The distribution of the genus *Rhoptropus* (Reptilia, Gekkonidae) in the central Namib Desert

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CONTENTS

1 INTRODUCTION

The gekkonid genus *Rhoptropus* (Peters) occurs over the western parts of Namibia and Angola from 24°S northwards to about 11°S. The latest check-list (Wermuth, 1965) recognises seven species, three of which extend as far as and reach their southern range limits in the area of the Namib-Naukluft Park. Although an impression of the general distribution of these three species may be obtained from the literature (FitzSimons, 1943; Haacke, 1965; Loveridge, 1947; Mertens, 1955 and 1971; Wermuth, 1965), published information is rather scanty.

A more detailed survey of the entire range of this genus has been in progress for some time by the senior author and has produced a clearer overall picture. *R. afer* (Plate 1) occurs in a coastal strip, closely coinciding with the fog-belt rarely extending inland further than about 60 km, ranging from just south of the Kuiseb River at Gobabeb to just north of the mouth of the Kunene River. *R. bradfieldi* (Plate 3) has a relatively limited range, namely from the south bank of the Kuiseb River near Homeb to western Damaraland just north of Twyfelfontein and although it occurs on the coast as far south as Swakopmund it swings inland and seems to be absent from the western part of the Namib-Naukluft Park. *R. barnardi* (Plate 2) is by far the most widely distributed member of the genus and the least specific with regard to habitat preference. It occurs from coastal desert through the pro-Namib into tropical savannah woodland in the Otavi Mountains and even miombo woodland in the Angolan highlands, and ranges from Rehoboth-Solitaire (24°S) to the latitude of Novo Redondo in Angola (11°S) (Transvaal Museum records).

On a microgeographic level FitzSimons (1943) pointed out that *R. afer* is "usually confined to the dry open flats of gravelly sand and stones . . ." while *R. barnardi* is "found living both on rocky koppies (hills) and among small outcrops on the flats". Loveridge (1947) stated

ABSTRACT

The diurnal gecko genus *Rhoptropus* is typical to the northern Namib Desert and adjacent inland areas. Three species extend southwards into the Namib-Naukluft Park. A detailed survey of the distribution shows very diverging patterns for each of these species south of the Swakop River and this situation is discussed with reference to habitat preference related to stratigraphy, substratum and possible effect of competition with sympatric lizard species.

that the habitat of *R. bradfieldi* consists of "black rocky outcrops in the Namib Desert". Mertens (1955) also noted that *R. barnardi* occurs on large as well as small boulders and reported that he had seen them on the same rocks as *R. bradfieldi* as well as having seen *R. bradfieldi* and *R. afer* 1 m from one another. Odendaal (1979) also pointed out that *R. afer* may generally be regarded as an inhabitant of the gravel plains while the other two species generally inhabit rock outcrops or ridges. *R. afer* utilises a habitat which one usually would associate with fast-moving lacertids rather than a climbing gecko since it almost exclusively occupies the horizontal or slightly sloping aspects of a site. *R. bradfieldi* and *R. barnardi* are good climbers exploiting all angles of the rock-face.

The above-mentioned observations were largely confirmed during the major survey and as a consequence it was suggested to the second author to investigate ecological aspects such as niche separation in areas of sympatry. Due to the accessibility of the central Namib Desert within the limits of the Namib-Naukluft Park this area was found to be the most convenient for this study. During this investigation, which included a combined field trip of both authors, extensive additional distributional information was gathered. Since the detail available for the central Namib is bulky, and exceeds the data available for the rest of the generic range, it was considered useful to present this information in this paper prior to a discussion of the entire range (Haacke, in prep.) and ecological investigations (Odendaal, in prep.).

2 METHODS

The distribution of the three species in the central Namib (Fig. 1–3) was investigated by extensive travelling over as much of the area as was practical. It was documented by collected voucher specimens which are deposited in the Transvaal Museum, Pretoria, and the State Museum, Windhoek. Material was also contributed by a number of other collectors. Published records and specimens in a number of other institutions were also incorporated. Of the various sites which were visited on one or more occasions, seven were studied more intensively by the second author and are described elsewhere in this paper. They are referred to by the following names: Gobabeb Site A, Gobabeb Site B, Mirabib Site, New Road Site, Bad Earth Site, Bakenkoppie Site and Bloedkoppie Site.

Two methods were used to derive relative density estimates for the three species at some of the main study sites, although in some cases time did not allow more than one method per site. The first method is the recording of individuals by means of a thumb counter while walking random transects across the study site for 45-minute periods during the peak activity period in the late morning (cf. Odendaal, 1978). The second i involved the recording of all individuals on four r ly established quadrangular areas of 40×60 m, equals 960 m² per site. Six metres is a convenien for observing the number of individuals on the cated area while walking down the middle of minimise disturbance and the possibility of lizard ing under cover, these transects were only done day during the morning peak activity period. The obtained for 960 m² were converted to values o m². The results obtained in this way do not nec reflect absolute densities and probably underes the population size, but may be used to compar For various reasons marking / recapture was i tical.

Co-occurring species were recorded at the seve study sites in order to establish whether a correlat isted between the distribution of *Rhoptropus* spec the presence or absence of other lizard species strate types were investigated in an attempt to es their effect on the distribution of the three spec

3 RESULTS

3.1 Recorded localities

The known distribution of the three *Rhoptropus* s in the central Namib is shown in Figures 1, 2 and localities from where material is available and t stitutions in which the specimens are housed are below:

AM = Albany Museum, Grahamstown
CAS = California Academy of Science, San cisco
DERU = Desert Ecological Research Unit, Go
HM = Zoologisches Institut und Museum, burg
LACM = Los Angeles County Museum
NMP = Natal Museum, Pietermaritzburg
PEM = Port Elizabeth Museum
SMF = Senckenberg Museum, Frankfurt/Main
SMW = State Museum, Windhoek
TM = Transvaal Museum, Pretoria
UZM = Zoological Museum of the University, Copenhagen
ZMB = Zoologisches Museum der Humboldt versität, Berlin

Rhoptropus afer (Plate 1): Arandis (SMF); B koppie (SMW), 5 km, 6 km and 13 km E, 13 km 14 km SE, 8 km SSE and 8 km S of Bakenkoppie Bloedkoppie (TM, SMW); Carp Rock, 4 km E km NE of Carp Rock (TM); Goanikontes (AM, S Gobabeb (TM, DERU, NMP, CAS, AM); Gobal of Kuiseb River (TM, DERU, UZM); Gobabeb n strip (DERU), 10 km and 12 km from Gob Mirabib, 30 km NW of Gobabeb, 19 km NN

PLATE 1: *Rhoptropus afer* Peters, 1869, from Gobabeb (Photo W. D. Haacke).

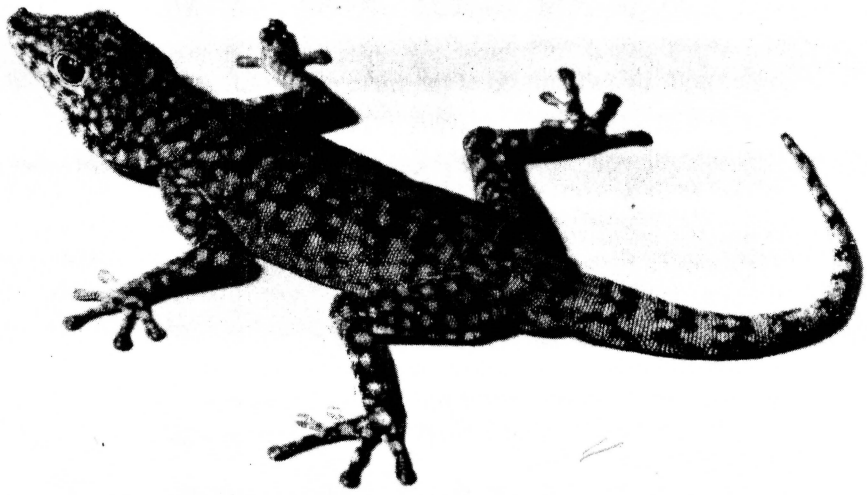

PLATE 2: *Rhoptropus barnardi* Hewitt, 1926. (Photo W. D. Haacke).

Gobabeb (TM); 20 km NNW of Gobabeb, 4 km NE of Gobabeb (SMW); N and S end of Gungochoab Mtn., 2,5 km and 3 km SE and 5 km NW of Gungochoab Mtn., Hamilton Mtn., 1 km SE of Homeb turn-off, Husab Drift, 3 km and 5 km SE and 9 km E of Klein Klipneus (TM); Kuiseb River nr. Rooibank (AM); Namib Station (SMF); btwn. Natab-Rooibank, "New Road Site", btwn. Nonidas-Namib, nr. Nonidas Station (TM); Otjimbingwe? (SMF); Palmenhorst (TM); Rooibank (TM, SMF, ZMB); ±40 km SE of Rooibank (TM); Rooikop (SMF); Rössing Mine (TM); Rössing (TM, AM, AMF); 5 km NW of Schieferberg Pass, Schierilatz (TM); btwn. Sphinx-Pforte (AM); Swakopmund (TM, AM, SMF, LACM); 5 km E of Swakopmund (UZM); 10 km E of Swakopmund (NMP); 13 km and 40 km E of Swakopmund (TM); 16 km E of Swakopmund (NMP); 3 km E of Swakop River bridge (CAS); 30 km and 42 km SE of Swakopmund (TM); 38 km SE of Swakopmund on Khomashochland Road, 11 km and 16 km from Swakopmund–Usakos (CAS); 20 km N of Swakopmund (SMF); 22 km N of Swakopmund (TM); Swartbankberg (TM, NMP); Swartbank S of Kuiseb River, 3,5 km and 8 km E of Swartbank Village (TM); Swartkoppies (SAM); Ubib, 3 km W and 5 km NNE of Ubib, nr. Vogelfederberg, Von Stryk Mine (TM); Walvis Bay area (SMF), 80 km E of Walvis Bay on Gamsberg Road, Welwitschia flats, Welwitschia Station, 5 km SSW of Witpoortberg (TM).

km W, 10 km SE, 5 km NNE of Ubib, N side of Witpoort (TM).

3.2 Density estimates

Table 1 shows the density estimates for some of the sites, indicating variations in population densities between species. The cause for the variation in relative densities between sites with more than one species represented may be sought in the availability of suitable preferred habitat. Some sites with the same species composition vary drastically in relative densities. For instance, *R. bradfieldi* occurs in much higher numbers than *R. afer* at Bad Earth Site while at New Road Site they occur in nearly even numbers (Table 1). These differences may be explained by comparing the suitability of the substrata. At Bad Earth Site the low vertical ridges are occupied by *R. bradfieldi* while *R. afer* occurs on the gravel sheets between the ridges. It appears that a lack of flat rocky areas with loose lying slab shelters in the presence of *R. bradfieldi* reduces the suitability of the site as *R. afer* habitat, resulting in low densities. Although *R. afer* will ascend even large rock outcrops in the absence of *R. bradfieldi*, as at Swartbankberg, Vogelfederberg, Carp Rock, Rooikop and even Gobabeb Site B, and others, this species in areas of sympatry will take to flat rocky areas as at Bloedkoppie and Bad Earth Site. In contrast at New Road Site the numbers of the two species are reasonably even. This site has large flat to near horizontal surfaces suitable for *R. afer* which are avoided by *R. bradfieldi*, which occurs on the many monolithic boulders with vertical and overhanging surfaces which are available.

During March/April 1977 generally higher density estimates were obtained for both *R. afer* and *R. bradfieldi* in contrast to December/January 1976/7 at Gobabeb Site A and Mirabib Site (Odendaal, unpubl. data). This could be due to the high relative abundance of hatchlings during early autumn. At present hardly anything is known about the population dynamics of the three species and whether their reproductive patterns show noticeable peaks which might be synchronised or staggered as in the lacertid *Ichnotropis* (Broadley, 1979).

3.3 Description of seven sites

These sites were given code names and used by the junior author for more intensive studies.

Gobabeb Site A (Plate 4)

Locality: 4 km SE of Gobabeb in an interdune valley.

The site consists of low but extensive granite outcrops situated in an interdune valley. These granite outcrops are surrounded by sand. The rock type is of a weathered flaky nature, providing suitable shelters for the lizards. The site is fairly homogenous without proper boulders and the granite is not quite as weathered as that of Mirabib and is of a lighter colour (more or less grey to whitish-grey). The time of insolation is more or less the same for the entire site, since it is flat. Hardly any shade is available at mid-day except under the flakes and on the vertical surfaces of the few concave larger rocks. There are also a few small outcrops of white quartzite (± a metre in diameter). This site is completely isolated by sand from any other suitable habitat with respect to *Rhoptropus*. Only *R. afer* occurs on this site and in high numbers (Table 1).

SITE	SPECIES	Method	$\bar{x}$	SE	n
Gobabeb Site A	*R. afer*	A	65,6	3,95	5
		B	6,2	0,91	9
Gobabeb Site B	*R. afer*	A	5,6	5,7	4
		B	5,8	0,86	5
Mirabib Site	*R. bradfieldi*	B	4,14	0,25	7
Bad Earth Site	*R. afer*	A	6	1,50	3
		B	0,25	0,25	4
	R. bradfieldi	A	40	6,57	3
		B	3,25	0,57	4
New Road Site	*R. afer*	A	25	2,02	3
		B	1,2	0,37	5
	R. bradfieldi	A	27	0,57	3
		B	2,6	1,02	5
Bloedkoppie Site	*R. afer*	A	2,5	1,50	2
	R. bradfieldi	A	28,5	7,51	2
	R. barnardi	A	25,5	2,50	2

TABLE 1: Estimates of densities for some of the main study sites done during March/April 1977. A=thumb counter method; B= estimated total number per 1 000 m².

Gobabeb Site B (Plate 5)

Locality: Gobabeb, directly across the road from the Research Station.

As Gobabeb Site A lacks boulders, a similar site with granite boulders was selected for the sake of comparison. With respect to the morphology of the rocks it differs from Gobabeb Site A only by the presence of large numbers of boulders. Again only *R. afer* occurs here and in high numbers (Table 1), although *R. bradfieldi*'s range extends to within 1 km from this site along the Kuiseb River.

Mirabib Site (Plate 6)

Locality: 40 km NE of Gobabeb, an isolated koppie on the SE side of the range, about half-way between Mirabib and Gorob Mine.

This site is a prominent outcrop consisting of many boulders of varying sizes and a substantial amount of flat areas, much of which is of the flaky nature comparable to that of the sites of Gobabeb. Many of its boulders and rock-faces are much larger than those at Gobabeb Site B. Shade is available throughout the day.

PLATE 5: Gobabeb Site B. Only *R. afer* occurs here utilising even the larger boulders (Photo W. D. Haacke).

PLATE 6: Mirabib Site. Only *R. bradfieldi* occurs here, mainly on the sides of the larger boulders (Photo F. Odendaal).

Habitat diversity and temperature microclimate is much more diverse than that of the relatively homogenous sites at Gobabeb. As far as *Rhoptropus* is concerned, this site is completely isolated by sandy plains from any other suitable rock outcrop. Since this site lies further east than Gobabeb, New Road, Bakenkoppie and Bad Earth Sites, its vegetation is much more diverse. Only *R. bradfieldi* occurs here and in high numbers (Table 1). This site lies east of the known range limit of *R. afer*.

New Road Site (Plate 7)

Locality: 20 km from Gobabeb on the road to Vogelfederberg.

Very similar in all morphological respects to Gobabeb Site B. It consists of granite boulders and flaky areas, situated next to a dry river-bed on the gravel flats. Both *R. afer* and *R. bradfieldi* occur here in approximately equal numbers (Table 1), although it is near the SE range limit of *R. afer* and at the southern tip of a band-like extension of *R. bradfieldi*'s range from the Langer Heinrich area in the Swakop Valley across the plains of the central Namib (cf. Figs. 1 and 3).

Bad Earth Site (Plate 8)

Situation: 40 km NNW from Gobabeb on road to Vogelfederberg.

Formation consists of low ridges, usually less than one metre in height, separated by gravelly sand. Rock type is black schistose amphibolite, marble and small patches of granitic formations. These ridges form part of the dark formations in the centre of the Namib Park gravel flats (cf. satellite photo, Plate 11), their strike is NNE to SSW and they disappear 4 km SSW of the intersection

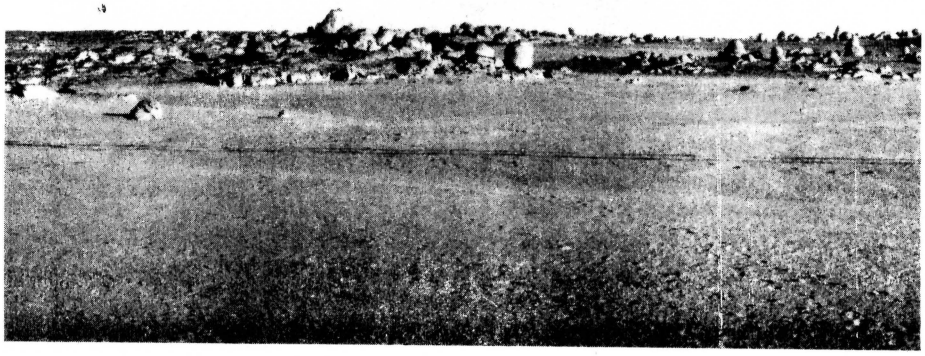

PLATE 7: New Road Site. *R. bradfieldi* occurs mostly on the larger boulders, while *R. afer* tends to utilise the flatter aspects and sheet-rock in between the boulders (Photo F. Odendaal).

PLATE 8: Bad Earth Site. *R. bradfieldi* is found on the near vertical schistose slabs, while *R. afer* tends to inhabit the area between the dykes (Photo F. Odendaal).

with the road which is also the limit of the range of *R. bradfieldi* at that point. The latter occurs in high densities at this study site. *R. afer* which does not utilise the ridges to any extent, but occurs more on the gravel flats in between them is not affected by the disappearance of the rocky ridges. *R. bradfieldi* occurs in very high numbers on rocks unusually low for this species while *R. afer* is relatively rare utilising the horizontal gravelly areas in between the rocky ridges (Table 1).

Bakenkoppie Site (Plate 9)

Locality: 32 km from Gobabeb and 4 km E of the new road to Vogelfederberg.

The site is an isolated koppie about 20 to 30 m high, consisting of large granite boulders and flat flaky areas. It is similar to Mirabib but the flat area around the base of the hill might be more extensive. *R. bradfieldi* occupies the large boulders while *R. afer* utilises the flat areas and slight inclines. No comparative estimates available.

Bloedkoppie Site (Plate 10)

Locality: In the NE of the Namib-Naukluft Park, 10 km N of Swakopmund–Khomashochland–Windhoek road.

This study site consists of three rocky systems namely the main hill (a on Plate 8) which consists of granite, a series of hills to the west (b on Plate 8) which are part of the Schieferberge and flat granite surfaces with low boulders (c on Plate 8) 3–4 km SE of the main hill. A

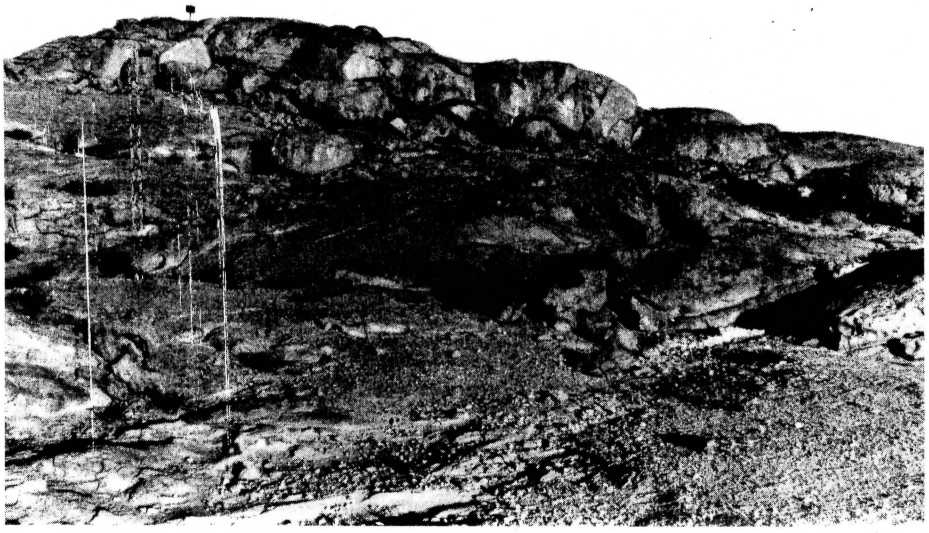

PLATE 9: Bakenkoppie Site. Although *R. afer* utilises the slopes of the hill, only *R. bradfieldi* occurs on the large boulders on top (Photo DERU).

PLATE 10: Bloedkoppie Site. *R. afer* occurs on sheet-rock in the foreground, *R. barnardi* occurs on the dark schistose formations of the hill to the left behind the tree aloe (*Aloe dichotoma*) while *R. bradfieldi* is found all over the large granite dome of Bloedkoppie to the right of the aloe (Photo F. Odendaal).

possible fourth system can be described consisting of loose granite boulders at ground level strewn around the base of the koppie and the immediately adjacent area. The main hill is comparable to the Mirabib Site in morphology consisting of a large granite dome with large boulders of varying sizes and flat flaky surfaces, but of much greater dimensions. The hills to the west with ridges of shales and amphibolites were well vegetated during the survey, mostly by grasses. Just within these hills on the side facing the main granite dome is a small isolated granite area (some 20 m × 20 m) encircled by shales and amphibolites. This site has a greater plant species diversity than any of the others (Odendaal unpubl. records).

R. bradfieldi occurs exclusively on the main hill while *R. barnardi* occurs exclusively on the shales and amphibolites of the hills to the west of the main hill. Some *R. bradfieldi* occur on the small granite patch encircled by the shales and amphibolites. *R. afer* occurs exclusively on the flat granite surfaces south of the main hill. Both *R. bradfieldi* and *R. barnardi* occur in high numbers while *R. afer* is rare, possibly due to the fact that this is a marginal population at the eastern range limit.

3.4 Co-occurring species

The following lizard species occur sympatrically with *Rhoptropus* at the following four sites: Gobabeb Sites A and B, Mirabib and Bloedkoppie and a brief general indication of their spatial and time niches is provided in Table 2.

TABLE 2: Lizards co-occurring at four study sites

	Occurrence on study sites:				General indication of time and spatial niches:			
	Gobabeb Site A	Gobabeb Site B	Mirabib	Bloed-koppie	Terres-trial	Rupi-colous	Diurnal	Nocturnal
GEKKONIDAE								
Rhoptropus afer	X	X		X		X	X	
R. barnardi				X		X	X	
R. bradfieldi			X	X		X	X	
Afroedura a. africana				X		X		X
Chondrodactylus a. namibensis		X	X	/	X			X
Narudasia festiva			X			X		X
Pachydactylus bibronii			/	X		X		X
P. bicolor				X		X		X
P. kochii		X			X			X
P. laevigatus	X	X	/	X		X		X
P. punctatus amoenoides		X	X	X	X			X
P. weberi werneri		X	X	/		X		X
Palmatogecko rangei	X				X			X
Ptenopus carpi		X			X			X
P. garrulus maculatus	X	X	X	X	X			X
P. kochi	X				X			X
AGAMIDAE								
Agama anchietae		X	X	X		X	X	
A. hispida aculeata		X	/		X		X	
A. planiceps				X		X	X	
CHAMAELEONTIDAE								
Chamaeleo namaquensis		X	/	/	X		X	
SCINCIDAE								
Mabuya acutilabris				X	X	X		X
M. hoeschi			X	X		X	X	
M. occidentalis	X	/		X	X		X	
M. spilogaster				/		X	X	
M. s. sulcata			/	X		X	X	
M. variegata		X	/	X		X	X	
LACERTIDAE								
Eremias breviceps		X	X		X		X	
E. namaquensis			/	X	X		X	
E. undata			X	X		X	X	
Meroles cuneirostris	X				X		X	
M. suborbitalis		X	X	X	X		X	
	6	14	18	20				

X=Confirmed presence
/ =Sight record

The combination of the diurnal/rupicolous *Rhoptropus* species present at these four sites in relation to the number of lizard species representing certain time/niche preferences is listed in Table 3.

Although *R. afer* has terrestrial tendencies in the absence of suitable rock, all species of *Rhoptropus* may be considered to be rupicolous and diurnal in comparison to other potentially competitive species (Table 2). With reference to Table 3 *R. afer* does not have any competitive lizard species with a similar niche preference at Gobabeb Site A, while at Gobabeb Site B two species are listed as potential competitors. Of these *Agama anchietae* is of very rare occurrence at that locality and is therefore of no consequence. Even within its normal distribution this species tends to occur in isolated pairs or as single individuals which are widely spaced. *Mabuya variegata* tends to be more common along the bed of the Kuiseb River with isolated individuals occurring on Gobabeb Site B.

TABLE 3: Distribution of lizard types on four study sites.

Study sites:	Occurrence of *Rhoptropus* species on study sites:			General indication of time and spatial niches of co-occurring species			
				Rupicolous		Terrestrial	
	R. afer	*R. barnardi*	*R. bradfieldi*	Diurnal	Nocturnal	Diurnal	Nocturnal
Gobabeb Site A	X			/	1	2	3
Gobabeb Site B	X			2	2	5	5
Mirabib			X	5	4	6	3
Bloedkoppie	X	X	X	7	5	5	3

At Mirabib no congeneric competitors have been recorded for *R. b. bradfieldi* (Table 2), while five other potential competitors are recorded. Of these both *Agama anchietae* and *Mabuya hoeschi* are non-social species which occur as widely spaced pairs or individuals and are therefore of little consequence as competitors. The small non-social *Mabuya variegata* also tends to occur as single individuals and apparently because of its low density its occurrence has not yet been confirmed by a voucher specimen. The larger rock living skink *Mabuya sulcata* which may occur in high densities in similar situations as *R. bradfieldi* may be of competitive significance under such circumstances, although, due to greater body thickness in adult form, it may lose its importance as competitor for narrow crevice retreats. At Mirabib it has only been recorded as a sight record by the second author, indicating a low density situation unimportant to *R. bradfieldi*. *Eremias undata* is an actively foraging lacertid avoiding vertical and overhanging rock-faces where it would encounter *R. bradfieldi*.

The presence of three *Rhoptropus* species at Bloedkoppie appears to significantly affect one another's occurrence at that site resulting in a patchy distribution with no direct overlap as discussed in the site description (cf. Page 00). All other diurnal rupicolous species recorded here are non-gekkonids of which *Agama anchietae* could co-occur with *R. afer* and *R. barnardi* but would only enter *R. bradfieldi* area on smaller rocks around the base of the granite dome. *Agama planiceps*, a social species, occurs in relatively high concentrations mainly in *R. bradfieldi* area as does *Mabuya sulcata*. Both the latter species could be considered to be potential competitors within the rupicolous / diurnal niche, although all occur in high densities. *Mabuya variegata* and *Eremias undata* have been discussed above, as being relatively insignificant and the unconfirmed sight record of *Mabuya spilogaster*, which usually prefers trees but in their absence will also use rocks, must be rated of similarly low significance.

In conclusion it appears as if other diurnal / rupicolous lizards do not significantly affect the distribution of *Rhoptropus* species and that the congeneric species give way locally to *R. bradfieldi* with *R. afer* restricting itself to low boulders and sheet-rock while *R. barnardi* restricts itself to rock types avoided by the others (cf. Table 3).

3.5 Substrate types

According to Logan (1960) "the rocky outcrops and canyons of the central Namib consist of coarse-grained, well-eroded granite, mica schists, feldspar formations or lime deposits".

The second author had rock samples from 38 sites in the Namib-Naukluft Park analysed. According to this analysis *R. afer* occurs almost exclusively on granitic plutonic rocks as are found from south of the Kuiseb at Gobabeb over most of its documented range, although within this area occasionally it has also been encountered on other rock types such as quartzites and marbles. *R. bradfieldi* usually associates with granitic substrates but has also been observed on marble (Bad Earth Site, Witpoortberge), quartzite (Gungochoab, and others) and other rock formations. Very coarse, crumbly granitic sites are avoided by all three *Rhoptropus* species. *R. barnardi* over its entire range shows hardly any habitat preference and will utilise practically any rock type except very coarse crystalline granitic formations.

4 DISCUSSION

The occurrence of this genus is dependent on the presence of a rocky substrate. Rocky areas utilised by *Rhoptropus* are often partially or completely isolated from one another by sandy terrain thereby creating biological island populations. These areas could only have been colonised at a time when rocky "passages" existed which provided migration routes or when ancestral forms of these geckos were still less specialised and therefore more likely to cross sandy stretches. The lack

PLATE 11: Satellite photo of the central Namib Desert. The Kuiseb River bed forming the border between the sand-sea and the gravel plains, the eroded Swakop and Khan River Valleys and the dark rock formations which affect the distribution of *Rhoptropus* are clearly visible. (NASA-Photo: 65-2652, SCI-1195, Gemini V, taken by G. Cooper and C. P. Conrad 27.8.1965).

of fossil evidence and uncertainty of the geomorphologic history of the area make discussions of the development of the present distribution pattern only a speculation.

The evolutionary centre of the genus appears to lie further north in the pro-Namib area, where several other species of *Rhoptropus* occur (Haacke, in prep.). For this reason the present-day pattern of distribution in the central Namib may be viewed as the dispersal front of a southern expansion which has reached its potential limits. The limiting effect may be due to pure physical conditions, such as the absence of suitable substratum, limits of suitable ecological conditions or biological pressures such as the presence of competitive species. Another aspect may be the withdrawal by extermination from areas which appear to be suitable but are not occupied today ("Island effect" MacArthur, 1972).

In the light of these concepts the southern range limits may be analysed as follows: Considering the entire range of *R. afer*, it is the most deserticolous species since it is restricted to the most arid parts of the Namib along the coast from the Kuiseb River into southern Angola reaching its eastern range limits at about 80 to 100 km from the coast. This is the area most affected by the coastal fog. The eastern margin of this area reaches an area with a marked increase in rainfall approaching what is referred to as Pro-Namib (Coetzee, 1969) or Inner Namib (Logan, 1960). The southern limits of *R. afer* (Fig. 1) are obviously determined by the disappearance of available sheet-rock surfaces due to the northward expansion of the sand-sea. In this case the possibility actually exists that *R. afer*'s range has been pushed back by sand encroachment if it is considered that for instance the mouth of the Kuiseb River formerly was at Sandvis and that the course of the Kuiseb used to run due west from Swartbank as indicated by subterranean water seepage (R.M. Huyssen, geologist, C.S.I.R., pers. comm.). The record of *R. afer* from Lüderitz (HM4005, 3 specs, coll. 1911, Werner, 1915) must be regarded as unreliable. The collector, C. Manger, a naval engineer during colonial times, provided material from the Swakopmund as well as the Lüderitzbucht area and since neither the ardent collector F. Eberlanz, who lived there his whole life nor the present authors ever managed to secure any specimens from there, nor from any of the rock islands in between, such as Hottentot Bay, Saddle Hill and the Meob-Conception Bay enclave, this record must be disregarded. Other doubtful records are those from Salem (Falk, 1914 in Mertens, 1971) on the Swakop River NE of Langer Heinrich Mountain since the description dates from a time when no other species had been described yet and it is highly likely that another species was actually involved. The specimens (SMF 22681–3) supposedly from Otjimbingwe also pose a problem, since they are from a considerable distance further east than the known and apparently acceptable eastern range limits of the species and the general ecology of that area is classified by Giess (1970) as semi-desert and savannah transition which is quite different to that of the coastal Namib. Although these specimens are correctly identified their origin is suspect and not acceptable, since no confirming material from the same locality has been obtained yet.

Although *R. afer* will utilise rocks such as those found at Gobabeb Site B and even ascend large outcrops such as Swartbank Mountain, Vogelfederberg and Carp Rock in the absence of the more specific boulder dwelling *R. bradfieldi*, it will yield in situations of sympatry by largely giving up the boulders and staying on the sheet-rock areas or gravel with flakes, to where *R. bradfieldi* is not inclined to follow. This latter situation can be demonstrated at various points of sympatric co-occurrence as at Bloedkoppie, 5 km NW of Schieferberg Pass, Gungochoab Mountain and even Bad Earth, Bakenkoppie and New Road Sites, where *R. bradfieldi* will be found in areas with vertical and overhanging surfaces while *R. afer* utilises the plains closer to the horizontal and preferably away from *R. bradfieldi* occupied boulders. It appears thus that the range of *R. afer* is not seriously affected by sympatric populations of congeneric rupicolous species, provided sheet-rock areas or gravel with flakes are available.

The distribution of the larger rupicolous *R. bradfieldi* in the central Namib shows some interesting patterns (Fig. 3) illustrating its dependence of well-developed rock formations with near vertical surfaces. Penetrations of the central Namib plains can be followed along geological formations and in some cases the southern range limits can be defined to within metres (cf. Plate 11).

In general terms the pattern may be described as ending in the Swakop River Valley with two southward extensions towards the Kuiseb Valley. This pattern correlates well with the dark formations which are clearly visible on satellite photos (Plate 11) which extend SW from the Langer Heinrich–Tinkas area and reach beyond the New Road Site and beyond Bad Earth Site to the tip of the Gungochoab Mountain. The other prong of the southward extension appears to extend along the lower altitudes of the escarpment along the eastern boundary of the park into the erosion valley of the Kuiseb. It extends down-stream along rocky outcrops of the banks to close to Gobabeb. An unsolved question at present is the presence of high density populations on Mirabib and the Mirabib Hills, since no clearly defined access routes have been identified to date and in fact this might be a trapped island population which has been cut off from the rest. It appears most likely that a connection existed towards the Kuiseb Valley from where these koppies might have been colonised.

As much as the presence of these geckos at one or other site might be particularly interesting, the absence from what appears to be perfectly good *Rhoptropus* biotope can certainly cause difficulty explaining. A major problem of this kind is the absence from all the mountains, hills and boulder fields between Mirabib Hill and probably the Onanis mountain. This includes the Arechadamab range N of Ganab, the Tumas, Amigab,

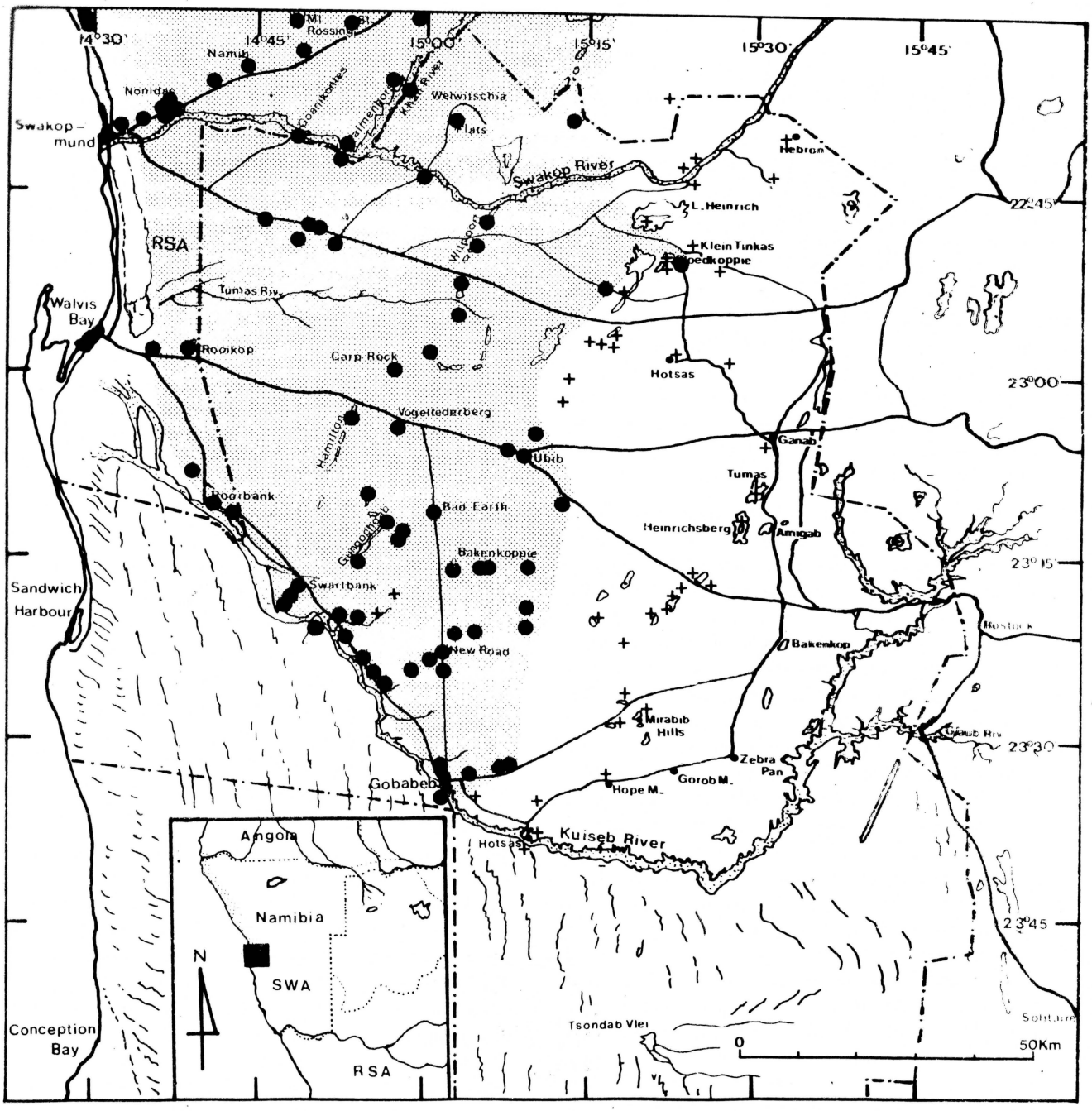

FIGURE 1: Distribution of *R. afer* in the central Namib. ●=confirmed records, +=negative checks.

Heinrichsberg and all the rocky hills and boulder fields from Kriess-se-rus westwards and southwards. If *R. bradfieldi* does occur on them it has not been found yet, although the rupicolous skink *Mabuya sulcata* extends from Hebron, Bloedkoppie and Gr. Tinkas past Tumas to Kriess-se-rus. If it did occur there in the past it might have died out due to an inability to survive natural pressures.

From the observations so far it appears that *R. bradfieldi*'s range limits are not affected by sympatry or parapatry of congeneric species. The deciding factor appears to be the presence of suitable rock formations with available access routes. Some excellent examples may be demonstrated. At Witpoort a wide valley separates two high rocky ridges which are part of the dyke which extends south from the Husab Mountains. On the N side *R. bradfieldi* is found on the top of the ridge with *R. afer* at the foot, while across the valley only *R. afer* is found. South-west of Bad Earth Site the presence can be followed to where the ridges disappear into a river-bank, while SW of the New Road Site a cliff on the bank of a dry wash is the terminal site. The rocky banks of the Kuiseb Valley as such act as a migration route and provide access to the cliffs in the vicinity of Gobabeb but not far enough to leave the river-bed and invade Gobabeb Site B no more than 2 km away.

R. barnardi, the smallest species, is extremely adaptable and occurs on a wide variety of rock types. In the

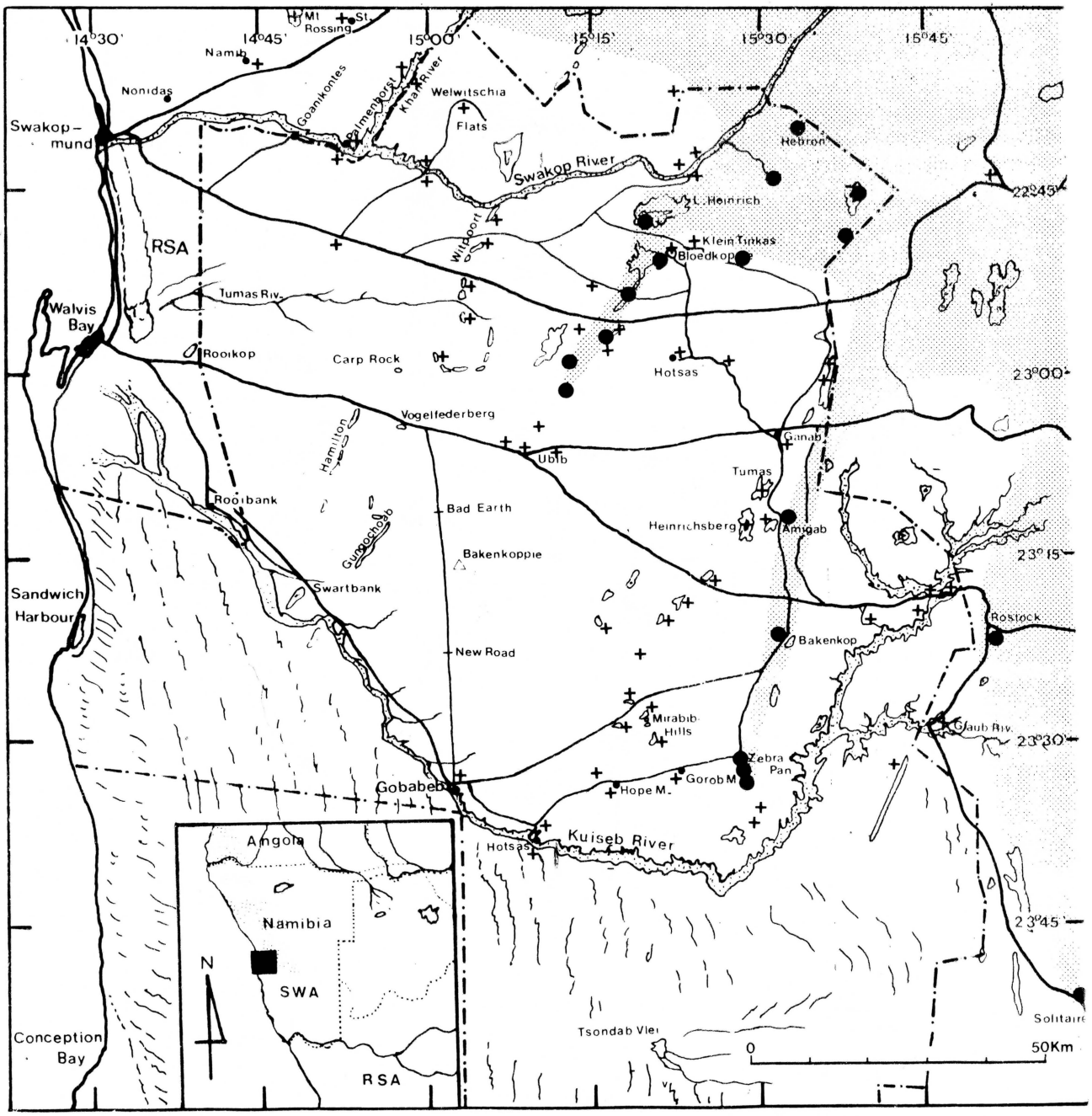

FIGURE 2: Distribution of *R. barnardi* in the central Namib. ●=confirmed records, +=negative checks.

central Namib (Fig. 2) it only occurs in the areas referable as "Inner Namib" (Logan, 1960) beyong the main fog-belt, thereby more or less excluding contact with *R. afer*. In general it may be said that *R. barnardi* avoids boulders occupied by the large *R. bradfieldi*. It will utilise small outcrops which are avoided by the larger species and exist along often very low ridges, as near Zebra Pan. This species also penetrates into the central parts of the Namib-Naukluft Park along the same formations as discussed for *R. bradfieldi* which extend SW from Langer Heinrich Mountain. Although it may occur sympatrically on the same ridge with *R. bradfieldi*, it usually appears to avoid direct contact and possibly physical aggression from the larger species, as was observed between *R. boultini* and *R. taeniostictus* at Caraculo, Angola (Haacke) by inhabiting formations which are not utilised by *R. bradfieldi*.

A striking example is a site at (2257S, 1517E) where *R. bradfieldi* occurs exclusively on the large boulders of a small granite outcrop situated in between and in contact with quartzite hills of lower rocky formations on which apparently only *R. barnardi* occurs.

The pattern in the central Namib-Naukluft Park appears to be that *R. barnardi* occurs in the inner Namib only, penetrating southwards in two tongues, one southward

sibility of avoiding direct competition with congenerics. Since at other sites all species are known to occur on the rock type apparently avoided here, the situation suggests that the occurrence of *Rhoptropus* in the central Namib Desert is a combined result of habitat selection and competition.

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7 GAZETTEER

Anigab (Vlei?)	2314S	1535E
Arandis Station	2226S	1459E
Bakenkoppie	2315S	1505E
Bakenkop	2322S	1533E
5 km E of Bakenkoppie	2315S	1507E
6 km E of Bakenkoppie	2314S	1508E
13 km E of Bakenkoppie	2314S	1512E
13 km ESE of Bakenkoppie	2317S	1512E
14 km SE of Bakenkoppie	2319S	1512E
8 km SSE of Bakenkoppie	2319S	1508E
8 km S of Bakenkoppie	2320S	1505E
nr Barrowberg	2337S	1532E
Bloedkoppie	2250S	1523E
1,6 km E of Bloedkoppie	2250S	1524E
5 km E of Bloedkoppie	2250S	1526E
Carp Rock	2259S	1500E
4 km E of Carp Rock	2259S	1522E
8 km NE of Carp Rock	2255S	1522E
Farm Donkerhuk	2247S	1549E
Goanikontes	2240S	1449E
Gobabeb	2334S	1503E
Gobabeb, S of Kuiseb River	2334S	1503E
Gobabeb nr airstrip	2332S	1503E
1,6 km SE of Gobabeb	2334S	1503E
10 km from Gobabeb-Mirabib	2333S	1508E
12 km from Gobabeb-Mirabib	2332S	1509E
30 km NW of Gobabeb	2329S	1519E
19 km NNW of Gobabeb	2324S	1502E
20 km NNW of Gobabeb	2324S	1501E
4 km NE of Gobabeb	2333S	1505E
5 km NNW of Gorob Mine	2329S	1524E

Farm Greylingshof	2329S	3046E
Gross Tinkas	2250S	1528E
N end of Gungochoab Mtn	2312S	1459E
S end of Gungochoab Mtn	2315S	1455E
2,5 km SE of Gungochoab Mtn	2312S	1459E
3 km SE of Gungochoab Mtn	2312S	1459E
5 km NW of Gungochoab Mtn	2309S	1456E
Haigamkab	2242S	1455E
Hamilton Mtn	2306S	1454E
btwn Hebron-Onanis River	2243S	1535E
3 km SE of Hebron	2243S	1540E
3 km SW of Hebron	2245S	1535E
6 km SW of Hebron	2248S	1532E
Homeb	2338S	1512E
km SE of Homeb turn-off	2337S	1511E
Husab drift	2245S	1503E
Khan Mine	2231S	1459E
0 km W of Khan Pforte		
km SE of Klein Klipneus	2326S	1457E
km SE of Klein Klipneus	2326S	1458E
km E of Klein Klipneus	2324S	1500E
Klein Tinkas	2249S	1526E
Farm Komuanab	2242S	1553E
Kuiseb Canyon and bridge	2318S	1547E
Kuiseb River nr Rooibank	2311S	1439E
Langer Heinrich	2247S	1520E
Mirabib	2327S	1522E
Mirabib Hills	2328S	1523E
Namib-Naukluft Park	2215DAd	
Namib Station	2234S	1444E
"New Road Site"	2320S	1502E
km W of "New Road Site"	2320S	1501E
Nonidas Stn	2236S	1438E
Nanisberg	2247S	1539E
Otjimbingwe	2222S	1608E
Palmenhorst	2241S	1453E
Piet	2244S	1520E
Rooibank	2310S	1439E
40 km SE of Rooibank	2325S	1456E
Rooikop	2259S	1439E
Rössing Mtn	2232S	1449E
Rössing Mine	2228S	1503E
Farm Rostock	2321S	1552E
Schieferberg Pass	2256S	1519E
5 km NW of Schieferberg Pass	2252S	1517E
Schierilatz	2240S	1435E
Btwn Sphinx-Pforte		
Swakopmund	2240S	1432E
5 km E of Swakopmund	2240S	1435E
10 km E of Swakopmund	2238S	1438E
13 km E of Swakopmund	2238S	1439E
16 km E of Swakopmund	2237S	1440E
42 km E of Swakopmund	2231S	1454E
30 km SE of Swakopmund	2247S	1413E
40 km SE of Swakopmund	2248S	1453E
38 km SE of Swakopmund on Khomashochland Road	2247S	1451E
20 km N of Swakopmund	2230S	1429E
22 km N of Swakopmund	2229S	1429E
11 km from Swakopmund—Usakos	2238S	1438E
16 km from Swakopmund—Usakos	2237S	1440E
3 km E of Swakop River bridge	2241S	1433E
Swartbankberg	2318S	1449E
Swartbank, S of Kuiseb River	2321S	1452E
3,5 km E of Swartbank Vill.	2321S	1454E
8 km E of Swartbank Vill.	2321S	1456E
Swartkoppies	2209S	1439E
Ubib	2307S	1511E
3 km W of Ubib	2306S	1508E
5 km NNE of Ubib	2304S	1512E
11 km NNE of Ubib	2301S	1513E
16 km NNE of Ubib	2259S	1513E
10 km SE of Ubib	2310S	1515E
nr Vogelfederberg	2303S	1459E
Von Stryk Mine	2249S	1454E
Walvis Bay area	2258S	1437E
80 km E of Walvis Bay on Gamsberg Rd	2309S	1514E
Welwitschia flats	2238S	1500E
Welwitschia Stn	2236S	1501E
N side of Witpoort	2248S	1506E
5 km SSW of Witpoortberg	2253S	1504E
Zebra Pan	2331S	1531E
2 km SSE of Zebra Pan	2332S	1530E
14 km SSE of Zebra Pan	2337S	1531E