Animals of the Namib Desert: Interactions with their physical environment

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The Namib Desert, located on the southwestern coast of Africa, supports a relatively rich and diverse fauna in an environment of extremely low primary productivity. Frequent advective fogs, a mosaic of substrate types including sand dunes, gravel plains and vegetated ephemeral riverine courses and the antiquity of arid climatic conditions are thought to have been important influences on the presence, abundance and distribution of the Namib fauna. Speciation has been particularly noticeable in the less mobile elements of the fauna, particularly invertebrates but also lizards, whereas in the more mobile larger vertebrates few endemic species have evolved. The available information concerning the Namib fauna varies considerably between groups and between trophic levels, thus the invertebrates and vertebrates are discussed separately and differing kinds of information are presented for different faunal elements.

Key words: Advective fog, climatic gradient, dune fauna, Namib Desert, substrate specificity.

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INTRODUCTION

Desert areas are often characterised by lack of rain, poor soil, few plants and animals, and extreme heat, cold, wind and dryness. Some deserts, however, are less extreme than others and the Namib is one such desert. Located on the southwestern coast of southern Africa, the climate of this long, narrow desert is moderated by the proximity of the South Atlantic Ocean and the cold water upwelling associated with the near-shore Benguela Current (Meigs, 1966; van Zinderen Bakker, 1975). One result of this moderate climate is the presence of a relatively rich and diverse fauna (Koch, 1961, 1962) in an environment of extremely low primary productivity.

The presence, abundance and distribution of the Namib Desert fauna are influenced by several major factors. Of primary importance, particularly to the invertebrate fauna, directly and indirectly, are the frequent, precipitating, advective fogs (Koch, 1962; Seely, 1978a). The alternation of sand dune, dry riverine woodland and gravel plain habitats (e.g. Coetzee, 1969) on the long axis of this narrow desert tract influences all plant and animal distribution patterns. The antiquity of the arid to semi-arid environments of western southern Africa including the Namib (Ward *et al.* 1983) is also thought to have influenced the character of the Namib fauna (Seely, 1978a).

Because of the long, narrow shape of the desert, the process of evolution has affected the more mobile and the less mobile elements of the fauna in different ways. Greater or lesser mobility combined with varying degrees of substrate specifity in the fauna have apparently led to differing rates of speciation with geo-

graphic and climatic changes through time. For example, in the highly mobile birds only three endemic Namib species, two small larks and a korhaan, have evolved (Maclean, 1985) in contrast to the less mobile, apterous tenbrionid beetles, for which over 200 endemic species have been described (Koch, 1962; see also Endrödy-Younga, 1978; Penrith, 1975, 1977, 1979).

As a matter of convenience and necessity, the invertebrate and vertebrate faunas are discussed below using separate formats. Different types of information are known and differing amounts of detail are available for these two major groups. Moreover, although the Namib extends from Angola to South Africa, most investigations have been carried out in the central core of this desert and it is material from this area which is herein emphasized.

INVERTEBRATES

Importance of fog

The Namib is a coastal desert extending inland to approximately the 100 mm rainfall isohyet and the 1000 m contour (Fig. 1). It is up to 160 km wide in the centre and narrows to the north and south. From a faunistic point of view the border tends to vary with fluctuations in rainfall. Because of the proximity of the cold Benguela Current along the coast, there is a steep climatic gradient from the cool, foggy coast inland to a warm desert savanna (Besler, 1972). In the central Namib near the coast, mean rainfall is less than 20 mm and fog occurs on average more than 60 days of the year; inland mean rainfall is approximately 90 mm and fog may occur only once or twice a year; temperature increases and humidity decreases from the coast inland (Lancaster *et al.* 1984). Toward the north, summer rainfall increases whereas in the southern Namib winter rainfall prevails. In effect, a mosaic of climatic conditions overlies another mosaic of substrate conditions, resulting in a complex of environmental conditions throughout this desert.

Quantitatively, fog is as important as rainfall as a source of water in the coastal half of the Namib (Lancaster *et al.* 1984) and is much more predictable (Pietruszka & Seely, 1985). Rain is essential for plant seed germination (Seely, 1978b; Seely & Louw, 1980) and recharges subsurface moisture reserves (Louw & Seely, 1982). Fog, on the other hand, produces water in only small amounts at one time, contributing to the continued growth of specialised perennial plant species (Louw & Seely, 1980; Seely *et al.* 1977) and to their continual or annual reproduction. In turn, the ephemeral and perennial plants provide the plant litter or wind-blown detritus component, an important source of energy in this environment (Robinson & Seely, 1980; Seely & Louw, 1980). Fog-water is also used directly as a moisture source by some desert invertebrates (Hamilton & Seely, 1976; Seely, 1979; Seely & Hamilton, 1976; Seely *et al.* 1983).

The invertebrate fauna at all trophic levels is dependent upon fog-water in this hyper-arid coastal desert environment. Herbivores associate with fog-using perennial shrubs and grasses. Although these animals have been little studied, Holm & Scholtz (1980) list 29 phytophagous insects living among sparsely vegetated sand dunes of the central Namib. These include members of the Orthoptera (Tettigoniidae, Acrididae (*s. lat.*); Hemiptera (Dictiopharidae, Cydnidae, Coreidae, unidentified *Heteroptera* spp.); Hymenoptera (unidentified *Apocrita* spp.).; Diptera (unidentified *Cyclorrhapha* spp.); and Coleoptera (Medoidae, Buprestidae, Histeridae, Curculionidae). Estimating the

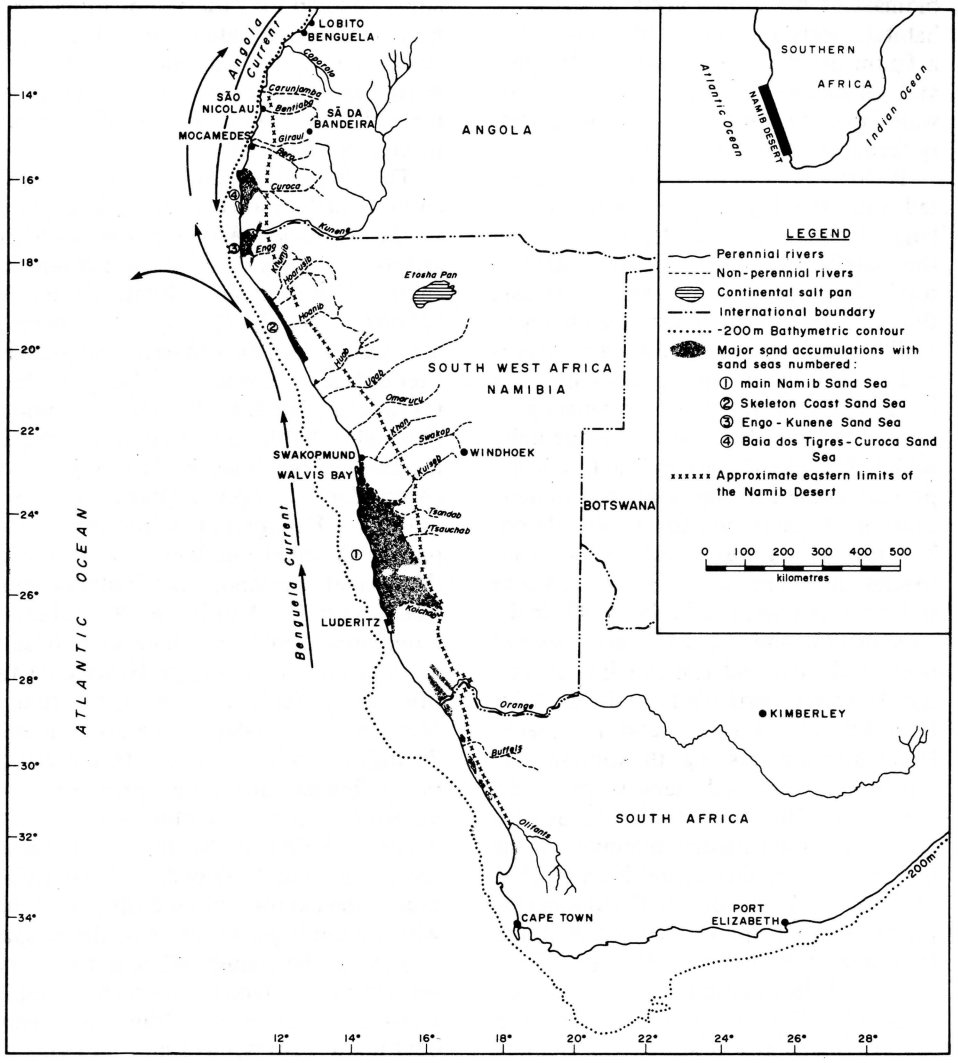

Fig. 1. - The Namib Desert (from Ward *et al.* 1983).

biomass of herbivores living in the same habitat, Seely & Louw (1980) arrived at a figure of 40 $mg.m^{-2}$ during a dry year and 84 $mg.m^{-2}$ during a wet year. Fog-water may be transferred through primary feeders to other trophic levels.

Perhaps even more intimately associated with the fog are the detritivores or large decomposers. In deserts including the Namib, the ratios of surface litter to total above ground biomass far exceed those of temperate forests (Schlesinger, 1977). Because rain almost never occurs and fog is only present for a few hours, if it occurs at all, fungi and bacteria(e.g. le Roux, 1970), which need a perpetually moist environment, are probably not important in the decomposition and mineralization of plant detritus in this desert. The role of organisms such as numerous species of nematodes (Proctor, 1982) or soil mites (Coineau & Seely, 1983) in decomposition and mineralization has not been evaluated and can not be discounted. However, particularly in the dune habitat but also on the sand-free plains, larger invertebrates, e.g. thysanurans and tenebrionids, probably serve as major decomposers. Holm & Scholtz (1980) list 36 species of detritivores/omnivores living in the dunes of the central Namib. They are included in the orders Thysanura (Lepismatidae); Isoptera (Hodotermitidae, Rhinotermitidae); and Coleoptera (Tenebrionidae). In the same habitat Seely and Louw (1980) found 29 $mg.m^{-2}$ of invertebrate omnivores in a dry year and 474 $mg.m^{-2}$ in a wet year.

The importance of larger desert detritivores as decomposers was recently described by Crawford & Taylor (1984) for a Chihuahuan desert environment. They emphasize the temporal and spatial patchiness of plant litter and its variable quality as factors which may detract from the effectiveness of microbial and fungal decomposers. In contrast, the guts of the larger decomposers they studied, particularly a highly abundant nocturnal camel cricket, (Raphidophoridae), provide a warm, moist and nutrient-rich environment for the break-down of detritus throughout the year.

The Namib fauna at the higher trophic levels is little known with the exception of the Solifugae (Wharton, 1981). Other arthropod predators and parasitoids in central Namib dune habitats (Holm & Scholtz, 1980; E. Griffin, pers. comm.) are Aranea (Ammoxonidae, Caponiidae, Ctenizidae, Eresidae, Gnaphosidae, Oxyopidae, Palpimanidae, Philodromidae, Pholicidae, Salticidae, Scytodidae, Eusparassidae, Thomisidae, Zodariidae); Acari (Anystidae); Scorpions (Buthidae, Scorpionidae); Hemiptera (Cydnidae); Neuroptera (Myrmeleontidae); Dectyoptera (Mantidae); Hymenoptera (Bradynobaenidae, Encyrtidae, Mutillidae, Philanthidae, Pompilidae, Scoliidae); Diptera (Asilidae); and Coleoptera (Carabidae, Histeridae). In this habitat Seely & Louw (1980) found 56 $mg.m^{-2}$ of predators in a dry year and 75 $mg.m^{-2}$ in a wet year. On the plains the following arthropod predators are known to occur (E. Griffin, pers. comm.): Araneae, Solifugae, Scorpiones, Pseudoscorpiones and Chilopoda. Of particular note is the extensively used silk-lined tube with camouflaged lid habit of the Eusparassidae in the Namib. While not primary users of fog, the fauna of the higher trophic levels is, nevertheless, ultimately dependent upon fog-water as a moisture source.

Importance of geography of the Namib

The Namib Desert extends some 2000 km from north to south between the Carunjamba River in Mocamedes District, Angola and the Olifants River in the Cape Province, South Africa (Ward *et al.* 1983), and occupies the Namib platform west of

the Great Escarpment. The configuration results in an extensive ecotonal area which contributes greatly to overall species richness of the Namib. Its effects are particularly well known for the vertebrate fauna, although for the lesser known invertebrate fauna it also undoubtedly has an influence. From north to south, four large dune areas (e.g. Ward *et al.* 1983) and many smaller dune patches occur. Where there is no sand cover, a gravel or rocky plain is exposed. Areas of similar substrate may be separated by great expanses of different substrate types. For example, the dunes of the southern/central Namib are separated by more than 300 km from the nearest part of the main northern dune field.

A number of ephemeral rivers and two perennial rivers, the Orange and the Kunene, cut across the Namib Desert from east to west. Headwaters of all these rivers lie inland from the desert. Several of the ephemeral systems, particularly those between the Orange and Kuiseb Rivers, no longer flow into the ocean but are impounded by the dune sea. Namib rivers often separate dune from plain habitats as a result of the predominantly southerly winds and coastal sand source. The winds tend to transport sand northwards and inland, building a sand deposit which eventually is transported into the water courses. When rivers flow, they carry sand to the ocean. New sand dunes may develop on the northern banks of the rivers near their mouths if wind direction and sand availability are complementary (e.g. Rogers, 1973). If not, sand-free plains may extend for a distance along the coast. The result is an alternating array of dunes, plains and rivers producing a mosaic of substrates available to desert animals.

The ephemeral water courses support a riparian woodland which acts as a linear oasis within the desert (Seely *et al.* 1980/81). Many animal and plant species occupying these oases would not otherwise be represented in the desert. The fauna of these dry rivers may also have supplied faunal elements which diversified and expanded into desert dunes and plains habitats.

A number of Namb invertebrates, particularly arachnids and representatives of the detritivore guild, are apterous and substrate specific (e.g. Penrith, 1975, 1977, 1979; Wharton, 1981). By contrast other species may occur in several major Namib habitats, including groups capable of travel between plants or, perhaps, carrion. In the central Namib, where three apterous groups have been relatively well studied, substrate specificity of tenebrionids (Endrödy-Younga, 1978; Penrith, 1977, 1979), solifugids (Wharton, 1981) and thysanura (pers. comm., J. Irish and R.T. Watson) is high. Table 1 identifies the number of species found in each of three major habitats.

In the Adesmiini of the Tenebrionidae, all dune genera of tenebrionids occur in the northern dunes whereas some are not represented in the southern dunes. Endrödy-Younga (1982) attributes this unusual pattern to a northward directed expansion of dune specialist elements. In the past, rivers which now are stopped by the dunes flowed further west (Besler, 1980; Seely & Sandelowsky, 1974), and an even more disrupted mosaic of habitat types occurred. This pattern of disruption and coalescence, the result of dimly understood geographic events permitting selective substrate connections and species exchanges, may have contributed to the contemporary diversity and distribution pattern of many substrate dependent animal groups.

Importance of the age of the Namib

The presence of fog in the Namib, for at least the last 5 million years (Siesser,

Table 1. - Substrate specificity of certain Namib invertebrates (from: Holm & Scholtz, 1980; Wharton, 1981; Wharton & Seely, 1982; J. Irish, R.T. Watson, pers. comm.)

	Dune sand	Riparian forest/ river sand	Gravel/ rocky plains
Tenebrionid beetles			
Adesmiini	8	5	6
Caenocrypticini	5	1	1
Calognathini	1	0	1
Cryptochilini	2	1	0
Drosochrini	0	1	1
Epitagini	0	1	0
Eurychorini	4	3	4
Melanimini	0	1	0
Molurini	2	2	6
Opatrini	2	6	4
Platynotini	0	1	0
Scaurini	1	2	0
Tentyriini	2	4	2
Zophosini	6	2	8
Solifuges			
Daesiidae	2	2	5
Gylippidae	1	0	2
Hexisopodidae	1	0	2
Melanoblossidae	1	0	2
Solpugidae	2	1	2
Thysanura	8	-	12

1980), contributed to the presence of a relatively diverse fauna in this arid environment. Fog may or may not have directly led to speciation among many Namib invertebrates but its presence was a necessary condition for the development and continued existence of at least a part of this fauna. Recent reconsiderations (Ward *et al.* 1983) support Koch's (1962) hypothesis that arid to semi-arid conditions have dominated the history of the Namib since the Cretaceous (± 80 my BP). This contradicts Endrödy-Younga's (1982) claim that dune movement rates identify a Namib antiquity dating < 100,000 yrs. These arid to semi-arid conditions were shared by much of the western half of the southern African continent (van Zinderen Bakker, 1975), with some variation at times. The fauna of the currently hyper-arid Namib is thus probably derived from a fauna living in at least semi-arid conditions for a prolonged interval (Seely, 1978a). When this long period of arid to semi-arid climate is viewed against the variation in the geography of the Namib,

including the dynamic mosaic of substrate types, the diversity and distribution of the invertebrate fauna in an area of such low primary productivity can begin to be understood.

VERTEBRATES

The presence and distribution of vertebrates is also closely linked to substrate. Rain, by producing open water and through its direct effect on primary production, has a major influence on most if not all vertebrates, whereas, fog, directly or indirectly, is less important and plays only a minor role in the lives of certain species that may feed upon fog-using plants or invertebrates. Most of the vertebrate faunas living in the Namib have a wide southern African distribution with many species only entering the desert on its eastern extremities, or temporarily invading during exceptional rainfall periods. Speciation within some groups has been exceptional, particularly those with relatively specialized substrate specificites and ecology. In these groups the relative proportion of endemics is high.

Fish

The two perennial rivers flowing through the Namib Desert have permanent fish populations whereas elsewhere fish occur only in flood water ponds and a few springs, none being endemic. Approximately 12 species of freshwater fish occur in the lower Orange river; many of these, including the endemic *Barbus hospes* (Cyprinidae), enter the Namib section (Cambray, 1984). Although the Kunene river lacks salt incursions or estuary characteristics, a number of marine fish permanently inhabit the mouth (Penrith, 1982).

Amphibians and reptiles

Despite their usual affinities for water, amphibians do live in the Namib Desert in a few selected habitats; two species which live in the winter rainfall area of the desert are independent of free water. In contrast, reptiles are common and conspicuous in most arid areas and the Namib is no exception. The highest proportion of endemic Namib species in any one vertebrate family (25 %) is found in the geckos. Many reptiles are as substrate dependent as the apterous invertebrates, which probably contributes to their overall species richness.

Approximately 15 species of frogs, some of which complete their life cycle without free water, have been recorded from the Namib Desert. Most frogs normally found in the Namib are adapted to rapid development, most in temporary pond situations. Others only become temporarily established in seasonal rivers during years of good rainfall. Tadpole metamorphosis takes place within the egg of two *Breviceps* (Microhylidae), both of which are endemic in the winter rainfall Namib. *Phrynomerus annectens* (Microhylidae) and *Bufo hoeschi* (Bufonidae) are flattened crevice-dwellers which can complete their tadpole stages in 8 and 3 weeks respectively (Channing, 1976). The Brandberg, a large arid mountain totally surrounded by arid gravel plains, has at least 5 species of frogs (van den Elzen, 1983), all dependent on intermittent rainwater pools for rearing tadpoles.

Five species of marine turtles (Cheloniidae and Dermocheylidae) are found along the Namib coast. The Nile Softshelled Turtle, *Trionyx triunguis* (Trionychidae), is also commonly observed in the Kunene river mouth. The Helmeted Terrapin, *Pelomedusa subrufa*, (Pelomedusidae) is sparsely distributed on the edge of the Namib. Six species of tortoises (Testudinidae) are recorded from the

Namib Desert (Greig and Burdett, 1976), mainly in the south. Only one species, *Homopus bergeri*, is nearly endemic. All species seem to prefer rocky or gravel plains substrate. Crocodiles (Crocodylidae) frequent the Kunene River.

Lizards, in general and geckos, in particular, have speciated to a great extent in the Namib (Table 2). Approximately 10 of the 40 species of gecko (Gekkonidae) in the Namib are endemic. Most of the endemic species are of the genera *Pachydactylus* and *Rhoptropus* and are mainly rupicolous (Haacke & Odendaal, 1981). However, three species of barking gecko, *Ptenopus* spp., are commonly found on gravel plains and sand flats (Haacke, 1975a), and *Lygodactylus Lawrencei* is a small, diurnal tree dweller. Of the two endemic web-footed geckos, *Palmatogecko rangei* prefers sandy substrates and *Kaokogecko vanzyli* gravel plains and sand flats (Haacke, 1976). Of approximately 10 species of legless skinks *Typhlosaurus* (Broadley, 1968) and *Typhlacontias* (Scincidae), which inhabit the South West arid zone, at least four are endemic to the Namib Desert. The Lacertidae have undergone considerable speciation in the South West arid zone, but few of the approximately 13 species of these diurnal lizards are endemic to the Namib Desert. Namib endemics include exclusively psammophilous species (Robinson & Cunningham, 1978) as well as some generalists, and those occupying gravel plains and sand flats. The ultra-psammophilous lizard, *Angolosaurus skoogi* (Cordylidae) (Fitzsimmons, 1955; Steyn, 1963), restricted to the dune areas of the northern Namib, is the most notable cordylid in the Namib Desert. The genus *Cordylus* shows considerable radiation in the South West arid zone, where there are 4 endemic and one

Table 2. - Approximate total of species and endemic species of amphibians and reptiles of the Namib.

	Species	Endemics
Frogs	14	2
Turtles and Tortoises	7	1
Lizards		
Geckos	40	10
Skinks	17	4
Lacertids	13	4
Cordylids	13	1
Varanids	2	0
Agamids	5	0
Chameleon	2	0
Amphisbainids	2	0
Snakes		
Vipers	6	2
Typhlops & Leptotyphlops	5	0
Colubrids	24	0
Elapids	5	0

wideranging species (Fitzsimmons, 1943). Several occur occasionally on rocky outcrops in the Namib but are more closely associated with the escarpment to the east. Two Monitor lizards (Varanidae), *Varanus niloticus* and *V. exanthematicus*, occur incidentally in the Namib. The Agamidae are medium-sized conspicuous, diurnal lizards generally associated with rocks, or are ground dwellers. The terrestrial Namaqua Chameleon, *Chamaelo namaquensis* (Chamaelionidae), is well known from all parts of the Namib but is most often associated with barren gravel plains. The Namaqua Dwarf Chameleon, *Bradypodion ventrale*, occurs sympatrically with the Namaqua chameleon in the southern Namib. Amphisbaenidae are poorly represented in the Namib Desert (see Broadley *et al.* 1976; Stewart, 1980a).

In contrast to lizards, snakes are poorly represented and less well known. Approximately 40 species have been recorded from the Namib, the majority of which are more widely distributed in the eastern Namib, escarpment and inland areas (Broadley, 1983). Two species of Typhlopidae and three species of Leptotyphlopidae have been recorded. They usually occur in sandy soils such as river beds, though specimens are also found in rocky areas. About 24 species of the family Colubridae have been recorded from the Namib (Broadley, 1983). Five species of diurnal sand snakes, *Psammophis* spp. the most conspicuous snakes in the Namib, are catholic in their habitat requirements and are the only colubrids regularly encountered in the sand dune areas.

Five species of Elapididae are known from the Namib, only entering the desert marginally. Exceptions are the shield-nose snake, *Aspidelaps scutatus*, and the coral snake, *A. lubricus*, which are know from the Namib Coast (Broadley, 1983), possibly from the eastern Namib via river courses. The only snakes endemic to the Namib Desert are the sand dwelling Namaqua dwarf adder, *Bitis schneideri*, and the Namib dwarf sand adder, *B. peringueyi*, which have evolved a "sidewinding" means of locomotion. *B. peringueyi* occurs in the sand seas from southern Angola to Luderitz, where it is replaced by *B. schneideri* to the south (Broadly, 1983). *B. peringueyi* is one of the few vertebrates known to directly use fog moisture (Louw, 1972; Robinson & Hughes, 1978). Four other adder species occur (Broadley, 1983).

Birds

Birds are a relatively mobile component of the Namib and approximately 220 bird species of 24 orders and 56 families occur in the Namib Desert. This excludes the pelagic procellariiformes, vagrants, and the predominantly inland species which enter the Namib only along the two perennial rivers. Endemic species include Gray's lark, *Ammomanes grayi* (Alaudidae), which occurs throughout the plains desert, the dune lark, *Mirafra erythrochlamys*, which occurs in the central and southern Namib on sandy substrates (Newman, 1983) and Ruppell's korhaan, *Eupodotis rueppellii* (Otidae), found throughout the central and northern Namib associated with stony substrates and gravel plains. Several coastal species occurring in the Namib are closely associated with the Benguela current and are considered "near endemics". The coastal wetlands of the central Namib Desert are extremely important for breeding and migration of many local residents as well as long distance migrants (pers. comm., A.J. Williams).

Mammals

Because of their intrinsic interest, the

mammals of the Namib are relatively well known (Coetzee, 1969; de Graaff, 1981; Smithers, 1983). Their distribution patterns are partially dependent upon substrate types although some species may occur throughout the desert. Many species are associated with the escarpment or eastern plains and only enter the Namib along perennial or ephemeral water courses. Some species may have a wide southern African distribution and enter the Namib only at its southern extremities. Other species, with a wide northern origin, may live in the northern and central Namib hills and plains. The presence of a large dune sea occupying much of the southern Namib, and contrasting topographically with mainly coastal dunes in the north, is a major factor in most distribution patterns.

Rainfall in the Namib may vary greatly, for example 100 fold, between years. Many mammals are able to take advantage of the increased resource base which results, and expand their Namib ranges considerably. For example, after good rains of greater than 100 mm on the plains of the central Namib, gerbils, ground squirrels and bat-eared foxes may become established 50 to 75 km west of their dry period ranges. In the same situation, riverine species can take temporary advantage of the more favourable conditions and expand their ranges onto dunes and plains. Only much further study will reveal the full extent of the plasticity of the distribution patterns of Namib mammals.

Shrews (Soricidae) are not a typical part of the Namib fauna although one common and three other species have been recorded. The hedgehog, *Erinaceus frontalis* (Erinaceidae), the pangolin, *Manis temminckii* (Manidae) (Stuart, 1980b), and baboons, *Papio ursinus* (Cercopitheridae), live in the escarpment and penetrate into the Namib via river courses. Vervet monkeys, *Cercopithecus pygerythrus*, live along the two perennial rivers only.

Three species of golden mole (Chrysochloridae) live in the Namib Desert, and are the only insectivores in sand dunes. The 3 species of elephant shrews (Macroscelididae), on the other hand, are usually associated with rocky areas or plains and for the most part are diurnal.

Approximately 20 species of bats have been recorded from the Namib Desert and another 5 or so species probably occur. *Laephotis namibensis* (Vespertilionidae), a rare species and the only Namib near-endemic, seems to be associated with riverine habitats in the central Namib and adjoining escarpment.

The Cape hare, *Lepus capensis* (Leporidae), is relatively common throughout the entire Namib and two species of red rock hares, *Pronolagus randensis* and *P. rupestris*, and the scrub hare, *Lepus saxatalis*, also occur. The Namaqua dune molerat, *Bathyergus janetta* (Bathyergidae), occurs in the southern coastal dune areas only, whereas the common molerat, *Cryptomys hottentotus*, penetrates the southern and northern sections (de Graaf, 1981). River beds and rocky outcrops are favoured by porcupines, *Hystrix afraeaustralis* (Hystricidae), which have been reported from the entire Namib. Loose soils of the eastern Namib provide springhares, *Pedetes capensis* (Pedetidae), with suitable burrrowing sites. The common ground squirrel, *Xerus inaurus* (Sciuridae), the Kaokoland ground squirrel, *X. princeps*, and the striped tree squirrel, *Funisciurus congicus*, live in the eastern Namib and escarpment. Dassie rats, *Petromus typicus* (Petromuridae), are one of the most conspicuous diurnal rodents restricted to rocky outcrops and inselbergs throughout the Namib (Coetzee, 1969).

Approximately 20 species of the families Muridae, Cricetidae and Gliridae have

been recorded. Most are species with wider inland distributions and may only enter the desert incidentally or during periods of high rainfall; some species are restricted to river courses, whereas others are restricted to rocky areas. Three species of Otomyinae are known from the Namib. Two of the six species of the subfamily Gerbillinae are endemic to the Namib. *Gerbillurus tytonis* is restricted to the sand seas of the southern and central Namib and *G. setzeri* to the gravel plains and river courses of the central and northen Namib. The pygmy gerbil, *G. paeba*, and the short tailed gerbil, *Desmodillus auriculairs*, occur throughout the Namib, and the bushveld gerbil, *Tatera leucogaster*, and *Gerbillurus vallinus* inhabit the pro-Namib and water courses.

Off the Namib coast approximately 40 species of cetaceans can be expected to occur. Approximately 22 carnivore species have been recorded from the Namib. Several are restricted to the perennial rivers and do not regularly enter the Namib section. Species which occur throughout the Namib and in all habitats are the honey badger, *Mellivora capensis*, the striped polecat, *Ictonyx striatus* (Mustalidae), the Cape wild cat, *Felis lybica* (Felidae), and the black-backed jackal, *Canis mesomelas* (Canidae). Others associate with the pro-Namib and escarpment but enter the desert via river beds: the caracal, *Felis caracal*, and the small spotted genet, *Genetta genetta*. After good rains the bat-eared fox, *Otocyon megalotis*, aardwolf, *Proteles cristatus* (Hyaenidae), cheetah, *Acinonyx jubatus*, cape fox, *Vulpes chama*, and the yellow mongoose, *Cynictis penicillata*, move into the Namib. The coastal Namib hosts suricates, *Suricata suricatta*, and lions, *Panthera leo*. The brown hyaena, *Hyaena brunnea*, is widely distributed in the Namib and is relatively common on the beach whereas the spotted hyaena, *Crocuta crocuta*, prefers the plains and river beds of the central and northen Namib. Leopard, *Felis pardalis, Galarella pulverulenta*, the small grey mongoose, and *G. sanguinea*, the slender mongoose occur wherever there is suitably dense vegetation or extensive rocky areas. Most carnivores avoid the high sand dunes.

Antbears, *Orycteropus afer* (Orycteropidae), are found throughout when conditions are favourable. Two species of rock dassies, *Procavia capensis* and *P. welwitschia* (Procavidae) occur in the Namib.

A number of larger mammals occur in the Namib, restricted to their appropriate habitat types. Elephant, *Loxodonta africana* (Elephantidae), giraffe, *Giraffa camelopardalis* (Giraffidae) (Viljoen, 1982), and black rhino, *Diceros bicornis* (Rhinocerotidae) (Joubert, 1971), are found only in the northern Namib typically associated with the river courses, pro-Namib or arid gravel plains. Burchells zebra, *Equus bruchelli*, may occur in the north incidentally whereas the mountain zebra, *Equus zebra hartmannae* occurs throughout. The warthog, *Phacochoerus aethiopicus* (Suidae), regularly moves down central and northern Namib rivers and has become established at some river mouths (pers. comm., R. Loutit), Hippopotamus, *Hippopotamus amphibius* (Hippopotamidae), previously occurred in the two perennial rivers. It is now considered extinct (Skead, 1980; Viljoen, 1982), the demise of the Kunene populations taking place within the last 10 years.

Approximately 14 species of ungulates occur in the Namib. Most are species that enter the desert only incidentally, but some such as the gemsbok, *Oryx gazella*, and the springbok, *Antidorcas marsupialis* (Bovidae), are cosmopolitan. Steenbok, *Raphicerus campestris*, have permanent populations in all the major Namib rivers. The klipspringer, *Oreotragus oreotragus*,

Table 3. - Approximate total species and endemic species of vertebrates in the Namib.

	Species	Endemics
Fish	12+	0
Amphibians & Reptiles	147	24
Birds	220	3
Mammals	150	5

occurs along the escarpment and is found irregularly throughout the Namib on mountain ranges, isolated inselbergs and in canyons.

Combining all vertebrate groups, approximately 529 species of which 32 are endemic to the area, occur in or very near the Namib Desert (Table 3). For invertebrates and vertebrates alike, the long narrow shape of the desert with alternating, distinctly different substrates has a major impact upon distribution patterns. In a similar manner, the transition from summer rainfall in the north to winter rainfall southwards and from a cool, foggy coast to a warm, dry savanna inland, influences presence, abundance and distribution of species. Thus an understanding of present dry conditions, superimposed on the long climatic history of the Namib and its attendant geomorphological changes, is an important component of our interpretation of the biota of this diverse desert.

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