

THE DISTRIBUTION OF MAMMALS IN THE NAMIB DESERT AND ADJOINING INLAND ESCARPMENT

by

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(With 1 map, 2 figures and 2 colour plates)

ABSTRACT

The mammals of the Namib Desert and adjoining escarpment zone are listed under the different habitats they occur in, viz. Sand Dunes, Coastal Hummocks, Gravel Plains, Rocky Outcrops and Canyons, Riverine Growth, pro-Namib and Adjoining Escarpment. Their utilization of these habitats and possible dispersion routes, are being discussed.

INTRODUCTION

The mammals of the Namib Desert have been listed amongst others, by Shortridge (1936), Roberts (1951), Ellerman *et al.* (1953), Hoesch & von Lehmann (1956), Bauer & Niethammer (1959), Meester (1962, 1964) and Niethammer (1968) and in reports by pioneers such as Pienaar and S. van Reenen in 1793 (in Vedder, 1934) and Alexander (1838) while their general distribution patterns have been discussed and mapped by Davis, 1962.

The subspecies represented in the Namib are in most cases not discussed in this paper as stress is laid rather on the presence of particular species in the different habitats of the Namib. Furthermore, this paper deals only with the mammal fauna of only the South West African section of the Namib Desert, with the exception of the bats and the Cape sea lion (*Arctocephalus pusillus*). The nomenclature used by Davis (1962, 1965) and Meester *et al.* (1964) is followed.

GENERAL TOPOGRAPHY (Map 1)

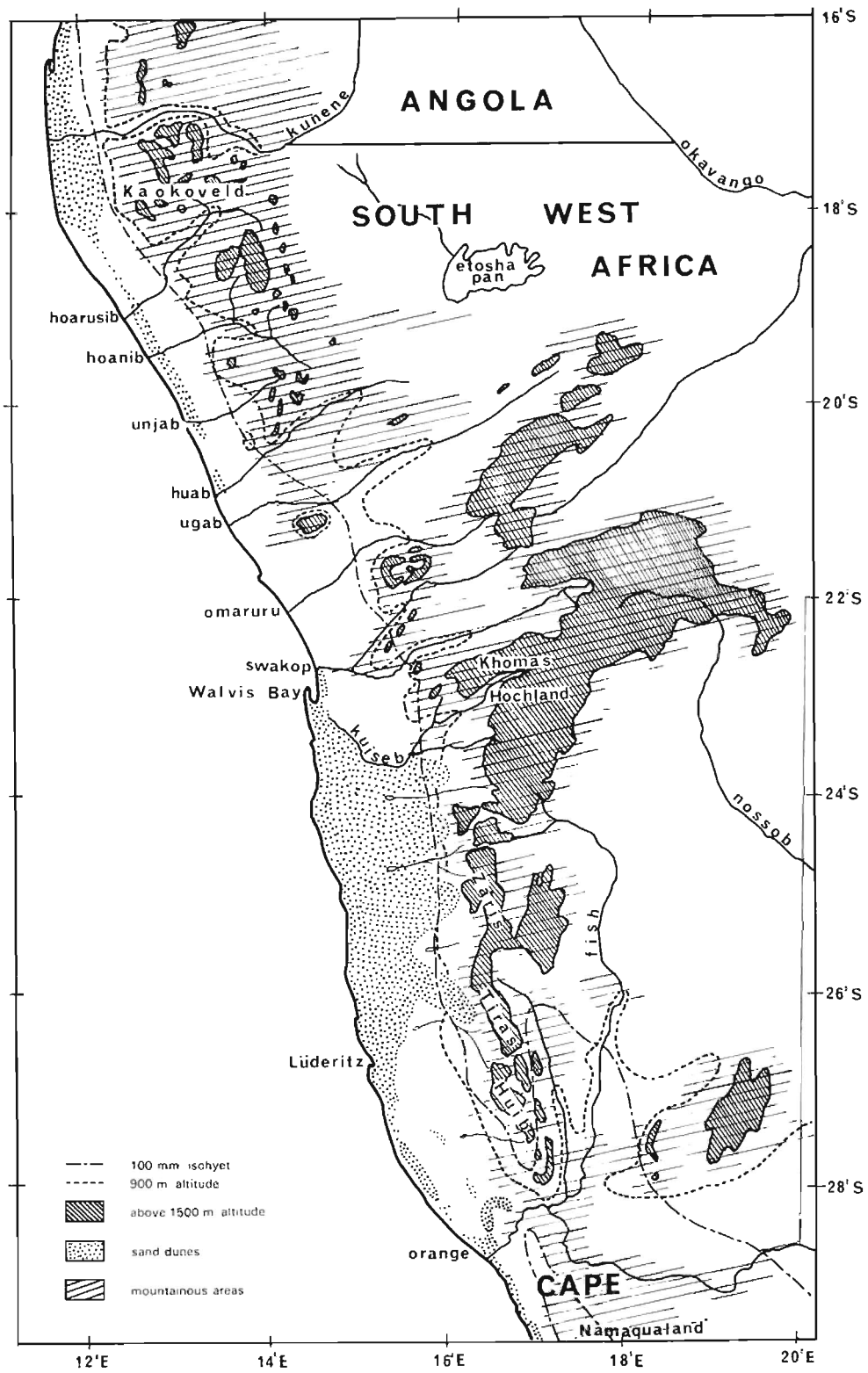
The Namib Desert forms a narrow coastal strip along a high inland plateau. The western edge of

this inland plateau is marked by either mountain chains which form distinct escarpments (Angolan and Kaokoveld mountains; Khomas Hochland, Gamsberg, Naukluft, Zaris and Tiras ranges; the Huib Plateau and Richtersveld Mountains of Namaqualand) or by a less clearly marked escarpment as in the area between the Kaokoveld and Khomas Hochland where the plateau has mountainous fingers stretching westwards and isolated mountains such as Brandberg, Erongo, Spitzkoppe and Chuos.

The Namib Desert consists mainly of gravel plains, unbroken sand dunes and dune stripes or barchan dunes on gravel plains (Koch, 1961).

The distribution of animal life (especially the small mammals) is, apart from the surface features mentioned, largely influenced by rocky outcrops and low mountain chains, by the rivers that cross or enter the Namib, as well as by coastal vegetation. The mountains and river beds form niches that differ vastly from the adjoining plains and dunes both in topography and micro-climate. The outcrops and river-beds may act as migration corridors leading from the inner plateau to the heart of the desert. The rivers crossing the Namib can be separated into:

- a) perennial rivers flowing from the central interior (Orange and Kunene);
- b) seasonal rivers from the interior of South West Africa (Huab, Ugab, Omaruru and Swakop); and
- c) seasonal rivers from the adjoining escarpment zone (Coroca from Sierra de Chela of Angola; Hoarusib, Khumib, Hoanib, Unjab etc. from the Kaokoveld and the Kulseb from the Khomas Hochland).



Map of South West Africa (approximately west of 20°E.), southern Angola and northern Namaqualand to show the sand dunes areas on the gravel plains, the escarpment zone and major rivers entering the Namib Desert.

A fourth group of rivers enter the Namib but do not have a clearly marked mouth. Some of these end amongst the dunes in lime plains or pans such as Tsondabvlei, Sossusvlei and Koichabpan.

The true desertic Namib occurs along the coast and is separated from the escarpment zone by the subdesertic pro-Namib. The pro-Namib is a rather ill-defined area of gradual change-over on the gravel plains or a clearly marked corridor, with scattered hills, wedged between the dunes and the escarpment. The 100 mm mean annual isohyet follows the eastern border of the Namib closely (Map), except along the Orange River Valley and environs. The area east of the Huib and Richtersveld Mountains and below the 100 mm isohyet is generally excluded from the accepted concept of the Namib. It could, however, zoogeographically be regarded as pro-Namib.

HABITAT TYPES AS UTILIZED BY MAMMALS

The habitats used by the mammals in the Namib could be basically be classified as Sand Dunes; Gravel Plains; Mountains, Rocky Outcrops and Canyons; Riverine Growth and halophytic shrubs in Coastal Hummocks (Plates I and II).

There are two main dune fields in the South West African Namib. The northern one lies south of the Kunene River and breaks-up towards the south to form either barchan dunes on soft gravel or a narrow littoral belt that stretches as far south as the Huab River. The Kuiseb River forms the northern limit of the central dune mass which averages a width of 60 miles and continues southwards as far as Lüderitz. Vegetation consists mainly of dune-grass clumps (*Aristida sabulicola*) while a variety of annual grasses appear after rain showers, especially in the more stable inter-dune 'streets'.

A large expanse of bare, rugged rock of the Damara System that lies south of the Huab River is an important topographical character hitherto not mentioned in discussions of biographical nature. This area of exposed rock stretches southwards beyond the Ugab River and some sixty miles inland to the east of the Doros Crater, north of Brandberg. This rugged terrain is separated from the sea by a 4 to 15 mile wide strip of sandy gravels similar to that found along the largest part of the coast between Swakopmund and the Unjab River. The influence of this rugged area on the distribution of animal life, mammals in particular, is yet unknown. It could be most important as it stretches across the Namib plains, leaving only a coastal corridor for north-south dispersion.

The Gravel Plains vary in regard to the firmness of the surface and the salinity of the soil. The surface may be sand, gravel or a near-exclusive flat-

stone covering. The surface can be vegetationless, vegetated with halophytes, with a sparse grass cover or with a good grass stand as in the pro-Namib.

Willoughby & Cade (1967) followed Logan (1960) in differentiating between the "Outer Gravel Flats" and "Inner Gravel Flats". The Outer Gravel Flats are virtually vegetationless with scattered halophytes such as *Arthroa leubnitziae* and *Zygophyllum stapfii*, while grasses and low, woody perennials form a sparse cover in the Inner Gravel Flats. Willoughby & Cade (*op. cit.*, p. 5) add: "This habitat is very open with little ground cover, and if rain fails to fall for more than a year the annual grasses disappear leaving hardly a trace". The 'Open Acacia Woodland' is used as a third habitat that can be compared with the 'pro-Namib habitat' as discussed in this article.

The Rocky Outcrops and Canyons consist of coarse grained, well eroded granite, mica schists, felspar formations or lime deposits (Logan, 1960). Vegetation varies remarkably, consisting not only of various grasses but also of a number of shrubs and succulents as *Sarcocaulon mossamedense*, *Pelargonium otaviense*, *Senecio longiflorus*, *Euphorbia lignosa*, *Orphanthera albida*, *Petalidium* sp., *Acacia reficiens*, *Commiphora saxicola* and *Hoodia* spp. (Giess 1962, and *in litt.*).

The variation in the riverine cover is discussed below in the comparison of the different species occurring in the river-beds, while full reference is given to the Coastal Hummocks in the discussion of the distribution pattern of *Parotomys littledalei*.

MATERIAL

The figure 1 was compiled from existing literature records, personal field notes and catalogues and after discussion of the distribution of the larger species with individuals having a sound knowledge of animal life in the Namib Desert during the last two decades.

The purpose of this figure is not only to mark the presence of the species in the different habitats, but also to give an approximate indication of their proportional abundance. In the figure 1, a solid bar indicates that the species is generally present in all the applicable niches throughout the habitat type, while a short bar indicates that the species is present in a restricted part of the habitat only. Hartman's zebra (*Equus zebra*), for example, was originally present throughout the escarpment zone (first column) as well as in most of the outcrops and in the rough terrain of the pro-Namib (third column). It was, however, restricted to the vegetated outcrops of the eastern desertic Namib (fourth column) and the gravel plains between these outcrops (fifth column).

PLATE I



a A barchan dune with small dunelets in the foreground. Photo P. Buys.



b A coastal hummock dune, about three feet high and densely overgrown with gannabush (*Salsola* sp.). The openings amongst the branches have been made by *Parotomys littledalei* to be used as sunning and lookout posts.



c Outerops on the central gravel plains at approximately 23° 30'S., 15° 30'E.

PLATE II

- a Rugged terrain. Hakos Mountains on the western escarpment of the Khomas Hochland. Altitude about 1800 m.



- b Kuiseb River bed at Gobabis with *Acacia albida*, *Tamarix usneoides*, *Salvadora persica* and *Nicotiana glauca* along the banks, a rock outcrop being a westerly remnant of the canyon shows on the right and a sand dune in the background.



- c Dense growth in the marshy bed of the Swakop River at its junction with the Khan River.



	ADJOINING INLAND PLATEAU	RIVERINE GROWTHS	PRO-NAMIB	ROCKY OUTCROPS & CANYONS	GRAVEL PLAINS	SAND DUNES	COASTAL HUMMOCKS
INSECTIVORA s.l.							
<i>Crocodyra cyanea</i>	██████████	██████████					
<i>Macroscelides proboscideus</i>	██████████		██████████				
<i>Elephantulus rupestris</i>	██████████		██████████				
<i>Elephantulus intufi</i>	██████████		██████████				
<i>Eremitalpa granti</i>						██████████	██████████
PRIMATES							
<i>Papio ursinus</i> [†]	██████████	██████████	██████████				
<i>Cercopithecus aethiops</i>	██████████	██████████					
CARNIVORA							
<i>Otocyon megalotis</i>	██████████		██████████		██████████		
<i>Vulpes chama</i>	██████████		██████████	██████████			
<i>Canis mesomelas</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
<i>Lycan pictus</i>	██████████	██████████	██████████		██████████		
<i>Ictonyx striatus</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
<i>Mellivora capensis</i>	██████████	██████████	██████████				
<i>Lutra maculicollis</i>	██████████	██████████					
<i>Genetta genetta</i>	██████████	██████████					
<i>Herpestes sanguineus</i>	██████████	██████████			██████████		
<i>Herpestes nigritus</i>	██████████	██████████					
<i>Atalapha pulchra</i>	██████████	██████████					
<i>Helogale parvula</i>	██████████	██████████	██████████	██████████			
<i>Mungos mungo</i>	██████████	██████████	██████████				
<i>Cynfelis penicillata</i>	██████████	██████████	██████████				
<i>Suricata suricatta</i>	██████████	██████████	██████████		██████████		
<i>Proteles cristatus</i>	██████████	██████████	██████████				
<i>Hyaena brunnea</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
<i>Crocuta crocuta</i>	██████████	██████████	██████████	██████████			██████████
<i>Felis libyca</i>	██████████	██████████	██████████	██████████			
<i>Felis caracal</i>	██████████	██████████	██████████	██████████			
<i>Felis nigripes</i>	██████████	██████████	██████████	██████████			
<i>Panthera pardus</i>	██████████	██████████	██████████	██████████			
<i>Panthera leo</i>	██████████	██████████	██████████	██████████			
<i>Acinonyx jubatus</i>	██████████	██████████	██████████	██████████	██████████		
TUBULIDENTATA							
<i>Orycteropus afer</i>	██████████	██████████	██████████				
PROBOSCIDEA							
<i>Loxodonta africana</i>	██████████	██████████	██████████	██████████	██████████		
HYRACOIDEA							
<i>Procavia capensis</i>	██████████	██████████	██████████	██████████			
<i>Procavia welwitschii</i>	██████████	██████████	██████████	██████████			
PERISSODACTYLA							
<i>Diceros bicornis</i>	██████████	██████████	██████████	██████████	██████████		
<i>Equus zebra</i>	██████████	██████████	██████████	██████████	██████████		
ARTIODACTYLA							
<i>Phacochoerus aethiopicus</i>	██████████	██████████	██████████	██████████	██████████		
<i>Giraffa camelopardalis</i>	██████████	██████████	██████████	██████████	██████████		
<i>Raphicerus campestris</i>	██████████	██████████	██████████	██████████	██████████		
<i>Oreotragus oreotragus</i>	██████████	██████████	██████████	██████████	██████████		
<i>Antidorcas marsupialis</i>	██████████	██████████	██████████	██████████	██████████		
<i>Oryx gazella</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
<i>Tragelaphus strepsiceros</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
LAGOMORPHA							
<i>Lepus capensis</i> (& ssp. <i>sabini</i>)	██████████	██████████	██████████	██████████	██████████		
<i>Pronolagus randensis</i>	██████████	██████████	██████████	██████████	██████████		
RODENTIA							
<i>Bathyergus janetta</i>	██████████	██████████	██████████	██████████			██████████
<i>Hystrix africaeaustralis</i>	██████████	██████████	██████████	██████████			
<i>Petromus typicus</i>	██████████	██████████	██████████	██████████	██████████		
<i>Xerus inauris</i>	██████████	██████████	██████████	██████████	██████████		
<i>Xerus princeps</i>	██████████	██████████	██████████	██████████	██████████		
<i>Pedetes capensis</i>	██████████	██████████	██████████	██████████	██████████		
<i>Aethomys namaquensis</i>	██████████	██████████	██████████	██████████	██████████		
<i>Mus minutoides</i>	██████████	██████████	██████████	██████████	██████████		
<i>Thalpomys paeduleus</i>	██████████	██████████	██████████	██████████	██████████		
<i>Rhabdomys pumilio</i>	██████████	██████████	██████████	██████████	██████████		
<i>Praomys natalensis</i>	██████████	██████████	██████████	██████████	██████████		
<i>Lemniscomys griselda</i>	██████████	██████████	██████████	██████████	██████████		
<i>Saccostomus campestris</i>	██████████	██████████	██████████	██████████	██████████		
<i>Petromyscus collinus</i>	██████████	██████████	██████████	██████████	██████████		
<i>Steatomys pratensis</i>	██████████	██████████	██████████	██████████	██████████		
<i>Malacothrix typica</i>	██████████	██████████	██████████	██████████	██████████		
<i>Parotomys littledalei</i>	██████████	██████████	██████████	██████████	██████████		
<i>Desmodillus auricularis</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
<i>Gerbillus paela</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
<i>Gerbillus vullinus</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████
<i>Tatera leucogaster</i>	██████████	██████████	██████████	██████████	██████████	██████████	██████████

DISCUSSION

The species listed in figure 1 are discussed under the different habitats. Species occurring in more than one of the habitats are discussed only once, usually under the habitat most commonly found.

Some mammals which occur in all habitats mentioned are the gemsbok (*Oryx gazella*), springbok (*Antidorcas marsupialis*), saddle-backed jackal (*Canis mesomelas*) and brown hyaena (*Hyaena brunnea*). The distribution of the two carnivores is greatly influenced by the presence of open water, although both these species are known to supplement the available water by eating vegetable matter such as narras (*Acanthosicyos horrida*), wild melons and other cucurbits, and in the case of the saddle-backed jackal, also berries. Saddle-backed jackals are extremely numerous along the coast as scavengers, a niche probably extensively utilized before by brown hyaenas, the number of which has become greatly reduced during the previous decades.

Although springbok penetrate into the dune areas, they usually follow the vegetation in the dune 'streets'. Gemsbok graze frequently on the sparse vegetation of the coastal plains and amongst the dunes.

Springbok and gemsbok are common on the Gravel Plains wherever there is vegetation. Being larger than most other mammals of the Namib and wanderers by nature, they often cross extremely dry areas for twenty or more miles to reach green vegetation after local rain showers. In contrast to the springbok, gemsbok are often found on rocky outcrops and against the steep slopes of canyons. Both these plains-loving antelopes will visit river-courses to drink but although they graze on the sedges or bushes in the river-beds, normally remain there for brief period only.

The Sand Dunes

The only mammal endemic to the Namib, the Namib golden mole (*Eremitalpa granti*) is represented by the typical form to the south of the Orange River and by the subspecies *namibensis* in the central dune system (Plate Ia).

There is a possibility that another species of golden mole exists in the Namib. This assumption is based on (a) an article on a golden mole collected during 1951 at Rooibank, 30 miles southeast of Walvis Bay (van der Merwe, 1964), and (b) reports of golden mole tracks observed in the bed

of the Swakop River, near its mouth, by amongst others, Dr. C. Koch. The golden mole mentioned in the article by Mr. van der Merwe not only appears to have the fore-claws different from that of *Eremitalpa* but it is also larger in size.

The golden mole seems to prefer dunes with scattered clumps of dune-grass (*Aristida sabulicola*). The large proportion of golden mole remains in owl pellets (Bauer & Niethammer, 1958 and Nel, in press) are due to the frequency with which these fossorial animals emerge and the large distances they cover on the surface. During these nocturnal surface wanderings they often cover a distance of 150 yards or more with intermittent submersion of a few inches only. However, they may also circle around just below the surface in dune-grass patches. Wandering around on the surface occurs more often on the hard windward side of dunes and adjoining parts of dune 'streets' but tracks have also been observed on the extremely soft sand of a rather sharp incline. *Eremitalpa granti* were recorded by Holm (1968) in the bed of the Kuiseb River near Gobabeb.

There are no insectivorous small mammals in the northern dunes, although a large number of rodent species, especially gerbils, probably take tenebrionid and other beetles on the dunes, as they do in captivity. The proteine-rich beetles may play an important part in their water metabolism.

The pigmy gerbil (*Gerbillus paebe*) is found throughout the drier sandy parts of southern Africa: along the south coast from the Alexandria District in the Eastern Cape to the Cape Flats, thence inland and northwards to South West Africa and the Angolan Namib, the Kalahari and sandy parts to the north of the Soutpansberg in the Transvaal.

G. paebe is the most widespread rodent of the Namib and is absent only from rocky areas and densely vegetated river-beds. It is often present on sandy patches in the gravel plains, amongst the coastal hummocks or in the high dune area where it more frequently occurs between the dunes, having its permanent burrows close to dune-grass clumps. Their tracks can nevertheless be followed up dune faces, indicating that it roams around at night and crosses the dunes.

The closely related *Gerbillus vallinus* has a more restricted distribution in southern Africa, being known only from the northwestern Karroo and the Namib. *G. vallinus* remains are exceptionally numerous in owl pellets from Sossusvlei (Bauer & Niethammer 1959, Nel, 1969), from near Hope Mine and from near Orupembe on the northern pro-Namib-Kaokoveld border (Davis, *pers. com.*).

Gerbillus vallinus is possibly the only Namib mammal of which a subspecies is restricted to the dunes and can be differentiated on cranial characters from the subspecies on the gravel plains.

Figure 1: The occurrence of mammals in the different habitats of the Namib Desert and in the adjoining inland escarpment. The length of each bar indicates the relative utilization by each species of the suitable niches in each habitat.

The Coastal Hummocks

Mammals found in the Coastal Hummocks comprise some of those already discussed, viz. saddle-backed jackal, hyaena, springbok, gemsbok and *Gerbillus pæba*.

The general distribution pattern of *Parotomys littledalei* corresponds remarkably with that of *G. vullinus*, both being present in the northwestern Karroo and Namib. *P. littledalei*, however is absent from the main dune systems and occurs only along the coast from as far south as the mouth of the Olifants River in the Cape Province to the north of the Rocky Point (Khumib River). It has not yet been recorded from further north although it is possibly present at or beyond the Kunene River mouth.

Although *P. littledalei* is also present in the southern pro-Namib parts of South West Africa, its distribution pattern in the central and northern parts of the Namib seems to be linked with the coastal hummock chain just above highwater mark and with the bush covered hummocks extending parallel or away from the coast, but in most cases not more than four miles inland (Plate I b).

There seems to be no contact between the *Parotomys littledalei* occurring in the Coastal Hummocks and those from the interior of South West Africa (Rehoboth District and southwest thereof) and the southern pro-Namib (opposite the southern plains).

The gannabush (*Salsola* sp.) hummocks seem to be the most commonly utilized by *P. littledalei* but they are also present in "inkbos" (*Suaeda plumosa*) and in the "podloodplant" (*Arthroaerua leubnitziae*). Although they often feed on the succulent *Zygophyllum stapffii*, judging from the numerous runways seen leading to these bushes, not one burrow system has been found in them.

P. littledalei, contrary to generally accepted belief, are territorial and not colonial, as is the case with *P. brantsi*. Tracks often lead from one hummock to another or from adjoining gannabush hummocks to the succulent *Zygophyllum* between the two. The only cases where more than one animal was found to utilize a single hummock were where females with young or two subadult animals were collected from the same lodge. Individual lodges can even be distinguished in river-beds with a dense "inkbos" cover, such as the Swakop River, close to its mouth. *Parotomys littledalei* are here present in the higher sandy parts of the river-bed but away from the damp brackish bottom.

It might be noted here that *P. littledalei* and the closely related *P. brantsi* are both present in the southeastern part of South West Africa, but have not yet been recorded as occurring sympatrically. The different niches that they occupy are indicated

by their plant community preferences. *P. littledalei* is found in *Salsola-Suaeda* communities while *P. brantsi* prefers the driedoring (*Rhigozum trichotomum*) covered dune 'streets'.

The Namaqua dune-mole (*Bathyergus janetta*) is found in the coastal dunes of Namaqualand in the Cape Province and in the area lying close to the mouth of the Orange River in South West Africa.

The Gravel Plains

Differentiation between the inhabitants of the desertic Gravel Plains and those of the pro-Namib is virtually impossible, as the pro-Namib consists mainly of vegetated gravel plains. The vegetation, on the other hand depends largely on rainfall which is an extremely unstable factor and consists nearly exclusively of local showers (Plate I c).

Of those mammals living on the Namib plains, mentioned above, the Namaqua gerbil (*Desmodillus auricularis*) is the most frequent. It may occur in the same general area as both *Gerbillus pæba* and *G. vullinus* but actually prefers gravel above sand and concentrates on exposed limestone areas, especially loose limestone amongst sand and gravel. *Desmodillus's* habit of storing seeds may be a factor contributing to its survival.

Ictonyx striatus, the polecat, is well adapted to life in the desert where it preys on rodents and ground birds. Polecats can be seen in the sandy rived-beds or way out on the plains, amongst sedges in river-beds or amongst boulders. Polecats have not yet been recorded from high mountains or steep ravines.

The validity of the Namib hare (*Lepus salai*) as a recognized species is still a question. Petter & Genest (1965) regard it as a subspecies of *L. capensis* and this view is followed here. It is recorded from the eastern parts of the Gravel Plains and pro-Namib, and is even present where the grass-cover is extremely sparse.

Suricates (*Suricata suricatta*) and ground squirrels (*Xerus inauris*) inhabit the pro-Namib plains and eastern parts of the desertic Gravel Plains. They sometimes live side by side but suricates normally have their main burrows amongst limestone while ground squirrels prefer softer soil.

The Namib suricate is distinctly smaller and paler in colour than the *S. s. hahni* from the interior of South West Africa. These differences are so marked that Roberts (1951) regarded the Namib form as a different species, viz. *S. marjoriae* Bradfield, 1936.

The distribution of the Kaokoveld bristly ground squirrel (*Xerus princeps*) is still rather unknown but appears to be restricted to the eastern part of

the South West African escarpment. Known from near Warmbad in the south (below 100 mm mean annual rainfall), Berseba area in the central Fish River Valley and from the Kaokoveld.

The Mountains, Rocky Outcrops and Canyons

Mountain fingers stretching from the escarpment, isolated mountain ranges, low outcrops on the gravel plains and canyons are to a large extent linked. Although the gap between outcrops might be sometimes several miles wide, they usually form a more or less continuous criss-cross pattern throughout the desert (Plate I c and Plate II a).

The small rock mouse (*Petromyscus collinus*) is one of the mammal species occurring in the rocky parts of the Namib. The general distribution pattern of this nocturnal species basically follows the western mountain area of Southern Africa, from southern Angola southwards to Namaqualand and from there along the mountainous zone eastwards to Cradock (Davis, 1962). *Petromyscus* penetrates into the Namib from the western highland area and thus invades an atypical region, although the niche itself is typical. *Petromyscus* were for instance, collected at Gobabeb and in the Zwartbank Mountain 20 miles northwest of Gobabeb in the desertic Namib. This is an excellent example of invasion of the Namib by use of rugged terrain.

Diurnal dassie-rats (*Petromus typicus*) are present in the mountain area of the escarpment zone, in pro-Namib outcrops and canyons and in similar habitats on the eastern side of the desertic Namib where they live sympatrically with *Petromyscus* and *Procavia*. In certain more westerly mountains the browser *Petromus* is absent where *Petromyscus*, which is largely a seed-eater, still occurs.

The insectivorous elephant shrews *Elephantulus intufi*, *E. rupestris* and *Macroscelides proboscideus* were previously regarded as occurring only in the western foothills of the escarpment, however, owl pellets collected near Gorob Mine during 1965, confirmed their presence in the Namib. (The nomenclature as used by Corbet, 1966, is being followed here, viz. *E. barlowi* of Lundholm, 1955 = *E. rupestris*). Different habitat preferences were found between two species of elephant shrews at Ganab in the pro-Namib; *E. rupestris* were collected amongst the boulders in the hills while *M. proboscideus* were found on low rocky outcrops, especially amongst limestone banks. Furthermore, *E. rupestris* appears to be diurnal and crepuscular while *M. proboscideus* were active at all hours of the day and night, they were seen basking in the early morning sun, dashing during midday from one hole to another, right amongst burrow entrances of a suricate warren and running around at midnight.

Of the larger species the dassie (*Procavia capensis*), red mountain hare (*Pronolagus randensis*) and the klipspringer (*Oreotragus oreotragus*) are also present on the eastern side of the typical desertic Namib. A factor not yet established is the dispersion and local migration of, amongst others, these species of animals. In visiting the same outcrops during consecutive years, dassies were found to be numerous during the year following exceptional good rains, hardly occurring the following year and gone without trace the year thereafter. This is apparently also true for the klipspringer, judging for the accumulations of their faecal pellets at different times.

These observations were made on the five mile long outcrop series to the north of the Gorob Mine. These outcrops are rather isolated, being about 15 miles from the Kuiseb canyons to the south and about 8 miles from higher mountains to the east.

An African wildcat (*Felis libyca*) has been seen at these hills, while black-footed cats (*Felis nigripes*) have been recorded from rocky banks of dry water courses in the plains to the north thereof (De la Bat, *in litt.*).

Porcupines (*Hystrix africae-australis*) use cave-like hollows amongst boulders for lying during daytime. This is also a species that does not penetrate into the true desert zone although they may be found in the proximity of water courses near the coast. Porcupines are, for example, absent from the gravel plain strip between the pro-Namib and northern dune-chain but are present between the vegetation of the river deltas.

The Riverine Growth

Mammals that are restricted to the vegetation in the river-beds or on the river-banks, may be recorded from these habitats in the heart of the desert, although they might not be able to survive in the adjoining desert (Plate II b, c). Spring-hares (*Pedetes capensis*), for example, have only been recorded from the sandy patches along the Khumib River in the northern Namib, about 5 miles inland.

Shrews of the genus *Crocidura* have been collected along the Kuiseb river-bed at Gobabeb and in the Swakop river-bed at Palmenhorst i.e. at the junction with the Khan River. These two places differ greatly in both the moisture contents of the soil which is sandy at Gobabeb and muddy sandy-silt at Palmenhorst and vegetation which at Gobabeb consist of trees (e.g. *Acacia albida*, *A. giraffae* and *Ficus sycomorus*) and shrubs (e.g. *Tamarix usneoides*, *Salvadora persica* and *Nicotiana glauca*) and at Palmenhorst of sedges (*Scirpus dioicus*) and reeds (*Phragmites communis*) (Giess, *pers. comm.*). A *Crocidura cyanea* was found in the same "inkbos" hummock as *Parotomys littledalei* near the mouth of the Swakop River.

Although the shrew *Myosorex varius* has been collected at Port Nolloth in the southern Namib (Meester, 1958), it is not yet known to be present in the South West African part of the Namib Desert.

The striped mouse (*Rhabdomys pumilio*) is widespread along the water courses, living in river-bed marshes, in low bushes on the banks, amongst flood debris or in narra bushes against dune-slopes. The presence of three subspecies, *bechuanae*, *namaquensis* and *namibensis* in the Namib (Meester, 1962) is highly unlikely. The main character used by Roberts (1951) in his "Key to the subspecies", viz. the relative tail length, has been questioned by Coetzee (*in press*).

The multimammate mouse (*Praomys natalensis*) on the other hand, being largely a mammal of Savanna Woodlands (Davis, 1962) and not of the desertic areas as is *Rhabdomys*, is not as well adapted to changing environments and is only present in the well-vegetated parts of some river-beds to the north of the Swakop River.

The tree rat (*Thallomys paedulcus*) nests in various species of trees in other parts of its range, but seems to be restricted to camelthorn trees (*Acacia giraffae*) in the Namib and its environs. The distribution of *T. paedulcus* thus coincides remarkably with that of the camelthorn tree, so that it occurs where these trees are fairly numerous e.g. along the larger water courses.

Niethammer (1968) found cranial remains of fat-mouse (*Steatomys pratensis*) in owl pellets from Sossusvlei. According to Smithers (1968) fat-mice are more abundant on sandy ground and sandy alluvium on the fringes of swamps and rivers of the Kalahari. This indicates that fat-mice could have used river-beds as dispersion routes. The dry river courses in the central parts of the escarpment, such as those leading to Sossusvlei, would suit fat-mice ideally as they do not have a marshy bed after seasonal rains but are regarded as open, well grassed valleys with occasional eroded gulleys.

The small-spotted genet (*Genetta genetta*) also use river courses in their dispersion as is shown by skins from near Walvis Bay and Gobabeb.

Of the two pachiderm animals, the elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*), which are frequent visitors to the river-beds, the rhinoceros can be regarded as a semi-permanent occupant and the elephant as a wanderer. Elephants still come right down to the coast along some river-beds, such as Hoarusib, while black rhinoceros are present in dry beds of a number of rivers entering the northern Namib. Pienaar (*in* Vedder, 1934) recorded a number of rhinoceros and elephant in the Swakop Valley during his short visit in 1793 and mentioned the presence of rhino-

ceros within "a day journey" of present day Walvis Bay. Mr. B. de la Bat (*pers. com.*) has informed the author of a remarkably well-preserved elephant tusk and a rhinoceros horn which were recently excavated near Tinkas water-hole, i.e. the desertic Namib/pro-Namib transitional area about 10 miles south of the Swakop River.

The pro-Namib

The mammals occurring in the subdesertic pro-Namib of South West Africa which have not yet been recorded from the desertic Namib or, if so, are regarded as occasional visitors are here listed.

Bat-eared fox (*Otocyon megalotis*): found in small family groups in the pro-Namib.

Silver jackal (*Vulpes chama*): penetrate the gravel plains on the western side of the pro-Namib under favourable conditions.

Hunting dog (*Lycan pictus*): present to the west of Usakos during 1947 and 1967, also recorded from the northern pro-Namib (Tinley, *pers. com.*).

Ratel (*Mellivora capensis*): although uncommon, present throughout the pro-Namib.

Slender mongoose (*Herpestes sanguineus*): sometimes also present in the more desertic parts of the west of the pro-Namib.

Dwarf mongoose (*Helogale parvula*): largely known from rocky outcrops in the pro-Namib.

Banded mongoose (*Mungos mungo*): more typically a central plateau species only found occasionally in the pro-Namib.

Yellow mongoose (*Cynictis penicillata*): widely distributed in the pro-Namib.

Aardwolf (*Proteles cristatus*): commonly found in parts of the pro-Namib where it rained.

Spotted hyaena (*Crocota crocuta*): only present in the pro-Namib area bordering the northern Kaokoveld.

Leopard (*Panthera pardus*): penetrate the pro-Namib from the escarpment, especially along canyons and mountain chains.

Lion (*Panthera leo*): existing in the Kaokoveld, and two decades ago still present to as far south as the Swakop River and western foothills of the Khomas Hochland in the pro-Namib.

Aardvark (*Orycteropus afer*): have been recorded from the eastern parts of the pro-Namib to the north of the Swakop River. Their distribution could be linked with that of termites (Isoptera).

White-spotted hyrax (*Procavia welwitschii*): replaces *P. capensis* in northern South West Africa. Known in the pro-Namib from the cliffs along the Hoarusib River and its tributaries (Tinley, *pers. com.*).

Mountain zebra (*Equus zebra hartmannae*) often found grazing on the pro-Namib plains, sometimes up to 12 miles away from water-holes situated in rugged terrain.

Warthog (*Phacochoerus aethiopicus*): westward distribution largely through the use of rived-beds and thence to the pro-Namib plains.

Giraffe (*Giraffa camelopardalis*): in the pro-Namib and even intruding into the more arid Namib to the west of the Kaokoveld.

Steenbok (*Raphicercus campestris*): present throughout the pro-Namib and perhaps spreading westwards along water courses (known from Ganab and Gobabeb).

Golden rock rat (*Aethomys namaquensis*): occur in rocky outcrops throughout the pro-Namib.

One-striped rat (*Lemniscomys griselda*) and the pouched mouse (*Saccostomus campestris*): present on the pro-Namib plains bordering the Kaokoveld.

Bushveld gerbil (*Tatera leucogaster*): commonly found in the northern pro-Namib, also on sandy patches along river-banks.

The Adjoining Inland Plateau

A number of mammals which are present in the areas adjoining the Namib, but not yet been recorded from the desert, or regarded as occasional visitors only, are:

Baboon (*Papio ursinus*): still numerous in the escarpment, being present right down to the edge of the pro-Namib eg. at the Erongo Mountains within the Savanna and at Gross Spitzkoppe which is on the pro-Namib's western margin. Alexander (1938) recorded baboons on the south bank of the lower Kuiseb canyon where it adjoins the central dune system. Sight records from Homeb and Gobabeb (Koch, *pers. com.*).

Vervet monkey (*Cercopithecus aethiops*): found along the Orange and Kunene rivers, not known from lower regions of the rivers.

Spotted-necked otter (*Lutra maculicollis*): although present in both the Orange and Kunene rivers, it remains to be recorded from lower regions of these rivers where they flow through true desert.

Herpestes nigratus ranging throughout the Kaokoveld and as far south as the Erongo Mountains, largely confined to granite outcrops.

Water mongoose (*Atilax paludinosus*): distribution could be compared with that of the spotted-necked otter.

Caracal (*Felis caracal*): known from the Erongo Mountains and Kaokoveld.

Kudu (*Tragelaphus strepsiceros*): throughout the escarpment and northern part of the inland plateau.

Large-ear mouse (*Malacothrix typica*): had been collected on limeish plains above the banks of the Swakop River at Otjimbingwe. They could perhaps have reached Otjimbingwe by migrating from the Kalahari sand at the headwaters of the Swakop River. The exact locality from where the owl pellets recorded by Niethammer (1968) as 'Karibib' were collected is unfortunately not given. The one *Malacothrix* found by him could thus either come from the Swakop or Khan rivers or from the plateau around Karibib which is situated inbetween these rivers. These seed eating rodents are not yet known from the true Namib.

Pigmy mouse (*Mus minutoides*): has been collected at the Hakos Mountain on the western side of Khomas Hochland (Hoesch & Lehmann, 1966), could occur in the pro-Namib.

REPRESENTATION OF NUMBER OF SPECIES PER HABITAT

The total number of species listed in figure 1 as well as the numbers being present in different pairs of habitats, are shown in figure 2. Of the total of 67 species listed in figure 1, 65 are known to be present in the Namib. The two not yet recorded from the desertic area are *Cercopithecus aethiops* and *Felis caracal*.

The representation of these 65 species in the different habitat groups used are shown in the outer ring of numbers of figure 2 while the number of species occurring in different pairs of habitats are indicated on the connecting lines. By comparing the number of species common in habitat pairs with species totals for each habitat one finds that nearly all the species that inhabit Riverine Growth, pro-Namib, Rocky Outcrops and Canyons and Gravel Plains are also present in the Adjoining Inland Plateau. This is not the case with the Sand Dunes and Coastal Hummocks to Inland Plateau relationship.

The relationship between number of species present in the different habitats are basically the following:

- a) About 50 to 66 per cent of the number of species present in the other habitat groups are also represented in the Riverine Growth.
- b) Nearly all those from Rocky Outcrops and Gravel Plains are also present on the pro-Namib plains, while those species from the Sand Dunes and Coastal Hummocks are not represented to the same extent.
- c) The Rocky Outcrops and Canyons group shares about all the species with the pro-Namib; about 75 per cent (15/28 ths.) with the Riverine Growth; 32 per cent (9/28 ths.) with the Gravel

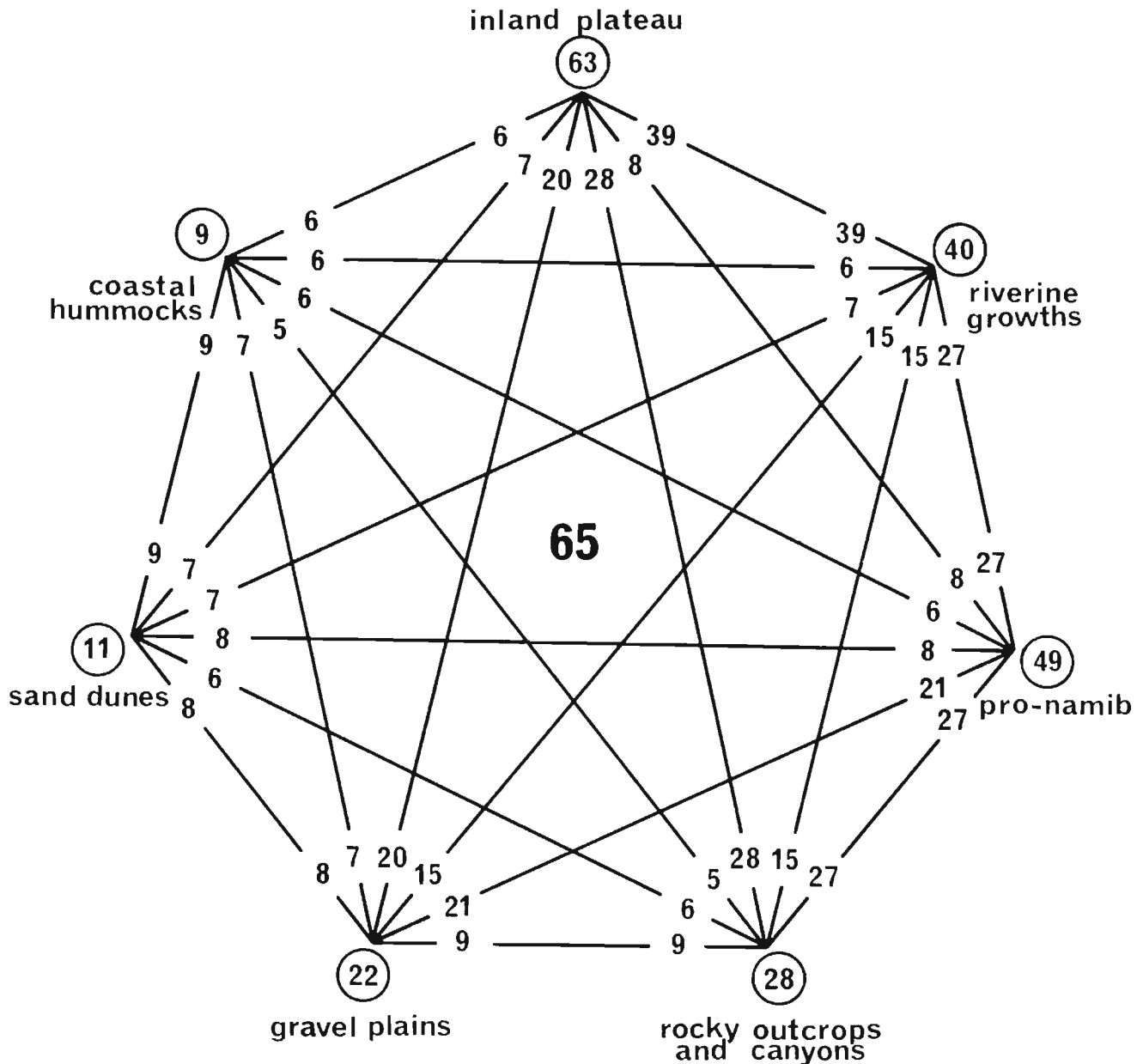


Figure 2: Relationship between the number of species found to be common to different pairs of habitats.

Plains and about 20 per cent with the Sand Dunes and Coastal Hummocks habitats.

- d) Nearly all the species to be found in the Gravel Plains are also present in the pro-Namib and to a lesser extent in the Riverine Growth. The species present in the Rocky Outcrops, Sand Dunes and Coastal Hummocks are about equally represented.
- e) The mammal species occurring in the Sand Dunes habitat share to more or less the same degree, the species present in the other habitats here used, listed in frequency order Coastal

Hummocks, Gravel Plains and pro-Namib; and Riverine Growth, Inland Plateau and Rocky Outcrops.

- f) As all species from the coastal Namib are to a larger or smaller degree also present in the Sand Dunes, the picture of mutual representation is virtually as in (e) above.

CONCLUSION

Figure 1 shows that mammals have filled most of the niches available in the Namib Desert. In discussing the possible utilization of niches, the

availability of food should be considered as well as the mobility of the mammal species.

A rich mammal fauna can hardly be expected on the vegetationless dunes were the only food source would be the invertebrates and reptiles that have a food chain based on the blown-in vegetable debris. Small mammals present in such an environment should then be basically insectivorous.

The rather bare gravel plains are even more unsuitable for mammal habitation. Those species found here are making full use of suitable niches created by depressions, outcrops and hummocks formed by the accumulation of sand against vegetation. A hummock topography thus formed creates a niche rich in fresh and decayed wind-blown plant material and a variety of invertebrates.

There are hardly any insurmountable physical barriers in the Namib if the sand dunes and plains are considered as separate entities.

Dispersion routes that could be followed in the sand dunes will be mainly along the dunes (*Eremitalpa*) or along the dune 'streets' (*Gerbillus*). The principal migration direction would thus follow the main dune direction which is longitudinal.

The main dispersion direction in the Coastal Hummocks will follow the coast because of the coast-bound existence of this habitat while a possible eastward migration of a lesser amplitude, when the hummocks spread towards the interior, might be of importance forming loops in the distribution, linking suitable coastal hummocks.

Although the slight geographical barriers (mountains) on the gravel plains would not prevent a multidirectional dispersion, the variation in aridity is a controlling factor as the majority of the species are able to spread westwards from the pro-Namib towards the desertic Namib.

The east-west distribution is especially important to the species frequenting riverine growth and to the rock-living species, particularly those found along the canyons.

In view of this, there will be an adequate gene flow between most of the populations living on the interior plateau and those on the pro-Namib plains which will inhibit extensive speciation or even subspeciation.

The presence of *Leemiscomys* and *Saccostomus* in the far northern pro-Namib parts, supports the idea of an east-west spread as these two rodents are present in the Kaokoveld but absent throughout the southern parts of the escarpment.

The geographical link and consequent possibility of gene flow, is barely present between the sand dunes of Namaqualand and those of the central Namib dune system and is virtually non-existent between the latter and the northern dunes. This is

indicated by the absence of the Namaqua dune mole (*Bathyergus janetta*) from the central dunes, although it is present in South West Africa at Oranjemund.

Equally so is *Eremitalpa* absent from the northern dunes but present in the central dunes and Namaqualand coastal dunes. This could indicate a more recent link between the central and Namaqualand dunes than between the central and northern dune system, and thus stress the importance of the isolated dunes on the plains inbetween the Orange River and Lüderitz area as a zoogeographical link (See Map).

The mammal fauna of the Namib Desert are remarkably unspecialized when the number of endemic species is used as a criterion. This is especially notable when compared with the high degree of speciation in invertebrates such as the Tenebrionidae (Koch, 1961) and could be due to:

- a) absence of topographical barriers, for larger animals, in large parts of the Namib;
- b) presence of migration routes that may be used by some species;
- c) possible contact with inland populations largely due to an east-west dispersion and
- d) the possibility of forced migration due to local changes, indirectly caused by scattered rain showers.

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GAZETTEER

Brandberg	21° 03—13' S.	14° 28—42' E.
Chuoss Mnt.	22° 16' S.	15° 35' E.
	to	
	22° 27' S.	15° 18' E.
Cradock, C.P.	32° 10' S.	25° 37' E.
Doros Crater	20° 46' S.	14° 17' E.
Erongo Mnt.	21° 26—33' S.	15° 30—50' E.
Gamsberg	23° 19' S.	16° 14' E.
Ganab	23° 06' S.	15° 27' E.
Gobabeb	23° 34' S.	15° 03' E.
Gorob Mine	23° 33' S.	15° 25' E.
Hope Mine	23° 34' S.	15° 15' E.
Koichab Pan	26° 18' S.	15° 36' E.
Naukluft Mnt.	24° 02' S.	15° 02' E.
	to	
	24° 28' S.	16° 20' E.
Oranjemund	28° 33' S.	16° 24' E.
Orupembe	18° 09' S.	12° 32' E.
Otjimbingwe	22° 22' S.	16° 08' E.
Palmenhorst	22° 42' S.	14° 54' E.
Rocky Point	18° 59' S.	12° 29' E.
Sossusvlei	24° 44' S.	15° 18' E.
Spitzkoppe (Gross)	21° 59' S.	15° 09' E.
Tsondabvlei	23° 58' S.	15° 22' E.
Usakos	21° 59' S.	15° 35' E.
Welwitschia	20° 22' S.	14° 57' E.
Zwartbank	23° 23' S.	14° 58' E.

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