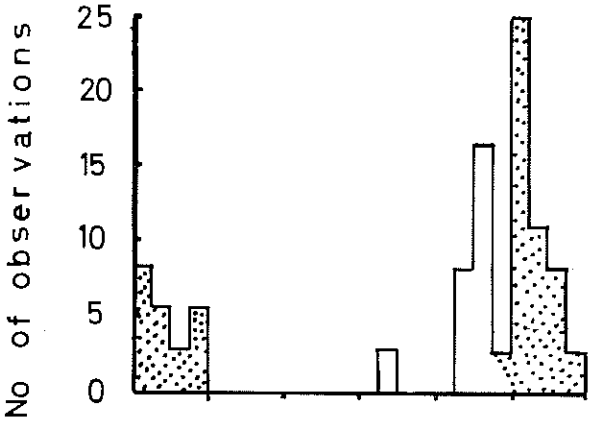


Fig 10 ELEPHANT (n=436)

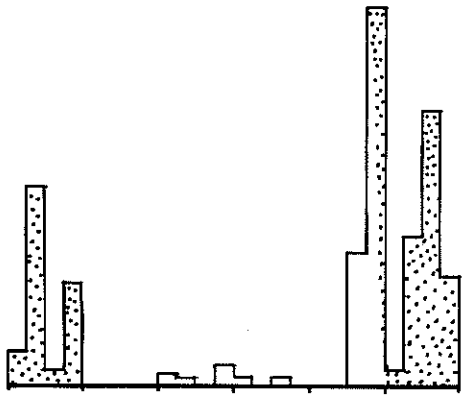


Fig 11 GIRAFFE (n=407)

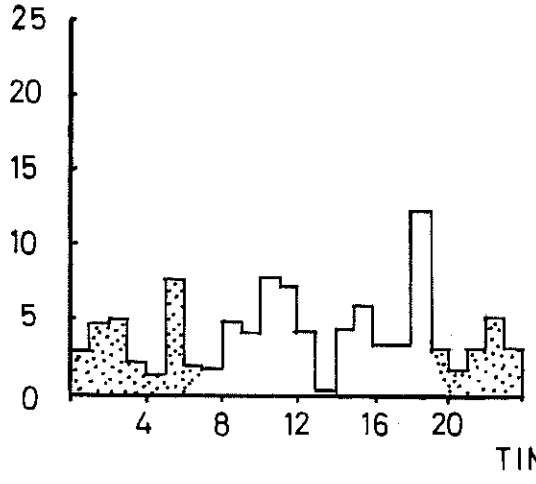
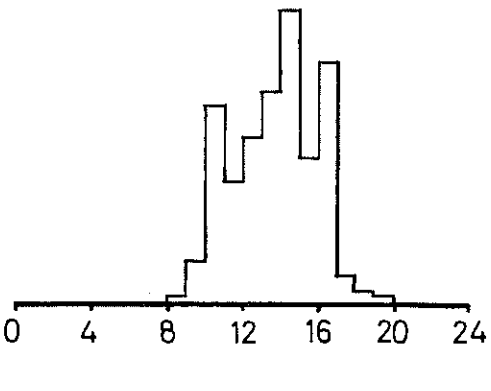


Fig 12 WARTHOG (n=203)



Drinking times (cont.)

Fig 13 OSTRICH (n= 221)

Fig 14 LION (n=133)

Fig 15 JACKAL (n = 676)

Fig 16 HYAENA (n=115)

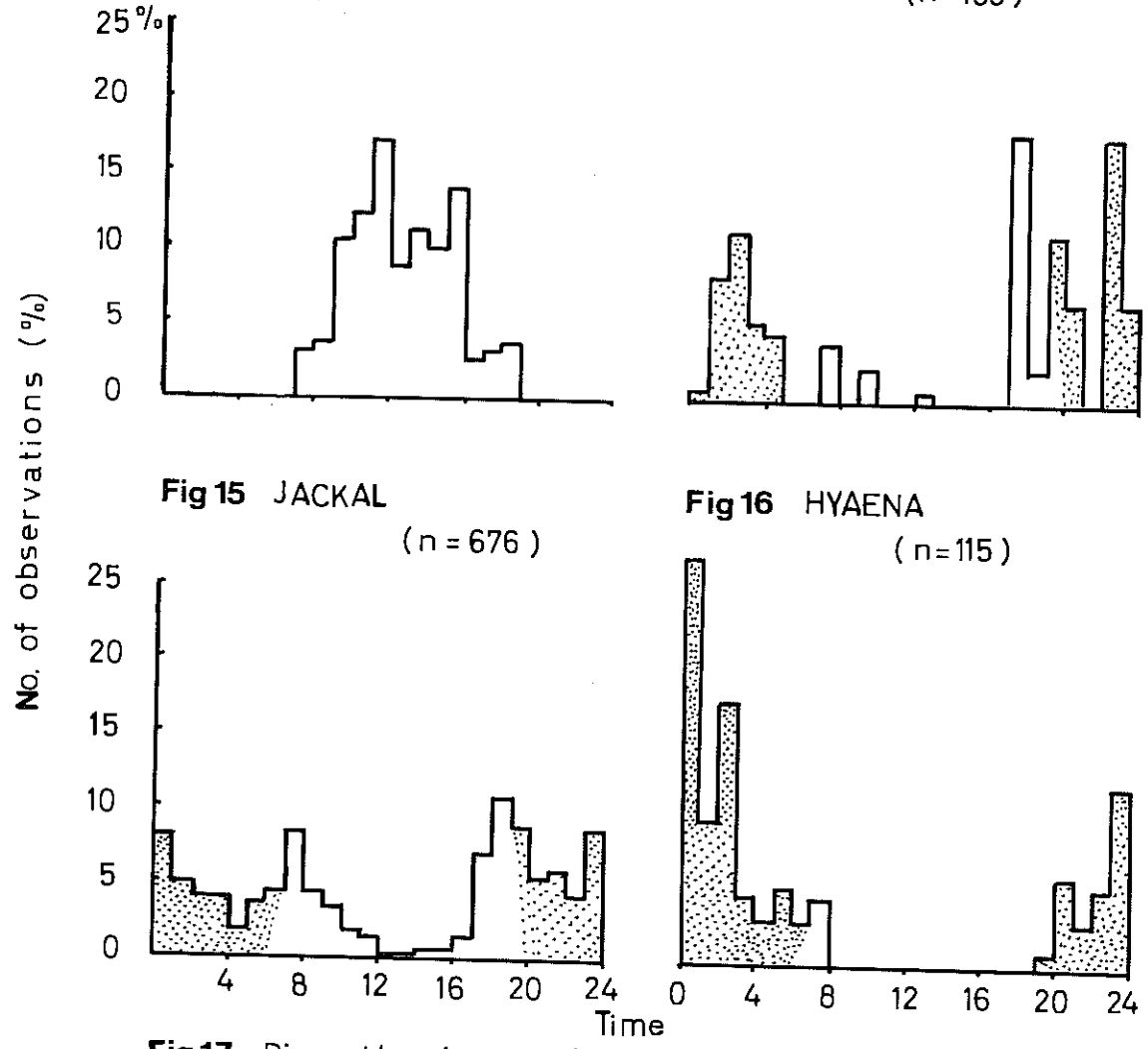


Fig 17 Diurnal/nocturnal drinking preference of 15 species

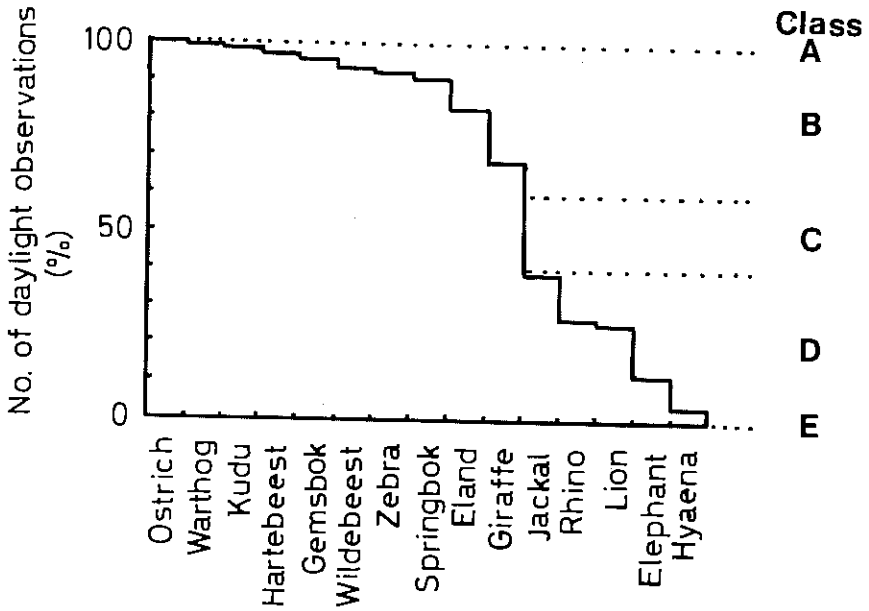
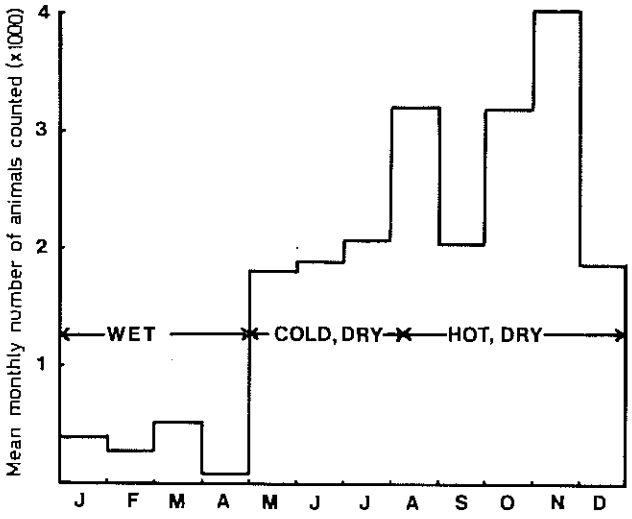


Fig 18 Game utilisation of a fountain (Gobaub) during a year, as shown by 14 24hour censuses.



The immobilisation of wildebeest *Connochaetes taurinus* with etorphine and the use of diprenorphine as an etorphine antagonist

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ABSTRACT

13 Blue wildebeest were successfully captured with a standard dose of 2,5 mg etorphine hcl and 20 mg triflupromazine hcl. The narcotic/tranquillizer mixture was prepared prior to the capture operation thus eliminating the mixing of "drug-cocktails" in the field.
Diprenorphine hcl effectively antagonised the narcotic effects of etorphine hcl at a ratio of 1:1.

1 INTRODUCTION

It has become common practice in Southern Africa to capture various species of wild antelope with etorphine hydrochloride (M-99, Reckitt) combined with hyoscine hydrobromide and various tranquillizers. In their comprehensive and excellent paper on the capture of 16 species of large wild herbivores, Pienaar, van Niekerk, Young, van Wyk and Fairall (1966) recommended drug mixture of 2 mg M-99, 20 mg acetylpromazine maleate and 10 mg hyoscine hydrobromide for the drug immobilisation of adult blue wildebeest *Connochaetes taurinus* (Burchell). Harthoorn and Bligh (1965) recommended similar drug-combinations. In a later publication Pienaar (1968) recommended the use of drug-combinations incorporating fentanyl (Janssen Pharmaceutica) and the butyrophenone neuroleptics such as azaperone and fluanisone (Janssen Pharmaceutica) as well as hyoscine hydromide. Nalorphine hydrobromide was recommended in all three papers for antagonising the narcotic effects of the etorphine.

In the Etosha National Park wildebeest were immobilised to evaluate the efficacy of etorphine hcl and to obtain samples and data for a project on anthrax. At the same time the animals were marked with collars and ear-tags for a preliminary migration study. In the case of 13 animals immobilized, a constant dosage of 2,5 mg etorphine hcl and 20 mg triflupromazine hcl (Siquil, Squibbs) and the etorphine antagonist — diprenorphine hydrochloride (R&S — 50—50 M. Hcl) was used. The results obtained are recorded in this paper.

2 METHOD AND MATERIALS

Wildebeest are shy and retiring animals and seldom allow a close approach by humans. In Etosha National Park they are found on open plains and usually gallop away when approached by a motor vehicle. Because of the disturbance caused at a waterhole, darting from waterhole hides cannot be recommended. Previously wildebeest were chased on an open plain and darted from a moving vehicle. This method required perfect co-ordination between the driver and the darter and good marksmanship. As wildebeest suddenly swerve and seldom run in a fixed direction many shots were missed. Chasing animals for long distances may precipitate muscular dystrophy and cause mortality (Ebedes, 1969).

For short periods during the rainy season territorial bulls congregate close to the main tourist roads in Etosha and are more concerned in defending

their territories against intruding bulls than in passing motor vehicles. They can therefore be approached up to 50 metres and darted with relative ease.

The Palmer Powder Charge Cap-chur gun, 1 ml projectile darts and either yellow or red ramsets were used for darting.

20 Mg etorphine hcl powder were dissolved in 8 ml triflupromazine hcl (Siquil, Squibbs) giving a solution of 2,5 mg etorphine and 20 mg triflupromazine hcl per ml. Hyoscine hydrobromide 100 mg/ml was used for three of the 13 animals darted.

Diprenorphine hydrochloride (R&S 50-50 M. Hcl) is a new potent morphine antagonist supplied for experimental purposes by Messrs. Reckitt and Colman, Main Road, Rosebank, Cape Town. The powder was supplied in sterile bottles containing 100 mg and a solution of 10 mg/ml was prepared by dissolving it in 10 ml of a special buffer solution consisting of 80 mg sodium citrate B.P., 80 mg anhydrous citric acid B.P., 41 mg sodium chloride B.P. and 0,1 % chlorocresol. The powder is very soluble and dissolves within a few minutes.

Although the exact antagonistic action on morphine and morphine-like drugs is not known it is possible that the morphine antagonists compete successfully with the narcotics for occupation of the receptor surfaces in the brain. (Bentley, 1964). In reversing the narcotic effects of etorphine in immobilised zebra, *Equus burchelli antiquorum*, Ebedes (1971) found that diprenorphine was effective at a ratio of 1:1 and 1:2. In the case of the wildebeest the ratio used was kept at 1:1 i.e. 2,5 mg diprenorphine hcl for antagonising 2,5 mg etorphine hcl.

All the animals captured were marked with collars and plastic ear-tags and injected intramuscularly with antibiotics and corticosteroids.

3 RESULTS

The table shows the results of the immobilisation of 13 wildebeest with 1 ml of a prepared standard dose containing 2,5 mg etorphine hcl and 20 mg triflupromazine hcl and the recovery times recorded after the injection of 2,5 mg diprenorphine hcl. The mean down time was less than 10 minutes (n = 13) and the mean recovery time recorded from the moment the intravenous injection of diprenorphine hcl was completed until the animal was on its feet was 1 minute 5 seconds (n = 12). In the case of No. 12 the antagonist was accidentally injected subcutaneously next to a superficial ear vein resulting in a delayed recovery time of 14 minutes. In all the other cases the diprenorphine was injected into the cephalic vein.

In the first three animals immobilised hyoscine hydrobromide was used, but for the remaining 10 animals this drug was left out of the immobilising-mixture and no effect on the immobilisation times was noted. Similar results were obtained with the capture of zebra (Ebedes, 1971).

None of the animals ran for long distances after darting and the rectal temperatures recorded shortly after recumbency were several degrees lower than the temperatures recorded in gemsbok *Oryx gazella* that were chased prior to darting (Ebedes, 1969).

The results obtained were highly satisfactory, a statement born out by the fact that all the marked animals were seen after the immobilisations and two wildebeest travelled a distance of more than 160 km from the area in which they were marked.

4 DISCUSSION AND CONCLUSIONS

By dissolving etorphine hcl in triflupromazine hcl to obtain a standard concentration of these drugs and by eliminating hyoscine hydrobromide, we eliminated the mixing of "drug-cocktails" in the field. This is important when large numbers of animals have to be captured by unqualified field staff under the supervision and direction of veterinary personnel. Field staff can now be instructed to fill the projectile darts with 1 ml of the combined etorphine/tranquillizer mixture and the mixing of capture drugs in the field thus simplified.

As in the case of zebra (Ebedes, 1971), hyoscine hydrobromide can be eliminated from drug mixtures used for capturing wildebeest.

Diprenorphine hcl proved to be an efficient and rapid etorphine antagonist in wildebeest and can be used intravenously with safety at a ratio of 1:1.

5 ACKNOWLEDGEMENTS

The writer wishes to thank all the Nature Conservators who assisted with the project. Some of them have left Etosha National Park, but their willingness and enthusiasm will always be appreciated. The complimentary samples of diprenorphine hcl received from Messrs Reckitt and Colman, P. O. Box 1097, Cape Town, are gratefully acknowledged by the writer on behalf of the South West African Nature Conservation and Tourism Branch.

Mrs H.-D. Smith is thanked for typing the manuscript Drs E. Young and M. Keep are thanked for their critical comments on the manuscript.

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Table. The immobilisation of wildebeest with 2,5 mg etorphine Hcl and 20 mg triflupromazine Hcl.

No.	Sex	Est. weight kg	Dart Site	Down Time	Temp. °C	Pulse	Resp.	** R&S 50-50 mg	Recovery Time
*1.	M	220	Hip	7 min 20 sec	—	80	34	2,5	1 min 57 sec
*2.	F	210	Shoulder	11 min 50 sec	—	98	34	2,5	1 min 21 sec
*3.	M	220	Neck	9 min 30 sec	—	92	40	2,5	57 sec
4.	M	230	Hip	6 min 30 sec	39,4	84	52	2,5	1 min 29 sec
5.	M	220	Shoulder	5 min 35 sec	39	94	26	2,5	1 min 5 sec
6.	M	220	Shoulder	4 min 47 sec	39,9	84	34	2,5	1 min 10 sec
7.	M	225	Triceps	4 min 35 sec	40	82	30	2,5	1 min 30 sec
8.	M	230	Thorax	12 min 7 sec	36	86	52	2,5	1 min
9.	M	220	Hip	15 min 30 sec	40,2	96	48	2,5	54 sec
10.	F	150	Shoulder	6 min 30 sec	40,3	106	52	2,5	52 sec
11.	M	240	Shoulder	12 min 30 sec	—	92	40	2,5	1 min 4 sec
12.	M	230	Hip	10 min 25 sec	40	88	24	2,5 subcut	14 min
13.	M	225	Hock	16 min 20 sec	39,5	90	26	2,5	50 sec

* 10 mg Hyoscine hydrobromide added to drug mixture
** R&S 50-50 = Diprenorphine hydrochloride (Reckitts)

Occurrence of C-4 plants in the Central Namib Desert

by

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CONTENTS

* Supported by the CSIR, Transvaal Museum and SWA Division of Nature Conservation.

ABSTRACT

A survey of the carbon isotope composition ($^{13}C/^{12}C$) of plants in the Central Namib Desert has been undertaken to ascertain the significance of the C-4 photosynthetic pathway to the desert flora. Using this criterion it is found that all the grasses and some sedges are of the C-4 type, while the majority of the other species are C-3. Of the latter group *Trianthema, Salsola, Gisekia* and *Blepheris* show the high ^{13}C-content characteristic of "Kranz" or strong CAM plants. The C-4 pathway is thus an efficient, but by no means an obligatory adaptive condition for survival in a hot desert environment.

1 INTRODUCTION

The 4-carbon (C-4) or Hatch-Slack mode of photosynthesis is an evolutionary adaptation to hot dry climates. This is evidenced in the fact that C-4 plants have the ability to photosynthesize at high temperatures and a high degree of water-use efficiency. They are thus, in general, more drought tolerant than plants that utilize the more widespread 3-carbon or Calvin cycle of CO_2 fixation (cf. Björkman & Berry, 1973). Several hundred C-4 species belonging to at least thirteen different families of the *Angiosperms* have been identified to date (Downton, 1975). They all exhibit the Kranz syndrome, i.e. their vascular bundles are surrounded by a sheath ('Kranz') of cells containing large specialized chloroplasts in which 4-carbon molecules such as malic and aspartic acid, initially formed in the mesophyll cells, are decarboxylated and the resulting CO_2 converted to sugars and starch via the normal Calvin cycle. The syndrome is especially common in the grass family, but is also present among the *Cyperaceae, Chenopodiaceae, Aezoaceae, Amaranthaceae* and others.

In addition to these 'Kranz' plants many succulents which exhibit the Crassulacean acid metabolism (CAM) also utilize the C-4 pathway, but they do this by night (Nuerenbergk, 1961; Sutton & Osmond, 1972). Malic acid is stored until the following day when it is decarboxylated, providing CO_2 for photosynthetic carbon reduction. The plants therefore can keep their stomata closed during the hot dry daytime and so minimize water loss. CAM thus also represents an adaptation for some species occupying a xerophytic niche (Neales *et al.*, 1968).

2 METHODOLOGY

In view of the obvious significance of the C-4 photosynthetic pathway for the ecology of arid zones, a survey has been made of the C-4 status of plants in the different ecosystems of the Namib desert. This represents a first attempt to evaluate the significance of the C-4 physiological process for the biomass of a region. A convenient means of doing this is to measure the $^{13}C/^{12}C$ ratios in the plants. 'Kranz' and C-3 plants show different degrees of isotope fractionation during the assimilation of CO_2 from the air (Bender, 1971; Smith & Epstein, 1971). As a result the relative ^{13}C con-

tent, δ^{13}, of the former ranges from -10 to $-16^0/_{00}$ (parts per thousand deviation from PDB standard carbon) while that of the latter group lies between -22 and $-32^0/_{00}$. Thus both modes of photosynthesis produce a slight depletion in the heavy ^{13}C isotope as compared with atmospheric CO_2 ($\delta^{13} = -7^0/_{00}$) but ranges do not overlap.

CAM plants, on the other hand, reveal δ^{13}-values over the whole range from $-10^0/_{00}$ to $-26^0/_{00}$ (Osmond *et al.*, 1973), depending on the ratio of nocturnal C-4-type assimilation to direct daily C-3 photosynthesis. This ratio is partially controlled by environmental conditions, notably by water stress, but is appears that the tendency to uitilize CAM differs between species. While some species can be induced to revert to the CAM mode only with difficulty and thus show δ^{13}-values in the C-3 range when growing in their natural habitat, others mainly assimilate CO_2 at night even under favourable conditions and always have δ^{13}-values in the C-4 range (Vogel, unpubl.). Isotope ratio measurements can thus only distinguish plants with an appreciable tendency to CAM from C-3 plants and not ones that are merely capable of CAM. ^{13}C analyses have the advantage that small dried samples can be used and it is not necessary to have physiologically active material to hand.

3 RESULTS AND DISCUSSION

The survey thus far has been confined mainly to the coastal tract in the vicinity of Sandwich Harbour (fog desert) and the sand desert further inland. The gravel plains north of the Kuiseb river and the Inselberge protruding from them harbour a much larger variety of species, the analysis of which is still under way. All three of these regions represent extremely arid habitats.

Rainfall along the coast amounts to less than 15 mm a year on average. An additional 40 mm of (saline) moisture is derived from the frequent early-morning fogs that are caused by advection from the adjacent cold sea (Goudie, 1972). In this adverse environment the limited plant communities are mainly restricted to such places where groundwater surfaces from below the desert floor. Inland from the coast average maximum temperatures rise rapidly from 19°C to 30°C while the precipitation increases only gradually to reach 100 mm annually on the inner margin of the desert. The very sparse vegetation in the sand desert and on the gravel plains is subject to extreme heat, high light intensities and long periods of aridity between the episodic showers. These conditions are somewhat tempered by the advective fogs which extend to the inner edge of the Namib several times each year and occur more frequently towards the coast (70 to 100 days per year 50 km inland).

Practically all the species occurring in the sand desert and along the coast are listed in Table 1 together with their relative δ^{13} contents. Some of the more common plants on the gravel plains are also included. The results show that all the grasses are of the C-4 type. In fact, of the 56 grass species listed for the entire region, including the inner desert margin, only three are 'Nonkranz' — two *Phragmites* and one *Polypogon* species, which are restricted to the river beds. This is in contrast to the findings for the coastal desert south of the Orange River where 95% of the grass species are 'Nonkranz' (Vogel *et al.*, 1977). Of the three sedges found on the coast one is Kranz and two 'Nonkranz'. Six of the seven other sedges on the regional check list are also Kranz so that, here too, the Kranz types predominate.

Most of the other plants in Table 1 are of the C-3 type. The only exceptions are the two species of *Trianthema* and those of *Salsola, Gisekia* and *Blepharis*. Microscopic examination of the small succulent leaves of *T. hereroensis* showed no sign of a bundle sheath so that it must be a strong uitilizer of CAM. The other species referred to with high ^{13}C contents (-11 to $-15^0/_{00}$) may either be CAM or 'Kranz' plants. It would be necessary to obtain fresh material of these plants to distinguish between the two possibilities. Two further samples, viz. *Mesembreanthemum querichianum* and *Welwitschia mirabilis* fall just outside the range for C-3 plants and are therefore probably weak utilizers of CAM in their natural habitat. In fact, *Welwitschia* has been reported to possess the necessary enzymes for CAM and to assimilate carbon dioxide at night (Dittrich & Huber, 1974). On the other hand experiments conducted by one of us (JSV) on a fresh leaf showed no nocturnal carbon dioxide fixation. Assimilation only took place in the early morning and late afternoon, in accordance with the findings of Bornman (1972). These observations together with the relatively low ^{13}C content of specimens collected in the Namib desert suggest that, although the species is capable of CAM, it predominantly utilizes the Calvin mode of photosynthesis in its natural environment.

The rest of the plants listed in Table 1 are classified as C-3 species on the basis of their low δ^{13} values. It cannot be excluded that some of them are also capable of exhibiting CAM, but this is clearly not their normal mode of photosynthesis. We observe that only ten (four genera) of the nearly fifty dicots thus far investigated from the Central Namib desert (20%) have adapted one of the two C-4 modes of carbon dioxide fixation.

4 CONCLUSIONS

The surprisingly low frequency of C-4 species encountered in this survey as well as the fact that several of the C-3 species are endemic to the Namib desert, suggest that the C-4 pathway may constitute an effectual but not an obligatory adaptive condition for survival in a hot desert environment. During prolonged isolation the endemic species have evolved satisfactory mechanisms of withstanding the dry heat of their habitat without converting to C-4. The high frequency of C-4 grasses, on the other hand, merely reflects the general situation in the interior of Southern Africa (Vogel *et al.*, 1977) and is not specific to the Namib desert.

5 ACKNOWLEDGEMENTS

We would like to thank Mrs A. Fuls for selecting many of the samples from the National Herbarium, Pretoria and Miss E. Lursen for performing the laboratory analyses.

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Table 1. Flora of the Central Namib Desert

A: *Dunefields south of the Kuiseb River*

	Family[1]	Species[2]	Collector Specimen No.[3]	Locality	Sa No M-	Anal. MC-	$\delta^{13}C$ ‰
26.	Molluginaceae	Limeum fenestratum	Seely & Vogel	NW of Tsondab	608	850	-22,6
		do.	Ward 166	Natab, W of Gobabeb	699	984	-23,5
		do.	Ward 213	12 km E of Tsondab	689	995	-23,9
27.	Aizoaceae	*Trianthema hereroensis	Giess 9841	16 km S of Gobabeb	616	879	-14,5
		do.	Seely & Vogel	NW of Tsondab	605	853	-12,5
		T. triquetra var. parvifolia	Jensen 276	S of Gobabeb	618	878	-11,7
47.	Capparaceae	Cleome paxii	Ward 214	12½ km E of Tsondab	688	985	-24,2
64.	Geraniaceae	*Monsonia ignorata	Seely & Vogel	NW of Tsondab	607	857	-24,5
84.	Sterculiaceae	Hermannia minimifolia	Ward 210	10 km E of Tsondab	691	993	-25,6
115.	Rubiaceae	*Kohautia ramosissima	Seely & Vogel	NW of Tsondab	604	852	-23,4
		do.	Ward 211	10 km E of Tsondab	690	994	-21,8
131.	Pedaliaceae	*Sesamum abbreviatum	Seely & Vogel	NW of Tsondab	609	859	-25,0
139.	Asteraceae	Helichrysum fleckii	Ward 216	6 km S of Hudaob	687	983	-27,3
147.	Liliaceae	Hexacyrtis dickiana	Seely & Vogel	NW of Tsondab	606	856	-24,0
		do.	Strey 2590	S of Hudaob	611	874	-26,6
160.	Gramineae	Asthenatherum glaucum	Seely & Vogel	near Tsondab	602	854	-12,8
		do.	Ward 161	Natab, W of Gobabeb	686	981	-15,1
		Eragrostis spinosa	Seely & Vogel	near Tsondab	599	847	-14,9
		Stipagrostis ciliata	do.	do.	601	851	-13,4
		*S. gonatostachys	do.	NW of Tsondab	596	846	-13,1
		*S. lutescens	do.	do.	598	844	-14,1
		S. namaquensis	do.	near Tsondab	600	848	-13,6
		*S. sabulicola	do.	NW of Tsondab	597	845	-13,2

B: *Coastal Area*

	Family[1]	Species[2]	Collector Specimen No.[3]	Locality	Sa No M-	Anal. MC-	$\delta^{13}C$ ‰
32.	Chenopodiaceae	Arthrocnemum affine	Ward 197	Sandwich harbour	695	987	-26,4
		Salsola nollothensis	Ward 203	10 km N of Sandwich ha.	693	989	-12,8
47.	Capparaceae	*Capparis hereroensis	Ward 202	10 km N of Sandwich ha.	694	988	-26,2
119.	Heliotropiaceae	Heliotropium curassavicum	Ward 195	Sandwich harbour	696	986	-24,6
124.	Solanaceae	Lycium tetrandrum	Ward 193	4 km S of Sandwich ha.	698	1007	-24,1
160.	Gramineae	Dactyloctenium aegyptium	Vogel	Spencer Bay N	654		-14,4
		Eragrostis cyperoides	Vogel	Spencer Bay N	674	628	-13,1
		do.	Ward 190	9½ km S of Sandwich ha.	692	991	-12,7
		Sporobolus virginicus	Ward 194	Sandwich harbour	697	997	-13,2
165.	Cyperaceae	Juncellus laevigatus	Rodin 2147	near Swakop ri.	628	906	-10,6
		Scirpus dioicus	De Winter 3442	Aroab, dunes	619	896	-22,4
		S. littoralis	Giess 3872	Kaokoveld	620	897	-23,5

C: *Plains North of the Kuiseb river and the Inselberge*

Family[1]	Species	Collector Specimen No.[3]	Locality	Sa No M–	Anal. MC–	$\delta^{13}C$ ‰
13. Welwitschiaceae	Welwitschia mirabilis	Bornman	Central Namib	C406	—	–19,9
	do.	Herre	near Swakopmund	C647	695	–22,4
25. Nyctaginaceae	Commicarpus squarrosus	Jensen 32	Arechadamab hills	764	1098	–24,5
26. Molluginaceae	Gisekia africana	Jensen 72	Hotsas hills	758	1108	–11,9
	G. pharnaceiodes	Tälken & Hardey 845	Outjo	753	1114	–12,1
	Limeum argute-coronatum	Jensen 138	near Ganab	754	1112	–24,8
27. Aizoaceae	Aizoanthemum dinteri	Ihlenfeldt & de Winter 3249	Twyfelfontein	755	1111	–22,9
	Galenia africana	Jensen	Hamilton range	756	1110	–25,9
	Mesembryanthemum guerichianum	Merxmüller & Giess 28713	Lüderitz-Süd	757	1109	–20,1
	Trianthema triquetra	Jensen 130	near Ganab	613	880	–12,2
32. Chenopodiaceae	Salsola aphylla	Jensen 9	W of Welwitschia	760	1105	–13,9
	S. tuberculata	de Winter & Giess 6223	Lüderitz	759	1107	–13,0
33. Amaranthaceae	Arthraerua leubnitziae	Jensen 46	Swartbank	752	1097	–24,4
	Calicorema capitata	Jensen 340	Gobabeb	751	1096	–25,6
65. Zygophyllaceae	Zygophyllum stapfii	Vogel	S of Swartbank	749	1094	–25,1
84. Sterculiaceae	Hermannia elliottiana	Jensen 453	Onanis	788	1141	–24,6
	H. modesta	Ihlenfeldt, de Winter & Hardey 3223	30 km from Torra bay	790	1143	–27,8
94. Cucurbitaceae	Citrullus ecirrhosus	de Winter 3193	Swakop-Usakos road	786	1139	–26,1
105. Plumbaginaceae	Dyerophytum africanum	Jensen 50	Hope Mine	789	1142	–24,4
114. Asclepiadaceae	Asclepias buchenaviana	Koch A13	Swakopmund	787	1140	–22,1
120. Boraginaceae	Trichodesma africanum			783	1136	–24,3
126. Scrophulariaceae	Sutera maxii	Jensen 155	N of Gobabeb	782	1134	–24,1
130. Acanthaceae	Blepharis bossii	Ihlenfeldt 1932	Kleinnabib ri.	776	1127	–11,6
	B. obmitrata	Jensen 147	Namib Desert Park	780	1131	–12,9
	Monechma arenicola	Tälken & Hardey 867	Swakopmund	781	1132	–24,6
	M. desertorum	Jensen 180	Kriesserus	779	1130	–23,5
	Petalidium setosum	Kinges 2409	Lüderitz	775	1126	–24,1
	Ruellia diversifolia	Jensen 197	Ojab farm	778	1129	–25,8
131. Pedaliaceae	Rogeria longiflora	Ihlenfeldt 1780	5 km N of Vioolsdrif	777	1128	–23,0
139. Asteraceae	Gnaphalium luteoalbum	Res. Sta. Gobabeb 00068	Gobabeb	774	1125	–28,5
	Helichrysum roseo-niveum	Pearson	Welwitschia	768	1118	–26,5
	Osteospermum microcarpum ssp. septentrionale	Barnard 102	Omaruru	767	1116	–23,7
	Pechuel-Loeschea leubnitziae	Keets 1230	Swakopmund	773	1124	–22,3
160. Gramineae	Erogrostis porosa	Kinges 2136	Lüderitz	761	1102	–12,9
	Sporobolus robustus	Jensen 523	Hudaob	762	1101	–13,9
	Stipagrostis obtusa	Jensen 181	6 km S of Kriesserus	763	1099	–12,8
	Triraphis ramosissima	Giess 3002	near Usakos	650	926	–13,8

[1] The numbering of the families is according to Merxmüller: Prodromus einer Flora von Südwestafrika.
[2] Endemic species are designated by an asterisk.
[3] The unnumbered samples were collected specifically for this investigation. In addition, J. D. Ward collected a number of specimens for us. These will be housed in the National Herbarium, Pretoria for possible future reference. The rest are samples taken from specimens in the National Herbarium.
In some cases the plants are not actually from the area under consideration, but only from the general region. In our experience the locality can only influence the isotopic composition insignificantly so that this procedure is acceptable. It has the advantage that the specimens are available to other investigators.

Observations on the mineral status of springbok (Antidorcas marsupialis Zimmerman) in South West Africa

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CONTENTS

ABSTRACT

The mineral status of 43 springbok was determined by liver analyses for phosphorus, calcium, magnesium, manganese, zinc, iron and copper. The animals were shot within a period of 14 months on a farm bordering the Kalahari. Mean values of the element concentrations were plotted according to season, and the probable causes of fluctuations are discussed.

1 INTRODUCTION

Little is known about the influence of specific minerals on the production of grazing animals, and much research work has to be carried out in this respect. Boyazoglu *et al.* (1972) have demonstrated that the mineral status of animals can be estimated by the analysis of the elements in the liver. It is planned to carry out, by liver analysis, a systematic survey of mineral imbalances of the economically important animals of South West Africa.

Little is known about the multiple factors influencing the mineral status of animals, and it is planned to determine the influences of pasture, and season, on the springbok, kept on several farms in South West Africa. Springbok are kept with a minimum of human influence. Factors applicable to domestic livestock but not applicable to them are rotational grazing, dosing and vaccinations. At most sea-salt is made available as a lick.

2 MATERIALS AND METHODS

Forty-three adult springbok (41♂, 2♀) were shot between April 1973 and June 1974 on the farm Gomnab (E 18°15′, S 23°36′), Rehoboth District, South West Africa. Within one hour after death a post mortem examination was carried out, and only animals in good state of health were used for this study. A wedge-shaped sample of about 30 grams of the thickest part of the edge of the liver, was taken from each animal, and was immediately preserved in 3% formaldehyde for later analysis. In the laboratory a one gram core sample was taken from the preserved liver, digested in acids, and the solution was analysed through a laminar flow burner on a "Beckman 979" atomic absorption spectrophotometer for copper, zinc, iron, magnesium, manganese and calcium (Boyazoglu *et al.*, 1972). Phosphorus was evaluated using a Technicon Autoanalyser. For the evaluation of the concentrations in each element group means of 8 observations were calculated. A mean date was also calculated for each group. By plotting the mean concentrations relative to the mean dates, the trends of the concentrations in each element are demonstrated. The means are shown in the relevant graph.

3 ENVIRONMENT AND FEEDING BEHAVIOUR

The farm studied lies on the border of the southern Kalahari Savannah, and can be characterized as

Table 1. Means and Standard Deviations of Mineral Concentrations in Livers from Springbok and other Livestock.

Species, origin	Month of collection	No. of animals	CU (PPM)	MN (PPM)	ZN (PPM)	MG (PPM)	CA (PPM)	FE (PPM)	P (%)
Springbok— Study Farm, Gomnab.	April '73— July '73	43	15,4 ±6,5	3,6 ±0,5	56,9 ±18,23	188,7 35,5	109,0 29,5	99,9 27,2	0,23 ±0,02
Springbok— Farm Dabib.	August '73	5	31,4 ±3,1	3,5 ±0,1	53,6 ±3,9	199,2 ±8,7	90,2 ±6,9	111,4 ±6,4	0,25 ±0,1
Springbok— Farm Campbellsdraai.	August '73	6	28,1 ±9,8	3,4 ±0,2	50,3 ±4,1	171,7 ±19,9	115,7 ±9,9	85,8 ±8,0	0,24 ±0,1
Springbok— Farm Galenbeck.	July '73	5	24,6 ±3,1	3,7 ±0,1	50,6 ±2,8	212,6 ±7,1	101,6 ±19,0	108,0 ±11,1	0,26 ±0,1
Republic of South Africa. Cattle (Means) Sheep (Means)	All year. 1973— 1974	8000	39 75	4,2 4,2	75 75	191 191	129 129	71 71	0,23 0,23

grass, mixed tree and shrub savannah (Giess, 1971). The area substrate is limestone, which appears in several flat ridges on the surface, covered mainly by red Kalahari sand, with a few "vleis" (wet areas) and salt pans interspaced. The rainfall of the 1972/73 season was 130 millimetres, which is only about 50% of the average annual precipitation. The last abundant rain fell in April 1973. As a result the pasture was poorly grown. In 1973 early October-rains did not bring any response to the grass, but flowers, fresh green leaves and green pods developed on the shrubs. The growth of the annual grasses started in December after a series of good rains, which lasted throughout January, February, March and April 1974 (Table 1).

The scattered shrubs *(Acacia mellifera* ssp. *detinens, Acacia karroo, Catophractes alexandri, Monechma australe)* were browsed by the springbok. During the dry season, flat herbs *(Helichrysum argyrosphaerum* — "sewejaartjies" and *Lotononis platycarpis)* grew on sandy areas, where the annual grass

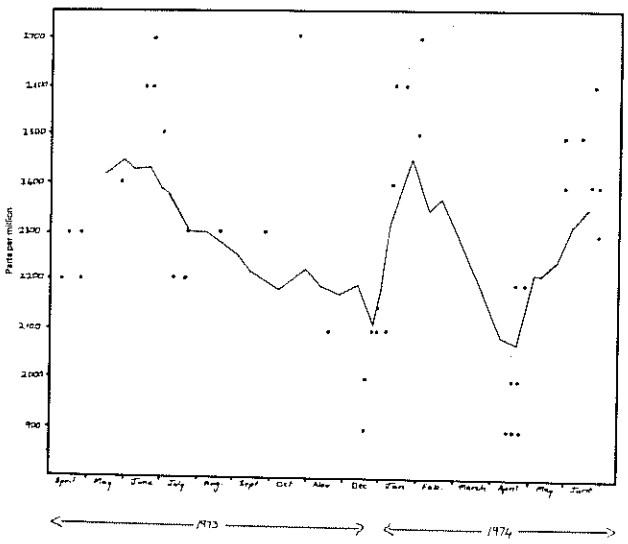

Figure 1. Correlation between Phosphorus concentration and season in springbok livers.

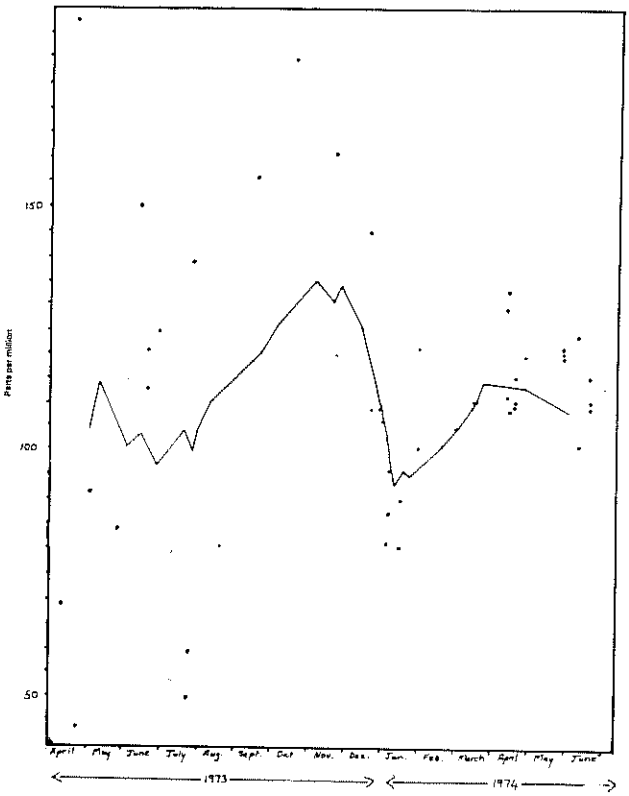

Figure 2. Correlation between Calcium concentration and season in springbok livers.

(Schmidtia kalahariensis) was scarce, and were grazed. In some areas of certain camps, where *Helichrysum argyrosphaerum* and *Lotononis platycarpis* were absent, green leaves of a grass *(Aristida congesta)* were grazed by the springbok. Water and rock salt blocks were available to the animals.

4 RESULTS AND DISCUSSION

Table 1 shows mean and standard deviations of the concentrations of the elements in the liver of

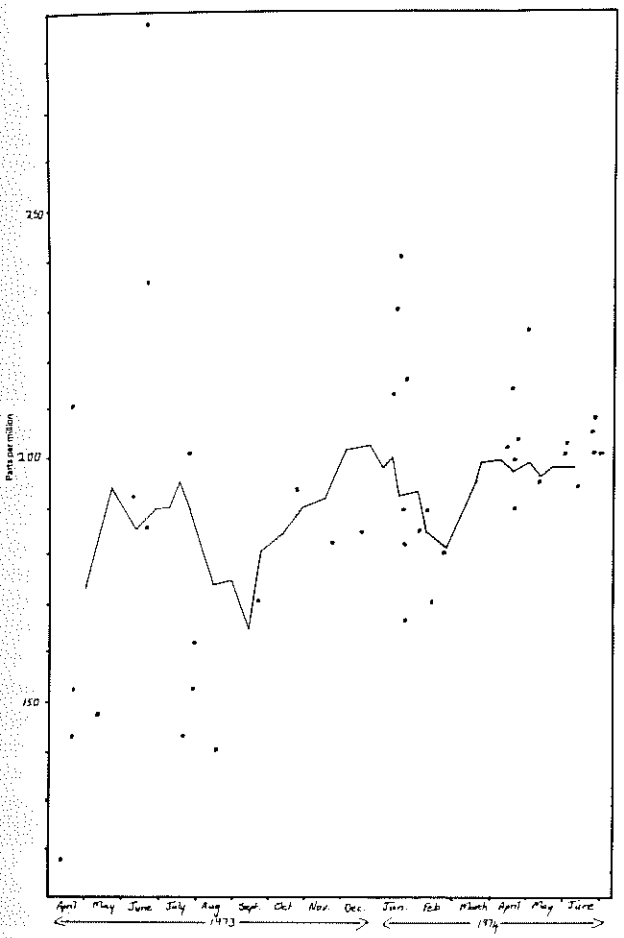

Figure 3. Correlation between Magnesium concentration and season in springbok livers.

springbok used in this study. Values are included from springbok of three other farms, 50 and 80 kilometres apart, partly comparable in soil and plant communities. Compared with the figures from the other farms, the animals studied at Gomnab had lower copper concentrations. The other elements did not differ. The lower copper concentration may be due to a less favourable state of the pasture and a lower copper concentration of the soil. In comparison to the "normal values" (table 2) determined in approximately 8 000 cattle and sheep in the Republic of South Africa by the same method (Boyazoglu, 1974), copper, manganese and zinc are lower in the springbok; the iron concentration however, is higher.

4.1 Seasonal influences

Figures 1 to 7 show concentrations of various elements in the livers collected over several months, indicating certain trends. The results were compared with those of mineral analyses by Freyer (1967) in 10 "palatable" grass and 4 shrub species collected on the Experimental Farm Uitkoms near Grootfontein, South West Africa. This area has a higher rainfall than the study farm, nearly all of the grasses and all the shrubs analysed were different from the pasture plants of the study farm. Nevertheless the seasonal influences on the mineral concentration of the plants are expected to be the same.

4.1.1 Phosphorus and Calcium (Figures 1 and 2)

The average concentration of phosphorus in the livers decreased during the dry season, rising after the rainy season had started.

This observation confirms Freyer's findings of a slight decrease of phosphorus in the palatable shrubs in winter, and a remarkable fall to traces in grasses during the dry winter season. The calcium concentration in the livers on the other hand, rose during the dry season and made the calcium/phosphorus balance unfavourable. This increase seems to be influenced by the increase of calcium in the pasture plants during the dry season, (Freyer 1967). Phosphorus fell during January, February and April 1974; calcium, however rose during the same time, and thereafter there were contrary trends in both these minerals. The antagonistic effect of high calcium intakes on phosphorus absorption, was also noted.

After the initial green, growth of the plants is completed, the fall of phosphorus, and slow rise of calcium in December/January, is suspected to be caused by a rise in calcium in the summer pasture plants and by a decrease of phosphorus (Freyer 1967) The second rise of phosphorus is obviously due to the first occurrance of the typical winter plants such as *Helichrysum argyrosphaerum* ("sewejaartjies") and *Lotononis platycarpis* in April/May, which were grazed by springbok during the dry season.

4.1.2 Magnesium (Figure 3)

Freyer 1976, found the magnesium and calsium concentration highest in the palatable shrubs. Mag-

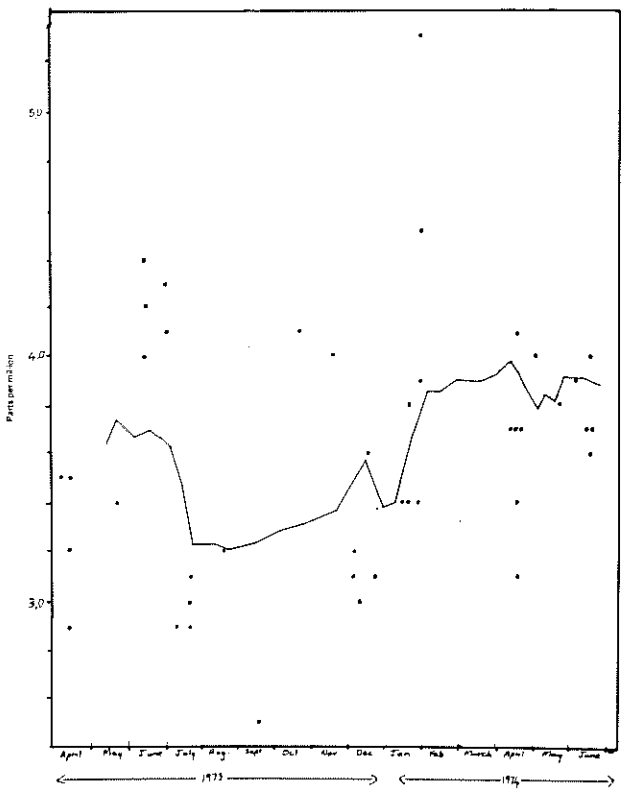

Figure 4. Correlation between Manganese concentration and season in springbok livers.

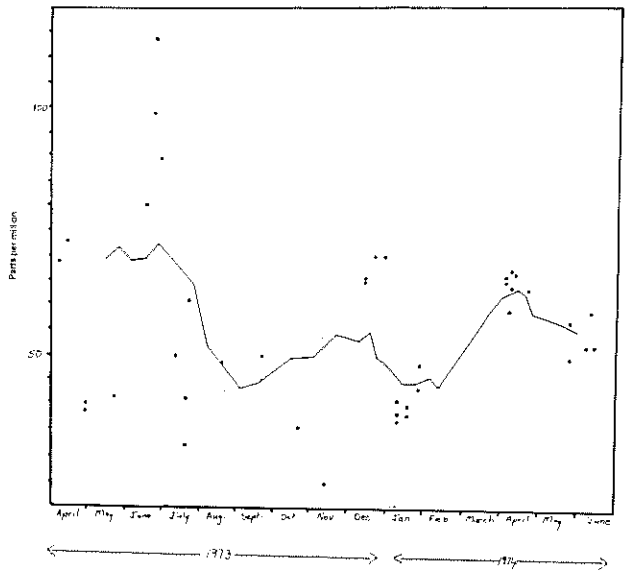

Figure 5. Correlation between Zinc concentration and season in springbok livers.

nesium hardly decreased in the pasture of the dry season, however, small variations and an antagonistic effect to phosphorus are suspected in the springbok. Except for the dry season 1973, the magnesium concentration of the livers followed a pattern similar to calcium.

4.1.3 Manganese (Figure 4)

In spite of the fact that Freyer *op cit* found only a slight decrease of manganese in the pasture during the dry season, there is a distinct difference between the relatively low concentration of this element in the livers collected during the dry season to those collected during the rainy season. The increase of the manganese concentration in December/January seems to be delayed long after the onset of the rainy season and the occurrance of the first green growth.

4.1.4 Zinc (Figure 5)

Freyer *op cit* found a slight decrease in the zinc concentration of the palatable shrubs, but a remarkable decrease in the zinc concentration of the pasture grasses during the dry season. The general trend of the graph confirms this finding. The expected rise of the zinc level at the beginning of the dry season however, seems to be delayed. There is again the question of whether the extremely high calcium concentrations at the beginning of the rainy season had a depressing effect on zinc absorption.

4.1.5 Iron (Figure 6)

There is an evident increase in the iron concentration of the springbok livers at the end of the dry season. Specific feeding patterns and changes in specific winter pasture plants seemed to be the cause, as Freyer *op cit* found a fairly constant level of iron in the pasture plants of different seasons.

4.1.6 Copper (Figure 7)

Freyer *op cit* found a decrease of copper only in the pasture grass of the dry season, but not in the palatable shrubs which contain 3 to 4 times more copper than grasses. In figure 7 there are two distinct rises in the copper concentrations of the livers.

The first increase, at the beginning of the rainy season, is suspected to be caused by two factors. Firstly, the grass has grown and becomes unattractive to the springbok, the animals browse more on the shrubs. Secondly, the values over the first peak, (over 24 ppm Cu) originate from animals in camps in the best condition of pasture and where *Acacia mellifera* ssp. *detinens* was abundantly available. The second rise is very much suspected to be caused by the occurrance of the winter plant *Helichrysum argyrosphaerum*, ("sewejaartjies"), one of the main feed sources of springbok during the winter season. This plant contains higher amounts of copper (Oelschläger and Schwerdtfeger, 1959) than other pasture plants, and usually occurs in larger numbers, mainly in overgrazed camps on the farm. This fact can be demonstrated by identifying the origin of the samples. From April to July 1974 (second rise of the graph), the springbok with the highest copper concentrations were shot in camps which were exceedingly overgrazed and of poorer quality, during the rainy season, whilst camps with the best pasture conditions were then found in the middel range.

In conclusion copper seems to be best supplied during the rainy season by pastures in generally good condition.

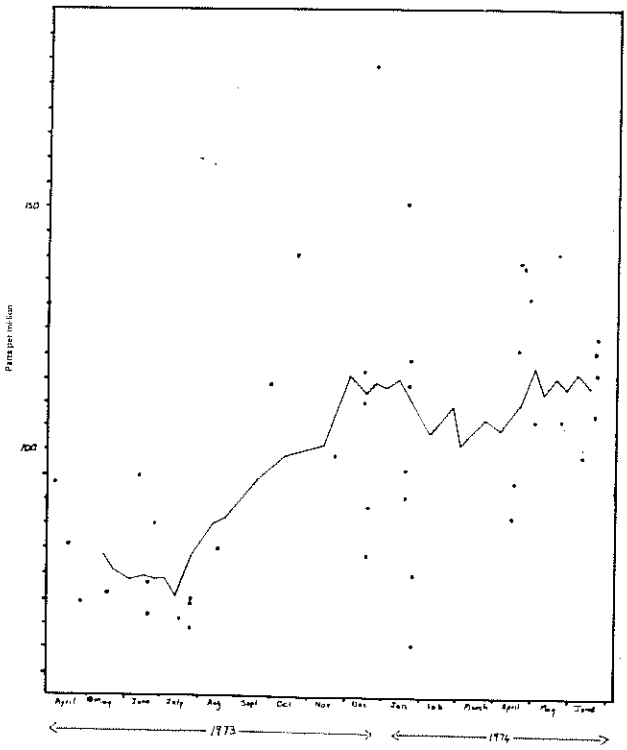

Figure 6. Correlation between Iron concentration and season in springbok livers.

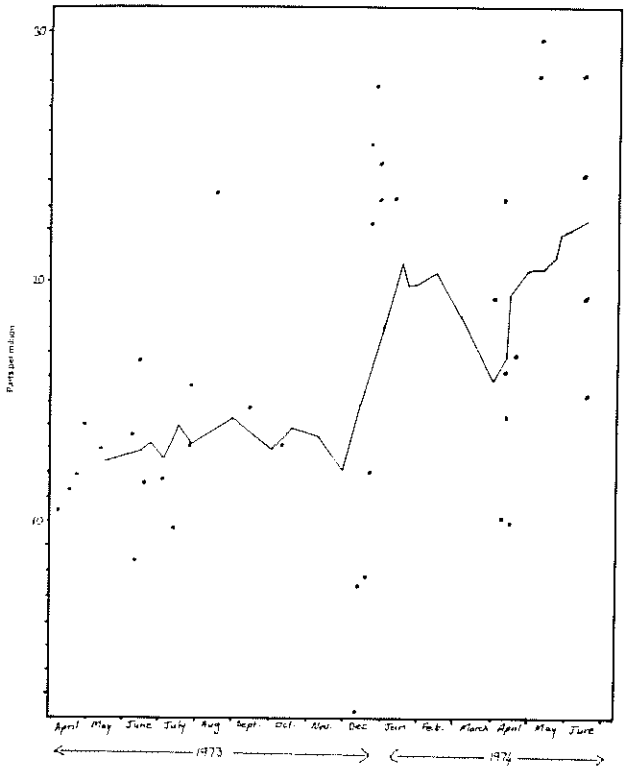

Figure 7. Correlation between Copper concentration and season in springbok livers.

During the dry season however, an overgrazed pasture is revaluated by the abundant growth of certain pioneer plants, if there is enough moisture in the soil.

5 ACKNOWLEDGEMENTS

Mr and Mrs H. Förtsch, and Mrs K. A. M. Förtsch for their great interest in the study, and for the kind help and friendliness during all the visits to the farm;

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SHORT NOTE

Radiocarbon dates for a shell midden complex from Wortel, Walvis Bay

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At the invitation of the Department of Nature Conservation, a preliminary excavation was carried out at a shell midden complex at Wortel near Walvis Bay during January, 1976. The site will be inundated upon completion of a salt evaporation pan. Although there is good reason to believe that cultural material has been previously collected from these middens and that any sampling of this material will thus be biased, it was nevertheless felt that the evidence of economic activities and exploitation patterns to be gained from the faunal analyses justified work on the site.

The site is situated in the delta of the Kuiseb River at the western edge of the dunes that have blocked the course of the river. A scatter of shell, bone and other material lies on a number of small dunes as well as on the intervening fluvial sediments. The sedimentary history of the area represents a complex interaction between dune movement across the delta and their truncation and burial by flood silts. This could have resulted in older sites being buried or washed away. The present midden complex could post date the last episode of fluvial deposition. However, a stream channel just to the west of the site could indicate continuing intermittent stream activity restricted to downcutting rather than flooding and deposition. This change in volume of the discharging river could have resulted from the river shifting its main channel elsewhere. Further work is planned to test this hypothesis.

The cultural material recovered includes ostrich eggshell beads and pendents, bone points, potsherds, quartzite flakes, quartz pebbles used as rubbers and grindstones or palettes of schist. In addition, a number of *Marginella capensis* shells appear to have been artificially bored. The mammal fauna consists of *Arctocephalus pusillus*, small medium bovids, large medium bovids and a Cetacean (R. Klein pers comm). The shell sample consists of *Lutraria lutraria, Perna perna, Choromytilus meridionalis, Nassarius plicatellus, Bullia laevissima, Patella argenvillei, Thais haemastoma, Hinnites sp, Marginella capensis* and *Donax serra*, (B. Kensley pers comm). Also recovered were fish and bird remains.

The radiocarbon dates are as follows:

Pta—1645	Wortel KM2	400±50 years B.P.
Pta—1651	Wortel KM3	260±50 years B.P.

According to the calibration curve, the most probable date for KM2 is AD 1460 and for KM3 AD 1635. The samples were taken from two separate middens and thus indicates the time period over which the site was utilised. The earliest known inhabitants of the Walvis Bay area were Topnaars and Damara (Alexander 1838; Galton 1853). It is thus possible that the middens at Wortel and at other places along the coast (Sandelowsky & Pendleton 1970) can be attributed to one or both of these people.

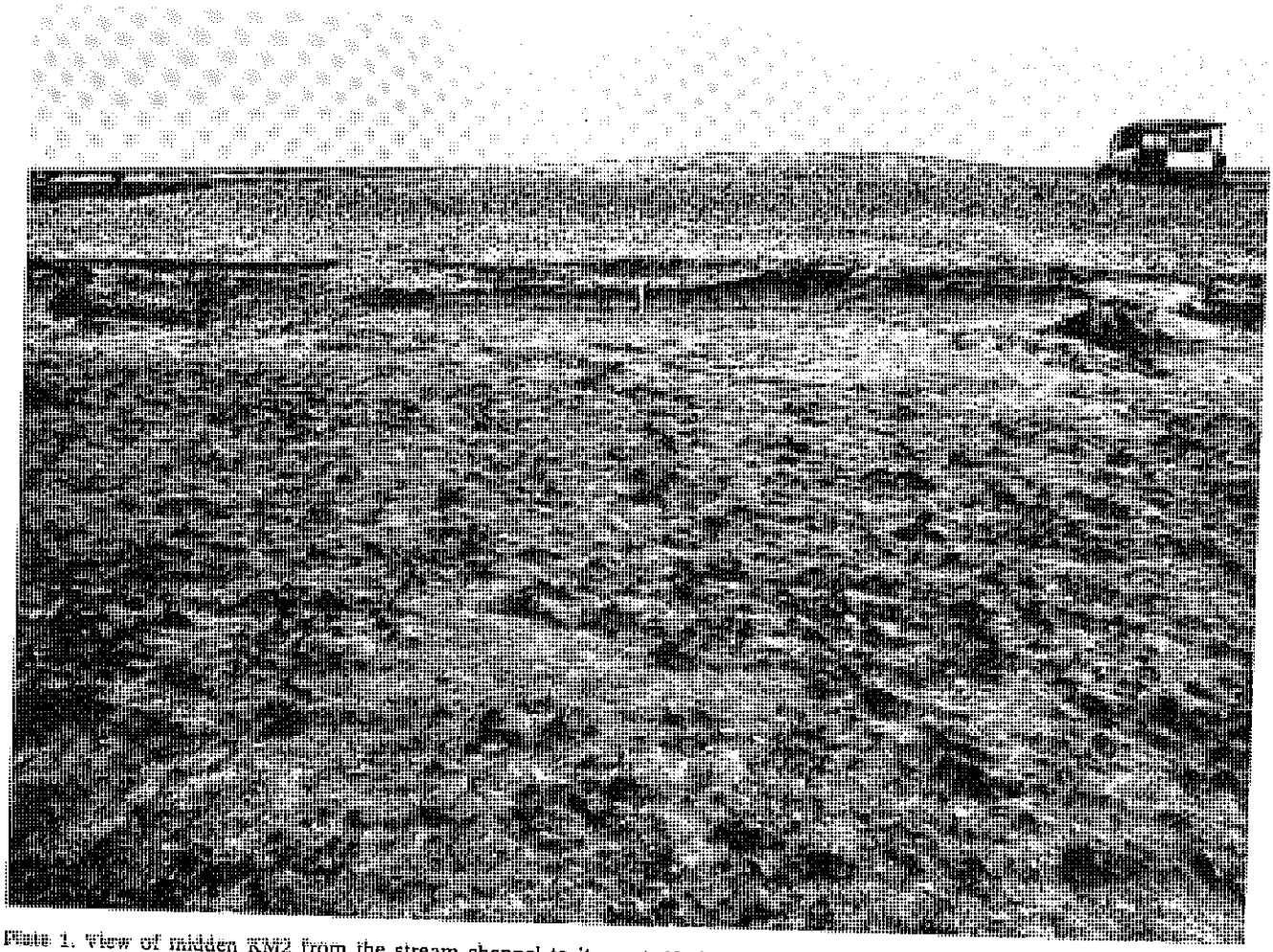

Plate 1. View of midden KM2 from the stream channel to its west. Notice how the midden has been truncated by the channel revealing the layered silts of the salt flats.

ACKNOWLEDGEMENTS

Sincere thanks are expressed to those who encouraged and supported the work at Wortel. They are: Mr C. G. Coetzee, Director of the State Museum; Mr B. de la Bat, Director, Dr E. Joubert and Mr C. Clinning of the Department of Nature Conservation and Mr F. E. Tworeck of Walvis Bay. The Secretary for National Education has granted permission (to L.J.) for this paper to be published.

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SHORT NOTE

Nesting association between Groundscraper Thrush *Turdus litsipsirupa* and Fork-tailed Drongo *Dicrurus adsimilis*

by

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and

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Nature Conservation and Tourism Division, South West Africa Administration, Windhoek

Nesting associations between birds and other living things (including other birds) have been described for many species (Talent 1937, Moreau 1942, Durango 1949, Walsh & Walsh 1976). In Africa the association of waxbills with wasps nests and several weaver species of the genera *Malimbus* and *Ploceus* with a variety of raptors are well known. An association between Groundscraper Thrushes and Fork-tailed Drongos does not appear to have been previously described. Present observations on such an association were made by CFC at Daan Viljoen Game Park, South West Africa (22°38′S, 16°58′E) in 1969/70 and by WRT at and near Nylsvley Nature Reserve, Transvaal (24°29′S, 28°42′E) in 1974/75.

At Daan Viljoen three active Groundscraper Thrush nests were found in the 1969/70 breeding season and all three were situated close to active Fork-tailed Drongo nests, two in the same tree and one in an adjacent tree. A fourth Groundscraper Thrush nest was found in 1974 near Daan Viljoen by R. Jensen (pers. comm.) and was in a tree adjacent to (45 m away) an active Fork-tailed Drongo nest. Five other nest records from South West Africa were not associated with drongo nests.

In two successive summers (1974/5 and 1975/6) at Nylsvley 32 active drongo nests and seven active Groundscraper Thrush nests were found. Six of the latter were probably the efforts of one pair of birds (the male was colour-ringed in December 1974 and the female in October 1975) which frequented the area around a homestead. They made three nesting attempts in 1974 and three in 1975. Five of the six nests were placed close to active drongo nests, ranging from 4—15 m away ($\bar{x}$=9 m). Two were in the same tree as the associated drongo nest and three in an adjacent tree. Figure 1 shows the positions of the respective thrush and drongo nests and Table 1 gives the chronology of each of the nesting attempts.

The thrushes laid three clutches of eggs in 1974 and one in 1975 and none were successful. The drongos raised young from their only nesting attempt in 1974 and were unsuccessful in all three of their 1975 nesting attempts. In none of the nests was the cause of nest failure ascertained.

The habit of Groundscraper Thrushes nesting in association with Forktailed Drongos is widespread, as evidenced by its occurrence both in Transvaal and South West Africa. In Transvaal five out of seven thrush nests were associated with drongo nests and in South West Africa four out of nine. The Transvaal sample is biased since all five associations were (probably) by the same thrush pair. The nesting efforts of this pair showed clearly that thrushes sought the association, not drongos. In five cases the associated drongo nest was already present when the thrushes commenced nest-buliding; in the sixth case (their first nest of 1975) the thrushes commenced building a nest about a month before the drongos started breeding, and the nest was deserted without being used.

The association between weavers and raptors and waxbills and wasps has generally assumed that the one affords protection to the other against predators (Moreau 1942, Walsh & Walsh 1976). It is well known that drongos are pugnacious towards predators (eg McLachlan & Liversidge 1969) and very bold when defending their nest (eg Gill 1950). Thrushes nesting close to nesting drongos will probably benefit from the drongos pugnacity towards predators, although the present observations provide no data to support this.

ACKNOWLEDGEMENTS

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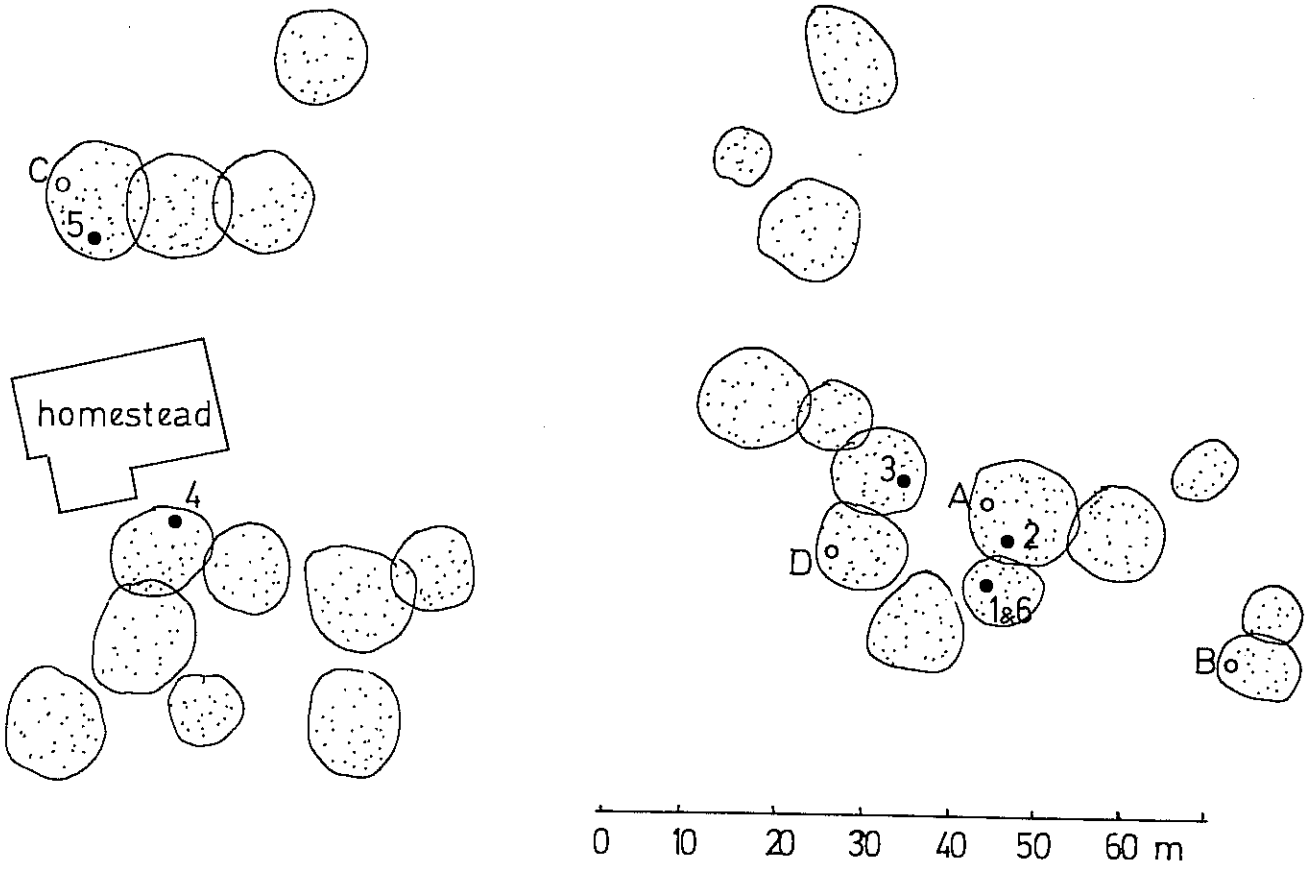

Figure 1. Positions of Fork-tailed Drongo nests (open circles, lettered A to D) and Groundscraper Thrush nests (solid circles, numbered 1 to 6) near Nylsvley Nature Reserve, Transvaal. The stippled shapes are individual trees.

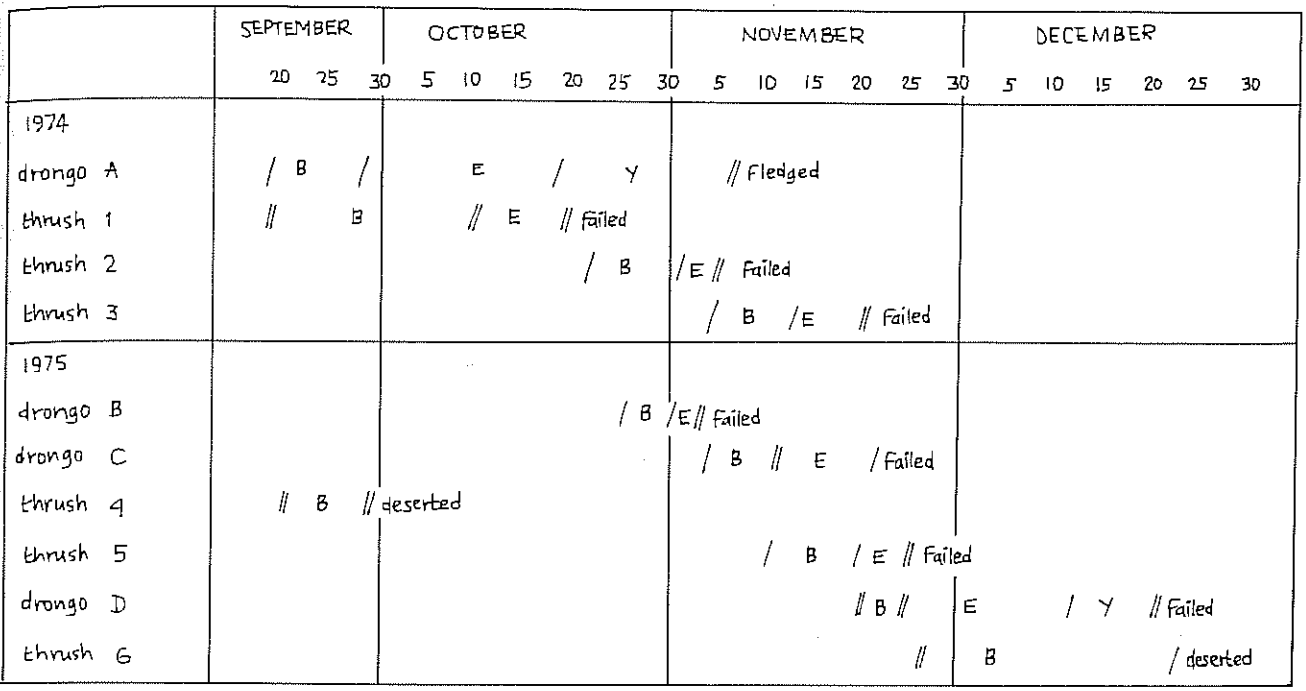

Table 1. Chronology of Fork-tailed Drongo and Groundscraper Thrush nests near Nylsvley Nature Reserve, Transvaal. Stages of each nesting cycle are denoted by: B — building, E — eggs, Y — young. The start and end of each stage is indicated by a single diagonal line (for estimated dates) or a double diagonal line (actual dates).

SHORT NOTE

Survey of populations of Aloes in the Namib Region south of the Swakop River

by

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A geological survey of the area shown on Figure 1 was carried out between February and June 1973. The area comprises 560 square kilometres and was traversed on 43 lines each one kilometre apart. In the course of the traversing, counts of the aloe populations were made. The object of the study was to determine the number of species and their respective densities in different parts of the area. The area is bounded on the northwest by the Swakop River and the ground to the southeast is very largely rocky and culminates in the Horebisberge which reach an altitude of some 1 200 metres above sea level. The area, classified as Inner Namib by Logan (1960), has a considerable range of temperature and a rainfall of about 100 mm per annum.

There are three different environments in which the aloes occur:

a) The generally rocky, hilly terrain rising from the Swakop River.
b) The Horebisberge and their southwest extension.
c) The sand and calcrete-covered flats southeast of the Horebisberge.

The three species of aloes recorded are *Aloe namibensis*, *A. dichotoma* and *A. hereroensis*. The former two are relatively common and counts were made so that population densities of each species could be evaluated. *Aloe hereroensis*, on the other hand, is extremely rare and only two specimens were recorded.

1 *Aloe namibensis*

The limits of occurrence of *Aloe namibensis* are shown in Figure 1 and the population density contours are derived from the numbers counted per line kilometre. It is estimated that these contours represent 2—5% of the actual population per square kilometre, as counts covered a strip extending some 30 m on either side of lines one kilometre apart. This aloe is most abundant on the undulating granitic terrain near the sandy flats east of the Horebisberge. An isolated population of *Aloe namibensis* was recorded in the mountains on the boundary between Rooikuiseb 109 and Tsaobismund 85. *Aloe namibensis* was noted in flower on April 17th which was about one month after the start of the rains.

2 *Aloe dichotoma*

The distribution of *Aloe dichotoma* is shown in Figure 2 and the contours represent the numbers counted per line kilometer. These figures probably represent about half the true population per square kilometer as counts covered a strip extending about 300m on either side of lines one kilometer apart. There is a forest of about 100 *Aloe dichotoma* on a south-facing hill slope near the Tinkas River and it is noteworthy that in general these aloes grow preferentially on south facing hill slopes. The principal population is on the south-easterly faces of the Horebisberge where more than 15 per line kilometer were observed over an area of 8 × 4 kilometers.

These aloes were in flower in May and supported a large population of Dusky Sunbirds (*Nectarinia fuscae*) at that time.

3 *Aloe hereroensis*

Two *Aloe hereroensis* were seen near the fence between Rooikuiseb 109 and Wilsonfontein 110 (Figure 1) in the extreme east of the area. They were in flower in the month of May. This is on the western limit of this species' distribution.

The principal populations of *Aloe namibensis* and *A. dichotoma* are east of the Horebisberge, probably due to a more favourable rainfall and development of soil in that area.

ACKNOWLEDGEMENTS

I would like to thank Mr W. Giess, of the Department of Agriculture, Windhoek, for his interest and assistance in compiling this report.

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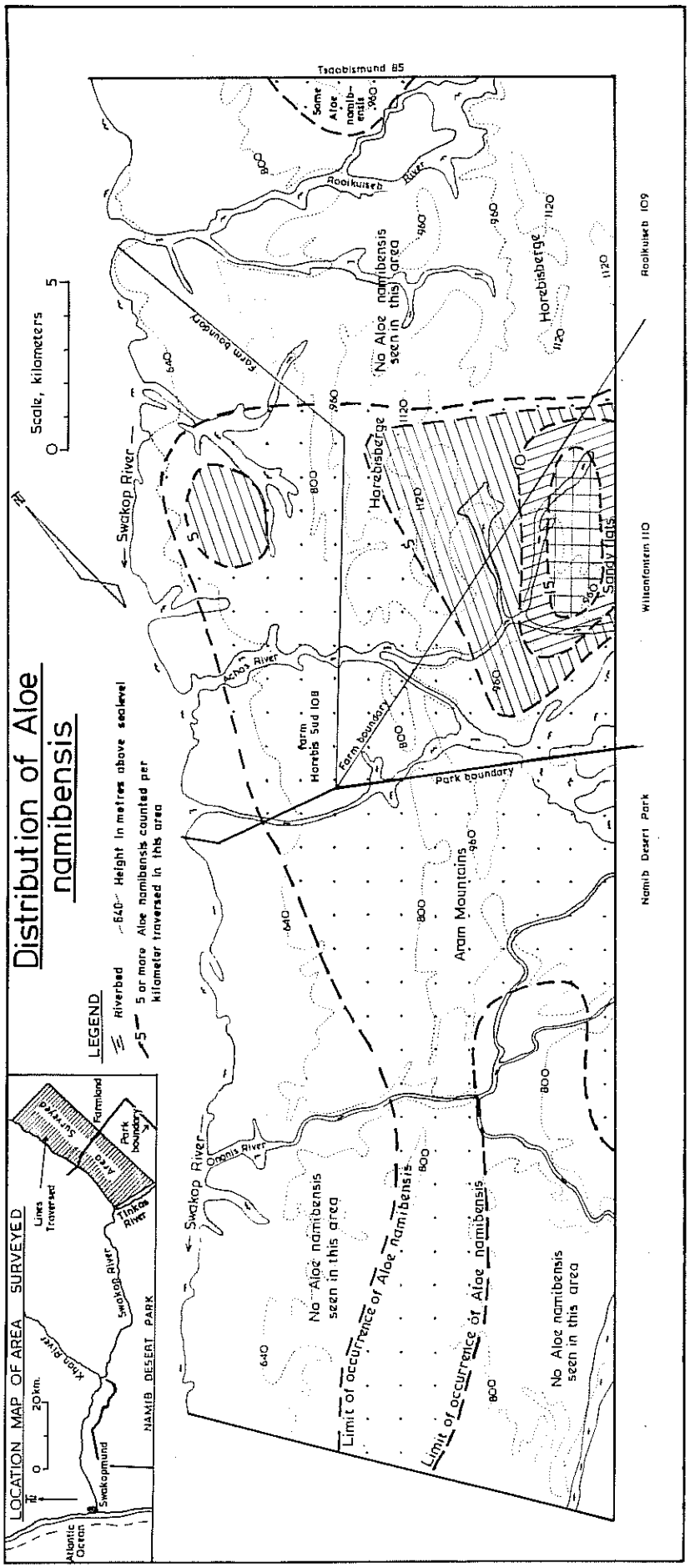
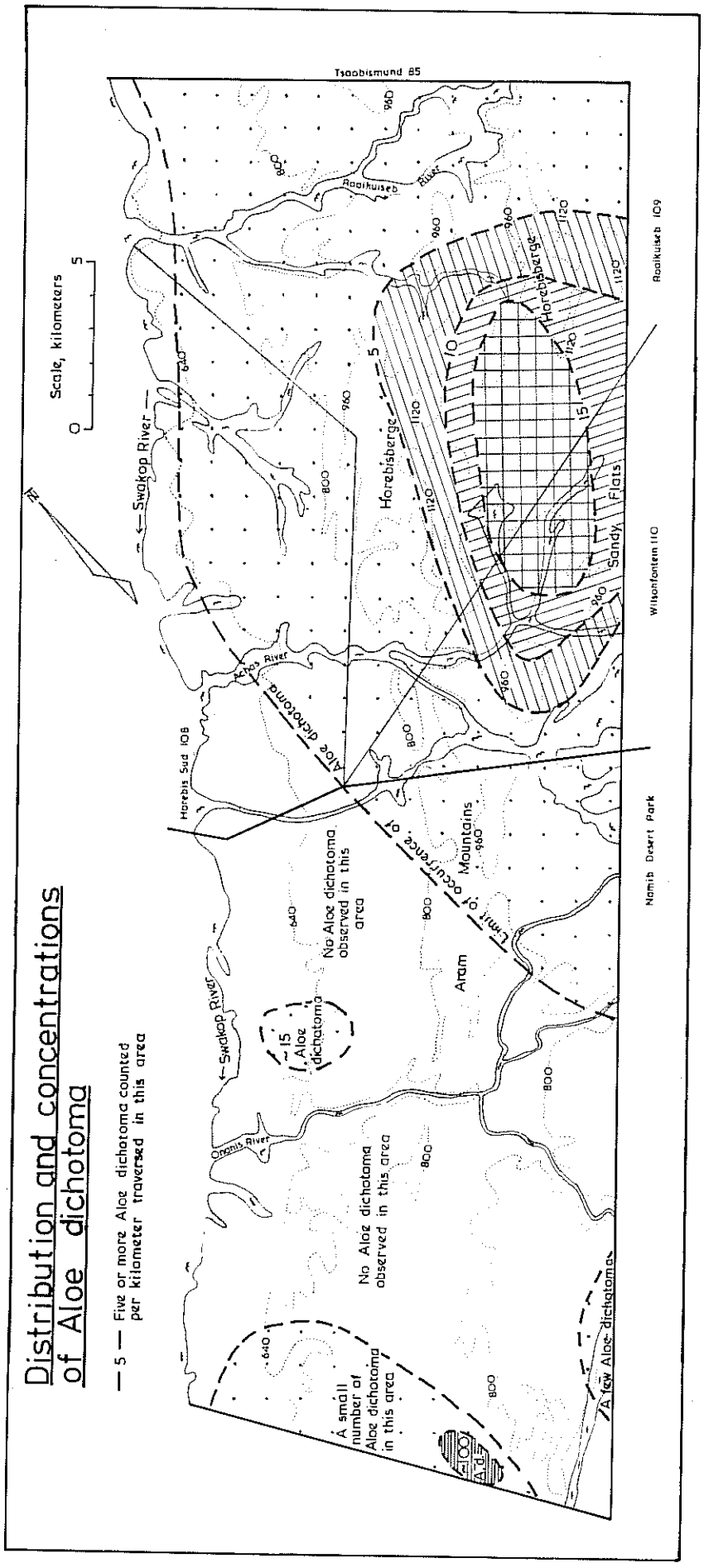

Distribution of Aloe namibensis
LEGEND
Riverbed
640 Height in metres above sealevel
5 5 or more Aloe namibensis counted per kilometer traversed in this area
Scale, kilometers
0
5
LOCATION MAP OF AREA SURVEYED
Lines Traversed
Farmland
Park boundary
Khan River
Swakop River
Swakopmund
Atlantic Ocean
NAMIB DESERT PARK
20km.
Tsaobismund 85
Some Aloe namibensis 960
Rooikuseb River
No Aloe namibensis seen in this area
Farm boundary
Swakop River
Horebisberge
Sandy Flats
Achas River
Farm Hambis Sud 108
Park boundary
Aram Mountains
Omaris River
Limit of occurrence of Aloe namibensis
Rooikuseb 109
Willemfontein 110
Namib Desert Park


Distribution and concentrations of Aloe dichotoma
— 5 — Five or more Aloe dichotoma counted per kilometer traversed in this area
Scale, kilometers
0
5
Tsaobismund 85
Swakop River
Khan River
Aloe dichotoma
Harebisberge
Sandy Flats
Wilsonfontein 110
Namib Desert Park
Harebis Sud 108
Mountains
Aram
Omaruru River
No Aloe dichotoma observed in this area
~15 Aloe dichotoma
A small number of Aloe dichotoma in this area
A few Aloe dichotoma
Roaikuiseb River
Roaikuiseb 109

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