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The Namib Dune Desert: an unusual ecosystem

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Namib Desert dunes of coastal southwestern Africa support a fauna including species adapted to a life committed exclusively to vegetationless dune crests and slipfaces. Fog and wind-blown plant detritus constitute a trophic base for this fauna, composed predominantly of tenebrionid beetles, arachnids and reptiles. Occurrence and characteristics of this fauna may be explained by the simultaneous presence of: (a) a cool, coastal climate in the dune areas; (b) extensive dune masses; (c) a rich, arid-adapted fauna over the western half of southern Africa including the Namib during the Quaternary.

Introduction

The vegetationless dune crests and slipfaces (Plate 1) of the Namib Desert of coastal southwestern Africa (Fig. 1) support a diverse, endemic fauna. Tenebrionid beetles are a major component of this fauna (Koch, 1960, 1961, 1962, Plate 2); reptiles (Mertens, 1955) and arachnids (Lawrence, 1969, 1972; Lamoral, 1972) are also well represented. No counterpart to this vegetationless-dune fauna is found in any other desert dunes of the world (Koch, 1960, 1961, 1962, Table 1). The only structurally comparable ecosystems are other detritus based systems such as occur on the highest mountains (Mani, 1968) or in the ocean abyss

Table 1. *Occurrence of endemic fauna (Coleoptera: Tenebrionidae) in Eastern Hemisphere deserts*

	All habitats		Vegetationless-dune habitats	
	Genera	Species	Genera	Species
Sahara	3	63	0	0
Somalia	—	—	0	0
Namib	35	±200	7	17[1]
Malagasi	—	—	0	0
Gobi	—	—	0	0
Australia	—	—	0	0

Modified from Koch (1962).

[1] Adesmiini: *Onymacris bicolor, O. unguicularis*; Eurychorini: *Lepidochora discoidalis, L. eberlanzi, L. kahani, L. nocturna, L. pilosa*; Zophosisi: *Anisosis caudata, Cardiosis eremitra, C. fairmairei, C. triangulifera, Cerosis hereroensis, Tarsosis damarensis*; Caenocrypticini: *Vernayella delabati, V. ephialtes, V. noctivaga, V. pauliani.*

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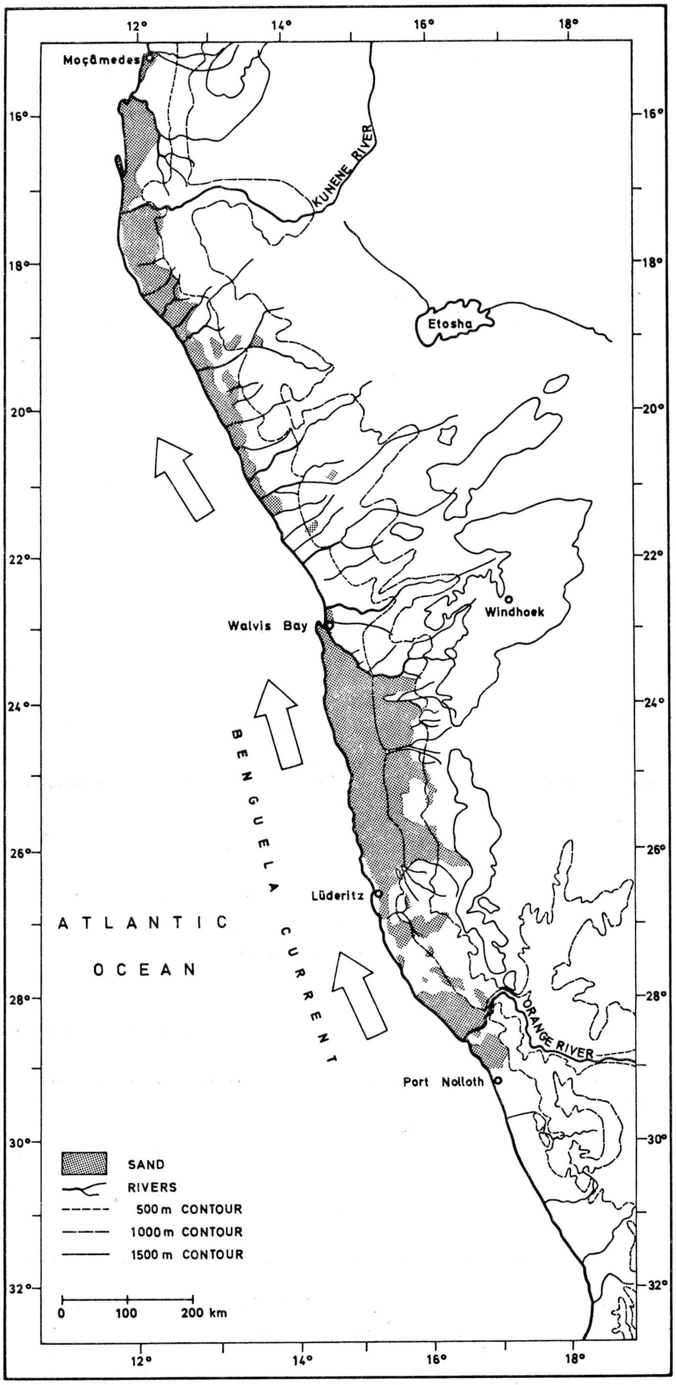

Figure 1. The Namib Desert of southwestern Africa parallels the coast and the Benguela Current.

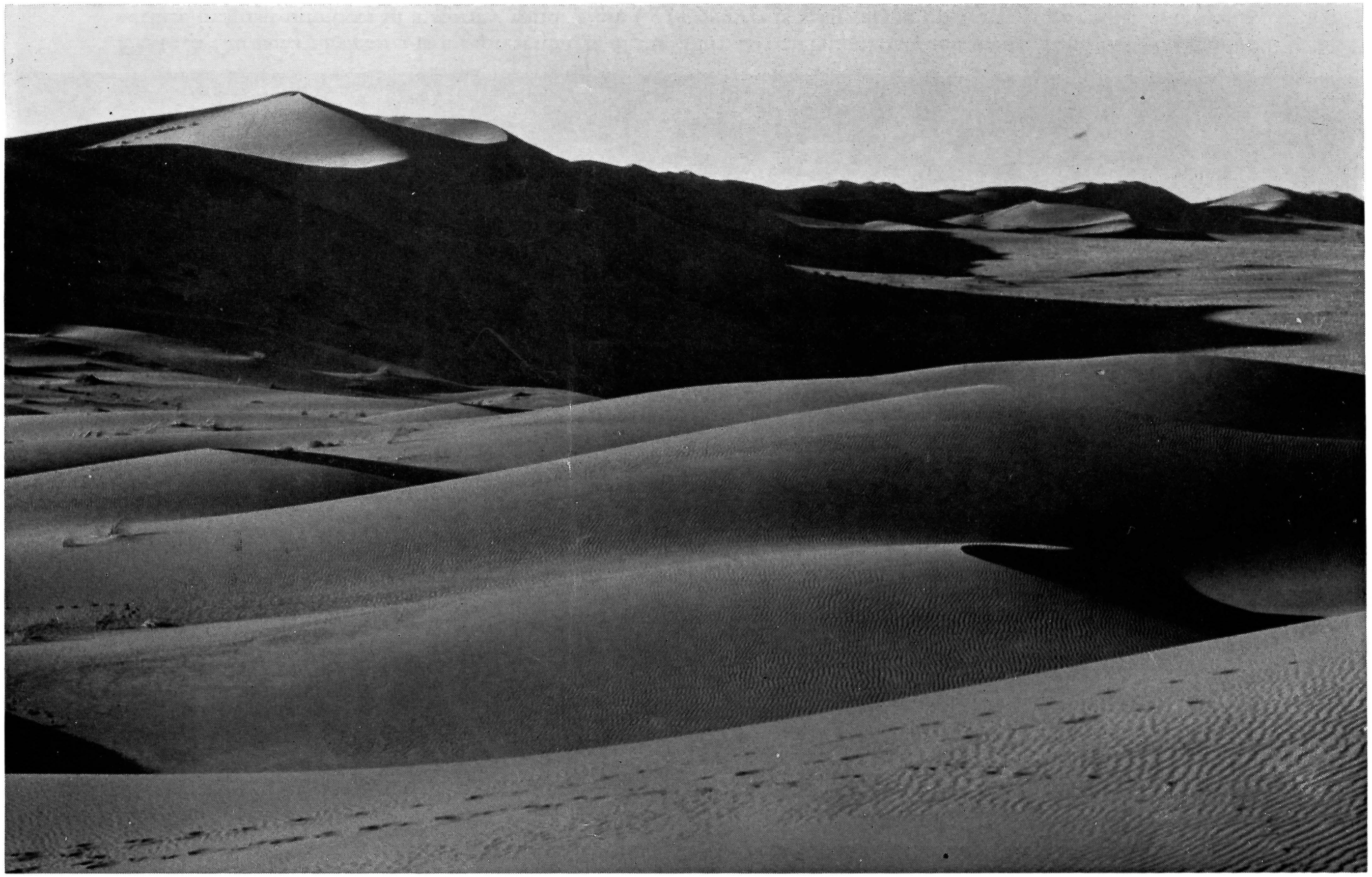

Plate 1. The vegetationless dune crests and slipfaces support a fauna independent of the slight vegetation cover of the dune base.

[*facing page 118*]

Plate 2. *Cardiosis fairmairei* is a representative of the diurnal, vegetationless dune fauna. It occurs on the sand surface in great numbers in a stormy wind. Here *C. fairmairei* is seen taking up water from moist dune sand.

[facing page 119]

(Koch, 1960). Here I will re-examine this fauna and, in the light of recent observations, re-evaluate explanations for its occurrence.

Four features of the fauna of the vegetationless dunes require explanation:

(a) What conditions have enabled a diverse fauna to evolve in this desert while no comparable fauna has developed in other vegetationless desert dune ecosystems ?

(b) What accounts for the peculiar distribution of the tenebrionid beetles of the vegetationless dunes within the Namib Desert ? The two large main dune masses are today separated by 200 km of rocky, dune-free desert, making it impossible for the flightless, substrate specific, dune species to cross the area. Despite this separation, a minimum of three tenebrionid species occur in both dune masses and at least two other endemic genera are represented by different species in the two dune areas (Table 2). Several genera have radiated into a number of sympatric species within both dune masses (Koch, 1962), a phenomenon which also requires explanation.

Table 2. *Species occupying the vegetationless dunes of the northern and southern Namib and genera with representatives in both vegetationless dune areas*

Onymacris unguicularis	*Cardiosis* sp.
Vernayella noctivaga	*Lepidochora* sp.
Tarsosis damarensis	*Onymacris* sp.
	Tarsosis sp.
	Vernayella sp.

Modified from Koch (1962).

(c) What accounts for the high degree of faunal endemism in the vegetationless and vegetated dunes ?

(d) What is the significance of the high degree of relatedness of the Namib fauna and flora, including the fauna of the vegetationless dunes, to that of arid northeastern Africa ? The disjunct distribution of related elements of the biota of the two arid regions includes tenebrionid beetles (Koch, 1962), other invertebrates (Connelly, 1931; Carcasson, 1964), mammals (Meester, 1965), birds (Moreau, 1966; Winterbottom, 1967) and plants (Volk, 1964; de Winter, 1966, 1971; Verdecourt, 1969).

Various hypotheses have been proposed to explain these features of the Namib biota. All centre around the 'great age' of the Namib (Koch, 1960, 1961, 1962) and the previous existence of an extensive arid area over much of Africa or at least a 'corridor' connecting the southwest and northeast arid zones (e.g. Balinsky, 1962). But alternative hypotheses may be supportable and are considered here. The coastal climate and its proximity to a large dune mass is a combination not found elsewhere and may have provided favourable conditions for the evolution of faunal elements with the specific characteristics of the distinctive Namib fauna. The relationship of climate and space to the tenebrionid beetle fauna is considered below.

Age of the Namib

Desertic Namib conditions are caused by the combined effects of the South Atlantic anticyclone, the cold Benguela Current, the upwelling of cold South Atlantic Central Water and the divergence of the South East Trades along the coast (van Zinderen Bakker, 1975, 1976). These conditions would have developed by Early Oligocene times, although the cold circum-Antarctic current developed only in the Early Miocene. During the Pleistocene the northern and southern boundaries of the climatic zones may have shifted, but desertic conditions prevailed constantly in the central core of the desert (van Zinderen Bakker, 1975). Tankard & Rogers (in press) stress the progressive development of aridity, which began in the late Tertiary but was only fully established in the Quaternary. They agree with van Zinderen Bakker (1975) that the effect of Quaternary global climatic conditions was to shift these climatic belts rather than eliminating them. The cold offshore Benguela Current is one of the major controlling factors of the extreme aridity in the Namib Desert. Thus initiation of major cooling and upwelling would have initiated the aridification of the Namib Desert. This development has recently been ascribed to early Late Miocene times (Siesser, in press). These three recent studies directed toward evaluating the age of the Namib Desert (Siesser, in press; Tankard & Rogers, in press; van Zinderen Bakker, 1975) broadly agree that initiation of desert conditions occurred in the late Tertiary. Yet while van Zinderen Bakker (1975) and Tankard and Rogers (in press) agree that arid conditions were developing in the Namib from the late Tertiary, van Zinderen Bakker (1975) concludes that the desert is of great age while Tankard and Rogers (in press) say that aridity was established relatively recently. Relative age appears to depend upon one's frame of reference. Hence to invoke the age of the Namib Desert as an explanation for the unique Namib biota, the age must be stated relative to that of other deserts.

The Sahara and Namib–Kalahari have never experienced truly humid conditions throughout most of geological history, although the boundaries have varied with time (Butzer, 1967). In northern Africa, the Libyan portion of the Sahara has been a desert since mid-Tertiary times (Mechelein, 1959) while the western Sahara supported Mediterranean scrub and dry woodland periodically during the Pleistocene (Moreau, 1966). Somalia Desert climate was never more mesic than semi-arid during the Pleistocene (Clark, 1954) although Azzaroli (1957, in Koch, 1962) attributes a 'recent' age to the Somalian dunes. Portions of the Asian deserts have a long history of aridity (Petrov, 1966, 1967). Development of aridity in Australia has paralleled that in the Namib Desert (Bowler, 1976). In South America evidence for aridity exists from the Pliocene, although the boundaries of these arid areas doubtlessly varied through the Quaternary (Solbrig, 1976), and paleobotanical analyses in North America indicate a comparable age for the Sonoran Desert (Axelrod, 1948). Thus tentatively we can conclude that the Namib Desert is no older than most other deserts and younger than some for which information is available.

Although the aridity of the Namib Desert may have existed throughout the Quaternary, we have no indication of the age of the dunes themselves. Selby, Hendy & Seely (in press) provide a minimum date of 210,000 years, for a lake deposit located on lightly cemented sandstone (Ollier, pers. comm.) within the present Namib dune field. No mesic conditions have existed since that date and the lake does not imply mesic conditions 210,000 years ago since the lake was small and may have formed from a single storm no more extensive than those which sometimes occur in the recent Namib Desert. I assume that development of the dune system paralleled that of aridity in the Namib, although the extent of the dune field may have changed considerably since then.

Arid conditions have not been limited to the Namib but prevailed across the western half of southern Africa (van Zinderen Bakker, 1975). Thus the Namib dunes throughout this duration have been exposed to a rich, arid-adapted tenebrionid fauna from which the present dune fauna is derived (Koch, 1962). This relationship undoubtedly influenced the character of the evolving Namib fauna, but it cannot be a complete explanation for its occurrence and character since the other African deserts, especially the Kalahari but also the Somalia and Saharan deserts, were also exposed to representatives of the same source groups. Additional factors must also have permitted and oriented the evolution of these groups in the Namib.

Present climate

The climate of the central Namib Desert (Table 3) is characterized by a low average temperature, high humidity, low rainfall and the presence of fog (Logan, 1960; Schulze, 1969; Besler, 1972; Seely & Stuart, 1976). Temperature increases and humidity decreases with distance from the coast (Logan, 1960; Besler, 1972). Within the coastal belt, moisture is supplied most commonly in the form of fog, inland most commonly as rainfall. Rain

Table 3. *Climatic characteristics of the Central Namib Desert*

km from coast	Avg max (°C)	Avg min (°C)	Avg relative humidity (%)	Avg daily amplitude (°C)	Pptn rain (mm)	Pptn fog (mm)	Fog (no. of days year^{-1})
2	18·6	12·9	85·4	5·7	13	38	81
22	25·2	11·1	65·5	14·0	10	67	75
33	28·2	10·9	57·9	17·2	7	161	88
56	30·0	11·8	51·0	19·3	16	29	37
110	28·5	15·3	41·9	13·3	64	—	5

H. Besler (1972). Desert Ecological Research Unit (original data).

distribution exhibits an east to west gradient opposite to that of fog. Consequently, the driest portion of the desert occurs where these two moisture régimes are decreasing and overlap (Besler, 1972). Although the coast receives less precipitation to that of a few kilometres inland, it experiences the higher humidity and lower evaporation associated with the more frequent occurrence of a low stratus cloud cover (Anon., 1944). Where this low stratus layer meets the ground several kilometres inland from the coast the greatest fog condensation in the Namib occurs (DERU, orig. data). Thus over the Central Namib Desert a mosaic of climatic régimes prevail (Fig. 2). These characteristics probably persisted through the climatic oscillations of the Quaternary while varying in magnitude and spatial distribution.

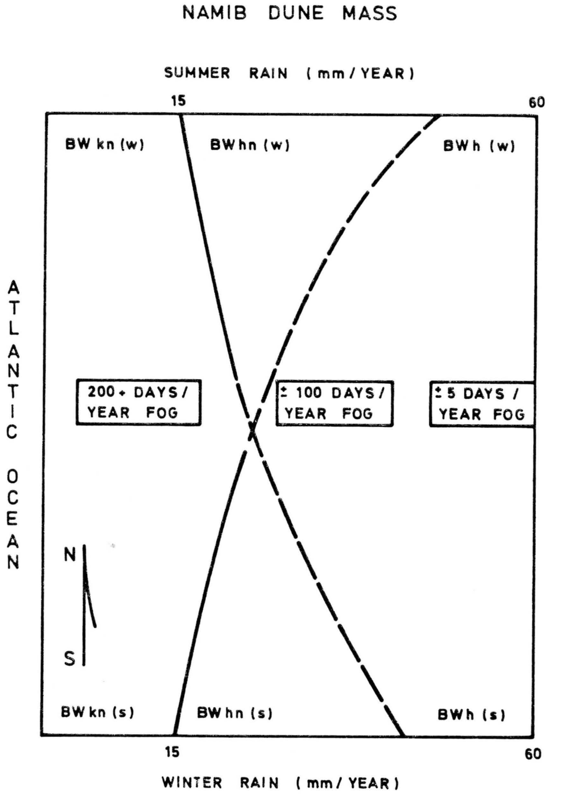

Figure 2. This diagram represents the climatic gradient existing over the southern Namib dune area.

Summer rainfall is greater towards the north and east whereas winter rainfall occurs towards the south. In the Central Namib, including the major portion of the southern dune mass, rain may occur during any month of the year but is most common from January to March (Schulze, 1969; Seely & Stuart, 1976). Because of the irregular nature of the convective rain, precipitation at any location may vary more than 100-fold between years. Rainfall events of approximately 20 mm allow germination of an ephemeral vegetation (Seely, in press). Storms of this magnitude or greater have occurred during five of the eight years records have been kept on the eastern edge of the Namib 110 km from the coast and once in 14 years 56 km inland (DERU, orig. data). Because spatially and temporally irregular rainfall increases with distance from the coast, vegetation, predominantly grasses, on the lower dune slopes and interdune valleys increases in occurrence and extent from the coast inland. When this ephemeral vegetation dries and disintegrates it is distributed by wind throughout the dune mass along with seeds and dead fragments from the sparse perennial vegetation. Some of this material enters the high dunes as detritus where it may last for several years, alternatively being covered and redistributed by the wind. Irregular rainfall thus provides a regular, long lasting energy source in the form of plant detritus, which is consumed by the fauna of the vegetationless dunes (Brink, 1956; Koch, 1961, 1962; Louw & Hamilton, 1972).

In contrast, it is the comparatively regular advective fog (Schulze, 1969; Seely & Stuart, 1976; Nieman *et al.*, in press) that provides the free water consumed by the fauna of the vegetationless dunes. Tenebrionid beetles (Hamilton & Seely, 1976; Seely & Hamilton, 1976) and reptiles (Louw, 1972; Robinson & Hughes, in press) use this source of free water. Water, a common limiting factor in desert ecosystems (Noy-Meir, 1973), is thus provided in the central Namib both by irregular rains and more frequent fogs. This climate, characterized particularly by the occurrence of advective fog and irregular rains, appears to be a permissive factor to the evolution of a fauna in the vegetationless Namib dunes.

Extent of the Namib dunes

The Namib has been broadly sub-divided into various zoogeographic zones including southern, central and northern Namib regions (Koch, 1962), and is further divided by Penrith (1977) to finer sub-divisions. Any zoogeographic sub-division of the Namib is arbitrary and oriented to a particular phyletic group. The Namib has received faunal components from various sources, and a source-oriented analysis is possible. However, the only strong substrate determined partitioning possible is by major substrate type, that is, to gravel plains, rivers and dunes (Koch, 1961) and to the major geographic separation of southern and northern dune masses. Hence in further analysis I emphasize these separations, which are particularly relevant to the flightless tenebrionids and less so to some other taxa.

Transitions between these Namib substrates are sharp even in the absence of major geographic separation such as occurs between the northern and southern Namib dunes. The dune sands of the Namib move northwards, ending at intermittent rivers crossing the desert from east to west. The major rivers (such as the Kuiseb, Swakop, Cunene and Curoca) arrest the northward march of sand, establishing habitat disjunctions and barriers to faunal movement (Koch, 1961).

Today the largest sand dune mass of the Namib Desert extends along the coast from Lüderitz (26°38′ S) to Walvis Bay (22°53′ S), its inland border varying between 50 and 140 km from the coast. Several rocky mountainous areas project through the dune mass and there is an occasional area of bare gravel plain. These disruptions comprise less than 10 per cent of the surrounding dune area. In addition, several rivers flow into but not through these dunes. This major dune area of the Namib between the Koichab and Kuiseb rivers consists of about 34,000 km^2 (Barnard, 1973) of contiguous, lightly vegetated and vegetationless dunes. To the north between 20°53′ S and 15°48′ S lies a second smaller dune mass.

Woody vegetation or other shelter for permanently resident birds and mammals is almost completely lacking from most of this dune area. Only at times of higher rainfall do perennial plants germinate and persist for several years, affording temporary shelter. At such times jackals (*Canis mesomelas*), bustards (*Neotis ludwigii*) and crows (*Corvus albus*) extend into these dunes to prey upon the greatly expanded populations of conspicuous, diurnal tenebrionid beetles. During the more enduring arid times these predators are lacking altogether from most dune areas and are present only in more persistent habitats at the dune periphery. Permanent resident dune predators consist predominantly of arachnids, reptiles and a mole (*Eremitalpa granti namibensis*), none of which prey upon the adult forms of the diurnal tenebrionids. The mole is largely limited to the more vegetated habitats and is lacking altogether from the coastwise dunes supporting little vegetation at any time.

The diurnal tenebrionids of the vegetationless dunes are relatively long lived, have a relatively low reproductive rate and possess no known morphological or poison defences. They are particularly conspicuous, when observed against the vegetationless red sand, especially the diurnal black and black and white species. Surface activity is strongly tied to surface climatic conditions. The number of individuals foraging on the surface depends upon the strength of the wind carrying detritus. Location of foraging is determined by the wind direction relative to the orientation of the slipfaces where detritus accumulates.

Sand surface temperatures further constrain the activity period (Hamilton, 1971, 1973; Holm & Edney, 1973). These diurnal species may also be found on the surface during the night or early morning, at otherwise unsuitable temperatures, in the course of fog water acquisition behaviour (Hamilton & Seely, 1976). Lack of strong predation pressure has probably been a factor enabling the evolution of these life-history characteristics, which include sluggish surface activity at low body temperatures. The characters expressed are the opposite of those resulting from predation pressure, e.g. defence via poison, morphology, crypsis and/or submergent behaviour (Maiorana, 1976). Thus lack of woody vegetation excludes large, opportunistic predators from permanent residence in the dune core and has been a possible permissive factor to the evolution of the conspicuous diurnal elements of the vegetationless-dune tenebrionid fauna.

Climatic oscillations during the Quaternary (van Zinderen Bakker, 1975) produced a diversity of physiognomic features within the major dune mass. Rivers at one time flowed across the present dune field (Seely & Sandelowsky, 1974) and what is now a continuous dune mass may once have been broken into several smaller dune areas. For substrate confined, flightless tenebrionids, these represent partial or complete barriers, perhaps sufficient to allow speciation. Morphological adaptations of contemporary Namib Desert tenebrionids, especially hypertrophied tarsal claws (Koch, 1961), enhance fit of morphology to the sandy substrate. The Namib Desert is characterized by sharp climatic gradients, so that in the space of 50 km macroclimate ranges from cool coastal conditions to a hot desert (Fig. 3). Quaternary climatic gradients were probably similar to those of today (Fig. 2) and would have been superimposed upon the more disjunct dunes. The sharp climatic gradient would have allowed diverse environments to persist, so that macroclimatic changes would have induced relatively small spatial shifts in specific climatic conditions rather than eliminating emerging forms highly adapted to specific climatic conditions.

Thus while the rich, arid-adapted Tertiary fauna may have provided the basic forms which adapted to the vegetationless dunes, the Quaternary provided conditions favouring the allopatric multiplication of species and their subsequent meeting to provide the species-rich contemporary fauna of these vegetationless dune and other Namib dune environments.

Discussion

To explain the unusual feature of the vegetationless-dune fauna, we must compare the Namib with other deserts. Despite much discussion of the extreme age of the Namib (Koch, 1960, 1961, 1962) recent evidence (Siesser, in press; Tankard & Rogers, in press; van

Figure 3. The steep climatic gradient of the coastal Namib Desert is seen here for mean maximum January temperatures in degrees centigrade. Mean daily temperature shows a similar steep gradient. After Jackson (1961).

Table 4. *Comparison of world deserts: age, climate, dune area*

Deserts (6)	Quaternary age or older	Cool, coastal climate	Extensive vegetation-less dunes
Sahara	+ (7)	− (8)	+ (6)
Somali-Chalbi	+ (5)	+ (8)	− (6)
Namib	+ (11)	+ (8)	+ (6)
Kalahari	+ (4)	− (8)	− (6)
Turkestan Desert		− (8)	+ (6)
Takla-Makan	+ (9)	− (8)	+ (9)
Gobi	+ (9)	− (8)	+ (9)
Iranian Desert		− (8)	− (6)
Thar		− (8)	− (6)
Arabian Desert		− (8)	+ (6)
North American Deserts	+ (1)	+ (8)	− (6)
Peruvian Desert	+ (10)	+ (8)	− (6)
Atacama Desert	+ (10)	+ (8)	− (6)
Monte	+ (10)	− (8)	− (6)
Patagonian	+ (10)	− (8)	− (6)
Australian Desert	+ (3)	− (8)	− (2)

Sources: (1) Axelrod (1948). (2) Beard (1976). (3) Bowler (1976). (4) Butzer (1966). (5) Clark (1954). (6) McGinnies (1968). (7) Mechelein (1959). (8) Meigs (1966). (9) Petrov (1966, 1967). (10) Solbrig (1976), (11) van Zinderen Bakker (1976).

Zinderen Bakker, 1975, 1976) suggests that the Namib has existed as a desert only since the late Tertiary, no longer than most other deserts (Table 4). Thus extreme age as a single causative factor of the unusual vegetationless-dune fauna appears to be an unviable hypothesis. Since the late Tertiary, arid conditions have affected not only the Namib but also the western part of southern Africa (van Zinderen Bakker, 1975). The rich, arid-adapted fauna of this extensive arid region contributed significantly to the present dune fauna (Koch, 1962). Similar arid conditions also prevailed in other African and Asian deserts. Thus proximity to extensive adjacent arid zones is also an inadequate sole explanation for the Namib vegetationless-dune fauna. Several other deserts share a cool, coastal climate (Meigs, 1966; Table 4). Some of these deserts are also of a similar age so that neither climate nor climate plus age are adequate explanations either. An extensive vegetationless-dune mass is also common to other deserts (Table 4) but not to any of those with a cool, coastal climate. The Namib is thus unique only in the combination of characteristics which include the coincidence of a cool, coastal climate and a large dune mass.

Given the evidence the special features of the Namib fauna originally identified can be re-examined. Conditions permitting the initial evolution of the Namib dune tenebrionid fauna included the occurrence of a large dune mass formed from sands transported seaward by rivers draining the entire southwestern side of Africa. These dunes formed next to an extensive arid zone which was inhabited by arid-adapted tenebrionids including many sand-dwelling forms. These forms contributed a stem stock some time during late Tertiary times. Oscillation in climatic conditions during the Quaternary shifted the location of climatic zones but did not obliterate the desertic core (van Zinderen Bakker, 1975, 1976). In the core of the Central Namib dunes the steepness of the climatic gradient involved relatively short spatial changes in the location of specific climatic conditions. Thus species adapting or adapted to specific climatic conditions could persist in the face of extensive climatic changes. We see a lesser manifestation of this process in present-day climatic fluctuations. During the past decade the distribution of various species has shifted east and west across the Central Namib from year to year with changes in rainfall and vegetation. Similar shifts, perhaps more extensive, would have been likely in response to climatic shifts in the past. Climatic fluctuations during this period also influenced global sea levels. A lower sea level could have established a coastal sand corridor permitting exchange of sand committed faunal elements between the southern and northern Namib.

Endemism of the vegetationless-dune fauna (Koch, 1962) and other components of the Namib dune tenebrionid fauna is related to the richness of the parent fauna and to subsequent radiation in response to the diverse conditions prevailing in the Namib and isolating barriers established in the course of physiognomic perturbations induced by the geological consequences of Quaternary climatic fluctuations. The high degree of relationship of the Namib arid-adapted fauna to that of northeast Africa (e.g. Balinsky, 1962) is best explained by the existence of an extensive arid area or at least a connecting arid corridor between these areas.

No single condition is in itself adequate to explain the unique character of the Namib vegetationless-dune fauna. But there is a unique *combination* of characteristics which have influenced the pattern and possibility of adaptation here. Long-term proximity to a rich arid-adapted fauna provided potential lines for adaptation. The strong climatic gradient across the Namib would have existed even in the face of strong climatic changes, and the persisting desertic core would include a diversity of geological and biological substrates. The large sand mass allowed arid-adapted, sand-committed insects to persist on substrates to which they may have adapted in spite of modest spatial changes in the location of their special environments. It is thus proposed that the distinctive features of the Namib dune fauna and especially the evolution of the vegetationless-dune tenebrionid fauna may be explained by an interacting combination of three factors which do not occur simultaneously in any other dune desert of the world (Table 4). Exposure through the Quaternary of the Namib dune habitat to a large contiguous area devoid of woody vegetation reduced predation pressure in the vegetationless-dune environment, thus permitting emphasis during faunal evolution upon conspicuous diurnal forms adapted to optimizing relationships to the substrate and to climate rather than to predator avoidance.

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