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

by

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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. *Rhoptropus afer* was the commonest reptile; it and *R. bradfieldi* are diurnal and their vertical pupils are remarkably insensitive to light. Pupils of *Pachydactylus laevigatus* and *P. punctatus amoenoides* are more, and of *Palmatogecko rangei* most light-sensitive. *Ptenopus garrulus* was heard but not seen.

In captivity *Pachydactylus laevigatus* 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.

CONTENTS

1 INTRODUCTION

Having taken a continued interest in deserticolous gekkonoid 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 Nurit, 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 laevigatus* 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, *Rhoptropus 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 bark-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 sunlit, 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 housefly 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 (HUJ-R) for preserved specimens, or in the author's research collection (GK) which includes also live animals. The Latin expression ra (rostrum-anus) signifies, where relevant, the snout-vent length of animals, in preference to the latter English expression (Werner, 1974). Taxonomical 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°–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 bareness (King, 1951; Wellington, 1955) except in restricted sites (Logan, 1960).

Gobabeb station is located on the Kuiseb 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 peneplain and, except near the sea, are stopped by the Kuiseb River (Coetzee, 1969: map; Louw & Holm, 1972: fig. 3) which is cleared by periodic floods (Logan, 1960). The superficially dry bed of the Kuiseb River, with its underground trickle of water, provides a contrasting green band of majectic trees (Coetzee, 1969: plate IIb), including many *Acacia albida* and *A. giraffa*, and a variety of shrubs (Logan, 1960). The *Acacia albida* 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 fogs are commoner 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 5 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.

TABLE 1.
Temperature and humidity data based on the records of the weather station (No. 649/37) at Gobabeb, for the period 5 – 10 August 1971.

Date and time	Temperature, °C. Air	Ground Surface	Relative humidity From hygrograph	from dry and wet bulb temperatures
5 August				
0800	9.8	8.6	83	63
1400	22.0	38.0	34	38
2000	18.4	–	59	56
6 August				
0800	6.2	9.3	100	98
1400	18.6	40.0	50	54
2000	14.2	14.8	70	70
7 August				
0800	7.4	6.0	93	79
1400	24.0	42.8	26	27
2000	18.6	17.5	34	34
8 August				
0800	–	–	–	–
1400	17.0	39.8	56	57
2000	15.7	14.8	65	63
9 August				
0800	6.1	5.9	103	92
1400	23.6	44.7	32	31
2000	17.1	15.3	53	47
10 August				
0800	7.1	6.4	82	85
1400	28.7	42.1	12	14
2000	22.2	19.8	28	23

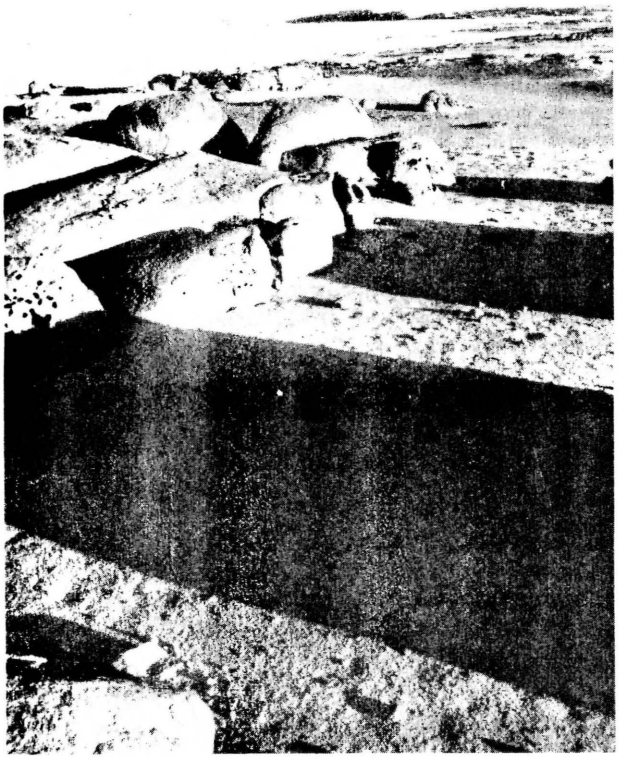


Plate 1. Landscape near Gobabeb, about 5 km east: Gravel plain with granite boulders, both inhabited by *Rhoptropus afer* (6 August 1971, at 1800 h).

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 *Meroles cuneirostris* (Strauch, 1867), adult male and juvenile, among Narras (*Acanthosicyos horrida*) bushes in the sands, active at 1100–1200 h on 6 August (HUJ-R 13283); *Aporosaura anchiatae* (Bocage, 1867), one caught by Alex Durr on the bare dunes, active at 1730–1800 h on August 9 (HUJ-R 11877); *Mabuya longiloba* (Methuen and Hewitt, 1914), on rocks next to sand, 1600–1700 h, on 7 August (HUJ-R 11878, 13246); and a snake, *Psammophis* sp., caught by Mr Finkelday, active in the forenoon of 7 August, in a river bed (HUJ-R 8639). As observed, i.e., by Lawrence (1959), the two first 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). Niche separation between the two has been dealt with by Louw & Holm (1972: fig. 4). 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.

Plate 2. Landscape near Gobabeb (South of Kuiseb river), about 5 km east: Wandering sand dunes, and in the foreground, flat sandstone and semi-fixed, vegetated, sand (wind rippled). The sandstone is inhabited by *Rhoptropus afer* (6 August, 1971 at 1630 h).

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 sepsoides* (Werner, 1968 b: fig. 2). However, the portion where the animal had moved upon the sand was not like *Sphenops* tracks, but continuously sinusoid. We failed to find the responsible animal. This, most probably was *Typhlosaurus braini* Haacke, 1964 (Lawrence, 1959: 235; Haacke, 1964: 5–7) for which these very dunes are the terra typica.

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 Uri). Kuiseb 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 (Frankenberg, 1975) of this animal when first seized is noteworthy in view of Kästle'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* ? *chloroscelis* 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 Kästle (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 × 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 euryoecy parallels that of *Oedura marmorata* 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 13275) 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 amoenoides* 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 *Rhoptropus afer* 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 (*Psammophis*, also captured).

Comments: Parker (1936: 130) and Loveridge (1947: 352–357) doubted the validity of any subspecies of *P. punctatus*, but the subspecies *amoenoides* was accepted by FitzSimons (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 rangei* 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 paraffin lux lamp one young *Palmatogecko rangei* 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; Haacke, 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. Finkelday 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 vertebrae 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 *Palmatogecko*.

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). Drove 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 (1843 h) and remained so till 1940 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, 1969, 1974). The near clicks sounded less loud and lower pitched than those of the Israeli *Ptyodactylus*. Each click sounded metallical, 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 Brain (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 *Ptyodactylus* (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 IIb).

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 *Ptyodactylus* (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

Plate 3. *Rhoptropus afer* on a wide, uniform gravel plain between Gobabeb and Rooibank (10 August 1971, afternoon).

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. Haacke 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 Kuiseb 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 *Ptyodactylus* (Werner, 1965: Fig. 8) and many other geckos, but single. Each "scar" was elongate about 15 × 9 mm. In one site the scars were numerous and in several layers, implying repeated use of the site for years as in *Ptyodactylus*, (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 Haacke (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. *Rhoptropus afer* basking on a granite rock, the colour of which it matches well. (Near Gobabeb, 7 August 1971, early afternoon.)

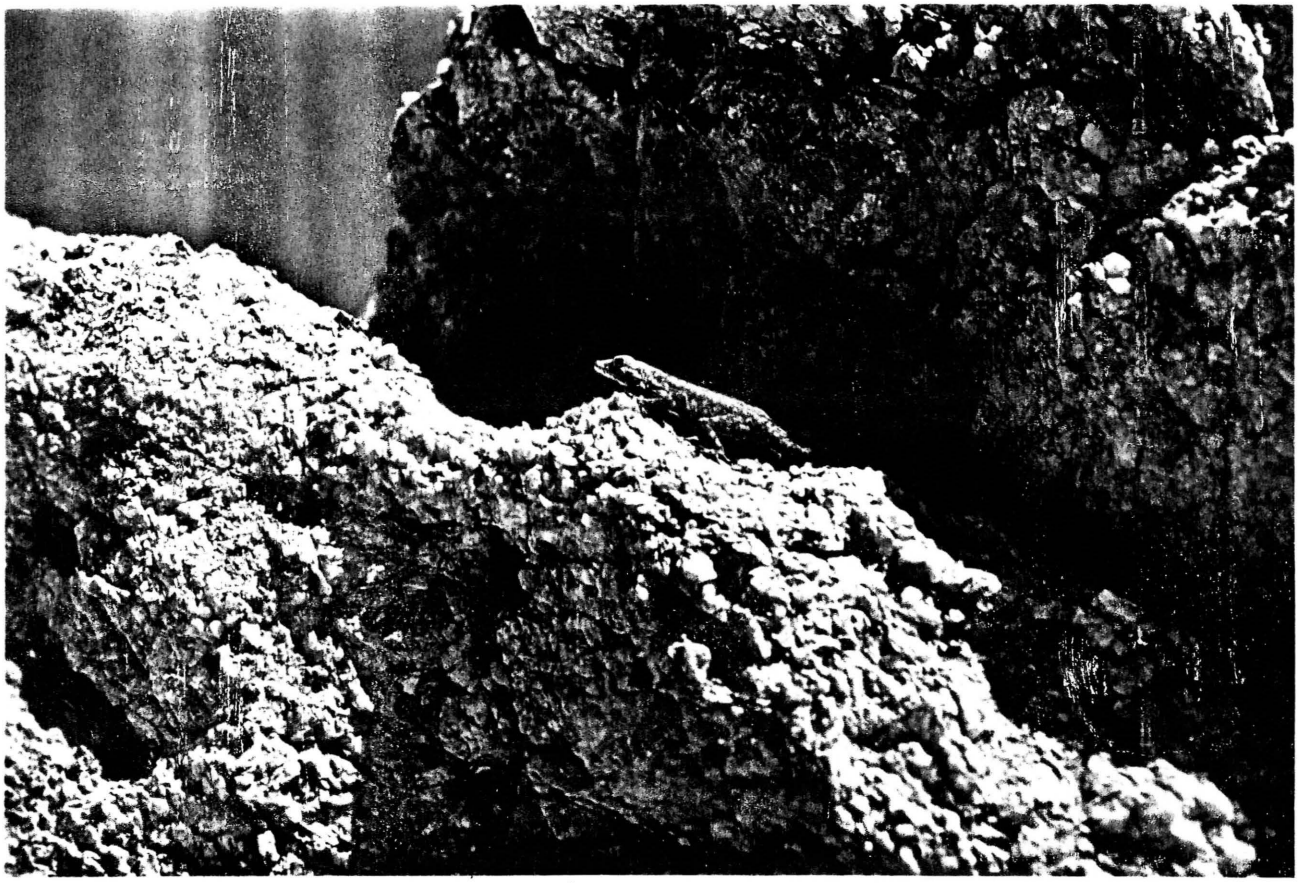


Plate 5. A dark *Rhoptropus bradfieldi* conspicuous against the whitish rock on which it basks. (Kuiseb river near Gobabeb, 9 August 1971, forenoon.)

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 × 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 × 14.89 × 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 *Palmatogecko* eggs (Haacke, 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* (*Bunopus*), *Ceramodactylus*, *Cyrtodactylus*, *Hemidactylus*, *Stenodactylus* and *Tropiocolotes*. 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* oviposit, 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 gecko*, for example, appears to be highly variable – Brodský, 1969), 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 Neonati (Plate 7)

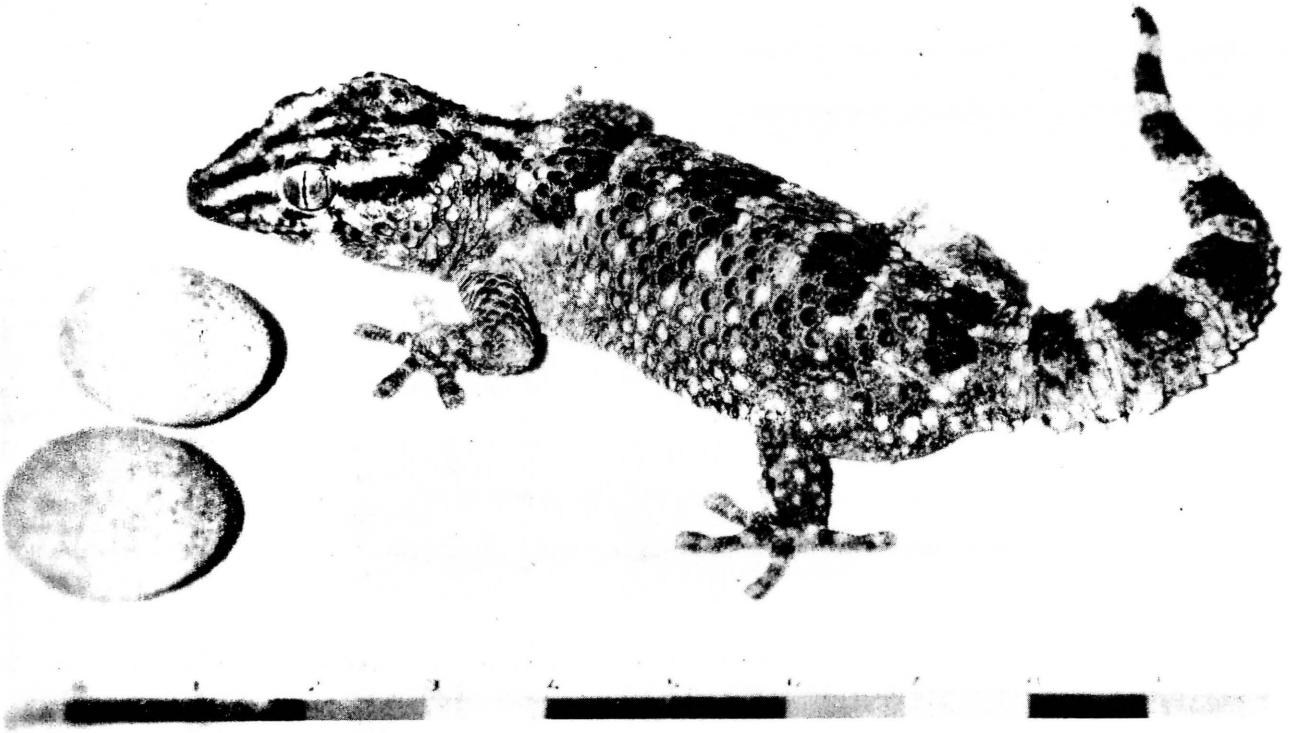
The time of day when hatching occurred is unknown for most eggs, because usually eggs were inspected only once daily. However, one egg is known to have hatched on 5 December 1972 between 0900 h and 1600 h, and another hatched on 25 March 1973 between 1400 and 1450 h. Thus, at least some of the hatchings 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 neonatus 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 hatchling rests for a while after extruding its head and before emerging completely (depicted for *Gekko gecko* by Brodský, 1969: Fig. 10).

The measurements of four normal hatchlings averaged 35.9 mm ra (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 neonati carried a remnant of the yolk sack. In the first case, an unusually small neonatus 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 ca. 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 *Hemidactylus 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 neonatus 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).



...*igatus*, female from the Gobabeb area with two eggs. (Jerusalem, 8 September 1972, from a Kodachrome transparency.) Scale, cen... ...illimeters.

...SSION

...ific Relationships

... of southwestern Asia (Werner, 1973) and ... 1972; Pianka & Pianka, 1976; Werner, in ... the Namib the gecko fauna is rich, including a ... and ground-dwelling species. The follow... ... restricted to the species actually observed. ... ground dwelling forms are practically excluded ... as our searches at night (with lamps) were ... p. 161). This may be due in part to the full moon ... of our visit. The effects of the moon and its ... activities have been investigated mainly in ... invertebrates (Sollberger, 1965) but Klauber ... presented data suggesting that the full moon depres... ... of desert snakes. Casual observations on ... nocturnal reptiles in Israel appear to point in the ... Interestingly, the one dark hour of full moon ... we spent on the dunes was not more fruitful (p. 161).

... appeared remarkable that two congeneric species, ... *afer* and *bradfieldi*, of similar size, and similarly ... should inhabit rocks in the same area. However, ... observation showed that they occupy two distinct ... with very little overlap: *R. bradfieldi*, a slightly heavier ... with "normally broad" digital pads, lives in vertical ... as befits an honest climbing species; FitzSimons ... termed it "essentially rupicolous". *R. afer*, with ... 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 Pianka and Pianka (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*.

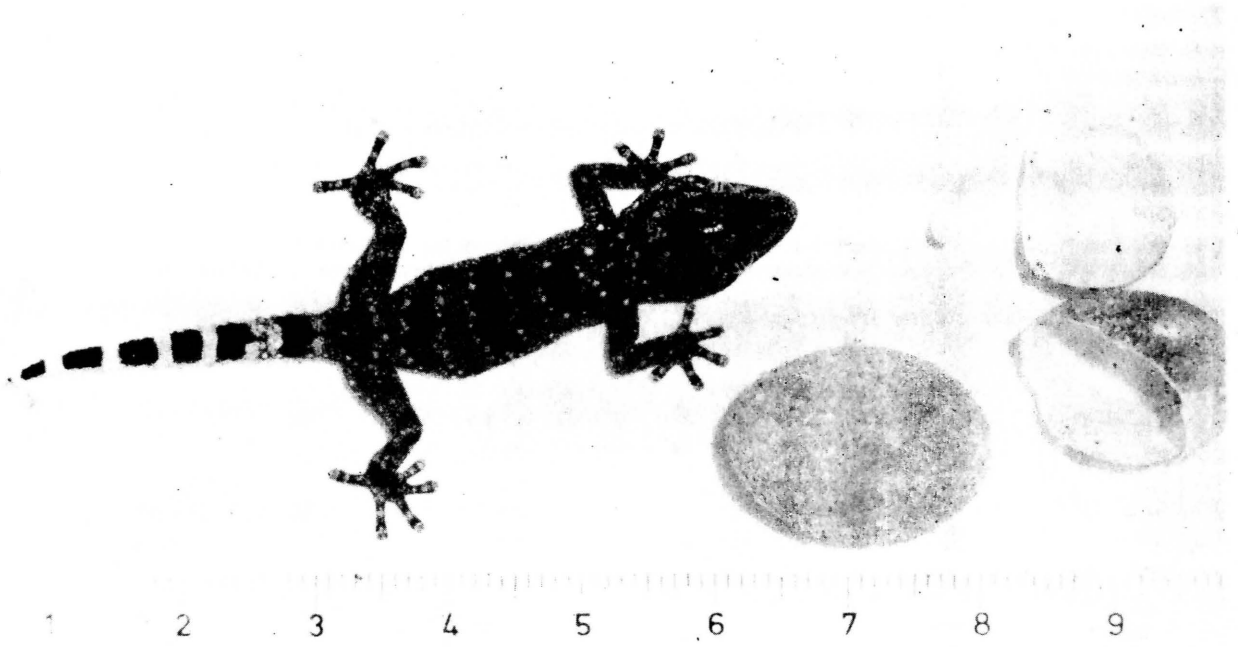


Plate 7. *Pachydactylus laevigatus*, neonatus, the shells of the egg from which it hatched (less than 24 h previously) and the yet unhatched twin egg. Note sar encrusted shell. (Parents from the Gobabeb area; Jerusalem, 14 October 1972, from a Kodachrome transparency.) Scale, centimeters and millimeter

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 pupil was that of *Palmatogecko* (Plate 8D), which would appear to be as completely nocturnal as the ecologically comparable Israeli psammophile geckos *Ceramodactylus doriae* 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 cycl more than a year after their transfer. I am not sure that the kept fully in pace with their original reproductive cycle. suspect, however, that they may have done so, because i August when they were caught, female *Rhoptropus* in th same habitat were commonly pregnant.

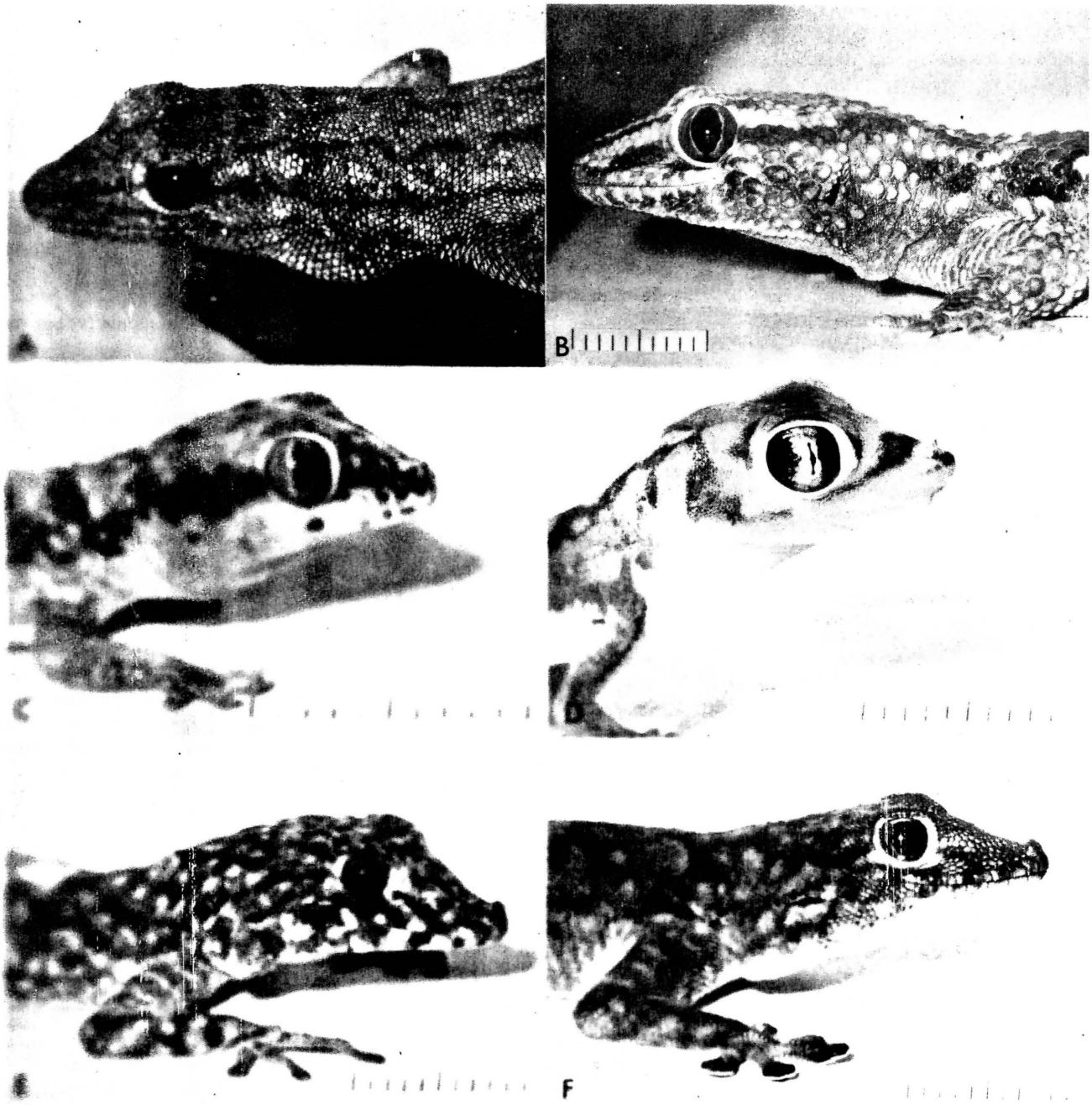
7 CONCLUSIONS

1 Concerning Gobabeb Station in August:

1. *Lygodactylus capensis* occurs on trees along the Kuise River at Gobabeb.
2. *Lygodactylus capensis*, although reputedly mute, cheep when seized (based on one case).
3. At Gobabeb, *Rhoptropus afer* occupies horizont habitats and small rocks whereas *R. bradfieldi* occupie larger steep rocks; there is little overlap between the tw
4. *Pachydactylus punctatus amoenoides* appears to coexi with *Rhoptropus afer* in the same habitat.
5. *Rhoptropus afer* and *bradfieldi* are diurnal, and their ve tical pupils are relatively insensitive to light.
6. The pupils of *Pachydactylus laevigatus* and *P. punctatu amoenoides* are much more light-sensitive than those *Rhoptropus*, and both species appear to be crepuscular nocturnal.
7. The pupil of *Palmatogecko* is more light-sensitive tha those of the *Pachydactylus* species.

2 Concerning *Pachydactylus laevigatus* in Captivity:

8. In captivity, *Pachydactylus laevigatus* lays eggs deposit loosely in the ground, that are initially soft and stick



... under comparable levels of illumination. All photographs ... originally photographed with the animal is included.

... (C)–(F) Light intensity ca. 30 lux (Jerusalem, 23 August 1971):

(C) *Pachydactylus punctatus amoenoides.*
(D) *Palmatogecko rangei.*
(E) *Rhoptropus afer.*
(F) *Rhoptropus bradfieldi.*

9. Each female lays ca. 3 clutches of 2 eggs each during August–November.
10. Eggs measure ca. 19 × 15 × 13 mm.
11. Incubation appears to last ca. 60 days at 29.5°C.
12. The neonatus measures ca. 36 mm, head and body; and 27 mm, tail.

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