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Ecological comments on some gekkonid lizards of the Namib Desert, South West Africa

by

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The Hebrew University of Jerusalem,
Jerusalem, Israel

ABSTRACT

Geckos were observed and collected around Gobabeb, the Namib Desert Research Station, during 5—10 August, 1971. Some specimens were taken alive to Jerusalem, Israel, for studies of pupillary responses and reproduction. *Lygodactylus capensis* is recorded for the area. *Rhopetropus afer* was the commonest reptile; it and *R. bradfieldi* are diurnal and their vertical pupils are remarkably insensitive to light. Pupils of *Pachydactylus laevis* and *P. punctatus ammonoides* are more, and of *Palmitogecko rangeli* most light-sensitive. *Ptenopus garrulus* was heard but not seen.

In captivity *Pachydactylus laevis* lay loose eggs measuring ca. 19 × 15 × 13 mm. Incubation lasts ca. 60 days at 29—30°C. Hatchlings measure ca. 63 mm (total).

These observations are discussed in comparison with available data on gecko biology elsewhere.

1 INTRODUCTION

Having taken a continued interest in deserticolous gekkonid lizards in Southwestern Asia (Werner, 1968, 1973) and having briefly observed them in the Sonoran desert of North America (Werner, 1972) and the Gibson desert in Western Australia (Werner, in Ms), I sought an opportunity for comparative observation in South Africa.

Thus, when my family and I were to return from a year in Western Australia to Israel, I directed our route through Gobabeb, the Namib Desert Research Station. Our party included my wife Nirit, our children Uri (6) and Sharon (4), all versed in the detection and capture of lizards; and, for part of the time, Mr. H. Finkelday of Windhoek, who kindly volunteered to introduce me to the local herpetofauna.

The visit to Gobabeb, 5—10 August 1971, was so brief that, despite the helpful cooperation of Mr. Finkelday, the station staff and the family, I could make only fragmentary observations on some of the local geckos. Nevertheless, the following presentation may add a little to previous records of gecko life in the Namib (quoted below). The more so, since the permission I received to take certain animals with me, enabled me to extend the observations on two points: the response of the eye's pupil to illumination, in gecko species possessing different habits of diurnality or nocturnality; and reproduction of *Pachydactylus laevis* in captivity.

2 TECHNICALITIES AND METHODS

The Namib Desert Research Station (P.O. Box 953, Walvis Bay, S.W.A.) is administered by the Desert Ecology Research Unit (supported by the S.A. Council for Scientific and Industrial Research). The station comprises a weather station, laboratory, library and several convenient, permanent, family bungalows for resident staff and visiting scientists. Transport facilities at the time included a light "dune buggy" Volkswagen that was useful on the dunes and a Landrover used over other surfaces and for longer excursions. My license to collect and export specified reptiles was issued by the Department of Nature Conservation and Tourism (Private Bag 13186, Windhoek). Only of one species, *Rhopetropus afer*,...
was a considerable excess of animals caught, examined and released.

Most collecting was done at about a 5 km distance from the station, in all directions, because on the one hand removal of animals was prohibited within this radius from the station, and on the other hand the unavailability of detailed maps and the lack of marked trails limited the cruising range.

Standard herpetological equipment and methods were used but emphasis was on scouting, reversible rock turning, and digging in the sand in "likely" spots. Crowbarring of rocks and bank-stripping were kept to a minimum.

Photographs were taken in the field with a Leica camera equipped with 28, 50, and 135 mm lenses, on Kodachrome II and Kodak plus-x films. Field observations on pupillary opening and shape were augmented by photographic observations in the laboratory (Fig. 9), under illumination-levels measured by a Gossen "Lunasix 3" photometer, as explained elsewhere (Werner, 1970).

Animals were initially identified by the keys of FitzSimons (1943, 1962) and Mertens (1971); and identifications of most were later kindly checked by Mr. W.D. Haacke. He also obligingly cared for the live animals for several days between our return to Pretoria and departure for Israel. Indeed, the majority reached Jerusalem alive when we arrived on 20 August.

In the laboratory animals were (and some are) kept in a suitable, air-conditioned reptile room, in wooden cages with a floor area of 27 × 27 or 47 × 37 cm. Summer day-time temperature is often around 30°C. The main food is houseflies and maggots. Water is available at all times. Survival times in captivity are appended to the comments on each species, as well as serial numbers in the Zoological Museum, the Hebrew University of Jerusalem (HUB-R) for preserved specimens, or in the author's research collection (OK) which includes also live animals. The Latin expression ræ (rostrum-anus) signifies, where relevant, the snout-vent length of animals, in preference to the latter English expression (Werner, 1974). Taxonomic problems are commented on only when needed to clarify the extent of the relevance of my observations.

3 THE ENVIRONMENT

The Namib Desert stretches along 1,900 kilometres of the Atlantic coast of South West Africa from 12° to 15°S (depending on definition) to 31°30′S but extends only up to some 145 km inland (Wellington, 1955; Logan, 1975). It is classified as a cool coastal desert (Logan, 1968) but it is one of the most extreme deserts of the world, being much more arid than the more famous neighbouring Kalahari "Desert" (Brain, 1962 b). The total annual precipitation averages only 12–50 mm, depending on location (Logan, 1975). The Namib Desert’s landscapes include three basic formations: in the north, (a) flat gravel plains (Coetzee, 1969; Plate Ic; Haacke, 1974: fig. 5) and (b) rocks, which often are similarly flat; these are usually granite (Plate 1) but sometimes sandstone (Plate 2). In the south, (c) sand dunes (Plate 2; also Mertens, 1954: fig. 12; Louw & Hamilton, 1972: fig. 1). All these landscapes have in common a plant cover approaching utter barrenness (Krieg, 1951: Wellington, 1955) except in restricted sites (Logan, 1960).

Gobabeb station is located on the Kuseb River some 97 km SSE of Walvis Bay at 23°33′41.5″S, 15°02′30.8″E (408 m above sea level), where the landscapes mentioned above meet.

The dunes, typical wandering dunes (Solger et al., 1910), advance from the south upon the gravel-and-rock penepale and, except near the sea, are stopped by the Kuseb River (Coetzee, 1969: map; Louw & Holm, 1972: fig. 3) which is cleared by periodic floods (Logan, 1960). The superficially dry bed of the Kuseb River, with its underground trickle of water, provides a contrasting green band of majestic trees (Coetzee, 1969: plate IIb), including many Acouta rubida and A. giraffa, and a variety of shrubs (Logan, 1960). The Acouta alba trees, incidentally, are very much larger than any I have seen in Israel, at the northern extreme of this tree’s distribution (Zohary, 1973: 18, 324, 544). A detailed report on the vegetation of the area is given by Giess (1962).

The climatic conditions at Gobabeb, which has its own weather station (No. 649/37), have been summarized by Schulze (1969): Mean daily maxima of air temperature are about 32°C in summer (December – April) and about 27°C in mid-winter; mean daily minima are about 15°C in summer, 10°C in winter; the absolute observed maximum was 42.3°C, and the minimum, 2.1°C. Mean monthly relative air humidity varies from 60% in February to 36% in May, Sunshine hours in mid-summer average 80% of the possible, but in winter over 90%, as clouds and fog are common in summer. The fogs occur in the night and morning; according to Logan (1975) the heavy dew is ecologically important in the coastal area. Rainfall occurs throughout the year but mainly around January–March; the mean annual precipitation is 24 mm.

Meterological data during our visit are relevant to activity times of reptiles and may be summarized as follows. Sunrise, 0734–0731 h; sunset, 1842–1844 h. The moon, full on 3 August, rose later each night, moonrise shifting from ca. 1900 h to ca. 2200. Wind was, at the most, moderate throughout. Temperature and humidity data are presented in Table 1 as kindly provided by Mr. Alex Durr from the weather station’s records. Some additional weather data recorded by me are mentioned in the text where relevant.

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The reptile fauna of the Namib has been studied from the taxonomical and zoogeographical standpoints and illustrated (FitzSimons, 1943, 1962; Mertens, 1955, 1971; Haacke, 1965) with a certain emphasis on geckos (FitzSimons, 1943: plates 1–17; Loveridge, 1947; Mertens, 1971: p. 6; Haacke, 1975, 1976). However, knowledge of the biology of reptiles in the area remains scant, despite a small number of detailed recent studies (e.g. Haacke, 1969, 1974, 1975, 1976; Hamilton & Coetzee, 1969; Louw & Holm, 1972; Mertens, 1972).

At Gobabeb reptile life seemed quite scant. Many man-hours were spent in futile search. The few reptiles which were seen besides the geckos reported, occurred almost exclusively on or near sand. Those secured, and thus identified, comprise *Merolea cuneirostris* (Strauch, 1867), adult male and juvenile, among *Nerura* (*Acanthosicyos horrida*) bushes in the sands, active at 1100–1200 h on 6 August (HUJ-R 13283); *Aporosaura anchiata* (Bocage, 1867), one caught by Alex Durr on the bare dunes, active at 1730–1800 h on August 9 (HUJ-R 11877); *Maduera longloba* (Methuen and Hewitt, 1914), on rocks next to sand, 1600–1700 h, on 7 August (HUJ-R 11878, 13246); and a snake, *Pammophis* sp., caught by Mr. Finkeley, active in the afternoon of 7 August, in a river bed (HUJ-R 8639). As observed, i.e., by Lawrence (1959), the two last named species, both lacertids, have fringed digits; they constitute two further examples of this convergent adaptation to life on sand, additional to those assembled by Buxton (1923: figs. 39–40). Of the two, *Aporosaura* has a *Scincus*-type snout and is the lacertid most extremely adapted to burrowing rapidly into the sand, as Mertens (1955) pointed out.
In addition, skink tracks were seen in the dunes (fresh at 1730–1800 h on 9 August). Where the animal obviously had moved under the surface, these resembled those of *Sphenops septiceps* (Werner, 1968: b: fig. 2). However, the portion where the animal had moved upon the sand was not like *Sphenops* tracks, but continuously sinuous. We failed to find the responsible animal. This, most probably was *Typhlatrachelus brauni* Haas, 1964 (Lawrence, 1959: 235; Haas, 1964: 5–7) for which these very dunes are the typical type.

4 FIELD NOTES AND COMMENTS

4.1 *Lygodactylus capensis* bradfieldi (Hewitt, 1932)

(Plate 8A)

Field Notes: 9 August 1971, ca. 1000 h (with Alex Durr and Uni). Kusnie River bed, ca. 5 km E of station. Stripped bark off a large dead (standing) *Acacia* tree. Flushed one female *L. capensis* from under the bark of an arm-thick branch, ca. 1 m above ground. Captured after search and chase. When grabbed, it cheeped. Thereupon removed much bark from this and adjacent dead trees, but found no more geckos. Under most of the dead bark there was a lot of the rotten sawdust-like material which is usually shunned by geckos.

Comments: This appears to be the first record of *Lygodactylus capensis* for the Gobabeb area.

Pasteur (1964) recognizes *bradfieldi* as a distinct species whereas Loveridge (1947) synonymizes it with *capensis*. I follow FitzSimons (1943) who regarded it as subspecifically distinct.

The distress call (Frenkemberg, 1975) of this animal when first seized is noteworthy in view of Kistelle’s (1964) observation that captive *Lygodactylus* behaved as if they were mute and communicated visually. This specimen, too, did not squeak again afterwards. I had the same experience with both *Phelsuma lineata* 7: chlorascellus Mertens, 1962, and *P. bimaculata* (Kauders, 1922) just east of Perinet, Madagascar, on 31 July 1971: when caught in the *Pandanus* bushes (in which both species occurred together) the animals cheeped. They also cheeped soon after capture, when grabbed. But later on they could not be made to cheep any more. This genus, too, has been described as mute, and communicating visually, by Kistell (1964). The phenomenon of cheeping at the initial capture but not later appears to be common, at least among certain gecko species.

The animal, adult when caught, survived in Jerusalem till 7 August 1972 (one year less a day) (HUJ-R 12357).

4.2 *Pachydactylus laevigatus* laevigatus Fischer, 1888

(Plates 6 & 8B)

Field Notes: 7 August 1971, ca. 1115 h (with the family and Mr Finkelday). In an open, bare riverbed ca. 5 km N of the station, an isolated, upright rock of exfoliating blackish sandstone, with a few small *Acacia* trees. Behind one of the thin vertical stone slabs found two adult female *P. laevigatus*, rather sluggish and easily captured. On the previously hidden rock face there were also oval whitish "scars", each ca. 14 x 11 mm, where gecko eggs had previously adhered. Further search of this rock revealed no more geckos.

7 August, ca. 2330 h. On returning to our residential bungalow, found and captured a half-grown male (regenerating tail) on the white-washed concrete wall of the "patio".

Comments: According to the experience of other collectors, too. *Pachydactylus laevigatus* occurs in houses as well as rock crevices (Loveridge, 1947: p. 399; Mertens, 1955: p. 46). However, FitzSimons (1956: p. 394) mentions a subadult found under the bark of a dry tree stem. This euryooxy parallel that of *Oedura mariorata* in the Australian deserts (Werner, in MS). The vertical pupil is moderately sensitive to light, implying predominantly, but not strict, nocturnal habits (Plate 8B).

Of the three animals, the two females, caught as adults, meanwhile died in captivity: one (HUJ-R 13273) in summer 1975, the other (GK 748) on 16 January 1976, four years, five months and nine days after capture, when it probably had already been at least two years old. The male caught half-grown, still thrives after five years (GK 747: August 1976: ra 79 mm). Some details are presented after the field notes.

It is doubtful that the egg "scars" found with the two females belong to this species. We shall return to this point when discussing the eggs laid in captivity (p. 164).

4.3 *Pachydactylus punctatus* amoenooides Hewitt, 1935

(Plate 8C)

Field Notes: 7 August, forenoon (with Mr. Finkelday and the family), low rocks near riverbed ca. 8 km N of the station. One specimen was caught under exfoliating granite indistinguishable from that inhabited by *Rhaptothelus* after which abounded in the same place. A second specimen was dug up by Mr. Finkelday from a hole between stones in the soil, into which a snake had escaped (*Psammodips*, also captured).

Comments: Parker (1936: 130) and Loveridge (1947: 352–357) doubted the validity of any subspecies of *P. punctatus*, but the subspecies *amoenooides* was accepted by Fitz-Simons (1943: 73) and Mertens (1955, 1971), whereas Wermuth (1965) even regarded the form as a distinct species.

The vertical pupil appears to be about as light sensitive as in *P. laevigatus*, probably implying a similar degree of nocturnality (Plate 8C).

One animal died on the journey, but the other survived in Jerusalem till 2 April 1972 (238 days) (HUJ-R 12108).

4.4 *Palmatogecko rangel* Anderson, 1908

(Plate 8D)

Field Notes: 9 August 1971, ca. 2030 h (with Alex Durr). Dunes south of the station. I discovered in the light of the paraffinlux lamp one young *Palmatogecko rangel* with perfect tail, walking slowly on the wind-rippled, hard-packed sand in a shallow depression between dunes. It was walking normally semi-erect (Werner and Broza, 1969) and its webbed feet (Mertens, 1955: figs. 17–20; Haaske, 1976: Plate 1) were impressing no tracks in the sand. No plants were close by. At the time there was little wind and the air did not feel cold. The animal, however, felt cold to my hand.

Comments: In order to observe and obtain this bizarre species I spent in the same area several hours searching with
lights at night, in vain, both before and after I found the above-mentioned specimen. The nocturnal search comprised both several hours of moonshine and a completely dark hour of the moon eclipse (6 August, 2100–2200 h). The fruitless search, in which Mr. Finkelsay and others participated, included also a morning (8 August, 1000–1200 h) when heavy fog made it likely that the geckos would indulge in digging - but we found no fresh holes.

The vertical pupil is by far more light sensitive than in the two Pachydactylus species. This would accord with rather strict nocturnal habits (Plate 8D).

Brain (1958) drew attention to the fact that geckos of this species only rarely lose the tail, and if they do — always from the base. Haacke (1976) confirms this phenomenon. An investigation of the comparable psammophile geckos of Southwestern Asia, Stenodactylus and Ceramodactylus, revealed that in them only few vertebrates at the base of the tail are provided with fracture planes, and the latter are mostly incomplete (Werner, 1965, 1968). It may be expected, but still remains to be proven, that the same is true of Pachydactylus.

The Palmatogecko reached Jerusalem alive but survived only a few days.

4.5 Ptenopus garrulus maculatus Gray, 1865

Field Notes: 8 August 1971 (with the family). Dr.ove to Zebra Pan, a grassy depression ca. 53 km NE of Gobabeb. Arrived before 1700 h, in full daylight. In the ground, between and at bases of grass clumps, saw many holes of various shapes and sizes. At 1800 h, with the sun low over the horizon, a chorus of Ptenopus calls gradually began. It became intense and continuous by sunset (1845 h) and remained so till 2100 h when the night became completely dark. It then abated abruptly and thereafter only little calling went on. We did not find the noise level deafening or disturbing as described by A. Smith (quoted in Brehm, 1893: 44).

While the chorus was on, there was a continuous background din, relatively high-pitched - the cumulative vocalization of many Ptenopus over a considerable area. Above this rose the occasional loud calls of nearby animals. Each single call consisted of an evenly spaced series of five clicks, rarely four or six, as is typical of this species in this area (Haacke, 1964, 1965, 1974). The near clicks sounded less loud and lower pitched than those of the Israeli Pseudactylus. Each click sounded metallic, like a low-pitched string organ. There was some qualitative variation among the calls. We tried consistently to locate and observe the calling animals with binoculars, and later also with electric torches, but failed completely. Not only was it very difficult to decide on the direction of a given call, but sometimes it seemed as if the source was moving fast (compare Haacke, 1969: 87). Often we had the definite impression of an organized chorus of animals responding to each other, or taking on from each other and carrying on.

Local air temperature was 16.5°C. At 1900 h when the chorus was going strong. We left the place at 2000 h after calling became very sporadic and before the moon rose.

Comments: The validity of a separate subspecies maculatus (for the S.W. African population) has been denied by Brin (1962 a) but accepted by Mertens (1971) and confirmed by Haacke (1974, 1975) who presents detailed distribution maps.

The vocalizing activity of Ptenopus at this low temperature is not surprising, because geckos of this genus have been seen in the open even at 10°C (Brain, 1962 b).

The geckos of the genus Ptenopus were the subject of the first study of gecko vocalizations ever published, by Haacke (1964, 1969, 1974). Among other details, he described differences between and within species, and depicts animals calling from the entrances to their burrows. However the function of the calls is even more obscure than in the geckos of the genus Pseudactylus (Frankenberg, 1974).

4.6 Rhoptropus afer Peters, 1969

(Plates 3, 4 & 8E)

Field Notes: These were the commonest reptiles near the station, and we must have seen several scores during our stay. They were basking on, and scampering over, the boulders (Plates 1 & 4), flat rocks (Plate 2) and gravel (Plate 3) throughout all or most of the sunshine hours. I have actual records of their activity in the open at these times:

6 August: 1600–1700 h; 1800 h
7 August: 1030–1240 h
10 August: 1000–1130 h; 1515 h

All but the last of these records are from the immediate vicinity of Gobabeb. The last (1515 h) is from the weather station between Gobabeb and Rooibank. This animal, a male, was on a gravel plain with few scattered, small to medium, loose stones. These geckos did not seem particular about the substratum, occupying sandstone outcrops (Plate 2), granite rocks (Plates 1 & 4) and flat gravel areas (Plate 3), and even small, more or less isolated flat rock outcrops in the sands (Plate 2). However, they appeared not to inhabit the few cliff-like rocks along the Kuiseb riverbed (Coetzee, 1969: Plate III).

We found some under stones or exfoliating rock slabs, in daytime, under circumstances that convinced us that it had not been our approach that made them hide there. Obviously they had to shelter from the sun occasionally to avoid overheating.

Depending on the hues of the rocks, the geckos were often camouflaged excellently (Fig. 4). When running, Rhoptropus afer always kept adpressed to the surface (Werner and Broza, 1969), with the limbs spread widely aside, regardless whether this surface was vertical or horizontal.

It was conspicuous that most R. afer we saw were adult males. Of the 18 animals caught and measured, 9 were males of 50–53 mm ra, and one a male of 46 mm ra. There were few juveniles (N=4; 36–44 mm ra) and females (N=5; 50–53 mm ra); the latter usually (N=3-4) pregnant. Despite the abundance and activity of these geckos, we heard no calls, in contrast with the usual experience with, e.g., the vociferous Pseudactylus (Werner, 1965; Frankenberg, 1974).

Comments: The habits of R. afer are remarkable in two ways. First, the animal has a vertical pupil (Plate 8E), as in predominantly nocturnal geckos (Walls, 1942), but appears to have fully diurnal habits. In agreement with this, the pupil is extraordinarily insensitive to light so that in average daylight it is broadly elliptical.

Second, its relatively narrow fingers and toes do possess digital pads, as in properly climbing species. Yet most R. afer inhabit horizontal or inclined rock surfaces, or even flat
gravel, and few occur in rocks with limited vertical surfaces. Even over horizontal surfaces they locomote as if they were climbing, in the adpressed posture, rather than in the semi-erect posture of proper ground-dwelling geckos (Werner & Broza, 1969).

Upon comparison with *R. bradfieldi* (below) it is tempting to suggest that *R. afer* represents a relatively recent ecological radiation and evolution, from an originally climbing stock, to occupy the daytime niche of horizontal and near-horizontal non-sandy desert ground. Presumably this niche was free and inviting at a certain time. During my visit, I only once saw a lizard other than *R. afer* in the daytime in this biotope around Gobabeb.

The specimens brought to Jerusalem survived only a few weeks. Mr. Haenke has also told me that this species is particularly difficult to keep in confinement (HUJ-R 11880–85).

4.7 *Rhoptropus bradfieldi* Hewitt, 1935
(Plates 5 & 8F)

**Field Notes:** This species, slightly larger and somewhat darker, occurred only on the vertical cliff-like rocks along the Kusseb River (Coetzee, 1969: Plate IIb), and on other rocks in the immediate vicinity of the cliffs. In this area it occurred on both the blackish, soft, layered sandstone and on the light-coloured granite (Plate 5). It always locomoted, of course, adpressed.

*R. bradfieldi* appeared to be just as diurnal and sun-loving as *R. afer* but due to its occurring in a restricted area, I have actual records of activity, including basking, for these times only:

7 August: 1530–1745 h
9 August: 1215 h (air temperature 24.5°C)

Most animals caught or observed were adult males. Adult females were rare, and only one juvenile was found.

In the rocks inhabited by *R. bradfieldi*, two egg-laying sites were uncovered behind vertical slabs of exfoliating sandstone on north-facing rocks (the sunny direction). The covering stone slabs were thin, only 1–2 cm thick in one case. The "scars" where eggs had adhered to the rock were not in pairs as in *Pyodactylus* (Werner, 1965: Fig. 8) and many other geckos, but single. Each "scar" was elongate about 15 x 9 mm. In one site the scars were numerous and in several layers, implying repeated use of the site for years as in *Pyodactylus*, (Werner, 1965: Fig. 6). Of course, it is only a surmise that these egg-laying sites belong to *Rhoptropus bradfieldi*.

**Comments:** The vertical pupil (Plate 8F) is about as insensitive as in *R. afer*, and this, again, would appear to relate to the diurnal habits, which are mentioned also by Haenke (1965). The ecological relationship of the two *Rhoptropus* species is considered in the Discussion (p. 165).

Of the specimens brought to Jerusalem, one survived for two years and three months but was preserved on 7 November 1973 when it appeared moribund (HUJ-R 12735; the others are HUJ-R 11879, 13242).
Plate 4. *Rhopetropus* after basking on a granite rock, the colour of which it matches well. (Near Gobabeb, 7 August 1971, early afternoon.)

Plate 5. A dark *Rhopetropus* bradfieldi conspicuous against the whitish rock on which it basks. (Kaiserb river near Gobabeb, 9 August 1971, forenoon.)
5 REPRODUCTION OF PACHYDACTYLUS LAEVIGATUS IN CAPTIVITY

5.1 Eggs and Oviposition

(Plate 6)

The two females and the young male (not identifiable as a male at the time) reached Jerusalem in good condition on 20 August 1971 and were placed in a wooden cage of ca. 27 x 27 cm floor which received the afternoon sun. The cage had about 3 cm of a sand-soil mixture on the bottom and was furnished with two diagonally leaning pieces of roof tiles. The animals were henceforth fed almost exclusively on housefly maggots, replenished every 2–3 days. For variety, grasshoppers were given every few weeks. During the succeeding months of September–October each female appeared to be pregnant at least twice. No eggs could be discovered and it was presumed that the eggs were eaten by the geckos, perhaps in relation to having been infertile.

However, during 1972 several eggs were discovered. By this time both the females and the male, now evidently mature, measured ca. 75–78 mm (ra).

All the eggs were nearly ellipsoid but somewhat flattened with three different diameters. The dimensions of seven eggs averaged 19.18 x 14.89 x 13.47 mm and the observed ranges were, respectively, 18.0–20.3; 14.4–15.8; and 12.9–14.2. Most eggs were buried in the ground, the rest were deposited on the ground. All eggs were discoloured by sand and soil particles stuck to the shell, obviously because the eggshell had been soft and sticky at the time of oviposition. This encrustation with sand occurs also in Pelmatogekko eggs (Haenke, 1976) but I have seen it in no other gecko species, including (i.a.) all the Israeli gecko genera that oviposit in the ground or under stones: Alsophylax (Bunophas), Ceramodactylus, Cryptodactylus, Hemithecodactylus, Stereocheilus and Tropidolepis. Many of the eggs were deformed by a depression or indentation at some spot — further evidence of their soft state when laid. This, of course, is the normal condition in species that stick the eggs to the substratum, and it remains to be seen how the Pachydactylus oviposits, when given a variety of artificial rock crevices that more closely resemble natural ones. It thus remains an intriguing open question whether the remains of eggs that were found sticking to the rock where the females were caught, did belong to this species.

Because in captivity most eggs were buried there remains a varying degree of uncertainty about the dates of oviposition and even about the eggs' arrangement in clutches, despite frequent inspection of the females and the ground. From the inspection of the females it was obvious that a clutch normally consisted of two eggs. The two females were not marked individually and it is not known which eggs were laid by what female; however, both females appeared similarly productive. Eggs, once discovered, were put in small glass jars in an incubator room at 29.5 ± 1°C.

Oviposition was first recorded on 31 August 1972, between inspections at 1400 and 1630 h. However, in the ground there were three eggs. One was broken accidentally; the other two hatched, one between the mornings of 12 and 13 October, and one between the mornings of 28 and 31 October. The second probably represents the full incubation period of ca. 59 days, whereas the first (42 days or more) probably implies an earlier oviposition in mid-August. Three additional clutches were laid by the middle of November, and a sixth, last of the season, was laid on 2 or 3 January 1973. (For none of these later clutches is the hour of oviposition known.) Hence each female (apparently) laid three clutches during the season August—December. Of two clutches each, only one egg was recovered, and in one of these cases the other egg was probably eaten, as the mother had been pregnant with two eggs.

5.2 Incubation

Of the ten eggs recovered, one was broken (as mentioned) and six hatched. Of those incubated at 29.5°C throughout (four), the longest incubation period was 61 days, and this was an egg almost certainly discovered within a day of oviposition. The second longest incubation lasted 59 days. Hence if this species has a uniform incubation period (that of Gekko gekko, for example, appears to be highly variable — Brodky, 1959), this would seem to be ca. 60 days at this temperature.

The last (January) clutch hatched only after 80–81 days but during this time the incubator was unstable and at least for one 3-day period the temperature sank to 22°C. This delayed hatching occurred on 23–25 March 1973, but prior to this, the last hatching was during 2–3 January 1973.

5.3 Hatching and Neonates

(Plate 7)

The time of day when hatching occurred is unknown for most eggs, because usually eggs were inspected only once daily. However, one egg is known to have hatched on 5 December 1972 between 0900 h and 1600 h, and another hatched on 25 March 1973 between 1400 and 1450 h. Thus, at least some of the hatchings occurred in daytime.

The hatching process, in the one case on which some information is available, was rather quick. On inspection on 25 March 1973 at 1400 h, one egg in the incubator displayed a slight crack. Wishing to photograph the hatching process, I inspected the egg at 5 min. intervals. No change was visible by 1445 h. However, by 1450 h the neonates had hatched and was found resting next to the eggshell with only the tail still inside. This was in contrast to the procedure common in geckos and other lizards, wherein the hatching resists for a while after extruding its head and before emerging completely (depicted for Gekko gekko by Brodky, 1959: Fig. 10).

The measurements of four normal hatchings averaged 35.9 mm (range 35–37) and tail, 26.8 mm (range 25.5–28).

In two other instances hatching appeared to be premature, though spontaneous, and the neonate carried a remnant of the yolk sac. In the first case, an unusually small neonate hatched on 5 December 1972, carrying a yolk sac (yolk volume about 1/6 that of the head); it looked otherwise healthy and climbed about in its jar. The yolk was not absorbed but dropped off and shrivelled after four days. On the 12 December this animal measured only ra. 32 mm and tail, 24 mm. During a severe cold spell, 15–17 January 1973, this animal was the only one of its species that died (together with two Hemithecodactylus mabouia, out of a collection of many geckos of over twenty species, several of them from deserts or the tropics).

In the second case, on 25 March 1973, the neonate carried a smaller yolk remnant (which similarly dropped off), and body size conformed to the minimal size of normal neonati (ra. 35; tail, 25 mm). This animal still thrives (August 1976: ra. 71; tail, 53 mm).
6 DISCUSSION

6.1 Inter-specific Relationships

As in the deserts of southwestern Asia (Werner, 1973) and Australia (Planka, 1972; Planka & Planka, 1976; Werner, in MS), so in the Namib the gecko fauna is rich, including a variety of climbing and ground-dwelling species. The following comments are restricted to the species actually observed. The nocturnal ground-dwelling forms are practically excluded from this category as our searches at night (with lamp) were nearly futile (p. 161). This may be due in part to the full moon at the beginning of our visit. The effects of the moon and its phases on animal activities have been investigated mainly in aquatic invertebrates (Sollberger, 1965) but Klauber (1939:50) presented data suggesting that the full moon depresses the activity of desert snakes. Casual observations on psammophile nocturnal reptiles in Israel appear to point in the same direction. Interestingly, the one dark hour of full moon eclipse we spent on the dunes was not more fruitful (p. 161).

At first it appeared remarkable that two congeneric species, Rhoptropus afer and bradfieldi, of similar size, and similarly diurnal, should inhabit rocks in the same area. However, closer observation showed that they occupy two distinct niches with very little overlap: R. bradfieldi, a slightly heavier animal with "normally broad" digital pads, lives in vertical rocks as befits an honest climbing species; FitzSimons (1943:117) termed it "essentially rupicolous". R. afer, with rather narrow digital pads, occupies smaller boulders and, especially, horizontal surfaces of rock or gravel (as previously noted by FitzSimons, 1943:115) that would normally be expected to harbour typical ground-dwelling lizards. But R. afer is revealed as originating from climbing stock by always locomoting adpressed as if climbing, rather than semi-erect (Werner and Broza, 1969). From the scarcity of proper diurnal ground lizards in this habitat, it would seem that the free niche "invited" R. afer to radiate into it, perhaps concurrently with competitive pressure from the slightly heavier R. bradfieldi. According to Mertens (1954), niche separation between these two species (at Rössing, only some 100 km to the north of Gobabeb) is based on their different colourations, which match different rocks. This was not the case at Gobabeb.

On the other hand, each of the two diurnal Rhoptropus species appeared to occur in the same spatial niche together with a predominantly nocturnal species of Pachydactylus: R. afer coexisted with P. punctatus amoenoides, which, however, is much smaller than R. afer. R. bradfieldi would seem to share its habitat with the much larger P. laevigatus. Besides the temporal division of the habitat between the Rhoptropus and the Pachydactylus species, the two members of a coexisting species-pair presumably eat partly different sizes of food organisms, in accordance with the geckos' different body sizes (and head sizes), as shown by Planka and Planka (1976) for Australian desert geckos.

It is noteworthy, that P. punctatus has somewhat narrower digital pads than P. laevigatus, in parallel with the (greater) difference between R. afer and R. bradfieldi.
6.2 Specific Diel Cycle and Pupillary Response
(Plate 8)

The gecko species observed appear to differ considerably in their diel cycles, although my scant observations provide no conclusive proof of the details. In the completely diurnal species, Lygodactylus capensis, the pupil of the eye is round (Plate 8A; Pasteur, 1964). Among the species with a vertical split pupil, we may expect a correlation between light-sensitivity and the normal diel cycle, so that under uniform illumination the pupil would be more widely open in the species with the stronger inclination towards diurnality. Indeed, observations on Israeli geckos confirm this (Frankenberg, in press).

Among the Namib geckos observed, the two Rhoptropus species appear to have completely or predominantly diurnal habits. In agreement, their vertical pupils were partly open in nature, even in full daylight. Their relative insensitivity is further demonstrated by the controlled laboratory observations (Plates 8E & F). On the other hand, the two Pachydactylus species were found at times and places compatible with a supposition that they are crepuscular or nocturnal. Their pupillary responses were by far more light-sensitive (Plates 8B & C). The most extremely sensitive pupill was that of Palmatogecko (Plate 8D), which would appear to be as completely nocturnal as the ecologically comparable Israeli psammophile geckos Ceramodactylus dorias and Stenodactylus petrii.

6.3 Annual Reproductive Cycle of Pachydactylus laevigatus

In Israel, geckos oviposit mainly during June—August (Werner, 1965, 1966 a, b). This generally holds true for Israeli geckos kept in my reptile room. The Pachydactylus laevigatus, ovipositing mainly during September—November, clearly failed to conform to their new environmental cycle, more than a year after their transfer. I am not sure that they kept fully in pace with their original reproductive cycle. I suspect, however, that they may have done so, because in August when they were caught, female Rhoptropus in the same habitat were commonly pregnant.

7 Conclusions

1 Concerning Gobabeb Station in August:
1. Lygodactylus capensis occurs on trees along the Kuiseb River at Gobabeb.
2. Lygodactylus capensis, although reputedly mute, cheeps when seized (based on one case).
3. At Gobabeb, Rhoptropus afer occupies horizontal habitats and small rocks whereas R. bradfieldi occupies larger steep rocks; there is little overlap between the two.
4. Pachydactylus punctatus amoenoideus appears to coexist with Rhoptropus afer in the same habitat.
5. Rhoptropus afer and bradfieldi are diurnal, and their vertical pupils are relatively insensitive to light.
6. The pupils of Pachydactylus laevigatus and P. punctatus amoenoideus are much more light-sensitive than those of Rhoptropus, and both species appear to be crepuscular or nocturnal.
7. The pupil of Palmatogecko is more light-sensitive than those of the Pachydactylus species.

2 Concerning Pachydactylus laevigatus in Captivity:

8. In captivity, Pachydactylus laevigatus lays eggs deposited loosely in the ground, that are initially soft and sticky.
Plate 8. Heads of geckos of six species from the Gobabeb area, to show the condition of the pupil under comparable levels of illumination. All photographs enlarged so that head length appears as 50 mm; where possible, 1 cm of a ruler originally photographed with the animal is included.

(A) & (B) Light intensity of ca. 20 lux (Jerusalem, 13 May 1972):
   (A) Lygodactylus capensis bradfieldi.
   (B) Pachydactylus laevigatus laevigatus.

(C) – (F) Light intensity ca. 30 lux (Jerusalem, 23 August 1971):
   (C) Pachydactylus punctatus amoenoide.
   (D) Palmitogecko rangel.
   (E) Rhapodopus afer.
   (F) Rhapodopus bradfieldi.
9. Each female lays ca. 3 clutches of 2 eggs each during August—November.
10. Eggs measure ca. 19 x 15 x 13 mm.
11. Incubation appears to last ca. 60 days at 29.5°C.
12. The neonate measures ca. 36 mm, head and body; and 27 mm, tail.

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Finally, I doubt when this report could have been written, had not Corporal M. Swarzinski understandingly lent me her desk during part of the 1973 war.

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On the origin of sheeting and laminae in granitic rocks: evidence from Antarctica, the Namib Desert and the Central Sahara

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ABSTRACT

Studies of granitic rock outcrops have been carried out in the McMurdo Oasis, Antarctica, and in the Namib Desert to test hypotheses of formation of large scale sheeting structures and of laminae. Laminae were also investigated in the Central Sahara. Evidence from Antarctica strongly supports the contention that sheeting may be a secondary feature resulting from unloading; evidence from the Namib is more equivocal but offers some support for this hypothesis. Samples of laminae have been studied in thin section and by X-ray diffraction. The weathering processes in Antarctica and the Namib are physical, but in the Sahara chemical. Taffoni may form both with and without case hardening or desert varnish on the outside of rock outcrops, and by both physical and chemical weathering processes. The almost ubiquitous occurrence of laminae on granitic rocks suggests that their formation may be caused by inherent features in the rock, such as in-built stress, and that this factor should be investigated in detail.

1 INTRODUCTION

In spite of a large literature and much debate a number of the problems of the origin of major and minor landforms on granitic rocks have not yet been resolved. It may be contended that much of the difficulty lies in the assumption that similar landforms must be produced by one set of processes, and that it is therefore, possible to recognise forms and to deduce origins for them. By contrast it has been postulated that few landforms are the result of unique processes, and that many processes may be responsible for landforms which converge towards similar forms (e.g. White, 1945; Berrangfey, 1950; Selby, 1977). If this last postulate is valid then it follows that the results of many processes must be similar and that each landform must be investigated in detail before any hypothesis of origin is adopted.

Two of the common features of granitic rock outcrops which have aroused much controversy are sheet structures and laminae. Both forms are very common on the granites of the Namib Desert and thin laminae are common on granites of the McMurdo Oasis, Antarctica: sheeting is not widespread in the McMurdo Oasis but its presence in certain places is believed to offer an opportunity to investigate one of the critical hypotheses which attempts to account for this phenomenon. Sheetimg is very common on bornhardts of the central Sahara, but as there is strong evidence that these bornhardts have been exhumed from beneath an ancient deep weathering profile and their detailed history can no longer be deciphered (Vogt and Bluek, 1963; Birot et al., 1955) they cannot be used to test hypotheses of the origin of sheeting.

1.1 Study areas

The McMurdo Oasis is a general term for the ice-free valleys of Victoria Land between 77°15'S and 77°45'S, and 160°E and 164°E. It consists of the Victoria Valley system, the Wright and Taylor Valleys which were created by outlet glaciers from the continental ice sheet. The glaciers cut through the Transantarctic Mountains, but they have now retreated and left wide open troughs with valley walls cut in metamorphic and intruded acid plutonic rocks. The geology has been described by McKelvey and Webb (1962) and Allen and
Gibson (1962). The geomorphic development of the valley walls has been described by Selby (1971a). The few climatological data on the area have been summarised by Bull (1966). Winter temperatures fall as low as −2°C but in midsummer screen temperatures may exceed +5°C for several days at a time. Precipitation is everywhere low but snowfall may exceed 10 cm a year in the eastern ends of the valleys and decline westwards. The relative humidity of the westerly winds ranges from 50% to 60% in midsummer with an average of around 45%. Near the coast the air from the east is more moist and relative humidities are commonly around 65% to 75%.

The climate, rocks and weathering phenomena of the central Namib Desert have been described by Goudie (1972), the climate by Schulze (1969), the soils by Scholz (1972) and the relationship between weathering phenomena and local climate by Bestler (1972). Their descriptions will not be repeated here. The main Namib Plain is cut across the basement Damara schist into which are intruded Salem granites (Clifford, 1967). To the east the plain is bounded by the Great Escarpment from which extend long spurs. The spurs are also predominantly of schist but granite intrusions outcrop in the core of many of them. In general, granite outcrops near the coast have very low relief (1–4 m). In the central desert around Mirabib outcrops with the configuration of low banks may rise 30 to 40 m above the plain, and near the escarpment some granite domes in spurs rise over 300 m above the plain.

In the area of the Mouyir Mountains and the Atakor, Hoggar Mountains central Sahara, there are many large granite bankheads formed in a variety of coarse and fine-grained granitic rocks (Rognon, 1967). The weathering skins and tafoni formed on a group of bankheads near Moulay Hassan, 24°40′N, 04°30′E, were investigated briefly during a traverse of the region.

2 SHEETING

2.1 Hypotheses

Many inselbergs and other exposures of massive rock in a variety of lithologies — granite, gneiss, quartzite, sandstone — are traversed by extensive curvilinear joints which transect closed joints and intruded dykes. These sheeting joints have a spacing, varying from about 0.3 m to 8 m, which becomes greater with depth from the surface; they are nearly parallel to each other and hence are approximately concentrically arranged (Dale, 1923; Twidale, 1971). Two schools of thought have arisen as a result of attempts to explain the frequent parallelism between sheet joints and the ground surface (Twidale, 1971, p. 63):

1. that sheet structure developed as a secondary feature, parallel to the surface of the land, through the removal of overburden permitting stress release in the rock;
2. that sheeting is a primary feature consequent upon internal structure in the rock so that the rock controls the surface relief.

The hypothesis of secondary origin through unloading was formally stated by Gilbert (1904) who argued that granitic rocks, whatever their origin, crystallise deep in the earth’s crust under high pressure conditions. As erosion removes the superincumbent load hydrostatic pressures decrease and the relief of pressure is expressed in a series of fractures aligned tangentially to the direction of stress and hence approximately parallel to the ground surface. Gilbert’s argument has been supported by many subsequent workers including Jahn (1943), Kieslinger (1958) and Bradley (1963). The mechanics of the unloading process have been examined by Johnson (1970) and by Brunner and Scheidegger (1973).

The unloading hypothesis is difficult to test in the field because the same evidence can be used to argue both for secondary unloading and for primary origin. Sheeting joints occur in rocks like sandstones which are usually cut by bedding planes and orthogonal joint systems, as well as in granitic rocks which also have orthogonal joint systems — even if such joints are closed. It is thus reasonable to ask why, if these orthogonal joints existed, was the inherent stress not released along joints of the orthogonal system? It has been pointed out by Twidale (1971, p. 67) that on Dartmoor, England, the main topography of the edge of the moor is of Quaternary age yet the sheeting joints are of Cenozoic age. Thus the unloading hypothesis is not applicable. A further argument is that inselbergs, especially bornhardts, are commonly believed to survive because of their lack of jointing — which is an indication that they are in a state of compressive stress — yet some of the best developed sheeting structures to be seen anywhere occur on the bornhardts of the central Sahara. There thus seem to be strong arguments against unloading as a universal cause of sheeting.

An exceptional case to the last conclusion is the occurrence of sheeting in areas of Quaternary valley glaciation where it is presumably caused by loading of valley floors with ice and then rapid unloading after deglaciation; this last hypothesis is widely supported (Gilbert, 1904; Lewis, 1954; Harland, 1957; Soen, 1965).

A closely allied hypothesis is that of Soen (1965) who suggested that the granites of Sermersooq, south Greenland, are associated with a negative gravity anomaly and that because of a mass deficiency in the crust gravitational forces tend to raise the deficient rock masses above their surroundings so that initially a vertical compression is exerted on the higher levels of the granite and surrounding country rocks, but that once the mass deficiency is compensated uplift ceases and a relative decompression takes place favouring large-scale sheeting in the near-surface rocks.

The hypothesis that contractional or tensional strains are set up during the emplacement and cooling of a granite intrusion, and that this leads to primary sheeting structure, has been supported by a number of workers including Oxnaed (1916) and Mounier (1961). Arguments and observations in favour of this hypothesis include the fact that compressive stresses at depth in mines frequently exceed the hydrostatic pressures which are exerted by the overburden. The most convincing argument, however, is that compressive stress offers in a single mechanism an explanation for the resistance and preservation of domed inselbergs and for the sheet structures characteristic of them (Twidale, 1971, p. 71). This hypothesis does not obviate the possibility that some sheeting may be caused by local unloading of ice, by faceting or by tectonic stresses.

If the compressive stress hypothesis is thus generally applicable then erosive processes will follow the line of joints and not the reverse.

2.2 Sheetin in Antarctica and the Namib

Sheet structures are not widely exposed in the McMurdo Oasis for the granite there is mostly well jointed. On the northern slopes of the Taylor Valley, however, above the
Plate 1. Joints in granite following the trend from the rectilinear slope to the free face, Taylor Valley, Antarctica.

Plate 2. Multiple dome forms in a granite outcrop surrounded by schists. The outcrop is close to the Great Escarpment, Namib Desert.
at the mouth of the Taylor Glacier there is an exposure of joints in granite which is interpreted as supplying convincing evidence in favour of a secondary origin for sheathing. The exposed joints occur at the junction between the rectilinear slope inclined at about 35° and the free face above inclined at about 80°. The joints follow the change of slope almost exactly (Plate 1). It was shown by Selby (1971) that the rectilinear slope increases its length by elimination of the free face above it, consequently the curved jointing is interpreted as a stress-release phenomenon adjusting to the evolving shape of the concavity between the free face and the rectilinear slope. It must be admitted that there are few places where so nice an adjustment can be seen, but there are also a few places where the joint blocks are sufficiently long for the curvilinear sheathing joints to develop.

Where sheathing is reported from other glaciated valleys it is described as forming convex or domed surfaces. Such forms cannot exclude the possibility that the joints reflect internal structure. A concave form exactly located in the angle between two slope facets, one of which is growing at the expense of the other, however, would be a remarkable coincidence if it were reflecting an internal structure.

In the Namib Desert many of the domes are isolated features and cannot be used to test the hypothesis of primary or secondary origin for sheet structures. A number of the outcrops, however, consist of multiple domes separated by widely spaced (0.3 km or more) megajoints (Plate 2). If the hypothesis of primary origin were to be accepted then it would be necessary to conclude that groups of dome-shaped rock masses occur within one intrusion and that these domes have preserved their form as the surrounding and overlying schists have been stripped away.

It has been contended (Selby, 1977) that relief in the Namib Desert has evolved by processes of escarp retreat across bedrock with the Great Escarment receding eastwards. If this hypothesis is justified the reduction of bornhardt size westwards is entirely conformable with a reduction of bornhardt volume by progressive sheathing parallel to the ground surface. The multiple-domed forms are also explicable by the incision of channels along megajoints and the development of sheathing parallel to the slopes above these channels. A primary origin for the compartmented domes would imply the existence of multi-domed intrusion forms.

3 LAMINAE

Laminae are scale, flake, flaggy or plate-like skins or shells of rock which are formed closely parallel to the surface of an outcrop (Twidale, 1971). Laminae may be up to 40 cm thick but are more commonly 1–5 cm thick; they conform closely to the rock surface even within tafoni or overhangs, beneath visors and on the outer surfaces of rounded boulders. The only general exception to this seems to be that they may intersect the walls of shallow pans (also called opferkesseln, gnannas, onciangas and kociiki). It seems evident then that laminae develop in conformity with the surface of almost any outcrop and that they continue to form as the rock body is reduced in volume. In the case of shallow pits it seems probable that pits may form in a surface already affected by lamination, but deeper pits (>10 cm) influence the formation of laminae (Plate 3).

Laminae develop in a great variety of rocks—granite, monzonite, syenite, quartzite, arkose, gneiss, limestone; they also develop in a great variety of climates ranging from the humid tropics through the subhumid and arid subtropical and temperate zones to the Arctic and Antarctic cold deserts (see Hedges, 1969; Dahl, 1966; Twidale, 1971, for reviews of the literature). They are thus very common features and likely to be produced by a variety of processes.
3.1 Laminae on granites from the Namib Desert

Field study of granite outcrops in the central Namib Desert has been carried out in the region of Gobabeb and Mirabib (Map 1). The granites of this region and their superficial weathering forms have been briefly described by Goudie (1972), Scholz (1972) and by Besler (1972) but no detailed analysis of the laminae is thought to have been carried out. One feature of the exfoliation of laminae from curved surfaces which these writers did not comment on is that many laminae are thinner at their edges than in the centre. This implies that such laminae being exfoliated from all flat or concave surfaces will initiate another concave depression or deepen an existing concavity, but convexities will be progressively eliminated. This observation may explain why so many of the interiors of Namib tafoni and overhangs have a multicellular appearance (Plate 4) and why boulders are rounded (Plate 5).

Specimens of laminae were removed from outcrops of granite in the Sout River bed about 5 km northwest of Gobabeb, and at Mirabib. The samples have been examined in thin section and by X-ray diffraction in the laboratory in the hope that they would provide information on the causes of lamination.

The specimens from Sout River were removed from outcrops which were greatly affected by honeycomb weathering and lamination (Plate 5) (see Goudie, 1972, p. 18–20 for descriptions). The granite has been weathered to form mushroom-shaped forms standing 1 to 2 m above a valley floor of alluvial silts and grus saturated with gypsum (CaSO₄.2H₂O), calcium carbonate and sodium chloride. In such an environment it seemed probable that salts, by crystallising in rock pores, could be responsible for rock weathering and the development of laminae.

In hand specimens and in thin section the rock samples showed only very slight yellow-brown discoloration of the outer surface and the discoloration was always around individual...
crystals had suffered swelling and separation of the plates forming the crystal and all had been noticeably discoloured. The red staining emanating from the biotites had spread along boundaries between feldspar and quartz crystals where these boundaries approximately corresponded with the lineation of stringers of biotite crystals. The staining was thus preferentially restricted to lines within the samples, but there was no evidence of separation along these lines. The strong red colours on the surface of the samples could be seen to emanate from a few slightly altered mica crystals. Within three of the samples there was some evidence that the biotite crystals were aligned and clustered, but these groupings were not dense or continuous and it is most unlikely that their arrangement could contribute to the formation of spalling of flakes larger than 1–2 cm². The granites all had a granular texture (hypidiomorphic—granular) with no suggestions of gneissic or schistose structures. Amongst the feldspars (microcline, albite, oligoclase and orthoclase) most crystals were fresh and unaltered. A few, however, showed signs of weak to locally moderate kaolinisation and sericitisation; a few large flakes of sericite were observed. These observations together with a few indications of spherulitic structures, which were probably chlorite, associated with biotite indicates that some slight chemical weathering had occurred. This would no doubt slightly weaken the rock but there was no indication that it had caused rock splitting.

The analysis showed that the red staining was caused by ferric hydroxides. These were mostly limonite but some could be goethite. The composition of the Mirribi granite is approximately: quartz 36%; microcline 16%; oligoclase with some albite 20%; orthoclase 20%; biotite 10%; muscovite <3%.

The average mineral grain of quartz and feldspar has a diameter of about 1.5 mm.

Samples taken from the inside of taffoni were also analysed but the results were uniformly uninformative. The rock crystals had suffered no visible chemical alteration and the fine dust from between laminae had approximately the same composition as the granite, with no soluble salts or chemical alteration products being detected.

In the Mirribi area many of the taffoni and cavernously undercut boulders and lips appeared to be suffering vigorous exfoliation. Fresh laminae could be seen separating from the walls and roofs of most cavities and the floors had a fresh-looking litter of fallen flakes. The only site where an indication of the rate of weathering could be obtained was in a very large cave which had been used as a shelter by early men. Occupation layers on the floor of the shelter contain charcoal which has been dated at about 10,000 B.P. (Sandeforsky, 1974). A crude measurement of the volume of fresh rock flakes in the occupation debris suggests a minimum rate of scaling of about 3 cm³/1,000 years. Because some of the fallen debris may have been removed by wind or people the possible maximum rate is unknown. The site may also be misleading for the roof and backwall are partly covered with soot which may have sealed the rock surface and reduced weathering rates.

3.2 Laminae on granites from Antarctica

The general nature of weathering crusts and taffoni on granite in the McMurdo Oasis has already been described by Selby (1971b, 1972). These forms are as common there as they are in the Namib and have similar dimensions.

Samples have also been taken from rock spalls and laminae within taffoni in the McMurdo Oasis. The results are no more informative than those obtained from samples from the Namib Desert. Chemical weathering was confined to biotite crystals near the surface of laminae taken from the outside of
boulders. The weathering crusts were also composed of ferric hydroxides but in Antarctica these formed a distinct crust — up to 0.5 mm thick — on some samples from the central zone of the valleys. It is notable that the largest taffoni, overhangs and visors occur in those areas where weathering crusts (desert varnish) are most prominent.

3.3 Weathering forms on granites from the central Sahara

The granites of the central Sahara were studied only briefly in the field as specimens for laboratory analysis could not be carried. Conclusions based on field evidence are therefore tentative. The outer surface of the granites was in places covered with a dark blue-black crust which appeared to be totally impervious, but this crust was in many places peeling and revealing fresh rock beneath it. More commonly the rock surface had a dull red-brown colour but there was no evidence on any of the outcrops examined that a crust had formed and the discolouration was superficial only, with no evidence that it had penetrated into the rock between crystal faces.

On the Sahara outcrops laminae were rare. Most boulders had the appearance of being subject to granular disintegration even though broken edges of sheets and boulders had some indications of platy structures in the rock. Hand specimens knocked from outcrops showed strong decomposition and leaching of the biotites, and some feldspars could be easily crumbled between the fingers (Plate 6). Taffoni everywhere were found to be actively growing with fresh quartz crystals falling out of a crumbling matrix of decomposed feldspars. The entrances to taffoni were often in the form of visors and overhangs, but there was no evidence that these apparently more resistant areas of rock were case-hardened or less deeply weathered. The ground around all outcrops consisted of a fine pea-gravel of quartz crystals surrounded by a pale brown silt and fine sand. Fresh feldspar crystals were not observed in this material.

In the central Sahara, then, granite weathering appears to have produced little laminar formation of the surface of outcrops. By contrast with Antarctica and the Namib the granites are strongly decomposed near the surface (to a depth of 5 to 10 cm). Weathering crusts exist but are exceedingly thin and do not cover all upper surfaces. Taffoni exist but their entrances do not have the sharp edges formed by case-hardened or laminated rock. The dominant exfoliation process seems to be granular rather than laminar.

4 CONCLUSIONS

Evidence from Antarctica clearly supports a secondary, or unloading, hypothesis for the origin of sheeting structures in granites of the Taylor Valley. The evidence from the Namib is more equivocal, but a primary origin seems improbable and the evidence favours a secondary origin.

The cause(s) of laminae in granites of the Namib and Antarctica is still unknown. Lamination is clearly a physical process and does not involve any chemical decomposition of the rock minerals other than possible release of ferric hydroxides from biotites. The investigations reported here throw no light on the relative effectiveness of such physical processes as salt weathering, differential thermal expansion and contraction, stress release, cryogenic weathering or sudden quenching of heated rock by rain — although, of course, some of these

Plate 6. Part of the surface of a large boulder near Moulay Hassan, central Sahara. The sheet of granite in the centre has a broken edge revealing decomposed feldspars and leached biotite crystals. Disintegration is largely granular. The boulders have small taffoni formed in their bases. Laminae are not present.
processes are inappropriate for the environments described — (see Schattner, 1961, for a review of these hypotheses). As with so many physical processes their action leaves no unique indicators of their occurrence.

The conclusion of Bester (1972) that the ferric hydroxide coating on rocks of the Namib is not a true, and impervious, desert varnish is supported. Her statement that the reddish-brown patina consists of montmorillonitic weathering products is not supported by the X-ray diffraction analyses.

It would appear from these observations that tafoni and laminae may form both with and without the development of desert varnish. The formation of tafoni in association with chemical weathering is also well established in the central Sahara, but the weak development of laminae there may be caused by chemical weathering. In a traverse through the humid and subhumid regions of central Africa the writer noted that although laminae do form on outcrops of granitic rock they were never as strongly developed as in the Namib and Antarctica. A tentative conclusion is that although laminae can form in all climates the existence of strong chemical weathering on the surface of outcrops reduces the effectiveness of lamination processes. The ubiquitous nature of laminar in granitic rocks suggests that its occurrence may be caused by the inherent properties of the rock — such as inbuilt stress — rather than by particular weathering processes, although physical processes obviously increase its effectiveness. The in-built stress of rocks needs further investigation.

5 ACKNOWLEDGEMENTS

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Biological survey of Sandvis 1, introduction and faunal list

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ABSTRACT

The topography of Sandvis is briefly introduced and changes in the area, based on charts, described. These show that the area has evolved, within 90 years, from an open harbour, suitable for large craft, to an almost completely landlocked generally shallow lagoon. A faunal list of the aquatic and marinal fauna is given. Excluding the planktonic component a total of 93 invertebrate and 25 vertebrates are recorded.

1 INTRODUCTION

During 1974 the authors were asked by the Nature Conservation and Tourism Division to undertake a survey of the marine invertebrates and fishes of Sandvis, to establish Inter alia its ecological importance and need for protection. The results of this survey will be published as a series. Part 1 describes the area in broad detail and contains a faunal list of the marine animals. Part 2 will deal in detail with the distribution and numbers of intertidal invertebrates. Subsequent reports will consider the distribution and biomass of subtidal invertebrates, the biology of the fishes, and the physical parameters.

Sandvis, or Sandwich Harbour (formerly Port D'Ilieu) is a large body of generally shallow water situated at approximately 23°20'S 14°25'E, some 50 km south of Walvis Bay. It is 11.1 kilometres long by 3.3 kilometres wide at its widest part. (fig. 1), with the long axis running roughly north-south. To the east the lagoon is bounded by high sand dunes of the central Namib system, along much of the eastern edge these dunes run directly into the lagoon. In the south-east corner the line of dunes is at an angle to the coast line and the dunes are separated by pools of seepage water and channels only open to the lagoon at high tide. The western side consists of a sand bar separating the lagoon from the sea. There are extensive shallows on the lagoon side of most of the sand bar. Although the lagoon has been known to be completely closed off to the sea (de la Bat pers comm) this has not occurred during the survey. The position and form of the mouth, however, is continually changing. In general it varies from a roughly central position to an opening at the northern half.

An extensive damp salt pan lies to the south of the lagoon, which appears devoid of macroscopic life apart from the insect Heterocerus peringueyi. The northern end is a large area of mud flats interspersed with pools and drainage channels. Above H.W.N. there are extensive beds of the halophyte Arthrocnemum and Sporobolus grass.

The high dunes of the land protect Sandvis from casterly winds. The dominant winds (at least 6 hours on 90% of days) are southerly however, and the salt pan provides no protection. This wind combined with the shallow water results in a very rough sea on most afternoons. The temperature within the lagoon due to solar warming is always higher than the sea outside. The degree of warming is dependant on several factors: apart from sunshine, air temperature, fog, evaporation and the time of high tide are all important. In general the temperature within the body of the lagoon is some 5–6°C above the ambient sea temperature in summer and 2–3°C in winter. In the semi-isolated pools of the northern mud flats and gullies near the south end, much higher temperatures can occur. Sea temperatures, measured at the mouth on an incoming tide, normally range between 12°C and 16°C; however, since the low water temperatures are dependant on wind induced upwelling, wide variations can occur, and sea temperatures in the area within the range of 10°C and 21°C occur.

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Initial water analysis suggest that underground seepage of freshwater has little effect on salinities and that Sandvis is best considered as a marine lagoon.

The higher temperature of Sandvis relative to the surrounding coast line has resulted in a number of animals becoming established outside their normal range.

Sandvis was a well known anchorage in the days of sail and is believed to have been used as a careening base by pirate vessels. It was certainly used for this purpose later by whalers both British and American. Near the end of the 19th century there was an ill-fated attempt to establish a meat canning factory there, while the Cape Town firm of de Pass & Spence operated a fishing station for many years. Later a company held the rights to collect guano.

Today it is difficult to imagine Sandvis being used as an anchorage for large vessels. The topography of Sandvis has however, undergone marked changes in the last 100 years. When surveyed in 1880 by Lt. C.F. Oldham in H.M.S. Sylvia, the northern end of the lagoon was an open bay with a depth of 5 fathoms. By 1892 the sandspit had extended northwards considerably and a bar of 10 foot was reported at the mouth. Later silted in the northern end continued. This was probably accelerated during the tenure of the guano company since, to increase the roosting areas and thus the guano yield, they used sandpumps to create artificial sand banks.

Due to its isolation very little marine biological work has been done at Sandvis. The only previous word was Lucks' (1970) study on the steenbras, *Lithognathus auret*. Nothing was known regarding the species composition of the invertebrate fauna.

Unfortunately during the course of this survey a short list of marine animals, randomly collected at Sandvis was published (Stuart 1975). The work has many inaccuracies and areas are vaguely defined. This is especially true of the beach which includes items washed up. Most serious however, is that in the mollusc list certain species are listed as dead shells, implying, to anyone not familiar with the area, that all other animals were collected alive in the habitats listed. This is certainly not always true. Among other dubious records Stuart lists Ostrea atherstonei Newton from the sand bar. For a living animal this would be both geographically and ecologically an exceptional record. We believe this record to refer to dead, beach rolled valves of *Hinnites* sp. which are common on the sand bar but having their origin well away from Sandvis.

The present faunal list records intertidal and benthic invertebrates and aquatic vertebrates. In addition parasitic animals and some of the larger planktonic invertebrates are listed but no attempt has been made to include the copepods and other smaller zooplankton. Birds, although in many cases, important in the marine ecosystem of the area, are not included. A detailed report on the birds has recently been published (Berry & Berry 1976). In all cases only material collected alive, and seen by us is listed.

2 COLLECTING AREAS AND METHODS

2.1 Hard substratum

The main hard substratum consists of three ridges of rock projecting from the dunes and exposed at low water. Other hard substrata for settling organisms are an iron cylinder north of the rocks, and the old wreck site to the south. This last consists of a scattering of iron work, bricks, bottles, cattle bones etc., lying between H.W.N. and L.W.S. It is assumed that these are connected with the illfated meat factory. In certain areas a secondary hard substratum fauna occurs where animals have settled on large *Perna* which themselves are anchored in mud or sand.

2.2 Sand

Coarse sand of marine origin occurs on the beach to seaward of the sand bar and in places on the lagoon side of the bar, especially in the region where the current mouth is. In the mouth area and outside the bar the sublittoral sand is very hard packed, probably by a combination of wave action and scour on the ebbtide.

Finer sand originating from the dunes occurs along much of the eastern edge. At the southern end, wind blown sand of dune origin forms a low ridge between the pan and the lagoon and overspills into the lagoon due to the prevailing wind.

2.3 Mud

In the main lagoon mud occurs wherever the depth exceeds about 2 metres L.W.S. These areas are referred to as green mud, the bottom consisting of very soft mud matted together with the tubes of amphipods of two species of *Amphithoe*.

The northern portion of the lagoon forms extensive mud flats exposed at low water except for semi-isolated pools and drainage channels. The higher portions of the mud banks are covered with dense growths of *Arthrocnemum* and *Sporobolus*, the former sheltering vast numbers of *Assiminea* snails. Unlike the green mud areas, this mud is very hard packed and often contains large numbers of dead bivalve shells, especially *Destria* and *Lutraria*.

2.4 Sand-mud mixtures

There are extensive areas of the lagoon where the depth is less than 2 metres L.W.S. Most of these areas consist of sand-mud mixtures. The physical constitution of the substratum varies in different areas due to influence of scour action, aeration and sand/mud ratios. This has resulted in differences in the dominant fauna of the different areas. They have been named for their dominant faunal constituent. (Map 3).

2.5 Shell

At the southern end, and to the south of the large Eastern bank there are areas of dead shell, mostly *Dosinia*. These are presumably the results of earlier mass mortalities.

Wherever possible collecting was done by hand, either directly on hard substratum or by means of digging and sieving on soft substrata. Below L.W.S. most collecting was done by dredging from a dinghy. Fish were collected by gillnetting, seining and hand nets, depending on habitat.
Map 3.

3 ACKNOWLEDGEMENTS

The survey was initiated by the Director of Nature Conservation and Tourism with the active co-operation of his staff. We especially acknowledge the help of Messrs. John Dixon and Charles Clinning, who, if not "hewers of wood and drawers of water," certainly provided these two very necessary items along with whole-hearted co-operation in many ways.

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The paper is published with the permission of the secretary to National Education.

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STUART C.T.

SPECIES LIST

SPECIES

MOLLUSCA
GASTEROPODA

Assiminea cf. stenesis Neville
Bulla digitalis Meusechen
Bulla laevissima (Gmelin)
Epitaphium kraussi (Nycti)
Gibbula benzi (Krass)
Litortina knysnensis Philippi
Marinula irishanensis Connolly
Melampus ocellatus Morelet
Nassarius koehni (Danker)
Nassarius plecost tus (Adams)
Natica vitana Gmelin
Patella granatina Linnaeus
Patella granollaris Linnaeus
Siphonaria capensis Quay & Guimard

MOLLUSCA
Pelecypoda

Aulacomya ater (Mollina)
Charonia variegata Lamarck (Krauss)
Donax serrata (Chermitz)
Dosinia lupinus Linnaeus
Gastropods motadous (Gmelin)
Gregarrella barbatula (Cuvier)
Leporimela lanikei (Dunker)
Lutraria leitaria (Linneaus)

OCCURRENCE AT SANDVIS

Very abundant in northern weed-flats, especially in Arthrocnemum
Taxonomic position very uncertain
On sandbar at lagoon mouth
On sandbar at lagoon mouth; dredged from mud in channel near mouth
Present in Perna area near mouth, 8 m
Fairly common in Perna area near mouth, 8 m
Juveniles abundant on rocks, adults abundant in weeds at northern end
Common in weed beds at northern end
Common in sand/mud at bases of weed, especially Arthrocnemum
Fairly common in starfish area; common in channel near mouth; in mud around rocks
Fairly common starfish area
Common in mud around rocks; dredged from mud in channels and from Perna area
Present on rocks
Fairly common on rocks
Abundant on rocks

DISTRIBUTION

Natal to Port Alfred; Hong Kong; Sumatra
Port Elizabeth to Lüderitzbucht
Port Elizabeth to Lüderitzbucht
Natal to False Bay; Mōwe Point; Bain des Tigres
East London to Saldanha Bay
Natal to Rocky Point, S.W.A.
Campe Bay, Cape; Tristan da Cunha; Gough Island; Dassen Island;
Port Alfred to False Bay
Port Alfred to Table Bay; Rocky Point, S.W.A.
Table Bay to Muizenbodes
Morocco to Senegal
Agulhas to Rocky Point, S.W.A.
Zululand to Muizenbodes
Natal to Rocky Point, S.W.A.
Persea pernii (Linnaeus)  Abundant on rocks; many juveniles on algae at 8 m; in mud channel at northern end and in starfish area
Petricola bicolor Sowerby  Fairly common amongst barnacles on rocks in rusty iron ruins of wreck
Semiaulax algatus (Gould)  Abundant on rocks; on algae at 8 m
Tapes corrugata (Gmelin)  Common on sandbar at mouth; in mudflats at northern and southern end; rare on rocks; fairly common in starfish area and amongst algae
Telfinia trilobata Gmelin  Present on sandbar at mouth; fairly common on sea-beach

BRACHIOPODA
Discinella tenella (Sowerby)  Present on rocks; abundant in Perna area

ECHINODERMATA
Amphipholis squamata (Delle Chiaje)  Fairly common in starfish area
Asteroidea bufo Gisbert  Abundant in channel and starfish area, present on Perina in channels
Ophiochis trigalica Millier  Fairly common in starfish area
Pachyactis angulatus (Lea)  Fairly common in starfish area

ARTHROPODA INSECTA
Heteroctopus peringueyi Grouvelle  Abundant in super layer of mud/organic detritus in northern mud flats

POLYCHAETA
Boccardia polymorpha (Haswell)  Abundant in crevices in rocks and in mud flats at low tide
Cirropiasa tentaculata (Moniag)  Abundant in mud banks at northern and southern end
Dispatia melapiotana neopallotana  Abundant in northern and southern mud flats; from mouth to sand dune basins
Dolichonea sanguinea Oersted  Common in starfish area
Glycera tridacynila Schmarda  Present in mud banks

Harmonia anomala Oesqueta (Kinberg)  Fairly common in starfish area
Limbrinora terrara (Schmarda)  Present in Perua area
Nephtila kowchegi Savigny  Common in southern mud banks, and sand bank close to sea beach
Nereis (Nentheus) victoria Fry & Leuckart  Fairly common in Perina and starfish areas
Nereis (Nereis) fala  Common in mud banks
Quatrofages  Present in Perina area
Pseudos supplied Schmarda  Present in Perina area
Phyphiletoea crassicauda (Marenzeller)  Fairly common in northern mud banks
Phyphiletoea schmardel Day  Present in Perina area; fairly common in starfish area
Platyconus demeli (Audouin & Edwards)  Common amongst Perina on rocks
Pseudonereis voriatega (Grube)  Taken in plankton
Solenopsis squamata (Muller)  Taken in plankton
Sclopetes (Sclopetes) sp.  Present in Perina area
Syllidae armata Quatrefages  Present in Perina area

Mocambique to Table Bay; Yzerfontein; Mocambique to Mocambique; Mediterranean; West Africa; Brazil; Straits of Magellan; Red Sea
Ishoqua Island to Walvis Bay
Mocambique to Angola; Ongra Fria, S.W.A.; Ecuador; Chile; Juan Fernandez Island
Natal to Rocky Point; Mediterranean; West Africa to Angola
Port Alfred to False Bay; Saldanha Bay
Walvis Bay to Mowe Point; Chile; Peru
Mocambique to Luderitzbucht
Luderitzbucht to Torra Bay
East London to Luderitzbucht
Zululand to Rocky Point
Port Alfred to Olifants River
Cape to S.W.A.; Subantarctic; Australia; New Zealand; Japan; Mediterranean; Europe
Mocambique to S.W.A.; Europe to West Africa; Indo-Pacific
Natal to S.W.A.; Mediterranean
Mocambique to Cape; Rocky Point; cosmopolitan in tropical and temperate waters
Mocambique to S.W.A.; Mediterranean to West Africa; Tristan da Cunha; Madagascar; Persian Gulf; Japan
Natal to S.W.A.
Natal to S.W.A.; cosmopolitan in tropical and temperate waters
Natal to S.W.A.; Norway; Mediterranean to Angola
Natal to S.W.A.; North Sea; North and South Atlantic; Pacific
Natal to S.W.A.; Mediterranean to West Africa; Madagascar
Natal to S.W.A.; Madagascar; Australia; Chile; California to Alaska
Mocambique to Rocky Point; Indo-Pacific
False Bay
Natal to S.W.A.; cosmopolitan in tropical and temperate waters
Mocambique to S.W.A.; circumtropical
Mocambique to S.W.A.; Mediterranean to West Africa; Indo-Pacific
Cape to S.W.A.; Mediterranean to West Africa
POLYZOA

Electra verticillata
(Lamouroux)

Abundant on algae on Perna
East London to Rocky Point

PORIFERA

Ciocalyptus alleni de Laubenfels

Abundant in patches in southern shallow end of lagoon
Durban to Lüderitzbucht

Hymaniasodon perlvis (Montagu)

Common on rocks and amongst ruins of wreck
East London to Lüderitzbucht

CRUSTACEA

CIRRIPEDIA

Balanus amphitrite Darwin

Common on rocks and in Perna area near mouth
Mocambique to Cape

Chthamalus dentatus Krauss

Abundant on rocks
Mocambique to Cape; Lüderitzbucht to tropical West Africa

CRUSTACEA

CUCUMACEA

Upicaeus caparti (Page)

Common in plankton; taken from stomach contents of Argyrosoma
Walvis Bay plankton

CRUSTACEA

MYSiDACEA

Mecopodopsis slabberi van Beneden

Common in plankton; taken from stomach contents of grebe and Trachurus
Transkei to Lüderitzbucht

CRUSTACEA

LEPTOSTRACA

Nebalia capensis Barnard

Fairly common in algal area; taken in plankton
False Bay to Orange River Mouth

Nebalia illuensis Kensley

Taken from stomach contents of Argyrosoma
So far known only from Sandvis

CRUSTACEA

COPEPODA (Parasitic forms only)

Brochoclista lithognathus
Kensley & Grindley

From Lithognathus aureti
Table Bay; Rocky Point

Caligus exanthelidus Barnard

From Mugil cephalus; Hypanus annula; free-swimming in plankton
Port Elizabeth

Caligus sp.

On Diplognathus torquus; Lithognathus aureti; Argyrosoma holoepistoma
Durban to Table Bay

Pandarina bicolor Leach

From Triakis megalopterus

CRUSTACEA

ISOPODA

Eurydice longicornis (Studer)

Common in sea embayment where new mouth is forming
False Bay to Lüderitzbucht

Exosphaeroma linnulatum
(Hecker)

Between mytilids on rocks
Cape Peninsula to Lüderitzbucht

Idiaecus indica H.M. Edwards

Present amongst algae 8 m
Table Bay to Rocky Point

Nereocila orbignyi
(Gautier-Menecelle)

Free swimming in plankton; parasitic on Mugil, Thysites
Agatha to St. Helena Bay; North Africa

Niaamla tranacca (Brandt)

Abundant in Arthroscyam and other weed patches under bushes along shore
Port Elizabeth; southern Cape; Namibianland; Walvis Bay; Okahandja

Pontogelodes latipes
Barnard

Free-swimming in pools; burrowing in detritus; common in sand at sand dune bases
Mocambique to Walvis Bay

Tylus granulatus Krauss

Common on sand dune beaches, and on inner (land) side of sea beach sandbar
Cape Point to Möwe Point
CRUSTACEA

AMPHIPODA

Amosella macragnathalma
(Costa)

E                                                                   
Fairly common in Perna area
Abundant in mud flats, especially
below low tide level
Abundant in mud flats, especially
below low tide level
Fairly common in starfish area
Abundant in Perna area, in sponge
Cleopatra and in starfish area
Abundant in starfish area and Perna area; fairly
common in sponge Cleopatra
Abundant in Perna area
Common in Perna area
Common on sand dune beach

ABUNDANT IN Perna AREA

Port Elizabeth to S.W.A.; Indo-Pacific
False Bay to S.W.A.

Mozambique to S.W.A.: austral
Mozambique to S.W.A.; cosmopolitan
Mozambique to S.W.A.; Atlantic
Mozambique to Olifants River; circumtropical
Natal to S.W.A.
Saldanha Bay to S.W.A.
Natal to S.W.A.; austral
Port Elizabeth to S.W.A., Indo-Pacific
False Bay to S.W.A.

CRUSTACEA

DECAPODA

Hymenosoma orbitale
Desmarest

Macrostephanus africana (Balon)

Nastillioecystes ocellata
(Gray)

Oreilipes punctatus
(de Haan)

Palaemon (Palaemon) pacificus
Simpson

Palaemon (Palaemon) pacificus
Simpson

Palaemonetes pulchellus (Poeppig)

Upogebia euphron
(Krauss)

ABUNDANT IN MUD-BOTTOM AREAS, IN Perna
AND STARFISH AREA, IN WOOD POSTS,
IN Arthroperamum patches
Fairly common in channel near mouth
From Mustelus gut (probably does
not occur in lagoon)
From Mustelus gut; fresh dead
specimens washed ashore
Abundant in algal area and northern
channel
Abundant in algal area and northern
channels, common in night plankton
Partly common amongst mysids on
rocks, in algal area
Fairly common amongst rusty ruin
of week

Present in Perna area
Abundant in Perna and especially starfish
area, and on rocks
Common around rocks
Present in plankton
Present in plankton

COELENTERATA

Aglaophenia plumula dichotomy
(M. Sars)

Amblyodon simpsoni
(Verrill)

Bunodosoma capensis (Lesson)

Kellikerina cf. fasciculata
(Pern & Lessur)

Platybranchus sp.

VERTEBRATA

PISCES

Chondrichthytes

Mustelus mawiius
(Linnaeus)

Triakis megalopterus
(A. Smith)

Rhombates bimini
Muller & Henle

Myliobates aquila (Linnaeus)

Dasyatis pastinacea (Linnaeus)

Caudorhynchus capensis Dumeril

OSTEICHTHYES

Engraulis capensis
Globispira
Sardinae areolata
(Pappe)

Common over bank. Usually gravid ♀ ♂
Less common than preceding species.
Again usually gravid ♀ ♂
Abundant in all shallow areas
Seasonally abundant in midwater
Shallow water over banks. Uncommon
Rare

Small schools of juveniles
occasionally in lagoon
Not Common

E. Atlantic
South Africa, S. Angola
E. Atlantic
England to South Africa
Baltic to South Africa
South Africa

South Angola, Cape
South Angola to Natal
Tetrahyurus feliceps
(Valenciennes in C & V)
Lethia amia (Linnaeus)

Trachurus trachurus
(Linnaeus)

Pomatomus saltator (Linnaeus)
Argyrotaenia hololepidotus
(Linnaeus)

Diplodus sargus Linnaeus
Lithognathus areolatus Smith
Lithognathus lithognathus
(Cuvier in C & V)

Thyrephora atropurpurea
Magellanicus Linnaeus

Liza Trachinops
(Smith)
Liza richardsoni A. Smith

Hypostomus breviceps
(Cuvier in C & V)
Gobius rufescens
Cuvier in C & V

Blemius cornutus Linnaeus
Clupeus superciliosus Linnaeus
Trigata sp.
Opistodus serpens Linnaeus

MAMMALIA

Arctocephalus pusillus
(Schreber)
Cephalorhynchus bairdii
(Gray)

Rather rare in shallow areas
Pelagic. Always present, possibly an isolated population
Always present but numbers vary

Pelagic, rather rare in Sandvis
Common in midwater
Abundant over sand banks
Abundant over banks and midwater
Only found once (Penrhith 1977)

Pelagic, only young found
Rare in main lagoon, abundant adults and juveniles found in pools and gullies
Rare
Large schools in main lagoon, juveniles in shallows
Common in shallow areas. Important food of predators
Channels of N. mud flats, between Perna, wreck site
Common at wreck site, and Perna
Rocks and dredged at Perna
Juveniles very common at times
Common in mud banks

Varying population of young adults
Based on sight records of 1 pair

South Angola to Natal
Europe to South Africa, very rare on S.W.A. coast
There is confusion over the name of this species. juveniles, cupressis, trachurus have all been used.
Cosmopolitan (missing inshore on W. coast)
Congo to Mozambique

Mediterranean to W. Indian Ocean
Cape Frio to Luderitz
Sandvis to S. Mozambique

Circumglobal in S. temperate waters
Circum-Tropical

Sandvis to Natal, Possibly a synonym of L. narutau Kino
S. Angola to South Cape
Cape Cress to St. Lucia

Cape Cross to Natal
Rocky Point to Kei River
Cosmopolitan

S. Angola to E. Cape
Southern hemisphere
The digestive enzymes of some psammophilous tenebrionid beetles from South West Africa

by

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Margherita Turchetto Lafisca

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University of Padova.

1 INTRODUCTION

This investigation evaluates the role of terrestrial invertebrates in the process of degradation and secondary humification of litter. This process is known particularly in many temperate, humid and moderately humid environments but little is known about desert species. We have assessed the action of the digestive enzymes of some Namib Desert tenebrionid beetles. (Onymacris plana Pet., O. laeviceps Gebien, O. rugatipennis Haag and Physosterna g. globosa Haag), feeding on dead vegetation.

The natural history of these species is summarised below:

1.1 Onymacris plana

Lives on sand dunes and about perennial grasses and the Narra plant, Acanthosicyos horrida in the Namib Desert, south and west of the Kuiseb River (Koch, 1961, 1962; Helmut and Edney, 1973). It is a common tenebrionid of dunes and less common in the flat interdune valleys and is sometimes found on the dune crests. It is mainly a summer species, though it is present all through the year. Strictly diurnal, it runs rapidly on the hot sand. It is omnivorous and feeds mainly on vegetal debris, but also on green plants and dead animals. In the summer it is present during intervals when it can maintain body temperatures below 44°C.

1.2 Onymacris laeviceps

Is also an inhabitant of sand dunes. It is diurnal to crepuscular and also mainly a summer species. Its habitat and food habits are similar to those of O. plana, although this species spends more time foraging at the base of dune slipfaces. This insect occasionally climbs into the thorny grass Stipagrostis subulata and feeds on its seeds.

1.3 Physosterna globosa

This is a typical example of river inhabiting beetles on the margins of the Namib dunes. It is common along river-beds, floodplains and occasionally occurs on the gravel plains. In this respect it differs sharply from Onymacris plana which exclusively inhabits niches of the dunes. In some habitats Physosterna globosa and Onymacris rugatipennis are sympatric, e.g., the Kuiseb riverbed and the reddish sand, are consolidated and more vegetated marginal dunes at the eastern fringes of the central Namib. These are the typical habitats for O. rugatipennis and the closest habitats of P. globosa to the true Namib dune. The feeding habits of P. globosa have adjusted to the available organic material as have those of the dune species. All of them apparently feed on any debris available, from drifted and dry plant debris to dead animal materials. As the habitats of P. globosa and O. rugatipennis are richer in all these materials, food is more plentiful and the selection wider. Both P. globosa and O. rugatipennis are abundant in summer and strictly diurnal with an activity cycle similar to that of O. plana, which is not usually found in the river bed.
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Figure 1: Thin-layer chromatography of reduced sugars

1-blank of cellulobiose; 2-blank of maltose; 3-blank of melibiose; 4-blank of lactose; 5-\textit{Onymacris plana} + cellulobiose; 6-\textit{Onymacris plana} + maltose; 7-\textit{Onymacris plana} + melibiose; 8-\textit{Onymacris plana} + lactose; 9-\textit{Physosterna} g. globosa + cellulobiose; 10-P. g. globosa + maltose; 11-P. g. globosa + melibiose; 12-P. g. globosa + lactose; 13-\textit{Onymacris laevicpes} + cellulobiose; 14-\textit{O. laevicpes} + maltose; 15-\textit{O. laevicpes} + melibiose; 16-\textit{O. laevicpes} + lactose
a - melibiose; b - lactose; c - cellulobiose; d - maltose; e - galactose; f - glucose.

Separation on Kieselgel 60 buffered with 0.1 N boric acid. Solvent: butanol + acetone H$_2$O (40 - 50 - 10). Indicator: 20% sulphuric acid + 0.2% ethanol solution of naphthoresorcinol (v/v) heated to 100-105°C for 5-10 minutes.

2 METHODS

For the extraction of digestive enzymes, the whole digestive tract was used. It was ground in a crucible with quartz sand and distilled in water at 4°C. We thus obtained both exo- and endoenzymes, contained in about 10 mg of fresh tissue per 1 cm$^3$ of water, which represents a high concentration of standard enzyme units.

In order to demonstrate the enzymatic action on oligo- and polysaccharides, Fehling's reagent was used for all non-reducing saccharides, whereas chromatography was employed for the reducing substances (Figure 1). Here we used ascending thin-layer chromatography, on plates of Kieselgel 60, buffered with 0.1 N boric acid and activated at high temperature. The solvent was butanol/acetone/water (40/50/10). Staining was accomplished by means of a solution of 20% sulphuric acid and 0.2% alcoholic solution of 1:3 dihydroxy-naphthalene (naphtho-resorcinol) (v/v) and heated to 100-105°C for 5-10 minutes. For the determination of N acetyl-glucosamin, the product from splitting of chitin, the method described by Aminoff (1952) was used. For quantitative detection of the amino acids, obtained acids, we used a method by which formaldehyde reacts with the amino groups so that the existing carboxylic groups can be titrated. For oils, beeswax and tributyrin we used bromothymol blue as an indicator. When enzymatic attack occurs the colour change shows an increase in acidity of the solution, owing to the formulation of fatty acids. For the different kinds of cork (common cork, or \textit{Quercus suber} cork, birch cork and maple cork) the production of succinic acid was taken into consideration, which gives the solution an intense dark colouration.

All the determinations were made by incubating the intestinal tract and the substrate for 24 hours at 37°C. For oligo- and polysaccharides a pH equal to that of the digestive extract of the different beetles was maintained (ranging from 5.2 to 5.8), since our previous research has shown that the optimal pH for the digestion of carbohydrates is slightly acid. In contrast, for proteases and esterases the determinations were done at pH 7.5.

3 RESULTS AND DISCUSSION

The results are presented in tables 1, 2 and 3.

As far as oligo-saccharides are concerned, both \textit{Onymacris} and \textit{Physosterna} show a remarkable digestive activity in comparison to all the assayed black beetles so far, some of which come from arid environments, such as Israel, Arizona, Sicily, etc. (cfr. Maruzzi and Turchetto 1975: Maruzzi and Turchetto, in press). They seem therefore, to possess $\alpha$- and $\beta$-glucosidases, fructosidases and $\alpha$- and $\beta$-galactosidases, with the exception of \textit{O. plana} and \textit{O. rugatipennis}, which appear not to possess an $\alpha$-galactosidase, since they do not split melibiose, while \textit{O. rugatipennis} digestion does not even attack raffinose. These results are consistent with our previous observations on different tenebrionids, which are easily able to break down di- and trisaccharides.

The polysaccharides as a whole seem to be less well digested, except glycopycin which is first broken down by an amylase and then by an $\alpha$-glucosidase into glucose, as we have shown. Among the species considered, only \textit{O. laevicpes} is able to utilise a broader alimentary system, compared with the other species, since it demonstrated an enzyme activity on all the polysaccharides we assayed. This species is able - within limits - to digest cotton, rayon and filter paper, which suggests the existence of an holocellulase. The ability of the animal to split several kinds of holocellulose in the presence of bacteriostatic substances, such as tolune and thymol, which were always included in the substrate, (already used with success by Zinkler 1971; Nielsen 1962; Parkin 1940; Ripper 1930, etc.) can be attributed to the presence of a true animal cellulase. The phenomenon has so far never been demonstrated in tenebrionids, and is, moreover, very rare in the animal kingdom (cfr. also Monsour & Monsour-Bek, 1934).

Among the proteins we assayed, only gelatin, salmin and albumine were consistently broken down by our species: \textit{O. laevicpes} is able to break down elastin and sericine as well. A remarkable digestive ability in \textit{O. laevicpes} is also shown as far as oils, vegetal esters, beeswax and tributyrin are con-
cerned. Only *O. rugatipennis* seems to possess very few esterases in which it differs from the other species.

We are not able at the present stage of research to say whether this feature can be correlated with ecology of the various species. Further research both in the laboratory and in the field should prove to be very rewarding.

<table>
<thead>
<tr>
<th>TABLE 1: Enzymatic action on oligo- and polysaccharides</th>
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</thead>
<tbody>
<tr>
<td><strong>OLIGO- AND POLYSACCHARIDES</strong></td>
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<tr>
<td></td>
</tr>
<tr>
<td>Trehalose</td>
</tr>
<tr>
<td>Sucrose</td>
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<tr>
<td>Cellobiose</td>
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<tr>
<td>Maltose</td>
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<tr>
<td>Melibiose</td>
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<tr>
<td>Lactose</td>
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<tr>
<td>Arbutin</td>
</tr>
<tr>
<td>Salicin</td>
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<tr>
<td>Mellezitose</td>
</tr>
<tr>
<td>Raffinose</td>
</tr>
<tr>
<td>Starch</td>
</tr>
<tr>
<td>Glucogen</td>
</tr>
<tr>
<td>Cotton wool</td>
</tr>
<tr>
<td>Rayon</td>
</tr>
<tr>
<td>Gaize</td>
</tr>
<tr>
<td>Carob</td>
</tr>
<tr>
<td>Ivory nut</td>
</tr>
<tr>
<td>Chitosan</td>
</tr>
<tr>
<td>Chitin</td>
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<tr>
<td></td>
</tr>
<tr>
<td><strong>Oryctes plan</strong></td>
</tr>
<tr>
<td><strong>Oryctes rugatipennis</strong></td>
</tr>
<tr>
<td><strong>Oryctes lacteolus</strong></td>
</tr>
<tr>
<td><strong>Physosterna gibbona</strong></td>
</tr>
</tbody>
</table>

Di- and trisaccharides, arbutin, salicin, starch and glycogen are pure substances; cotton wool is pure holocellulose; rayon is regenerated cellulose; gaize is hydrocellulose treated with H₂PO₄ (not present in nature); carob is a galactomannan extracted from carob seeds (*Cercidium microphyllum*); ivory nut is a marmalade of *Phylophalus microcarpa* seeds, consisting of mannose A (97.6%) and mannose B; chitin and chitosan were extracted from the beetles' elytra.

<table>
<thead>
<tr>
<th>TABLE 2: Enzymatic action on proteins</th>
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</thead>
<tbody>
<tr>
<td><strong>PROTEINS</strong></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Gelatin</td>
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<tr>
<td>Casein</td>
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<tr>
<td>Salmiin</td>
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<tr>
<td>Elastin</td>
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<td>Fibroin</td>
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<tr>
<td>Sericin</td>
</tr>
<tr>
<td>Albumin</td>
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<tr>
<td></td>
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<tr>
<td><strong>Oryctes plan</strong></td>
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<tr>
<td><strong>Oryctes rugatipennis</strong></td>
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<tr>
<td><strong>Oryctes lacteolus</strong></td>
</tr>
<tr>
<td><strong>Physosterna gibbona</strong></td>
</tr>
</tbody>
</table>

All chemically pure substances were used with the exception of elastin (prepared and purified by the Institute of Anatomy of this University), fibrin and sericin (obtained from silk worm cocoons by means of a prolonged solubilization). The gelatin used is that employed in photographic plates; these are exposed to digestion and then developed to reveal the degree of enzymatic attack on the gelatin.

<table>
<thead>
<tr>
<th>TABLE 3: Enzymatic action on oils and esters</th>
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</thead>
<tbody>
<tr>
<td><strong>OILS AND ESTERS</strong></td>
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<tr>
<td></td>
</tr>
<tr>
<td>Olive oil</td>
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<tr>
<td>Grape seed oil</td>
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<tr>
<td>Corn oil</td>
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<tr>
<td>Peanut oil</td>
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<tr>
<td>Sunflower oil</td>
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<tr>
<td>Soy bean oil</td>
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<tr>
<td>Linseed oil</td>
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<tr>
<td>Castor oil</td>
</tr>
<tr>
<td>Oak cork</td>
</tr>
<tr>
<td>Birch cork</td>
</tr>
<tr>
<td>Maple cork</td>
</tr>
<tr>
<td>Bee wax</td>
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<tr>
<td>Tributyrin</td>
</tr>
</tbody>
</table>

We used pure, refined oils; the corks are raw, natural substances; the beewax is crude i.e. a complex mixture of cerotic, melissitic and palmitic acids, linked with melissic and celtic acids.

4 **ACKNOWLEDGEMENTS**

Thanks to the kindess of Dr. M.K. Seedy, Director, Desert Ecological Research Unit, Walvis Bay and of Dr. E. Endrody-Younga, Senior Professional Officer of the Transvaal Museum, Pretoria, we have been able to carry out this research.

Permission to conduct this study was granted by the Nature Conservation Division, Administration, South West Africa.

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MARCUZZI, G. and TURCHETTO, M.

NIELSEN, C.D.

PARKIN, E.A.

RIFFER, W.

ZINKLER, D.
Paleowind directions in the Central Namib Desert, as indicated by ventifacts

by

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Abstract

Ventifacts cut from dolerite boulders are exposed along the flanks of the Swartbankberg in the Central Namib Desert. Approximately 93 per cent of all ventifacts studied have facets indicating that the dominant sand-bearing wind has been from the north-east. It is therefore, concluded that this wind has played some part in preventing the extension of the Southern Namib dunes across the rock platform of the Central Namib.

1 Introduction

The main dunes of the southern Namib Desert trend approximately south to north, and extend northwards as far as the Kuiseb River which forms a sharp boundary of the dune field (Map 1). Goudie (1972) lists five main hypotheses which may account for why the dunes terminate so abruptly at the Kuiseb channel:

1. Big dunes move so slowly that the almost annual floods of the Kuiseb remove sand encroaching into the channel and only at the coast, which the river rarely reaches, can sand drift further northwards;
2. Rare northerly winds of high velocity play a role in keeping dunes from crossing the River;
3. A large volume of sand would be required to fill the river bed and this would require a considerable period of time;
4. It is possible that the dunes are still growing northwards and that their northern boundary coincides purely fortuitously with the Kuiseb River;
5. The River may have shifted its course northwards under the influence of the advancing dunes.

It is difficult to test these hypotheses in the absence of long-period records but the presence of ventifacts in parts of the Central Namib suggests that some indication of the direction of dominant sand-bearing winds may be obtained. On the open gravel plains north of the Kuiseb River many quartz pebbles appear to have been polished smooth, and are not faceted, by sand abrasion, and the pebbles derived from the common schists weather too rapidly to preserve evidence of abrasion by wind-driven sand. In the area of the Swartbankberg and Hamilton Range, however, dolerite dyke rocks and, more rarely, some marble boulders preserve evidence of wind-cut facets and oriented excavation pits (Allen, 1971). Experience in Antarctica (Selby et al., 1973) has shown that ventifacts are usually aligned so that the abraded facets face the direction of the wind which was responsible for their formation. If, therefore, the facets of ventifacts are found to have a uniform alignment it can be assumed that these facets indicate the direction of a dominant sand-bearing wind, and it seems probable that this same wind would be a dominant one in transporting sand in neighbouring dune fields.

2 Swartbankberg Ventifacts

The hills of the Swartbankberg and Hamilton Range are composed of marbles and schists of the Precambrian Damara System (Smith, 1962). The rocks have the same general strike as the trend of the hills and are intruded by younger dykes of fine-grained dolerite. Few of the dykes extend to the edges of the hills and into the plain where a sand supply for wind abrasion exists, but on the northern end of Swartbankberg one...
The results of the traverses are given in Table 1, which indicates clearly the importance of north-easterly winds for carrying abraded sand, for approximately 93 per cent of the boulders sampled have facets facing that direction. Confirmation of this evidence was obtained from a dyke in one of the hills in the centre of the Hamilton Range and from a number of marble boulders, which bear facets and aligned excavation grooves. No evidence was found which conflicted with the trend indicated by the ventifacts on Swartbankberg.

3 CONCLUSION

There seems to be little doubt that winds from the northeast have been, and are still, very important in the transport of sand. There is no available evidence to suggest how long it takes for a dolerite boulder to be faceted by the wind, but it is probably thousands of years. It seems likely therefore, that the northeast wind has been effective for at least much of Holocene time and has played some part in preventing sands of the main dune field from crossing the Kuiseb River and invading the gravel plains of the Central Namib.
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Plate 1. Typical ventifacts from Swartbankberg.

physical

Plate 2. A marble boulder showing evidence of ventifact and excavation pits.
4 ACKNOWLEDGEMENTS

I am indebted to Dr. Mary Seely, Director of the Namib Desert Research Station, Gobabeb, for her hospitality and help in completing this work, and to the University of Waikato for study leave and financial assistance.

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SMITH, D.A.H.,
Aspects of the geomorphology of the Kuiseb River, South West Africa

by
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University of Fort Hare
Alice, Cape Province

Abstract
Geomorphological aspects of the Kuiseb river catchment in central South West Africa are analysed. The characteristics of the Kuiseb drainage are compared with other Atlantic drainage systems in terms of pattern and discharge potential. The detailed morphology of Kuiseb longitudinal and cross profiles, derived from map analysis, are scrutinised and relevant terrace deposits are considered in an attempt to elucidate a sequential history for the catchment.

1 Introduction
The Kuiseb-Gaub drainage system, a component of South West African Atlantic drainage, rises in the Khomas Highlands to cross the central Namib desert and reach the coast near Walvis Bay (Map 1). The siting of the Desert Ecological Research Unit at Gobabeb on the north bank of the middle Kuiseb river has resulted in considerable research effort being expended in the middle Kuiseb catchment, but no overall synopsis of the catchment geomorphology is, as yet, available. This paper outlines the characteristics of the Kuiseb drainage system as compared with other central Namib drainage components. Salient geomorphological features of the middle Kuiseb valley between Hudaob and Rooibank are emphasised.

2 The Kuiseb System as a Component of Atlantic Drainage
2.1 Drainage patterns
The watershed between Atlantic and Kalahari drainage lies east of the Escarpment, approximately along the longitude of Windhoek (17°E) in central South West Africa. Further south the watershed between the Namib endoreic drainage and the captured Fish-Orange system trends further west along latitude of 16°E (Map 1). Drainage has been pronounced consequent on post Jurassic continental break up and to have undergone subsequent modification by capture (Mabbutt, 1955). Atlantic drainage has been affected by periodic uplift, marginalised in the Escarpment zone, with the concomitant necessity to extend courses seaward.

North of the Kuiseb river, the prevailing alignment is west south west, whereas to the south, the trend becomes more generally due west (Map 1). By comparison, the orientation of the Kuiseb-Gaub system appears distinctly anomalous. From its source to Hudaob, the Kuiseb river is aligned southwest. The direction alters abruptly westward at Hudaob. From Homeb a northerly component is added and downstream of Gobabeb the alignment changes again to become northwest between Swartbank and Walvis Bay. Delta course alteration also to the northwest, downstream of Rooibank, has been documented for the historic period since 1885 (Stengel, 1970). It has also been suggested that a progressive northward shift of the entire lower Kuiseb downstream of Gobabeb has occurred over a longer time span, that the Kuiseb river originally flowed west to Conception Bay (van Zyl, unpub.). Advancing dunes, attendant on aridification in the late Cenozoic period have been cited as the controlling mechanism for these shifts (Wienecke & Rust, 1973).
The course pattern of the Kuiseb river requires explanation. The Hudaob bend is now constrained by structural weaknesses in the basement rocks, as in detail is much of the bedrock upper course. Furthermore the seaward extension of all river systems following emergence might explain changes in direction coastwards. Although both factors have affected the Kuiseb system, they are not unique to it, yet the anomaly is confined to its catchment. Localised warping may have been significant and river capture has also been postulated on little evidence. Changes in discharge affect river pattern but climatically induced drainage changes are also unlikely to be restricted to a single catchment. The Kuiseb-Gaub drainage pattern is a legacy of its past evolution, for which a detailed explanation cannot be offered at present.

2.2 Discharge characteristics

Even in the highland zone few rivers flow perennially in South West Africa. Between 22° and 29°S only the Omururu, Swakop-Khan and Orange rivers are able to maintain courses to the Atlantic. Other systems cease to flow where evaporation exceeds discharge and end in vleis, either on the gravel plain like the Tubas river, or among dunes, as is the case of the Tsodab, Tsauach and Tsams rivers (Map 2). The Kuiseb-Gaub system is intermediate in character. Although normally flowing for a period annually in its middle course, discharge rarely enters the Atlantic Ocean. Since 1837 the Kuiseb river has discharged into the sea on only 14 occasions, an average of once in 10 years (Stengel, 1970). The construction of pumping works at Rooibank with direct loss by extraction now inhibits coastal discharge further. It occurs only exceptionally, as in 1963, but it is probable that given pre-1951 conditions, discharge to the sea would have occurred in 1974 and in 1976.

Discharge characteristics are a function of catchment size and precipitation patterns, on average over the catchment and in terms of seasonal distribution. Seasonal variation in totals and the incidence of high intensity storms are critical. Throughout South West Africa annual evaporation exceeds annual precipitation. Only high intensity storms, resulting in short-lived water surplus conditions, create sufficient discharge to promote channel flow. Comparative statistics for six Namib catchments have been derived from map analysis of 1:100,000 topographic and annual average rainfall map sheets (Table 1). Of these six catchments only the Swakop-Khan system maintains a course to the coast regularly. The Kuiseb-Gaub system flows through the dune barrier across its delta only periodically and the other four systems are endoreic (Map 1).

Midgley and Pitman (1969), for the North West Cape Province, have calculated that, given the evaporation rate that obtain (which may be lower than in the central Namib), discharge is minimal where annual precipitation does not exceed 200 mm (Table 1.2). Applying their expected discharge figures to the central Namib catchments, demonstrates that the two critical parameters are catchment size and area of catchment with precipitation exceeding 200 mm pa. (Table 1.1). Mean annual precipitation does not exceed 200 mm in any portion of the catchments analysed.

Long-return, large-magnitude precipitation events (storms) cause significant discharge even in the endoreic systems and lead to geomorphological changes in bed and valley forms. However extension of regular fluvial discharge downstream to affect large-scale changes in valley geometry, such as
evidenced by the terrace sequence west of Tsaondab Vlei and as postulated by Seely and Sandefurrowsky (1974) requires long-term changes in either precipitation totals or in evaporation rates or in both simultaneously. Since the catchment area in receipt of over 200 mm annual precipitation appears to be critical, relatively small amplitude changes in climate could cause significant changes in discharge regimes and in the energy potential of the rivers. The Kuiseb system's intermediate position with respect to discharge characteristics, renders it particularly susceptible to such changes.

3 THE KUISEB CATCHMENT WEST OF THE ESCRAPMENT

3.1 Catchment subdivisions

The Kuiseb-Gaub drainage system can be divided into four distinct sections on the basis of catchment characteristics and valley morphology (Map 2). East of the Escarpment in the Khomas Highlands headwater region, the highland zone, the river drains a planed bedrock plateau. The open valley is only shallowly incised into the former planation surface (Sprattizer, 1966). The margin of the highland zone is however more dissected and the valley becomes more entrenched immediately upstream of the canyon section. West of the Escarpment, the Kuiseb river demarcates the dune and gravel-pediment Namib. Dunes conceal detail of the south bank in the three sections west of the highland zone. Between the highland front and Homeb, the Kuiseb river has incised through a calcite fanglomerate into underlying bedrock. Incision, reaches its most spectacular proportions in the Kuiseb canyon, extending from the Kuiseb-Gaub confluence approximately to some 5 km upstream of Homeb. From this point downstream to Gobabeb in the lower canyon section, bedrock cliffs are visible but incision becomes progressively more open and less pronounced. From Gobabeb to Swartbank, although the river bed remains clearly defined, the valley is shallow, less than 10 m depth within rock-defined banks. Seaward of the Swartbank ridges, the valley itself becomes indistinct for the sides are formed of less coherent deposits, while below Rooibank, no valley exists. River channels are braided and create the delta overlying a recently emerged marine plain. (Fig. 1) (Davies 1971).

The four sub-sections of the Kuiseb catchment comprise a bedrock highland zone, where incision has been minimal in the core region; the main and lower canyon downstream to Gobabeb superimposed from a calcite veneered footslope; a shallow valley section between Gobabeb and some kilometres downstream of Swartbank where course shifts became apparent and the plain and delta section from Rooibank to the coast where bed changes result from every flood.

3.2 Geological components

Upstream the drainage system crosses Basement Complex rocks. Their geological variation is of significance as a control of local pattern and for the provision of load components. The

Map 2: The Kuiseb Catchment showing major subdivisions.
TABLE 1: Catchment and Drainage

(0 indicates no portion of catchment fell in zone)

<table>
<thead>
<tr>
<th>CATCHMENT</th>
<th>SWAKOP KAHN</th>
<th>KUISEB-GAUB</th>
<th>TUBAS</th>
<th>TSONDAB</th>
<th>TSAMS</th>
<th>TSAUCHAB</th>
</tr>
</thead>
<tbody>
<tr>
<td>Catchment Area (Km²)</td>
<td>30 636</td>
<td>16 896</td>
<td>2 748</td>
<td>5 780</td>
<td>2 040</td>
<td>5 572</td>
</tr>
<tr>
<td>% Catchment receiving over 200 mm pa.</td>
<td>68</td>
<td>55</td>
<td>6</td>
<td>35</td>
<td>0</td>
<td>0</td>
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<tr>
<td>% Catchment with up to 100 mm pa.</td>
<td>15</td>
<td>32</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>% Catchment in Namib (after Stengel 1970)</td>
<td>16</td>
<td>20.5</td>
<td>94</td>
<td>?</td>
<td>?</td>
<td>?</td>
</tr>
</tbody>
</table>

CALCULATED DISCHARGE (million m³)

| From over 200 mm pa. | 266.5 | 93.4 | 1.5 | 20.4 | 0 | 0 |
| From 100 - 200 mm pa. | 26.3 | 10.7 | 5.2 | 18.7 | 10.2 | 27.9 |
| From less than 100 mm pa. | < 9.1 | < 10.8 | < 3.1 | 0 | 0 | 0 |
| TOTAL | 301.9 | 115.0 | 9.8 | 39.1 | 10.2 | 27.9 |

1.2) Expected Discharge (mm) (allowance made for evaporation) after Midgley & Pitman, 1969

ANNUAL PRECIPITATION | DISCHARGE
<table>
<thead>
<tr>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>105</td>
<td>2</td>
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<td>160</td>
<td>6</td>
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<tr>
<td>220</td>
<td>10</td>
</tr>
<tr>
<td>295</td>
<td>20</td>
</tr>
<tr>
<td>445</td>
<td>50</td>
</tr>
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</table>

Basement Complex Pro-Cambrian rocks are locally concealed by calcrete sheets and other Cenozoic components which have not yet been widely reported. The importance of these Cenozoic sediments was noted by Kaiser (1923) who discussed their relationship with the older rocks in the southern Namib and similar relationships appear to obtain in the Kuseb catchment. The Pro-Cambrian Basement Complex consists chiefly of Damara System schists and marbles and Salem granite containing a high proportion of quartz and pegmatite. The older rocks have been intruded by presumed Karoo-age dolerite dykes (Clifford, 1967; Martin, 1965; Smith, 1963).

A red calcified sandrock impregnated with calcified nodules overlies the schists and granite between the Kuseb and Tsodab drainage basins and outcrops along the Kuseb valley. The sandrock appears to be of more than one age and to incorporate flat-bedded and cross-bedded sands. It is often capped and preserved by thick calcrete sheets but the full extent of the outcrop is concealed by calcrete and Namib dune sand. Thick calcrete sheets rest on planed bedrock on both banks of the middle Kuseb catchment immediately west of the Escarpment. Further downstream on the north bank the calcrete sheets rest on Basement Complex rocks and have been dissected by the close granadulla valley network. Dissection is not restricted to the dune free north bank, however. On the south bank the calcrete capping, that at Hudaob has a thickness of over 10 m, also exhibits valley dissection. These valleys are now sand filled and interrupted by dunes (Goudie 1972; Smith, 1965). The Kusseb river has apparently been superimposed from the calcrete caprock and has adjusted to flow approximately along the geological contact between sandrock and Basement Complex rocks for sandrock has been traced upstream of the Gaub confluence. Renewed incision has since stripped the sandrock to expose Basement schists underlying sandrock at Hudaob, Homeb, Osseweter and Gobabeb. The structure of the underlying Basement Complex now exerts constraints on river bed alignment in detail.

Components of the bed-load of the Kuseb river derive from the rocks outcropping in the catchment. However at present the bed material in the middle and lower Kuseb consists dominantly of re-worked dune sand from the dune field, encroaching from the south, and micaceous slits. Pebbles are rare downstream of Homeb. However, the presence of well-rounded fluvial pebbles in the calcrete caprock, indicate that past discharge was more effective than that at present. These river pebbles, being largely of quartz and quartzite, remain in the system and are re-incorporated in a number of younger sediments. They may also be reworked as terrace deposits within the present valley having been let down from altitudinally higher calcrete sheets.

3.3 The morphology of the Kuseb valley

The present morphology of the Kuseb valley is the product of interaction between geomorphological processes and past climatic events through discharge control, acting on bedrock geology. The whole of southern Africa, including South West Africa, has been affected by base-level impermanence throughout the Cenozoic period. Glacially controlled eustatic variations in sea-level have been superimposed on general but differentiated tectonic uplift. Regional warping has been presumed on the basis of the Fish River system incision and attendant capture of Kalahari drainage (Mabbutt, 1955). All western river courses are also progressively younger upstream since the coastal platform across which they pass is constituted by a series of emergent marine shelves. Progressive emergence implies progressive reduction in gradient and concomitant loss of fluvial energy. Associated with periodic desiccation, some river systems have been unable to maintain their channels to the coast throughout their evolution. The degree of rejuvenation thus varies between catchments. Although a relict suite of terraces exists downstream of the present Tsodab river endpoint, the depth of rejuvenation in that catchment is considerably less than in the Kuseb system.
Valley-in-valley profiles are characteristic, only shallowly incised upstream of the Goagis confluence but becoming progressively more pronounced in the canyon section between the Gaub confluence and Homeb. At Hudseb the entire valley depth exceeds 200 m and within this valley, the 500 m wide canyon slot has a depth of 150 m. Downstream of Homeb, although the valley-in-valley form persists, the incised valley is wider and shallower. The markedly slot-like effects of rejuvenation manifest in the localized canyon zone, may well have resulted from differential warping along the mountain front as suggested by Wieneske & Rust (1975) in another context.

Downstream of Gobabeb the valley form is far less pronounced and from Rooibank it is indistinct since the river flows across marine plains into which incision has not taken place. On such small-scale cross sections terrace details are masked. Field analysis of valley deposits between Homeb and Gobabeb, however, demonstrate that periodic incision was not sequential. Periodic changes of base level occasioned by eustatic sea level fluctuations were superimposed on tectonic uplift, resulting in phases of downcutting and an alternation of incision and aggravation.

The long profile of the Kuiseb river, similarly constructed from map data, confirms the evidence of the cross profiles (Fig. 1). Overall the long profile of the Kuiseb river, like that of many arid zone rivers, is convex. This convexity has been attributed to increasing desiccation seawards and loss of energy since an adjusted bed slope is essentially a transport slope in equilibrium with the load and energy available (Doddie, 1972; Rust & Wieneske, 1974; Stengel, 1970). Steepening may therefore, be a response to energy loss or to increased load. In detail the Kuiseb profile exhibits localized marked irregularities of gradient (Fig. 1). These variations in gradient become obvious when expressed as a histogram (Fig. 2).
The presence of at least four knick points marking risers of about 40 m, 60 m, 100 m and 200 m respectively inland can be identified.

Localised steepening upstream of Hudaob and of the Gaub-Kuiseb confluence are interpreted as knick points associated with the canyon incision and the valley-in-valley profiles upstream of the canyon proper. Steeper gradients are also apparent at Swartbank and Rooibank respectively and these are also interpreted as knick points, superimposed on a regional convexity resultant from coastal emergence and possibly progressive desiccation (Fig. 2). The general convexity of the lower Kuiseb is therefore, a function of emergence rather than of desiccation.

Between the zones of knick point steepening, where gradients are less than 1:200, the bed gradient is extremely gentle. Upstream of the Gaub confluence, mean gradient is 1:385; between Hudaob and the Aussinani confluence it is 1:420 and even seawards of the postulated Rooibank knick point where convexity is maximised, gradients exceed 1:200. The mean gradient of the Kuiseb channel is furthermore considerably less than that of the pedimented surfaces into which it is incised. Mean pediment gradients can be calculated for the gravel Namib north of the river with ease but to the south establishment of the interdune surface gradient is complicated by the presence of dune sand. A gradient of 1:100 appears to be average for the pediment surface wash slopes. Being also transport slopes, the steeper gradient may be a response to reduced efficiency. However it is likely that the surface has also been steepened by warping (Wienecke & Rust, 1973). Reactivation of the Kuiseb river in the steepened zone would inevitably result in incision upstream, with concomitant deposition downstream, a pattern that is apparent in the Kuiseb system (Fig. 3). Nevertheless it should be pointed out that a similar result can occur attendant on a change from braided to channel flow as a function of greater flow efficiency.
3.4 Terrace deposits and sequences

Periodic rejuvenation and changes in discharge cause depositional sequences which provide evidence of past events. West of Hudaab, the Kuiseb valley shows a number of minor valleyside bevels and within the incised valley, terrace deposits have been preserved. The earliest and most extensive surface is the high level calcrete caprock which is now in process of dissection (Besler, 1972). In many places it is no longer a single surface. Calcrete duplication occurs and even the highest, and presumably oldest calcrete sheets contain inclu- sions of rolled calcrete pebbles indicating a prior deposit. East of the Escarpment similar surface limestones resting on fluvial sands and gravels are considered to be part of the Kalahari System and to be Early Tertiary in age (Mabbett, 1955). In the Namib, the oldest, thick calcrete rests either on sandrock or directly on planed Basement Complex rocks. Similarity in geological relationships may thus indicate that the high level calcretes of the Kuiseb system may be a Kalahari System equivalent and also an Early Tertiary deposit.

The Kuiseb river has incised through these deposits to expose extensive areas of both Basement Complex schists and sandrock. Although the tributary granodurra valleys are reputed to show some duplication of incision (Rust & Wienecke, 1974) the pronounced break of gradient in most channels is likely to be a function of more effective incision by the main Kuiseb channel. Sandfilled channels interrupted by longitudinal dunes dissect the high level calcretes to the south and are also totally unadjusted to the present Kuiseb channel. Where the Kuiseb Canyon widens, some kilometres upstream of Homeb, a number of distinct deposits and associated terraces can be identified and traced downstream (Map 3). Remnants of a pebble-packed, calcrete-cemented conglomerate occur high on the valley sides but only one 30 m exposure is known; all other remnants have depths of 1 to 2 m only. This calcrete conglomerate differs from the high level calcrete caprock in the concentration of pebbles. It is likely to represent a reworked lag deposit derived from destruction of the higher calcrete caprock. The location of the cliff exposure in the Kuiseb valley indicates that aggradation was subsequent to the initial canyon incision (Fig. 4.2). Water-laid micaceous slits creating at least two distinct terrace levels have been preserved in side valleys from a few kilometres upstream of Homeb to Gobabeb (Map 3). At Homeb these slits can be seen to rest on cross-bedded dune sand and the upper terrace level is accordant with that of the pebble conglomerate surface.

<table>
<thead>
<tr>
<th>LOCALITY</th>
<th>POSITION (Alt. m)</th>
<th>DISTANCE UPSTREAM (km)</th>
<th>CHANNEL GRADE (ratio)</th>
<th>PEDIMENT GRADE (ratio)</th>
<th>TOTAL VALLEY WIDTH (m)</th>
<th>INCISION WIDTH (m)</th>
<th>OVERALL DEPTH (m)</th>
<th>INCISION DEPTH (±m)</th>
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<tbody>
<tr>
<td>50</td>
<td>14</td>
<td>280</td>
<td>423</td>
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<td>—</td>
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<td>225</td>
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<td>—</td>
</tr>
<tr>
<td>Norkoach</td>
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<td>195</td>
<td>100</td>
<td>No valley</td>
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<td>—</td>
<td>—</td>
<td>—</td>
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<td>Swaribank</td>
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<td>Ausimnus</td>
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<td>100</td>
<td>2,500</td>
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<td>—</td>
<td>60 - 100</td>
<td>—</td>
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<td>400</td>
<td>370</td>
<td>110</td>
<td>2,800</td>
<td>200</td>
<td>60 - 100</td>
<td>—</td>
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<td>Gaub Confluence</td>
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<td>Gogas Confluence</td>
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TABLE 3: Postulated sequence of events for the Middle Kuiseb

<table>
<thead>
<tr>
<th>GEOGRAPHICAL EVIDENCE</th>
<th>HYDROLOGICAL REGIME</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erosional</td>
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<tr>
<td>Depositional</td>
<td>Channel</td>
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<tr>
<td>1 m Flood plain terrace</td>
<td>Channel</td>
</tr>
<tr>
<td>Colluvial terrace</td>
<td>Sheetwash : braided</td>
</tr>
<tr>
<td>Incision</td>
<td>?</td>
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<tr>
<td>Incision</td>
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<td>Meandering scarred river</td>
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<tr>
<td>Channel</td>
<td>Braided</td>
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<tr>
<td>Loose pebbles of low terrace</td>
<td>Braided</td>
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<tr>
<td>Sand filled channels</td>
<td>Braided</td>
</tr>
<tr>
<td>Pebble packed channels</td>
<td>Braided</td>
</tr>
<tr>
<td>Braided channel</td>
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<tr>
<td>Incision</td>
<td>Pebble conglomerate (calcification)</td>
</tr>
<tr>
<td>High level calcrete (calcification)</td>
<td>Fan channels</td>
</tr>
</tbody>
</table>

3.4 Terrace deposits and sequences
A low colluvial fan with a steeper surface gradient abuts against the silts and occupies valleys excised in them. It consists of waterlain angular gravel derived from bedrock disintegration, interbedded with lenses of reworked dune sand. Below this level, lies the present flood plain terrace consistently at +1 m above the dry river bed, built of micaceous silt and sand. Four distinct terrace deposits are thus present within the incised valley, pebble conglomerate, grey micaceous silts, colluvial gravel and sand and the present flood plain deposits.

An attempt to clarify the relationships between the deposits, all of which must post-date canyon incision, will be based on three depositional sequences located between Ossuwater and Gobabeb (Fig. 4). The pebble calcrete that caps the high terrace at Gobabeb is similar to that of the cliff exposure and to the outcrops along the south bank at Ossuwater. The depth and location of the 30 m cliff deposit demonstrates that the phase of pebble deposition post-dates canyon incision. The pebble conglomerate calcrete must have filled the incised valley and overlapped onto both Basement rocks and sandrock on the upper valley slopes. The silts post-date the subsequent removal of the pebble conglomerate by renewed incision since they abut against the calcrete as well as against Basement Complex rocks. It is probably fortuitous that the upper silt level accords with the surface of the pebble calcrete. Nevertheless, calcrete remnants may have acted as silt traps and caused the accumulation. Incision to cut the initial canyon was followed by aggradation and calcification. This cycle was superseded by renewed incision and then by silt aggradation. The duplication of the silt terraces may in fact represent a third cycle of renewed incision and aggradation.

The gravel and sand fan deposit is younger than both the pebble calcrete and the silts. It occupies tributary valleys incised into the silt and is adjusted to a level lower than the lower silt terrace but above present flood plain level. The steeper surface gradient suggests that it was of colluvial sheet-flow origin rather than of fluvial or lake provenance. It thus records a further change in hydrology. The youngest member of the sedimentary suite is the 1 m silty-sand flood plain that abuts against all the other deposits and is aggraded whenever flooding occurs.

At Gobabeb, where the Kuiseb valley is much wider, the terrace evidence permits postulation of a sequence in the destruction of the pebble conglomerate (Fig. 4). A braided channel system, now sand-filled, dissects the pebble conglomerate. A series of lower channels have incised the pebble conglomerate, stripped sandrock and exposed Basement Complex bedrock. The bedrock channels appear to represent a gradual fluvial shift northwards to spread derived pebbles over weathered bedrock up to 2 km north of the present Kuiseb channel (Map 3). The bedrock valleys south of the present Kuiseb channel have since been aggraded with dissected and uncremented pebbles. This fill has itself undergone some dissection. At a late stage the Kuiseb river shifted to its present position to cut a broad meander-scarred valley. In these meander scars are preserved silts similar in texture to those upstream but here not &ndash; the only evidence of the pebble conglomerate level (Table 3).

It has been postulated that the northwesterly trend of the Kuiseb valley was caused by dune advance under conditions of increasing aridity (Wieeneke & Rust, 1973). The channels dissecting the pebble conglomerate of the high terrace and those at lower altitudes in bedrock all prolong the westerly alignment of the Kuiseb course between Hudob and Natab (Map 3). The northerly shift is therefore, subsequent to the phase of re-incision. If the silts are all of the same age, then the river had reached its present position prior to the emplacement. It is possible that the cause of the northward shift, which is repeated in the deltaic channels seawards of Rooibank in historic time (Stiegel, 1970), is to be sought during a phase of marine regression which would have increased continentality making maintenance of the Kuiseb course to the sea more difficult. Preliminary analysis of the depositional sequence suggests cyclic incision and aggradation (Table 3).

Cross-valley and long profile sections have demonstrated the effect of episodic rejuvenation on which are superimposed the effects of discharge variation. The cyclic nature of the Cenozoic events that have moulded the geomorphology of the Kuiseb River system is clearly apparent.

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Outline geological and geomorphic history of the Central Namib Desert

by

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Abstract

The history of the Central Namib includes the following: deposition, metamorphism and granitization of the Precambrian;planation of the Precambrian to form the Namib Unconformity Surface, an unweathered pediplain with a few inselbergs thought to be of Jurassic age; deposition of the Tsondab Sandstone, a terrestrial sandstone thought to be equivalent to the Kalahari System, and of Upper Cretaceous and Tertiary age; planation to form the Tsondab Planation Surface, a vast pediment crossed by east-west drainage; incision of the Tsondab and Kuiseb Rivers with formation of minor terraces; formation of the modern sand dunes.

Numerous workers have made contributions to the geomorphology of the Namib and some have constructed partial geological histories, or placed events of landform history in an order of succession (e.g. Rust and Wiencke, 1973, 1974; Selby, 1976; Wiencke and Rust, 1973a, 1973b; Markert, in press). No one seems to have tried to construct a full geological and geomorphic history of the region, possibly because they feel available data is inadequate. Such a history should be constructed as a fundamental basis for geological work, to provide a scheme which can be tested, modified, improved or even refuted. The existence of such a geological outline constrains workers to either fit data into the scheme, or to challenge the data or the proposed relationships. In an area of limited knowledge a formal geological history, with all its imperfections, has its uses. It is to provide such a starting point that the following outline is offered.

1 Precambrian

Varied sedimentary rocks, shales, sandstones and limestones, were laid down and later metamorphosed to schist, gneiss, quartzite and marble. These rocks were injected by veins of quartz, aplite and pegmatite, sills of dolerite (Swartbank), and in places converted to or intruded by granite. There has evidently been uplift since these metamorphic rocks were created, followed by erosion to form the ground surface that truncates the rock structures.

2 Namib Unconformity Surface

Long continued erosion across the Precambrian rocks formed a plain. This plain is a fundamental datum in the area, separating the metamorphic bedrock from all younger deposits. I shall call this plain the Namib Unconformity Surface. Although generally flat, the Namib Unconformity Surface has some irregularities which rise as hills, strike-ridges, cuestas or inselbergs above the general surface of the plain. The age of the planation will be discussed later.

Upon the Namib Unconformity Surface were deposited a basal conglomerate, here simply termed the Basal Conglomerate, and a red sandstone, here called the Tsondab Sandstone.

3 The Basal Conglomerate

The Basal Conglomerate on the south side of the Kuiseb Canyon near Hudacb contains very angular quartz fragments and a basal concentration of garnets which can be matched in
the immediately underlying bedrock. The detritus that is incorporated in this conglomerate is not marine and, if fluvial, it has suffered very little wear and is not far travelled. At this locality the rock could be termed a breccia, but elsewhere equivalents are conglomeratic. There are some places north of the Kuiseb (as on the road to Mirribib) where limestone capping mesas of Precambrian rock has no pebble content, but this limestone is probably equivalent to the Basement Conglomerate.

Carbonate has thoroughly permeated the Basal Conglomerate either contemporaneously with deposition of the conglomerate or as a later introduction. In some places there appear to be two similar conglomeratic hard bands with softer material between, the upper one making a distinct mesa. Airphoto Strip 14 No. 56 provides an example (Fig. 00)

4 TSONDAB SANDSTONE

South of Gobabeb, at Tsondab, and at many other localities, there is a red sandstone as bedrock. I shall call this the Tsondab Sandstone. This may be a lateral equivalent of the Basement Conglomerate in part, but most of it overlies the conglomerate and is younger. At Gobabeb the sandstone appears to overlie Precambrian metamorphic rock and granite directly, so the Basal Conglomerate is locally absent.

The Tsondab Sandstone is a quartz sandstone cemented by carbonate. In places it has cross bedding, consistent with being originally deposited as dune sand, but also possible foreset beds of a delta deposit. There are also plane bedded sandstones. There are no pebble bands as might be expected in a water-deposited sediment, and most authors have assumed that this sandstone is consolidated dune sand. This sandstone is considerably older than the dunes of the present day and should not be confused with them. An analogy may be found in Britain where the Old Red Sandstone (Devonian) and the New Red Sandstone (Triassic) mark two periods of aridity in the same area separated by millions of years, a whole geological Period. The two episodes of dune formation in the Namib may be separated by a similar time span.

The Tsondab Sandstone has been referred to as “sandrock” (Marker, in press), a term that adds nothing to the concept of “sandstone”, and as “consolidated red desert sands” by Selby (1976). This sort of terminology tends to link the Tsondab Sandstone with the modern sand dunes and I suggest that the simple term “sandstone” be stressed to emphasize that this is not merely the consolidated (“calcretes”) base of the present dunes but a stratigraphically quite distinct unit.

There is no direct evidence of the age of either the Basal Conglomerate or the Tsondab Sandstone, and they could be anything from Precambrian to Tertiary. They are unfoliated and have no materials suitable for radiometric dating. A good possibility for dating would be a palaeomagnetic study of the Tsondab Sandstone. It is well oxidised and, if it has sufficiently intense and stable magnetisation, its magnetic direction and dip could be fitted onto the palaeomagnetic wander curve for Africa and so give the age of magnetisation and a minimum age for the rock itself.

The age of the Tsondab Sandstone can only be estimated by comparison with similar deposits elsewhere. They may be equivalent to the Kalahari System of Botswana and the Republic of South Africa. The similarity may be gauged from the following description of the Kalahari deposits (Trueswell, 1970): “Rivers draining into this region ... deposited clay, more calcareous marls, sands, and occasional gravel bands in

the basin to form the primary Kalahari beds. Covered by the ubiquitous later sands as they are, information on these beds comes largely from boreholes. Their age is uncertain, but generally believed to be early Tertiary. They are capped by one or more sheets of calcrete and silcrete ... The age of these deposits is again uncertain, and made more so since they appear to have formed at several different times ... Subsequently the underlying material was reworked to produce the widespread blanket of Kalahari sands.”

According to Haughton (1969, p. 427) the lowest horizons of the Kalahari System may be of Lower Cretaceous age, and this could also apply to the Tsondab Sandstone.

5 THE TSONDAB PLANATION SURFACE

After deposition of the Tsondab Sandstone a new erosion surface was cut across the sandstones. This was probably in the form of a vast pediment stretching from the Naukluft Mountains to the sea, and was traversed by drainage flowing from east to west. The terraces and vleis preserved in interdune corridors bear gravel derived from the east. Those of the Tsondab area have dolomite from the Naukluft Mountains which is absent from the Kuiseb area. There was presumably a period of sheet-flood activity when these gravels were deposited over a huge pediplain cut across sandstone and Precambrian basement rock. This activity, which pre-dates dune formation, would presumably also affect the gravel plains to the north of the Kuiseb. Thick deposits of gravels were laid down which have since been cemented into conglomerates (calcretes).

This planation surface is another fundamental surface in the history of the area, separating the period of accumulation of the Tsondab Sandstone from the later history of fluvial erosion and wind deposition.

Again we can find a comparison with the Kalahari, where the geomorphic history, according to Grove (1969) appears to be similar to that of the Namib. The deposition of the lacustrine and terrestrial Kalahari Beds with numerous calcretes was
succeeded by a period of river incision, and renewed wind dominance created the present dunes.

The Tsondab Plantation Surface is best preserved as the upper terrace at Tsondab Vlei, where it is about 100 m above the vlei surface. The age of the plantation surface is not known but will be considered further later in this paper.

6 FLUVIAL INCISION PERIOD

The broad plain that existed after the formation of the Tsondab Plantation Surface was later cut into by the major rivers crossing it from east to west to form major valleys. At times downcutting was replaced by lateral erosion and terraces were carved across the sandstone.

South of Gobabeb an old course of the Kuiseb is preserved within the dunes. The terraces have carbonate cemented terrace gravels and are essentially rock cut terraces eroded across the Tsondab Sandstone and Precambrian bedrock with a thin veneer of gravels. The terraces and river course are older than the present Kuiseb course, and the gravels can be distinguished from those of younger Kuiseb terraces by the abundant desert varnish on quartz pebbles.

At Tsondab Vlei the Tsondab Sandstone has been eroded to form a terrace about 50 m above the present valley bottom and 50 m below the Tsondab Plantation Surface. The terrace has a cover of terrace gravels, now carbonate cemented. The size of the valley and the size and roundness of the pebbles in the terrace deposits indicate that the Tsondab River had a high flow, at least intermittently, at the time of downcutting and terrace gravel deposition. At the time when the Tsondab Valley was occupied by an active river the present dune field did not exist. In a few places the Tsondab Sandstone has been stripped away exposing intrics of gneiss, usually in the form of hills or strike ridges. From this point on the geomorphic history of the area is best considered by areas: the Kuiseb River Valley, the dune area to the south and the gravel plains to the north.

6.1 The Kuiseb River Valley

The Kuiseb River flows in a canyon cut through the Precambrian bedrock, with bedland topography extensively developed on the northern side. Downstream from Homeb there are remnants of a river terrace preserved in cemented gravels, a deposit here called the Ossewater Conglomerate. The top of this terrace is about 30 m above the present valley floor, and the base of the conglomerate is a few metres above the present valley floor. Therefore the Kuiseb cut down almost to its present level and then built up its bed (aggraded) with river gravels to the level of the terrace. The gravels became cemented with carbonate either penecontemporaneously or subsequently. The river then cut down again, carving a valley through the Ossewater Conglomerate and eroding to the present river level.

Then came a new period of aggradation when the river built up its bed by deposition of the Homeb Silts, now preserved in the side-valleys around Homeb (Rust and Wieneke, 1974), overlying both Precambrian bedrock and the Ossewater Conglomerate. The silts themselves are fine sediments, near horizontal, and are fine material brought down by the Kuiseb in flood and deposited away from the actual river course. Interdigitating with the silts are wedges and lenses of angular gravels, hillwash derived from the local valley sides. The silts represent far-travelled debris brought down by the Kuiseb after rain in its upper catchment: the gravels represent hillwash brought down by local storms, washed onto a dry terrace top. If the hillwash had gone into a lake it would be waterworn, which it is not. When the hillwash was deposited the Kuiseb was either not flowing, or slightly flowing leaving the terrace top dry.

Some minor river terraces a few metres above present river level post-date the Homeb Silts. Further details of the geomorphology of the Kuiseb Valley and its terraces are provided by Markier (in press).

Table 1: The geomorphic history of the Kuiseb may be summarised as follows: (oldest events at the bottom): –
8. Formation of minor terraces and the present flood plain
7. Formation of the lower terraces of the Kuiseb
6. Re-excavation to bedrock, leaving remnants of Homeb Silts
5. Deposit Homeb Silts
4. Erode to bedrock at present river level
3. Deposit gravels of Ossewater Conglomerate to form a terrace. Cement.
2. Cut canyon, almost to present level; tributaries form badlands.
1. Initiate Kuiseb course on the Namib Unconformity surface or on the Tsondab Plantation Surface.

What sort of time periods can be associated with these events?

The erosion of the canyon and its tributaries would take hundreds of thousands of years, perhaps millions. It could occupy much of the Lower Pleistocene, or be of Tertiary origin. The Ossewater Conglomerate would require at the very least some tens of thousands of years, to accumulate, cement, and erode again. There is no need to invoke any special mechanism such as damming of the river by dunes to cause the accumulation of these river sediments.

The Homeb Silts could have been deposited in a few hundred but more probably a few thousand or tens of thousands of years. They are river sediments (deposited in tributary backwaters) rather than lake sediments, and could have accumulated during a period of general aggradation. If a lake were ever present it must have periodically dried up. The remnants of the Ossewater Conglomerate Terrace downstream could have acted as a partial barrier to the river, causing it to spread out and deposit its silt upstream of the barrier, where the silt is now found. As with the Ossewater Conglomerate, if the dune-dammed lake hypothesis is rejected it becomes impossible to tie to the Kuiseb fluvial history into the history of the dunes.

6.2 The dune area south of the Kuiseb River

This area has been covered by sand dunes at some time in the past and these dunes are still active to some extent. The date of the commencement of dune activity is not known.

The main mass of the sand is in essentially fixed north-south linear dunes. Only the crests and minor dunes are active and it is thus invalid to use (as some authors have) movement rates of minor dunes as a general figure for migration of the dune field as a whole.

As water courses flow east-west and the dunes are north-south it should be possible to study the interplay of the two to
some extent, and some estimates of the age of termination of
the rivers in the dunes can be attained (Seely and
Sandelowsky, 1974). The amount of interplay is probably
quite small and the dunes simply post-date the valleys.

One of the most spectacular features of the Namib is the
abrupt termination of the dunes at the Kuiseb River. It would
seem that the Kuiseb carries away any sand deposited in its
bed and prevents the dunes from crossing its valley. It is possi-
bile towards the coast that dunes may have deflected the
Kuiseb to the north, but in the central part of its course the
river is dominant and dunes do not cross it. If dunes ever cross-
the river there should be evidence of them on the north
side, and there is none. Dunes blocking the Kuiseb have been
invoked to account for the deposition of the Homeb Silts. The
lack of necessity for a dune-dammed lake has already been ex-
plained; if such a lake did exist there should be remnants of
the damming dune to the north of the Kuiseb. Alternatively
one may postulate that any dune sand that did cross the
Kuiseb was carried across the gravel plains and dispersed to
the north. It cannot be demonstrated that this process did or
did not happen in the past, but there is no evidence that it is
going on now. Sand dunes do cross intermittent rivers. In the
Kalahari, as in the Namib, longitudinal dunes approached a
river course at near right angles, and the dunes stop abruptly
at the river. When the river flows it carries away sand. But
some sand does cross the river. There is a dune-free strip
parallel to the river on the downwind side, then a strip of sand
parallel to the river where the sand re-assembles. This is then
blown out into further parallel dunes.

What is the explanation for the difference between this situ-
ation and that of the Kuiseb? The Kuiseb flows sufficiently fre-
quently and with sufficient velocity to remove the sand blown
into its bed, whereas the Kalahari type of stream described
above is inadequate for removing all the sand.

This further suggests that the Kuiseb River valley was in ex-
inestence, and the river was flowing before the sand dunes came
into existence. If the sand dune field pre-dated the river, old
dunes should be found to the north.

The Tsondab valley to the south is similar. The river had to be
large (at least in flood time) to carve the deep valley and ter-
racies; and it could not be simultaneously eroding its bed and
being blocked by sand. The sand dunes post-date the terraces
and the lower course of the Tsondab. The present dune field is
therefore relatively young, and is separated from the Tsondab
Sandstone by (a) the planation of the Tsondab Planation Sur-
fce and the spread of gravels on the resulting pediplain, and
(b) the incision of the Tsondab and Kuiseb valleys, with the
complications of terrace formation, river course change from
the prior-Kuiseb to the present course, and probably the
various depositional terraces of the Kuiseb. The time gap
between the formation of the Tsondab Sandstone and the
modern dune is therefore great, probably millions or tens of
millions of years.

6.3 The gravel plains

The gravel plains north of the Kuiseb bear little evidence to
reveal their history. Present day weathering processes are
tending to make the plain ever flatter, and the slopes of in-
selbergs are retreating (Selby, 1976).

However, there are considerable remnants of an indurated
cover of surficial materials, calcetate up to 30 m thick, which is
apparently equivalent to the Basement Conglomerate of the
south side of the Kuiseb. No remnants of the Tsondab Sand-
stone are known north of the Kuiseb.

The present day processes are doing little more than bevel a
pre-existing plain (the Namib Unconformity Surface) which is
being exhumed from a calcetised cover of younger rocks.

Table 2: The history in brief appears to be:
5. Modern pedimentation and minor river and wind action
4. Erosional stripping of younger rock to re-expose the
Namib Unconformity Surface
3. (possibly deposit equivalent of Tsondab Sandstone)
2. Deposit "calcetate" equivalent of the Basement
Conglomerate
1. Erosion of the Namib Unconformity Surface.

The Kuiseb River runs along the geological contact between
the Precambrian rocks of the gravel plains and the Tsondab
Sandstone of the dune area to the south. It is possible that the
middle course of the river has moved south by unidirectional
shifting down the slope of the Namib Unconformity Surface
as it stripped the cover rocks. Now, however, it is incised in
Precambrian rock and such movement, if it ever occurred, has
stopped.

7 Age of the erosion surfaces

King (1969, fig. 119) shows the gravel plain of the Namib as
part of the Post African Late Cenozoic land surface. It is
possible, however, that it is a downwarped part of the African
(early Cenozoic) or even Gondwana (Jurassic) land surface
preserved on the Komas Highlands.
On his latest terminology (King, 1976) the planation surfaces are called the Gondwana (Jurassic), Kretea (early-mid Cretaceous) and Moorland (late Cretaceous to mid Cenozoic). According to King the Moorland surface is characterised by calcrite and silcrete, and on this basis is the most likely to be equated with the Tsodab Planation Surface. Its postulated age is greater than that of the previously postulated Post-African surface and would not conflict with any information currently available. Another approach to the age of the erosion surfaces (Selby, 1976) is to equate the gravel plain of the Central Namib with a similar plain in the South Namib where there is a silcrete — the Pomona sandstone — which is thought to be pre-middle Eocene. However, according to Haughton (1969, p. 436) the Pomona sandstone is not dated by fossil evidence, so this approach is also speculative.

The situation is complex, for there are two erosion surfaces in the area, the Namib Unconformity Surface cut across the Precambrian rocks, and the Tsodab Planation Surface cut across the Tsodab Sandstone and possibly continuous with the bevelled surface where the calcrites are being stripped from the gravel plain. The concepts and terminology involved in this situation of closely coincident surface and exhumed surfaces are beyond the scope of this brief paper. The Namib Unconformity Surface is probably pre-Lower Cretaceous and/or Jurassic, and the Tsodab Planation Surface is probably middle to late Tertiary. The cross section shown in Figure 40 shows diagrammatically the main features which have to be fitted into a geological and geomorphic history.

Table 3 is a suggested outline geomorphic history from the Namib Unconformity Surface to the present.

It must be remembered that, as with all geomorphic histories, this one is a minimal history. Whole episodes may be missing, and all the events that are included could be elaborated.

**Table 3: Outline of geomorphic history from Namib Unconformity Surface to the present.**

<table>
<thead>
<tr>
<th>Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>10. Deposit: young terrace gravel and floodplain</td>
</tr>
<tr>
<td>9. Erode to river level</td>
</tr>
<tr>
<td>8. Deposit: Homeb Silts</td>
</tr>
<tr>
<td>7. Erode to present river level</td>
</tr>
<tr>
<td>6. Deposit: Ossewater Conglomerate</td>
</tr>
<tr>
<td>5. Erode almost to canyon bottom</td>
</tr>
</tbody>
</table>

**Kuliseb**

8. Deposition of modern dune field
7. Erode to Vlei level, leaving the 50 m terrace
6. Erode to 50 m level
5. Deposit gravels from the east
4. Erosion of Tsodab Planation Surface
3. Deposition of the Tsodab Sandstone
2. Deposition of the Basal Conglomerate
1. Formation of the Namib Unconformity Surface

**8 Geomorphic History and Climatic Change**

It is very superficial to attribute climatic changes to every change in geomorphic history. With present knowledge this cannot be done in a satisfactory way. The various possible combinations of rainfall, vegetation growth, runoff, soil formation, and erosion are too complex to allow conclusions to be drawn from a single geomorphic event. Much more abundant, varied and accurately dated data are required for more than the most general speculation.

For example, in South-eastern Australia where abundant dated stratigraphic material has been studied in detail, it has been found that periods of world glaciation were represented in south-eastern Australia by arid conditions, in the sense that vegetation was reduced, strong winds blew and dunes were active. But the rivers at that time were bigger than those of the present day and lakes were generally full. If only part of the data had been found who would have thought that full rivers were correlated with arid periods?
In the Namib, until the geomorphic-stratigraphic evidence is much more detailed, climatic inferences are highly speculative. The area has been arid to some degree for a very long time, perhaps back to Mesozoic. Periods of river downcutting indicate the flow of rivers, but they may have been (like the present Kuiseb) that collect their water outside the desert. The modern period of dune building may indicate greater aridity than before, or it may, for example, result from greater flow of the Orange River bringing more sand to the area.

At the present state-of-the-art of geomorphology more direct conclusions are likely to come from study of lakes or sediments in or around the Namib than from study of the relatively barren dunes and gravel plains. However, to establish the correlations necessary for a sound history, the stratigraphy, sedimentology and geomorphic history of the Namib needs to be known in greater detail than it is present.

9 A NOTE ON CALCARETES

Various different materials in the Namib area have been referred to as calcarete, to the point where the term has little meaning or value. According to Netterberg, an authority on the calcaretes of Southern Africa, "A calcarete may be defined as almost any terrestrial material which has been cemented and/or replaced by dominantly calcium carbonate... calcaretes may be of pedogenic or non pedogenic origin". (quoted in Goudie, 1975).

In the Namib area it is clear that carbonate cementation of sands and gravels has taken place many times, and deposits of very different age have been termed "calcarete." It must be stressed that "calcarete" has no value whatever for correlation of deposits from different areas. It has no time significance, and if used as in Netterberg's definition it has little biogeographical value. I have avoided it as much as possible in this paper, and recommend that it should be used as little as possible.

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Patterned ground near Gobabeb, Central Namib Desert

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Two major types of patterned ground and one minor type are found in the interdune valleys south of the Kuiseb River at Gobabeb and are particularly distinct after good rains (e.g., 1976 with 125 mm). The patterns are polygons bounded by straight lines with little regularity. The average distance across a polygon is approximately 5 m although some reach 20 m. The polygons have been briefly described by Goudie (1972), who does not distinguish two types and proffers no explanation. The patterned ground described here is quite distinct from the simple mud cracks figured by Scholz (1972). Besler (1972) described polygons near Gobabeb and Swartbank and relates their formation to the past or present gypsum content of the soil.

The three types are distinguished by the vegetation growing on them: in one kind (Type A) the grass (Stipagrostis gonaustachys) grows inside the polygon but not along the bounding lines; in the second kind (Type B) some grass species grow along the lines but not within the polygon. A third type (Type C) supports a slight growth of Stipagrostis gonaustachys within the polygon and a more dense growth along the lines. Vegetative growth requires optimum water conditions, so the three types can be re-defined in terms of available soil moisture as:

Type A. Patches within the polygon have available soil water but the lines are too dry for plant growth.

Type B. Patches within the polygon are too dry but soil water is available in the lines.

The three types are shown in Figs. 1, 2, 3, 4 & 5.

Type A: Within the patches there is shallow soil over calcrite which occurs at a depth of about 10 cm. The lines are joint cracks about 20 cm wide, penetrating the calcrite and filled with soft soil. It would seem that the calcrite is a barrier to percolation so any water that falls on the patch is held in the soil above. On the cracks there is no limit to percolation so water goes below the depth of root penetration.

The difference between patch and line can even be detected by firmness of the surface: the patches afford firm ground while the lines are soft.

The lines are utilized by burrowing animals which may exaggerate and perpetuate the difference between line and patch, but the animals are not the original cause of the polygons.

These cracks are essentially joints in limestone (calcrite). The joints cannot have a tectonic origin in this stable area, and are therefore, a local phenomenon, most probably resulting from shrinkage of the calcrite upon drying. This suggests that the polygons are fossil. The patterned ground is not the result of active process continuing at the present time but it was created at a specific time when the calcrite dried out. This particular calcrite is therefore of a specific age, and possibly dates to the last onset of true aridity.

Type B: The patches in this type occur on bare rock, an indurated pebble-free, red sandstone, which may or may not have a slight calcrite development on the surface. The sandstone is probably of Tertiary age and has been called the Tsondab Sandstone (Ollier 1977). These lines are joint cracks up to 20 cm wide filled with sand, pebbles and calcrite fragments.

The bare rock cannot hold enough moisture for plant growth, but the infilled joints full of varied debris can sometimes support growth (though even at the best the growth is sparser than in the patches of Type A). Burrowing animals do not seem to live in the cracks of Type B.

The joints were formed during the lithification of the original sand into sandstone by drying, consolidation and chemical
This sandstone is exposed on a river terrace. The rock was almost certainly consolidated and jointed before fluvial erosion carved the rock-cut terrace. Minor erosion at the time of terrace cutting widened the joints. The terrace was probably covered in alluvium, some of which filled the widened joints. Much later erosion has stripped the alluvium from most of the sandstone, but it has remained in the cracks. Where deep alluvium is preserved on a terrace it may have developed a calcrite pan and could eventually give rise to Type A patterned ground.

The two types of patterned ground thus seem to be related to the nature of river terrace. Where the terrace is rock-cut and bare sandstone is exposed at the ground surface type B patterns appear; where sufficient depth of alluvial fill is preserved on a terrace Type A pattern may be present.

Type C: The third type of patterned ground occurs below the terrace remnants, within the dry interdune valleys south of Gobabeb. On the surface the pattern is similar to Type B, with grass growth more developed in the lines and only slight vegetative growth within the polygons. The soil is about 20 cm deep, under both line and patch, and preliminary investigations failed to find any cause for the vegetation pattern. The age and origin of this type is unknown.

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An observation on parental care of young in the steenbok in South West Africa

by

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The steenbok (*Raphicerus campestris*) is a common antelope in southern Africa, but little information has been published on its behaviour. Recently Lent (1974) reviewed the mother-infant relationships in some species of African antelopes, but not the steenbok. The following observations, made on the eastern edge of the Namib Desert at Gobabeb, South West Africa (15°03'E, 23°34'S), are the first to describe parental care of newborn young and its possible adaptive significance.

At 19h00 on 9 August 1976, I observed a newly born steenbok kid with its mother near some large rocks on the gravel plain bordering the Kuiseb River. Birth appeared to have been quite recent as the kid was unsteady on its feet and used the mother's legs for support. The following day the female was seen at 16h00 in the same area, but the kid was not with her. In March 1974 M.K. Seeley observed another female at Gobabeb, who kept her kid hidden in one spot among the rocks for five days (pers. comm.).

At 09h00 on 13 August the female walked cautiously from the river vegetation to some rocks on the gravel plain where the young was lying hidden (Plate 1). She suckled the kid while lying on her side concealed between the rocks. When finished, she returned directly to the river, leaving the kid who remained prone in the same spot throughout the day, standing only twice to stretch and turn around. The female did not return to the kid until after sunset (19h00) when she was accompanied for the first time by an adult ram. When they were within three metres of the kid it responded to a nudge from the mother by standing up and running to her side. The two then returned to the hiding spot where she suckled it for approximately five minutes from both standing and recumbent positions. During feeding the male stood several metres away observing the river. After several minutes he returned approaching the standing female from the front and tapping her on the shoulder several times with his foreleg before moving around to her hindquarters where he began licking her genital region. She in turn started to lick the same area of the kid as it fed. The ram then attempted to mount the female but was promptly kicked off by the female's rear leg. The three steenbok then moved away slowly, the adults foraging on *Zygodontium simplex* and *Stipagrostis eilati* and the young intermittently running ahead several metres but returning quickly to its mother's side. They stopped again while the kid sucked whereupon the ram again tried unsuccessfully to mount the female. Observations had to be terminated at this point (19h45) from poor visibility. That night the kid was not returned to the former spot.

On 9 September 1977 at 11h15 I observed a female, who had been disturbed, leading a newborn lamb from exactly the previous year's "laying out" spot (Fig. 1) to the river. As I approached to within 20 m of the river vegetation, the female charged directly at me with her head lowered and ears lying flat, but when within 5 m of me she veered away suddenly and disappeared into the vegetation. She repeated this "mock charge" four times, whereupon I moved away.

Anti-predator behavioural adaptations found in some herb species of southern African bovids (e.g. group defence, synchronous birth, and aggregation at lambing time) are lacking in steenbok, which live singly, or in pairs during reproductive periods (Estes, 1974; Jarman, 1974). Although limited to two single instances, these observations imply that behavioural mechanisms to protect the vulnerable newborn young from predators have also evolved in the steenbok and other non-
herding antelope species, of which some possibly are leaving the young concealed and alone except for brief periods of suckling, and placement of the kid away from the greatest concentration of predators (e.g. Black-backed Jackal, Caracal Cat, and Spotted Hyaena), which at this locality is in the riparian vegetation, and aggressively threatening potential predators.

I am grateful to the CSIR and the Transvaal Museum for financial support and the S.W.A. Division of Nature Conservation for facilities and permission to work in the Namib Desert Park.

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1. MADOGUA publishes papers on original, basic and applied research concerning nature conservation and the deer in South West Africa.

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