

Physiological, morphological
and behavioural adaptations of
the ultrapsammophilous,
Namib Desert lizard
Aporosaura anchietae
(Bocage)

by
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The biology of desert amphibians and reptiles has recently been reviewed at some length by Mayhew (1968). He points out that, although a considerable number of desert lizards have been studied, very few have been found to possess specific physiological adaptations to the desert environment. In fact, the majority escape desert conditions almost entirely by well defined adaptive behaviour. Nevertheless, as he has indicated, most of these studies have been carried out on New World lizards and it is possible that the Old World forms may exhibit more specialised adaptations. Moreover, when lizards are able to escape thermal stress and desiccation by behaviour, the problem of survival is largely one of adaptation to a markedly fluctuating nutritional plane. The reason for this is that in most deserts a brief period of ample vegetation and dense insect populations is followed by a prolonged period of drought and a low nutritional plane.

When the above considerations are taken into account together with the preliminary observations of Hoesch (1960), it is clear that a study of the Namib Desert, sand-diving lizard *Aporosaura anchietae* should be most rewarding. This species (Figs. 1 and 2) was first described by Bocage in 1867 from Rio Coroco, near Mossamedes in Angola. Until fairly recently it was thought to be very rare but it is now considered to be one of the dominant species in the dune system of the Namib Desert. Furthermore, in view of the highly specialised fauna which has been described in the dune system of the Namib (Koch, 1961) and the apparent great geological age of this area, one

would expect this species to exhibit interesting adaptive characteristics. For these reasons then a study of the physiology, behaviour and ecology of *Aporosaura* was undertaken.

PROCEDURE

The investigation was carried out over a period of 18 months and consisted of intermittent observations while studying the general ecology of a dune ecosystem and three periods of three weeks, during which intensive field studies were carried out to examine the behaviour and ecology of the species. In addition, animals were collected from the field for either immediate dissection or held in captivity for laboratory studies. The following general procedure was adopted:

Distribution: In addition to distribution records kindly supplied by Mr. W. Haacke of the Transvaal Museum, records were kept of distribution during extensive field trips along the eastern perimeter of the dune system and during expeditions into the interior of this system.

Climate: As the Namib Desert Research Station is officially rated as a First Order weather station, daily records of meteorological data were available for the investigation. In addition the temperature on the surface of dunes was measured with fast-registering mercury thermometers and thermistor probes during periods of intensive field study.

Feeding habits: These were studied in the field through the use of powerful binoculars and in the laboratory by examination of gastro-intestinal tract contents of freshly killed specimens.

Water balance: The water relationships of *Aporosaura* were examined by (a) studying the behaviour of other organisms occurring in the food chain of *Aporosaura* (b) examining the water content of the gastro-intestinal tract in relation to prevailing weather situations (c) laboratory studies involving dehydration and rehydration of captive specimens (d) determinations of plasma osmolality under a variety of conditions using the method of Gross (1954).

Thermoregulation: This was studied in the field by observing the animals throughout the day from a remote position in conjunction with simultaneously monitored micro-climatic data. In addition the animals were observed at close range in the laboratory under a variety of temperature conditions and their behaviour analysed and recorded photographically.

Activity rhythms: These were recorded through field census made from a remote position while endogenous or circadian rhythms were examined in a series of temperature controlled containers which had been fitted with photo-cells and a continuous event recorder. Light intensity in these containers was kept at a constant minimum with just sufficient light to trigger the photo-cell mechan-



Figure 1. (Top) *Aporosaura anchietae* in threatening posture. (Photo: Dr. L. Schulze-Prozesky, Transvaal Museum).



Figure 2. (Bottom) *Aporosaura anchietae* painted by Klaus Schaefer

ism. The containers were provided with sand to a depth of 7.5 cm and the diameter measured 15 cm.

Morphology: Gross anatomy was routinely observed by macrodissection and in the case of one individual serial cross-sections were prepared of the entire animal in order to study the micro-anatomy.

RESULTS AND DISCUSSION

Distribution

The known distribution of *Aporosaura* has been illustrated in Fig. 3. These records are based on personal observation, records supplied by the Transvaal Museum and Mertens (1955). The data contained in Fig. 3 reveal that the distribution of

Aporosaura is governed by two main environmental factors. These are the presence of sand, particularly in the form of large dune systems, and the occurrence of advective sea fog. It should, however, be pointed out that meteorological data are not sufficiently complete to say with absolute certainty that all localities of distribution receive fog regularly, although there is good reason to believe this to be the case. The distribution of *Aporosaura* coincides with aeolian sand deposits throughout the Namib Desert. The importance of fine wind-blown sand and advective fog in the ecology of this species will become clear in the subsequent discussion.

The following records constitute the known distribution of *Aporosaura*:

Just N of Lüderitz
 Bogenfels
 Farm Namtib, 110 km NNW of Aus.
 Porto Alexandre, Angola
 Near Elizabeth Bay 33 km S of Lüderitz
 Gobabeb
 5 km S of Swartbank
 Swakopmund
 Sandwich Harbour
 Near Rechenberge, 48 km NE of Lüderitz
 Rooibank
 Unjab River, 8 km from mouth
 Sossus vlei
 ± 48 km NW of Ouhandjou, Kaokoveld
 56 km SW of Orupembe, Kaokoveld
 Okotuso area, Kaokoveld
 Near Awasib (Diamond Area 2)
 24 km S of Gobabeb
 32 km S of Natab
 Geluk farm (Maltahöhe district)
 Tsondabvlei
 Tsauchab River, 40 km W of Sesriem
 Between Uri-Hauchab mountain and Naribis
 8 km E of Walvis Bay

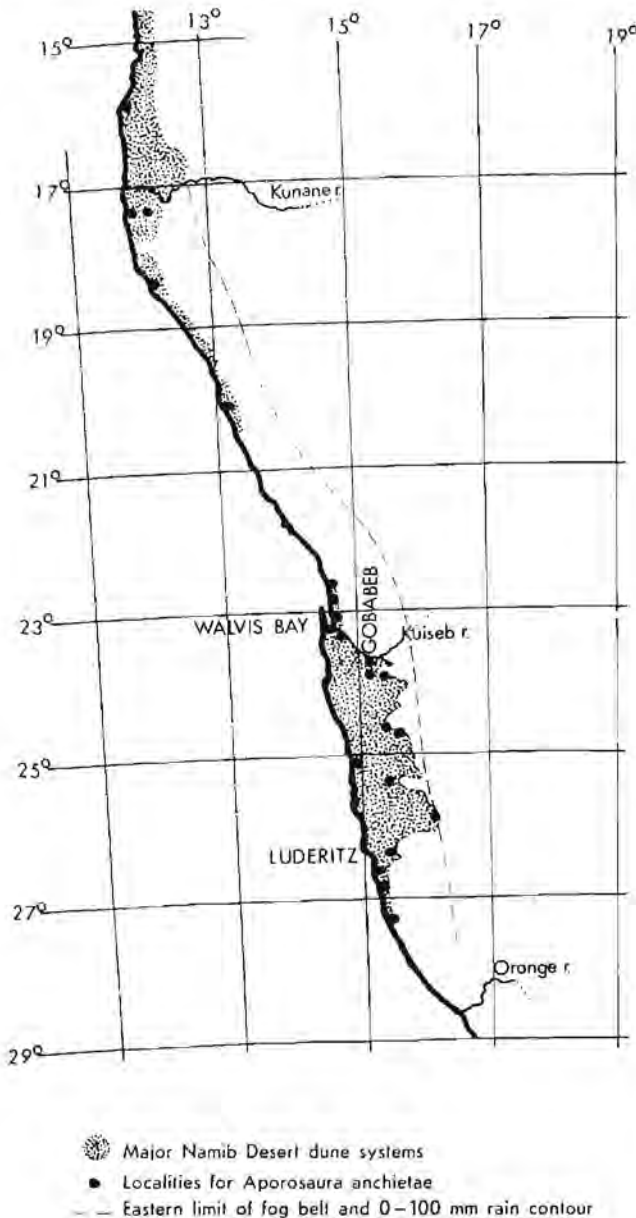


Figure 3. Map depicting distribution of *Aporosaura anchietae* together with certain climatic and geomorphological features. Schaefer.

Habitat

It is beyond the scope of this paper to outline the climate, vegetation and geomorphology of all the areas where *Aporosaura* is known to occur in the Namib. Instead, the main study area of the investigation, the large dune system south of the Desert Research Station at Gobabeb, will be briefly described. For more detailed discussion the reader is referred to Logan (1960), Meigs (1966) and Schulze (1969).

(a) **Climate:** The prevailing winds are an important feature of the climate at Gobabeb. The easterly mountain wind is a high velocity wind, gusting up to 80 mph, which occurs frequently during the winter months when low temperatures prevail on the high inland plateau to the east. This wind, due to the rapid drop in altitude over the escarpment, is dry and often very hot. During summer the easterly mountain wind is rare and the prevailing wind is from the Atlantic Ocean, i.e. from a westerly to south-westerly direction. The latter wind is cool and moist and together with the east wind is mainly responsible for the sculpting of the dune system. In addition the east wind, because of its high velocity and origin over an area with reasonably high rainfall, is responsible for carrying dry plant material or detritus into the dune system.

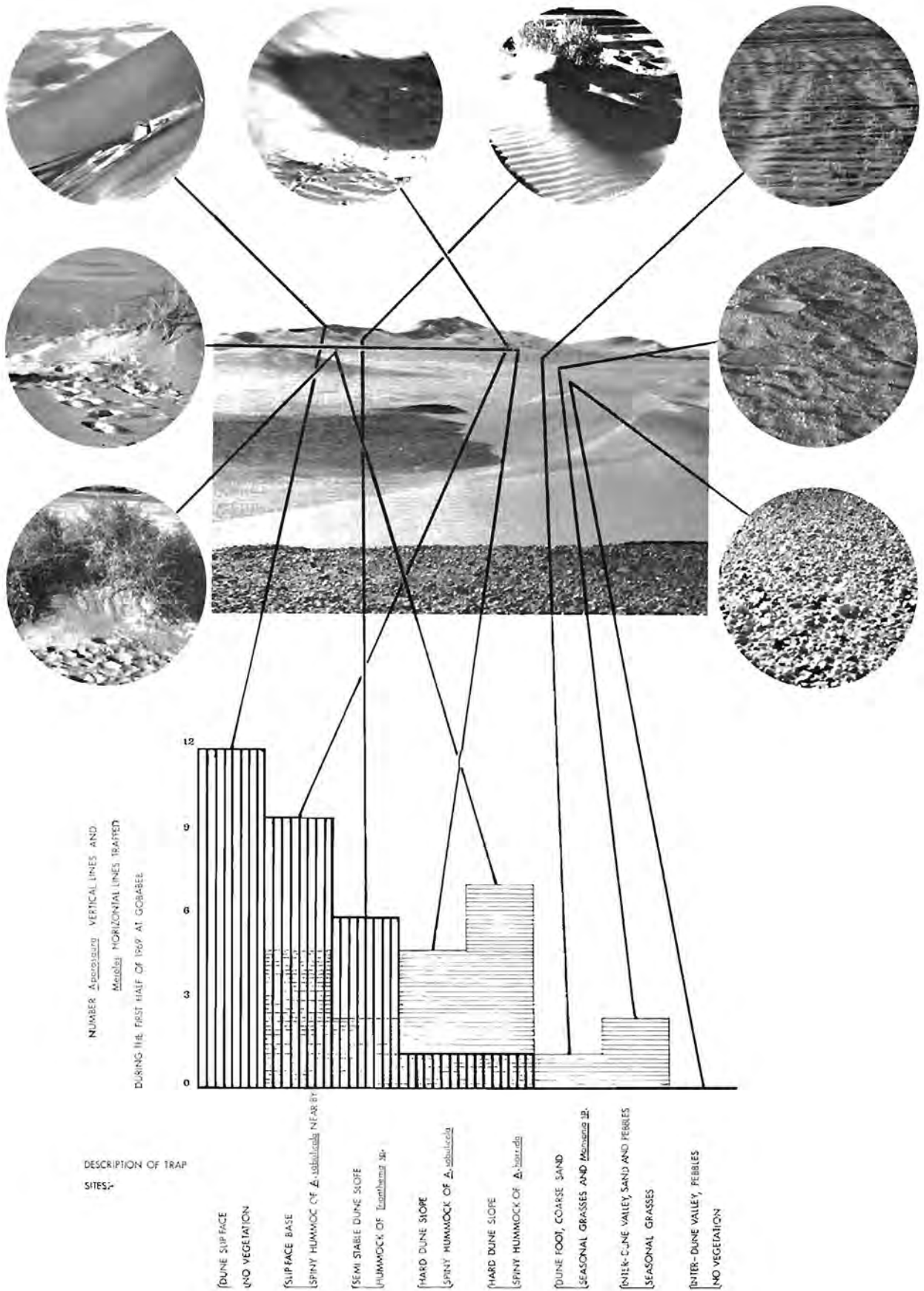


Figure 4. Frequency histogram of trappings of *Aporosaura archietae* and *Meroles cuneirostris* in the various micro habitats of a dune system near Gobabebe during the first half of 1969. (Unbaited pit-traps with 12" diameter were used.) The view on central plate is from the south onto the general trapping area, peripheral plates depict the trapping sites.

Advective sea fog is a regular feature of great importance to the ecology of the whole Namib Desert. The fog precipitates on the dunes, detritus cushions and plant hummocks, mainly during the night and early morning. For direct use by small animals, the frequency of precipitation is much more important than the amount, and the frequency of fog in the morning alone is about 40 days in the year (Schulze, 1969). Furthermore, the frequency distribution is fairly uniform, except for May and June, when fog is less frequent in the inland dunes (Gobabeb). The frequency at the coast is much higher, and when dew and rain are included, some form of precipitation can be expected at least once every three weeks in any part of the distributional range of *Aporosaura*. It is also of interest to note that the amount of precipitation in the form of fog exceeds the rainfall at Gobabeb and that rainfall increases inversely to fog precipitation in an easterly direction from the coast to the escarpment.

The temperature range experienced at Gobabeb is extreme although the average daily maximum is lower than would be expected, namely 30,1° C, while the absolute daily maximum is 42,3° C in the Stevenson screen (Schulze, 1969). The microclimate on the surface of the dunes will be discussed in more detail later, suffice it to say that surface temperatures above 60° C have repeatedly been measured while the highest reading recorded was 80° C (pers. comm., K. Schaer).

(b) *Vegetation*: *Aporosaura* is decidedly not dependent on active vegetation, since some parts of the distributional range are virtually vegetationless (viz. the coastal dunes). The inland dunes are sparsely vegetated with i.a. *Stipagrostis sabulicola*, *Acanthosicyos horrida* and *Eragrostis spinosa*, all of which are spiny and form hummocks. These plants are used as shelter from heat and enemies and as a source of arthropod food by *Meroles cuneirostris* and other lizards, but not by *Aporosaura*. Other plants in the southern Namib dune system include *Trianthema* sp., *Monsonia ignorata*, and various seasonal grasses, none of which, however, is of any direct importance to the habitat of *Aporosaura* (Figs. 3 and 4). By virtue of its complete independence of plants, *Aporosaura*, together with *Angolosaurus skoogi* of the northern Namib, may have no counterpart in other deserts, since the Namib seems to be the only desert with an ultrapsammophilous arthropod fauna extensive enough to support a reptile fauna in bare vegetationless sand (Koch, 1961; Koch, Hamilton and Monod, in preparation). Both the ultrapsammophilous arthropod and reptile fauna of the Namib depend directly or indirectly almost exclusively on the windblown vegetable detritus of local as well as distant origin. In this respect it should be mentioned that the eastern perimeter of the Namib is bordered by the Khomas Hochland escarpment which has a predominantly savannah-shrub vegetation. The high velocity easterly winds originating from this region could carry dry vegetation from this area and deposit it in the form of wind-blown detritus on the slip-faces of the dune system, although the exact origin of the detritus has not yet

been determined. Nevertheless, a large proportion of this detritus consists of small particles of naturally cured hay and grass seeds which could originate from the savannah vegetation.

(c) *Geomorphology*: Like all aeolian sand, the dunes in the Namib form compacted, often rippled surfaces on the windward side, with a steep slip-face on the leeward side. These slip-faces, sometimes referred to as leeward-faces, are at an angle of ca. 32° to the horizontal in the Namib dunes, varying somewhat with air moisture. The dunes in the Namib generally form on the barchan dune principle, the leeward side of the dune acts as a trap for wind-blown matter and both sand and organic particles sift down on the slip-face, as a result of wind action, to form a very loose and powdery layer of sand with the lighter organic matter mostly on the surface. This wind-blown organic detritus is then collected by the minor turbulences on the slip-face into detritus "cushions", which consist mainly of grass stems, seeds and arthropod shells. Unlike the smaller barchan dunes described by Hamilton and Coetzee (1969) at Torra Bay in the northern Namib Desert, the major southern dunes have no dune crest area, but only a sharp ridge.

These slip-faces therefore are extremely important in the ecology of *Aporosaura* for they provide an ideal medium in which to thermoregulate, to escape from predators and the wind-blown detritus which collects there is of both direct and indirect nutritional importance. Moreover, the soft wind-blown sand is well oxygenated and ideal for sand diving and subterranean respiration. The main dune ranges in the southern Namib, among the highest in the world, are orientated in a north-south direction and are approximately one to two miles apart. The slip-faces change with the wind direction but are predominantly east or west facing, depending on wind direction. This factor is of importance to the temperature accommodation of dune animals since western slopes heat up much later in the day, and stay warm much longer in the afternoon than eastern slopes. The difference between east facing and west facing slip-faces can be as much as 10° C at certain times of the day. Typical temperature conditions prevailing upon an east facing slip-face are illustrated in Fig. 5. These data also show the effect of wind upon slip-face temperature and the marked reduction in temperature 7,5 cm below the surface.

Feeding Behaviour and Nutrition

The feeding behaviour of *Aporosaura* is closely related to its thermoregulatory behaviour and activity rhythm which will be discussed later. Suffice it to say, at this stage, that when weather conditions are favourable during the day the animals emerge upon the steep slip-face to feed upon detritus and occasional arthropods. During this activity they frequently travel a considerable distance from the slip-face, traversing the hard rippled dune slopes

at great speed to examine distant slip-faces for suitable food. During this process they pay special attention to the detritus which collects at the foot of slip-faces in a calm wind-free vortex. They are also capable of tremendous speed on the soft surface of the slip-face and even catch flying insects with great ease.

Their foraging excursions are, however, not confined to the slip-faces, and, given favourable conditions, they will forage between the vegetation hummocks at the foot of the dunes and even on

occasion enter the inter-dune plains to a distance of 50 m to feed on termites and ants. During these excursions on the surface they frequently interrupt their rapid sprints across the surface of the sand and indulge in a characteristic behaviour pattern which is best described as "head tapping". This consists of moving the head up and down onto the sand surface in a rapid succession of movements. The reason for this behaviour is unknown and may be to assist olfactory processes as it is frequently more intense when the animal moves through detritus.

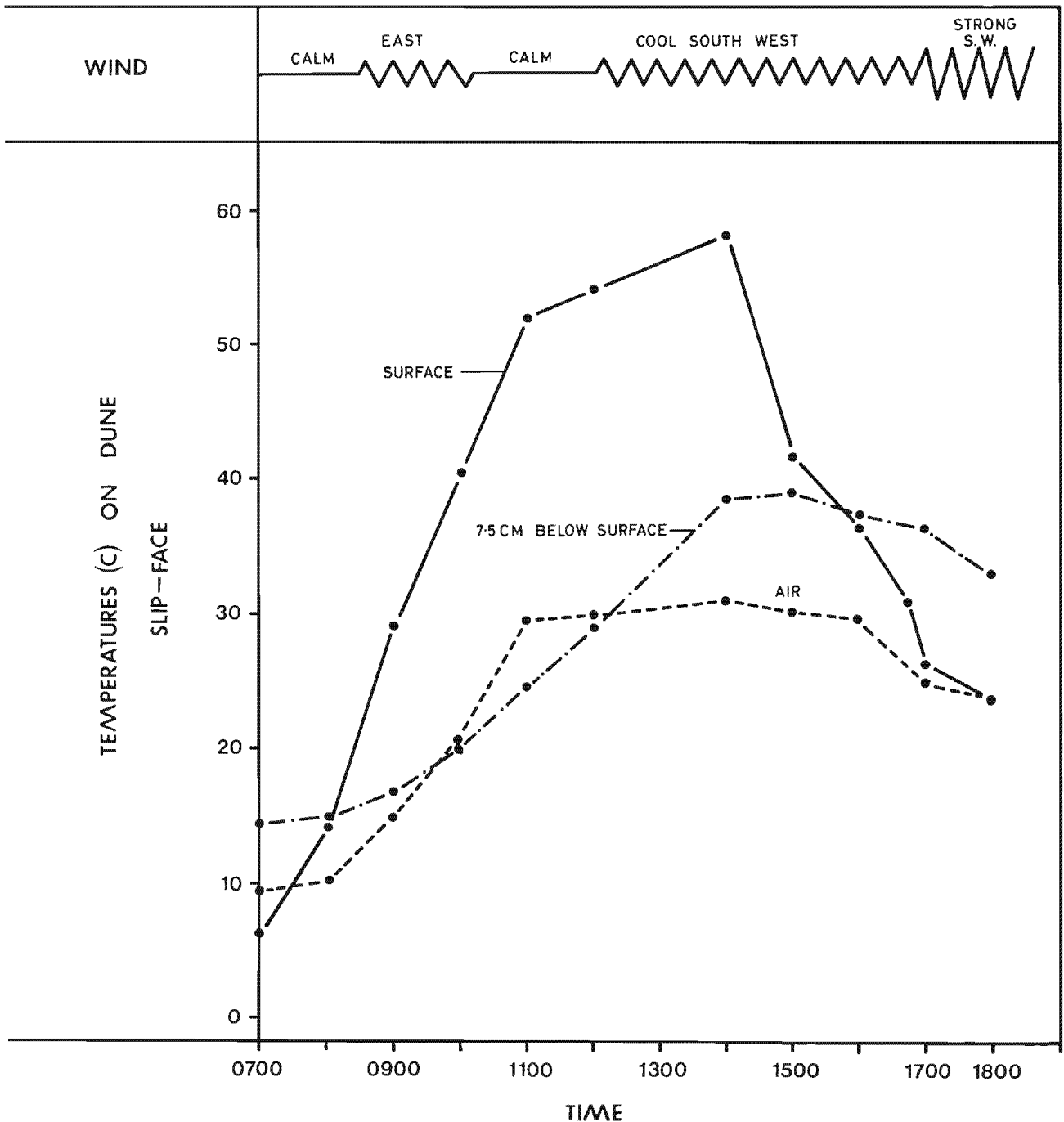


Figure 5. Typical temperature and wind conditions on dune slip-face which constitutes the micro-habitat of *Aporosaura anchietae*.

In the coastal dunes between Walvis Bay and Swakopmund there is virtually no vegetation and *Aporosaura* in this area are entirely dependent upon the arthropod fauna and particularly upon dipterans from the nearby sandy beaches. The latter are frequently caught in flight or while they are thermo-regulating upon a slip-face and it is in these circumstances that *Aporosaura* best demonstrates its tremendous speed and agility often leaping into the air to capture flying insects.

In captivity *Aporosaura* will always give preference to arthropods and can be maintained for many months on small grasshoppers and termites. Nevertheless, if no arthropods are offered to them they will eat commercial bird seed mixtures in reasonable quantity. Of greater interest, however, is their frequency of feeding in captivity. For example, when offered either termites or false codling moth *ad libitum* after three weeks of starvation they will feed voraciously. Towards the end of the feeding period the animal twists its body in a characteristic writhing motion, thereby forcing and assisting the passage of food into the stomach. This is a most pronounced behavioural pattern and the reason for it becomes clear if the animal is killed and the stomach examined immediately after feeding. The stomach is enormously distended, so much so that it fills a large volume of the abdominal cavity and in this distended condition the stomach wall is sufficiently transparent to enable one to see the contents. After feeding in this manner, captive animals exhibit little or no interest in feeding for a prolonged period and remain submerged beneath the sand for longer periods than usual.

The significance of this feeding behaviour under desert conditions, where the opportunity for feeding is often infrequent, is obvious. Moreover, it is possible that *Aporosaura* may be able to convert this food rapidly into fat reserves which would ensure its survival for long periods of unfavourable nutrition. In this connection it is of importance that Bustard (1967) found that starved *Coeleonyx variegatus* could convert sufficient food within four days into fat reserves which lasted for six to nine months.

In order to ascertain the exact nature of the diet of *Aporosaura*, the gastro-intestinal contents was examined of animals drawn from three sampling areas namely, Gobabeb, the coastal dunes between Walvis Bay and Swakopmund, and the small dunes near the Unjab River mouth. The results of these examinations are summarized in Tables 1, 2 and 3.

From the data contained in Tables 1, 2 and 3 it is evident that *Aporosaura* is extremely opportunistic in its feeding habits. At Gobabeb by far the greater portion of the gastro-intestinal contents consisted of grass seeds, with relatively few small arthropods which inhabit the same micro-habitat. On the coastal dunes near Swakopmund their diet consisted almost exclusively of kelp flies. At the Unjab River mouth, on the other hand, the diet consisted mainly of weevils. It would appear then that *Aporosaura* is well adapted to changing its diet according to the

Table 1. Gastro-intestinal contents of *Aporosaura anchietae* collected from the major dune system immediately south of Gobabeb.

Animal No.	Date	Contents
1	June, 1968	2 Thysanura (<i>Lepisma</i>) 1 <i>Psammogaster</i> beetle 84 Grass seeds
2	June, 1968	6 Termites 2 Grass seeds
3	June, 1968	1 Termite 38 Grass seeds
4	June, 1968	3 <i>Psammogaster</i> beetles 2 Dune ants 7 Termites 102 Grass seeds
5	June, 1968	1 <i>Psammogaster</i> beetle 16 Grass seeds
6	June, 1968	3 Thysanura (<i>Lepisma</i>) 3 Termites 8 Grass seeds
7	June, 1968	4 Thysanura (<i>Lepisma</i>) 1 Termite 72 Grass seeds
8	June, 1968	2 <i>Psammogaster</i> beetles 1 Thysanura (<i>Lepisma</i>) 2 Dune ants 2 Termites 2 Red solifuges 72 Grass seeds
9	June, 1968	4 <i>Psammogaster</i> beetles 1 Solifuge 1 Dune ant 5 Grass seeds
10	June, 1968	1 <i>Psammogaster</i> beetle 1 Termite 1 Aphid (<i>Pseudococcus</i>) 11 Grass seeds
11	June, 1968	42 Grass seeds
12	June, 1968	33 Grass seeds
13	September, 1968	1 <i>Cardiosis fairmairei</i> beetle 18 Grass seeds
14	September, 1968	1 Thysanura (<i>Lepisma</i>) 36 Grass seeds
15	September, 1968	2 <i>Cerosis hereroensis</i> beetles 70 Grass seeds

Table 1 (continued)

Animal No.	Date	Contents
16	September, 1968	1 Dune ant 119 Grass seeds
17	April, 1969	1 Thysanura (<i>Lepisma</i>) 1 Grasshopper (<i>Crypsicerus cubicus</i>)
18	April, 1969	1 Hymenopteron 2 Curculionidae 2 Grass seeds
19	April, 1969	2 Staphylinid beetles 1 Grasshopper (Fam. <i>Lathiceridae</i>) 1 <i>Cerosis hereroensis</i> beetle 34 Grass seeds
20	April, 1969	1 grass seed Unidentifiable remains of small arthropods
21	April, 1969	1 Tenebrionid larva 1 Grasshopper (Fam. <i>Lathiceridae</i>)
22	April, 1969	2 Curculionidae Fine grass stems (green)
23	April, 1969	14 Curculionidae
24	April, 1969	2 Grasshoppers (Fam. <i>Lathiceridae</i>) Fine grass stems
25	April, 1969	1 Hymenopteron Fine grass stems (green)
26	April, 1969	3 grass seeds Unidentifiable remains of small arthropods
27	April, 1969	10 Hymenoptera (small)

dictates of circumstances which must be of considerable advantage under desert conditions. The herbivorous nature of the diet at Gobabeb, however, is a decided disadvantage as the water requirement of an animal consuming dry grass seeds is considerably higher than when insects form the major portion of the diet. It would seem then that provision would have to be made for some form of water storage in these lizards when on a dry herbivorous diet and, as will be discussed later, this is in fact what occurs.

The data in Tables 1, 2 and 3 also confirm the large capacity of the digestive tract observed in captivity. For example in Table 1 it can be seen that in one individual the remains of 119 grass seeds were ob-

served and in Table 3 the remains of 191 dipterans were recorded. This represents a very large capacity when the size of *Aporosaura* ($\pm 3g$) is taken into consideration.

Finally, it was noted that a large amount of sand was present in the gastro-intestinal contents and in several lizards nematodes were found. The parasite load, however, was relatively light.

Water Balance

In order to survive in the desert environment lizards usually exhibit some form of adaptation, either behavioural or physiological, in order to balance water loss against gain. For example, insectivorous lizards, by the nature of the high moisture content

Table 2. Gastro-intestinal contents of *Aporosaura anchietae* collected from the coastal dunes between Walvis Bay and Swakopmund.

Animal No.	Date	Contents
1	April, 1969	101 Diptera
2	April, 1969	3 Staphylinid beetles 36 Diptera 1 White lady (<i>Carparachne alba</i>)
3	April, 1969	1 Tenebrionid (small) 1 Moth 191 Diptera
4	April, 1969	27 Diptera
5	April, 1969	2 Tenebrionid (small) 37 Diptera

Note: The majority of the Diptera annotated above belong to the family Canaceidae (genus *Canace*) and the family Coelopidae (*Coelopa (Pucomyia) africana*).

Table 3. Gastro-intestinal contents of *Aporosaura anchietae* collected from small dunes near Unjab River mouth.

Animal No.	Date	Contents
1	November, 1968	70 small Curculionidae
2	November, 1968	2 small scarab beetles 46 small Curculionidae
3	November, 1968	79 small Curculionidae
4	November, 1968	25 small Curculionidae 1 Plant bug (Fam. Pentatomidae)
5	November, 1968	1 Noctuid moth

of their diet, can accomplish this reasonably easily by avoiding high temperatures and low relative humidities which increase respiratory water loss and water loss through the skin. In addition, obligatory nitrogen excretion in the form of uric acid is a great advantage to these animals.

Other interesting forms of adaptation have been reported recently. For example, Bentley and Blumer (1962) have shown that when *Molloch horridus* comes into contact with water, the water enters fine capillary channels in the skin and spreads along these channels until it reaches the lips where it is absorbed by hygroscopic material produced in this area by mucous glands. In other lizards the actual skin has been shown to be permeable to water (Warburg, 1966) while in one species *Uromastix acanthinurus* the permeability of the skin is dependent upon the amount of moisture in the environment and is apparently permeable in water and impermeable in dry air (Tercafs, 1963). Moreover, in some herbivorous desert lizards water balance is facilitated by the presence of nasal salt glands which are capable of excreting a hyperosmotic fluid (Norris and Dawson, 1964), while some lizards are apparently capable of storing extra water in their tissues (Khalil and Abdel-Messeih, 1959 and 1961).

If the water balance of *Aporosaura* is considered against this background it is clear that it exhibits several of these adaptive mechanisms. For example, the activity rhythm, which will be discussed in detail later, is such that the animal spends prolonged periods submerged beneath the sand thus avoiding the desiccating effect of high temperatures and dry air to a great extent. In addition, a portion of the diet even at Gobabeb consists of small arthropods with a relatively high moisture content. In this context it has been possible by observing predator-prey relationships to construct a water chain concomitantly with one of the food chains at Gobabeb which leads up to *Aporosaura*. This water chain originates with advective sea fog which precipitates in fine droplets upon the tenebrionid beetle *Lepidochora argentogrisea*. These beetles are then preyed upon by the white lady spider (*Carparachne alba*) which in turn are taken by *Aporosaura*.

Similarly, in the coastal dunes at Swakopmund a more direct water chain exists. Here the frequency of advective sea fog is far greater and it was observed to condense in fine droplets upon the wings of Diptera which settle on the crests of these dunes overnight. The Diptera, chiefly Coelopidae or kelp flies, remove this moisture from the surface of the wings in characteristic fashion by drawing the wings across their legs, thus transporting the moisture in larger droplets to where it is, presumably, readily available to the organism either by imbibition through the proboscis or absorption through the integument. As the fog clears the Diptera can be seen thermoregulating on the warm surface of the slip-faces where shortly afterwards they are captured in large numbers by *Aporosaura*. The *Aporosaura* in turn have been seen to be captured by the side-winding adder (*Bitis peringueyi*), thus complet-

ing the water chain (Fig. 6). The osmotic gradient involved in this water chain has been assessed and it is of interest to note how dramatically the osmolality of the sea water differs from that of the advective sea fog. This is not surprising as the condensed fog is derived from water vapour which condenses above the cold Benguella sea current and need not necessarily be of direct marine origin. It is, however, of interest that the osmolality of the condensed fog is very low in spite of the proximity of the sea, as it often occurs that advective fog will condense around salt nuclei derived from sea spray.

Fog samples were collected in glass containers which had been rinsed in distilled water and placed about 0.5 km from the sea. These samples had an osmolality of 15-20 mOsm. The condensed fog ingested by reptiles will naturally have a higher osmolality than the above sample because of contamination from dust and the plant material upon which it settles. Nevertheless, even allowing for a four fold increase the fog water would still be most useful to the animals. In fact, a single fog water sample collected off plant material at Gobabeb had an osmolality of only 28 mOsm. Apparently then the condensed fog is ideal for supplementing the water balance of any animal that is able to utilise it. This fact, together with the relatively high frequency of the fog, confirms the belief that fog can be of great importance in the general ecology of the Namib. The osmolality of the haemolymph of the kelp flies and of *Aporosaura* is, as one would expect, considerably higher than that of the fog, while the osmolality of the dipterans exceeds that of *Aporosaura*. This would lead one to believe that *Aporosaura* may be obliged to utilise fog water in the coastal dunes. The association of the kelp flies with the highly saline medium in the kelp would presumably counterbalance the beneficial effects gained from fog water, although their malpighian tubules should also contribute towards maintaining water balance, thus benefitting *Aporosaura* indirectly.

In spite of the apparent ease with which *Aporosaura* is able to maintain water balance in the coastal dunes where it is exclusively insectivorous, the inland population at Gobabeb is faced with several difficulties in this regard. For example, although they remain submerged for the greater part of the day, they spend a considerable amount of time on the slip-faces of dunes in a micro-climate of 30-40°C and low relative humidity. This means that evaporative water loss during this period must be significant and when one considers that, in addition to this stress, the greater percentage of their diet consists of dry grass seed, then it would be expected that they would be compelled to make use of a source of free water. The obvious choice in this respect would be condensed sea fog on detritus and isolated plants and, although *Aporosaura* has not been observed to drink condensed fog, there is very strong circumstantial evidence that it does. For example, when animals are captured and dissected within two days after the occurrence of a heavy condensing fog the digestive tract is greatly distended and filled with clear fluid.

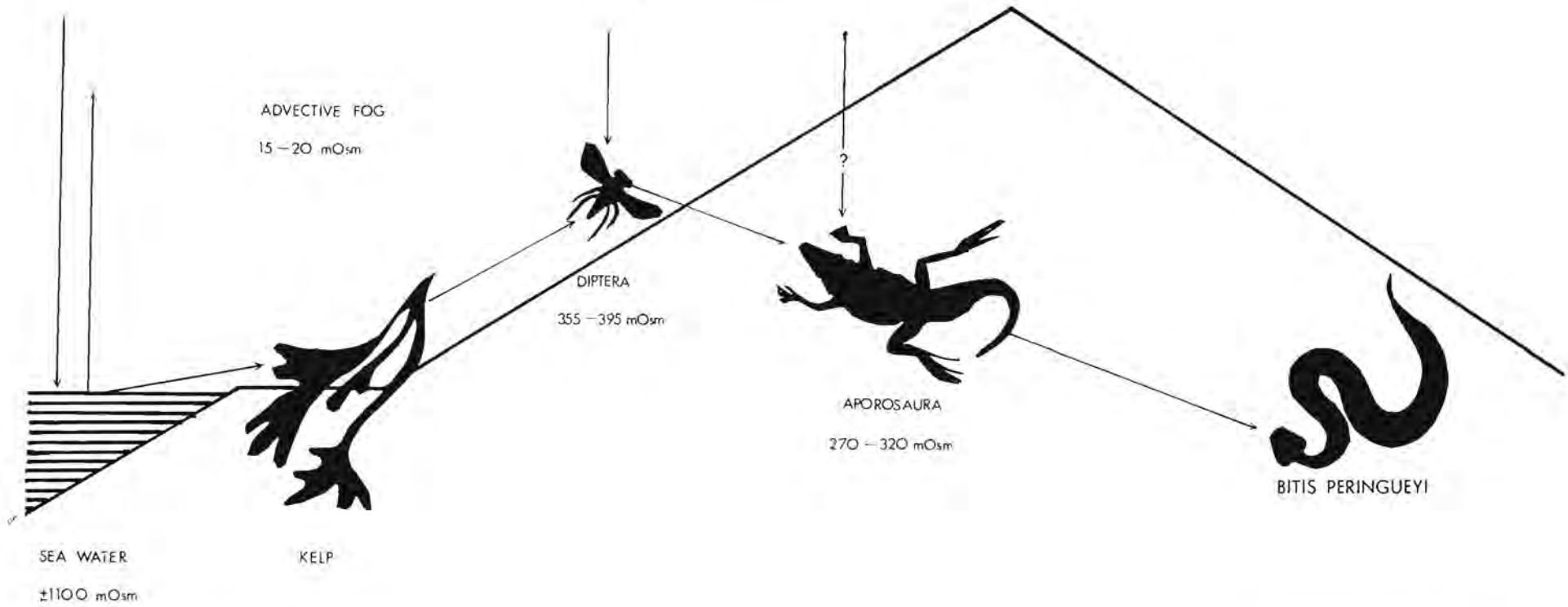


Figure 6. Schematic presentation of water and food chain passing through *Aporosaura anchietae* in the coastal dunes south of Swakopmund. The appropriate osmolality is indicated where known.

When, on the other hand, the dissections are carried out three weeks after the occurrence of the last fog this phenomenon is absent. Moreover, the animals drink water droplets, sprayed onto dead plant material, very readily when in captivity and, after 5 weeks of dehydration, will emerge from beneath the sand in response to the aerosol spraying of water upon plant material in the terrarium. Finally, *Aporosaura* has been trapped in a time-registering pit trap between 08,00 and 10,00 hours during heavy fog. The surface temperature at this time was between 13,5°C and 16,2°C which is far lower than the temperature normally required by them for activity.

In view then of the above circumstantial evidence for the drinking of condensed fog water, laboratory experiments were carried out to examine quantitatively how much water *Aporosaura* is capable of drinking in a brief period, what occurs with this water after ingestion and what effect the sudden intake of a large amount of water has on the osmolality of the plasma. In order to do this eight *Aporosaura* were withheld from water for three weeks and weighed before and after free access to water for a three minute period. The animals were then killed at intervals of 15 minutes, 24 hours, three weeks and eight weeks after receiving water (two animals at each interval) and the digestive tract examined and photographed. A further 10 individuals were divided into two groups after a three week dehydration period and the one group was immediately killed and blood samples collected for haematocrit and osmolality determinations. The second group was allowed free access to water before being killed after 15 minutes for similar blood samples. The results of these experiments are summarised in Fig. 7 and Tables 4 and 5.

The data in respect to water intake in Table 4 show that within three minutes *Aporosaura* is capable of ingesting approximately 11 per cent of its body weight. This is remarkable and equivalent to the

Table 4. Water consumption of *Aporosaura anchietae* during a three minute drinking period after three weeks of dehydration.

Animal No.	Weight before drinking (g)	Weight after drinking (g)	Intake	Intake as % of body weight
1	2,8272	3,0433	0,2161	7,6
2	3,3464	3,6157	0,2693	8,1
3	1,0869	1,2481	0,1612	14,8
4	2,5034	2,8074	0,3040	13,1
5	2,7265	3,0984	0,3719	13,6
6	2,3164	2,5328	0,2164	9,3
7	2,3939	2,6222	0,2283	9,5
8	5,7967	6,4345	0,6376	11,0
Mean	2,8747	3,1753	0,3006	10,8

Table 5. The effect of *ad lib.* drinking after three weeks of dehydration upon haematocrit values and plasma osmolality of *Aporosaura anchietae*. The animals were killed 15 minutes after drinking and values for animals freshly caught in the field are given as a comparison.

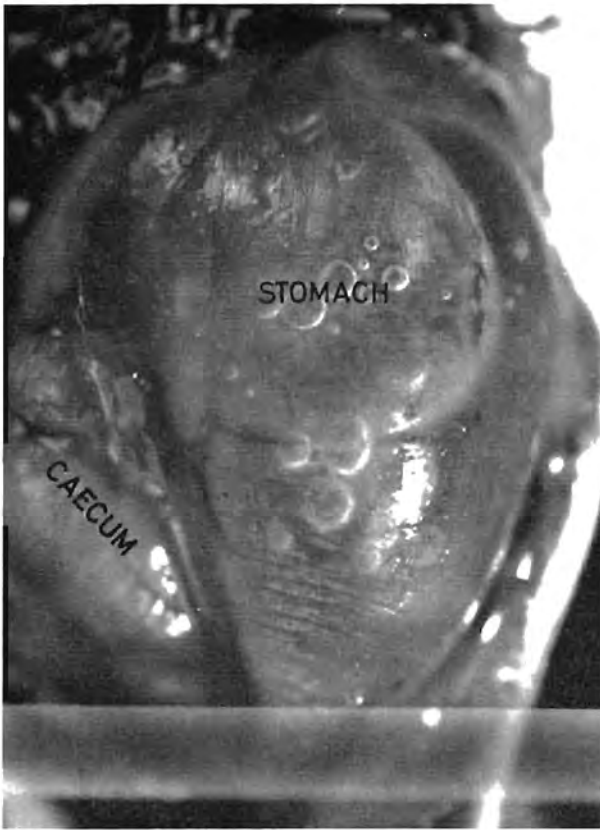
Treatment	No.	Haematocrit (%)		Plasma osmolality ^a (mOsm)	
		Range	Mean	Range	Mean
Dehydrated group	5	43-48	45	410-435	420
Hydrated group	5	41-46	44	390-415	406
Freshly captured	8	—	..	275-320	312

^a Plasma osmolality was determined in all cases on heparinised plasma for comparative purposes. Absolute serum values may be slightly different.

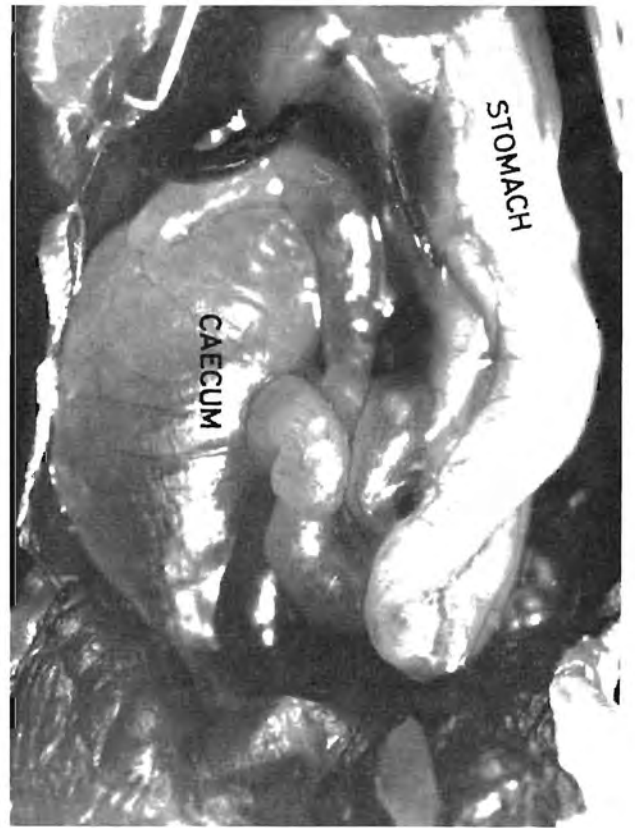
drinking of over 1,5 gallons of water by a 150 lb human although it is not as great as the drinking capacity of a ruminant such as the desert camel which, with its voluminous digestive tract is capable of drinking 30 per cent of its body weight (Schmidt-Nielsen, 1964). *Aporosaura*, on the other hand is a monogastric animal and this large intake of fluid causes tremendous distention of the stomach. The stomach, however, expands readily becoming transparent in the process (see Fig. 7). The same twisting and writhing movements of the body, which were observed during a voracious feeding period, were again observed during drinking. These movements are presumably associated with facilitating the ingestion of an abnormally large amount of water. It will also be seen from Fig. 7 that after 24 hours the major portion of the water has been shifted to the caecum which in turn expands proportionately to accommodate the water load. In this way it seems, therefore, that *Aporosaura* is capable of storing water in the digestive tract and that this water can be absorbed as required by the tissues. Moreover, it is also evident that after three weeks and eight weeks of dehydration, fluid in the digestive tract becomes progressively depleted although, even after eight weeks, a significant amount of fluid is still present in the caecum.

The gross expansion of the digestive tract after water ingestion is also reflected in the external appearance of the animals. After eight weeks of dehydration they have an emaciated appearance but after drinking the lateral abdominal folds fill out and within a short time the animal takes on a plump appearance.

The ingestion of such a large amount of water could cause severe disruption of the osmolality of the plasma but, as the data in Table 5 indicate, this was not the case. The haematocrit and osmolality values of the plasma were apparently little affected by the sudden water load although the dehydrated individuals exhibit a higher osmolality than those



A



B



C



D

Figure 7. (A) Immediately after water ingestion the stomach is greatly distended and stomach wall is transparent. (B) After 24 hours the water load is shifted to the caecum which expands to accommodate it. (C) Three weeks after water ingestion. (D) Eight weeks after water ingestion a significant amount of fluid is still present in caecum.

freshly captured from the field. The number of replications in the present investigation were, however, not sufficient to draw any definite conclusions and it is possible that sufficient time was not allowed between drinking and collection of the blood samples. Nevertheless, it would seem that the digestive tract is an efficient barrier between the sudden water load and the tissues, thus ensuring homeostasis of the tissue fluids.

In conclusion then it appears as if *Aporosaura* is singularly well adapted to making use of the peculiar weather pattern of the Namib Desert fog belt.

Thermoregulation

An examination of thermoregulation in *Aporosaura* revealed that from a physiological view point, this species is reasonably well adapted to extremely high temperatures, but not particularly so. For example, Brain (1962) during an expedition to the Namib assessed the critical maximum temperature of *Aporosaura* at 45,1°C compared with 44,2°C for the nocturnal gecko *Plenopus garrulus* which is never exposed to abnormally high temperatures. He also observed the "dishing" of the body of *Aporosaura* during warming. Our investigations confirmed the data of Brain (1962) in that critical maxima or incipient upper lethal limits for *Aporosaura* lie between 44°C and 46°C. Nevertheless, it is felt that, due to the variable heating time involved in experiments of this nature, comparisons are difficult to make. It is also felt that the success of *Aporosaura* under high temperatures is more closely associated with its specialised thermoregulatory behaviour than with physiological tolerance.

Thermoregulatory behaviour was examined in the field from a remote position during four entire days through binoculars and in the laboratory from close range. It was found that thermoregulation in this species is typically thigmothermic, with the animal relying heavily on heat conduction from the substrate for raising body temperature. Nevertheless, in view of the high radiation intensity usually encountered on the slip-face a considerable portion of the gain in body temperature must be via heliothermic mechanisms. The animals also, as will be discussed shortly, attempt to maintain body temperatures below critical levels for as long as possible by means of a behaviour pattern which would assist convective and radiant cooling.

Although this behaviour pattern, i.e. thigmothermia, is common to many lizards, in the case of *Aporosaura* it is dramatically exaggerated in order to allow the animals maximum use of the short period when surface temperatures are at the preferred level. In this respect it should be remembered that the animals inhabit the soft lee-side or slip-faces of the dunes. These lee-sides, by the very nature of their formation by the prevailing west and south-west winds, are virtually wind free and frequently

face the rising sun. The result is that surface temperatures rise very rapidly (see Fig. 5) and the preferred temperature limits for *Aporosaura* usually occur for a relatively short time.

Sequential photographic records, together with surface and body temperature records have made it possible to analyse this exaggerated thermoregulatory behaviour. When the surface temperature approaches 30°C the head emerges from the sand and shortly thereafter the animal emerges completely to press the ventral surface of the body against the sand substrate. In order to achieve maximum contact the body is dished convexly, the tail and all four limbs are held high in the air above the body. Body temperature rises rapidly during this phase and the animal then begins to forage on the dune face. It is capable of phenomenal speed at this temperature. As the substrate temperature approaches 40°C, however, the animal straightens its limbs to raise the body as far as possible above the sandy substrate. Periodically it will interrupt this stilt-like walk to raise diagonally opposite limbs while the base of the tail is used for support. This is presumably done to assist radiant and convective cooling. At surface temperatures above 40°C, the lizards dive swiftly beneath the soft sand to reach the cooler depths. Photographic records of this behaviour and a summary of temperature records at which the various stages occur are presented in Fig. 8 and Table 6 respectively. It is also of interest to compare the similarities in thermoregulatory behaviour of *Aporosaura* with that of *Angolosaurus skooei* which occupies a similar microhabitat in the northern Namib and which has been described by Hamilton and Coetzee (1969).

Table 6. The relationship between surface temperature and type of thermoregulatory behaviour in the laboratory. Surface of substrate heated from above by infra-red lamp.

Number of Animals	Temperature of Substrate (°C)		Type of Thermoregulatory Behaviour
	Range	Mean	
12	<5	<5	Immobile
12	23,0-27,2	26,2	Sudden increase in respiration
12	26,0-30,5	28,3	Tongue flicking in and out
12	27,5-34,1	30,5	Body is dished convexly and pressed against substrate
12	36,4-40,5	38,8	Stilt-like walk and lifting of diagonally opposite limbs
12	39,5-46,0	41,6	Diving reaction beneath sand to escape heat

A Surface temp. 31°C



B Surface temp. 33°C



C Surface temp. 39°C



D Surface temp. 44°C



Figure 8. Thermoregulatory dance employed by *Aporosaura anchietae*. (A and B) When substrate temperatures are $\pm 30^\circ\text{C}$ the ventral surface is pressed against the substrate with all four limbs held in the air. (C) As substrate temperature approaches 40°C the limbs are straightened to move the body away from the substrate and diagonally opposite limbs are lifted while tail is used for support. (D) Panting at 45°C , normally the animal dives beneath the surface before this temperature is reached. (Photographs: Alice Mertens.)

Although 12 body temperatures were recorded in the field in an attempt to estimate the preferred body temperature for *Aporosaura*, this was, by necessity, nearly always done after the animals had been chased for long distances until they were exhausted. The range obtained lay between 26.4°C and 38.3°C but no great reliance can be placed on these data. Nevertheless, the data in Table 6 and Fig. 8 reflect that *Aporosaura* gives preference to substrate temperatures between 30°C and 40°C.

Activity Rhythms

Laboratory studies, carried out to investigate the circadian or endogenous rhythm of *Aporosaura* showed that the species is strictly diurnal under constant conditions of light and temperature. Interesting effects of temperature and light upon the circadian rhythm were, however, also detected and these will be reported in detail elsewhere (Holm, 1972).

The activity cycle in the field under natural conditions was examined from a remote position, from which it was possible to keep 12 slip-faces under observation through binoculars from sunrise to sunset. Surface temperatures of the sand upon the slip-face and wind direction and velocity were simultaneously monitored and these data together with the periods when *Aporosaura* were active upon the surface have been summarised in Fig. 9. These data show the marked effect of substrate temperature upon the surface activity of the animals and the effect of wind upon surface temperature and emergence of the lizards. In Fig. 9A it can be clearly seen that in the absence of strong wind the east-facing slip-face heats up rapidly during the morning. As a result the *Aporosaura* emerge for only a brief period when the surface temperature is between approximately 30°C and 40°C. During the afternoon, however, the slip-face is in the shade and cooling of the substrate between 40°C and 30°C occurs over a longer period than the heating phase in the morning. The result is that the animals stay above the surface for a longer period at the apparently preferred range of approximately 30°C to 40°C.

The above bimodal activity cycle is typical for *Aporosaura* in the dune system near Gobabeb but is, nevertheless, influenced by daily change in wind velocity, wind direction and air temperature. For example in Fig. 9B the effect of strong east wind during winter is clearly shown. Although the wind, presumably by convective action, resulted in a slightly slower heating of the substrate surface during the morning when compared with Fig. 9A, the lizards did not emerge during the morning. This action is probably taken to avoid the desiccating effect of the east wind which frequently results in atmospheric temperatures of well above 35°C and relative humidities of less than 10%. In the afternoon, however, as is frequently the case, the cool and moist sea air resurged and during the westerly winds a large number of *Aporosaura* emerged on

the slip-faces, many of them feeding upon detritus. This detritus is brought into the dunes by the east wind and, in the afternoon, whirls back onto the eastern slip-faces as a result of the westerly wind. This effect of wind upon surface activity was first noticed by Hoesch (1960).

Finally, the data in Fig. 9C, show that *Aporosaura* are active throughout most of the day in the much cooler conditions prevailing in the coastal dunes between Walvis Bay and Swakopmund. Again however, it is evident that these lizards give preference to the approximate surface temperature range of 30°C to 40°C. Moreover, it was also noted that on cold days at the coast, when the surface temperatures remained below 20°C throughout the day, the lizards remained submerged for the entire day. It would seem then that the activity cycle of *Aporosaura* is well adapted to escape the exigencies of the desert environment and to exploit their micro-habitat as fully as possible.

General Behaviour

A specific study of general behaviour was not carried out but during the course of the investigation certain behavioural characteristics were observed and recorded.

Probably the most striking behaviour of *Aporosaura*, apart from the thermoregulatory dance described previously, is the ease with which it is able to dive beneath the sand. Sand diving occurs when surface temperatures are unfavourable and is also used in emergency when danger threatens. Frequently the first reaction to danger is a fast sprint followed by emergency diving beneath the sand. If the emergency dive occurs in unsuitable hard sand, the lizard will emerge after a short time and sprint towards a more favourable slip-face where it will disappear beneath the sand within a fraction of a second with a mere flick of the tail. This escape mechanism is aided further by excellent vision which appears to be a common characteristic of desert lizards (Mayhew, 1968). These reactions then provide *Aporosaura* with considerable protection against its natural predators which are the side-winding adder (*Bitis peringueyi*) and presumably the black-backed jackal (*Canis mesomelas*), the chanting goshawk (*Melierax musicus*) and the rock kestrel (*Falco tinnunculus*). The birds of prey, listed above, are frequently seen sitting on the dune crests watching the slip-faces (R. Jensen, pers. comm.).

Although the first reaction of *Aporosaura* to danger is escape, they will on occasion become aggressive when continuously pursued. This aggressive stance consists of straightening the front limbs and raising the head and thorax as far above the sand as possible. The threatening posture is illustrated in Fig. 1. If provoked further at this stage it will attack the aggressor, jumping forwards and lifting the body completely off the ground. In this process it snaps its jaws and may overturn in mid-air. It will also bite if it can gain purchase.

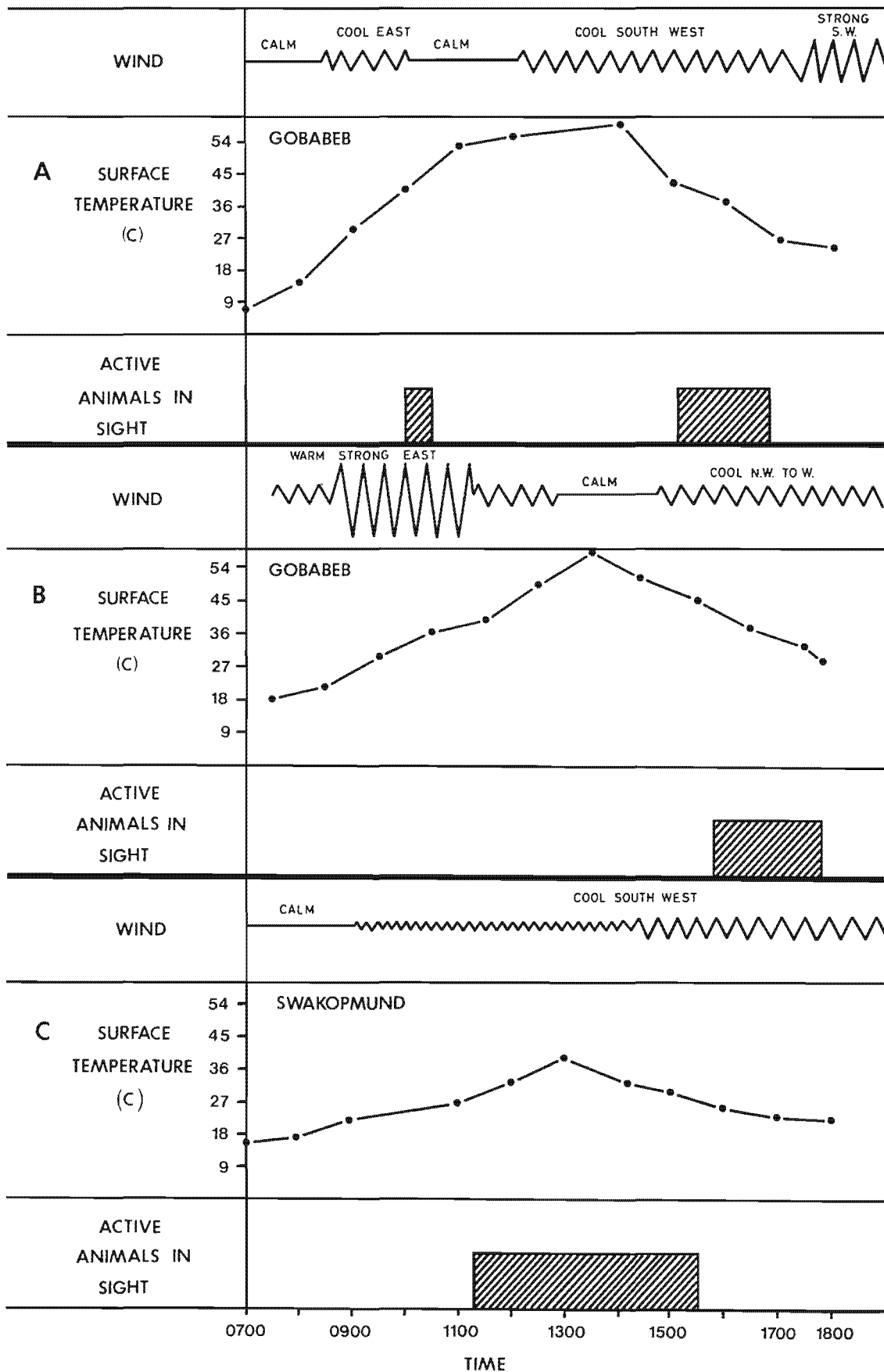


Figure 9. Effect of substrate temperature and wind upon the activity cycle of *Aporosaura anchietae*. (A) Typical bimodal activity cycle in major dune system south of Gobabeb with preference given to substrate temperatures between 30°C and 40°C. (B) Illustrates how strong east wind prevents the emergence of the lizards. (C) Unimodal activity cycle in coastal dunes where temperatures frequently remain between 30°C and 40°C for a longer period.

The reason for the peculiar behaviour pattern of head tapping, described under feeding behaviour, is not known. It could be an aid to olfaction while foraging on the dune face or may be involved in temperature sensing. Moreover, head tapping in *Aporosaura*, although similar, is not identical to the head bobbing displayed by many iguanid lizards. The latter is thought by Cowles (1956) to enhance depth perception by the lizards while Carpenter (1967) believes that it is a form of aggressive behaviour. As *Aporosaura* indulges in head tapping while alone it seems unlikely to be associated with aggression and to date there is no evidence of territoriality among *Aporosaura*. Head tapping was, however, observed to be an integral part of courtship behaviour in the male.

Reproduction

Ovaries and testes were examined from 37 animals collected during April, June, September and November. During these four months individuals with either active ovaries, yolked eggs or active testes were collected. It would therefore appear as if the reproductive cycle in *Aporosaura* is aseasonal.

During June, 1969 a pair were observed to mate 60 minutes after being captured from the coastal dunes south of Swakopmund. During and prior to coitus the male clasps the female firmly about the abdomen with the fore limbs and was seen to bite the nape of the female's neck repeatedly.

A female, captured in late June, 1969 and held in captivity with seven other *Aporosaura*, laid two eggs on the surface of the terrarium sand on 30 August, 1969. This female refused to feed for four weeks prior to laying and the abdomen and lateral abdominal folds were greatly distended. The eggs weighed 758 mg and 588 mg respectively and measured 16,5 mm and 16,0 mm in length while the diameter was 9,0 mm and 8,5 mm respectively. This is the first observation on the mode of reproduction in *Aporosaura* which was previously speculated to be ovo-viviparous.

Morphology

A cursory examination of the external anatomy of *Aporosaura* clearly reveals how well it is adapted to an ultra-psammophilous existence. The head and body are generally flattened and depressed allowing maximum contact with the substrate. The lateral abdominal folds are voluminous allowing marked distention of the digestive tract, described previously. The digits are attenuated and denticulated to facilitate sprinting on soft wind-blown sand. The snout is broad, depressed and spatulate (see Fig. 10A). Presumably this shovel-like form assists the animal in sand diving. A sagittal section through the skull (see Fig. 10B and C) reveals also that the external nares open posteriorly which would be of obvious advantage during sand diving. In addition

the nares are provided with a cartilaginous flap to which is attached a relatively well developed muscle. Contraction of this muscle would presumably occlude the nares and prevent the inflow of sand during diving. The position in which the head is held when the lizard is submerged is, however, not known and it is not possible to speculate on how the peculiar morphology of the nares may assist the animal when submerged. It was also noted that the epithelial lining of the vestibule of the nares was well developed and capable of copious mucus secretion which would be a distinct advantage in evacuating sand granules.

Apart from the marked elasticity of the digestive tract discussed previously, a superficial examination of the internal anatomy did not reveal further unusual adaptations. It would seem, however, that an histological study of the expanded and contracted stomach may reveal additional peculiarities and be a rewarding study. The abdominal cavity of *Aporosaura* is lined with a black peritoneum which is considered common among diurnal desert lizards and uncommon among nocturnal or fossorial species (Mayhew, 1968). Porter (1966) is of the opinion that a black peritoneum could be important in reducing the influx of radiation, particularly ultraviolet, which is intense under desert conditions and could cause biological damage to certain tissues.

The colour pattern of *Aporosaura* (see Figs. 1 and 2) has been described by *inter alia* Fitzsimons (1943). To this description the following could be added; the colour pattern is fairly cryptic and the population inhabiting the pale yellow coastal dunes near Swakopmund are paler in colour than those in the darker dunes near Gobabeb. Moreover, the transition from the characteristic yellow colouration of the juveniles to adult colouration seems to be gradual, since many specimens intermediate in size and colour are found. Finally, the general appearance of *Aporosaura* is aesthetically very pleasing and it must be counted among the more elegant reptiles.

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Finally, we wish to record our very sincere appreciation to the late Dr C. Koch, to whom this commemorative volume has been dedicated, for his valuable encouragement and advice.

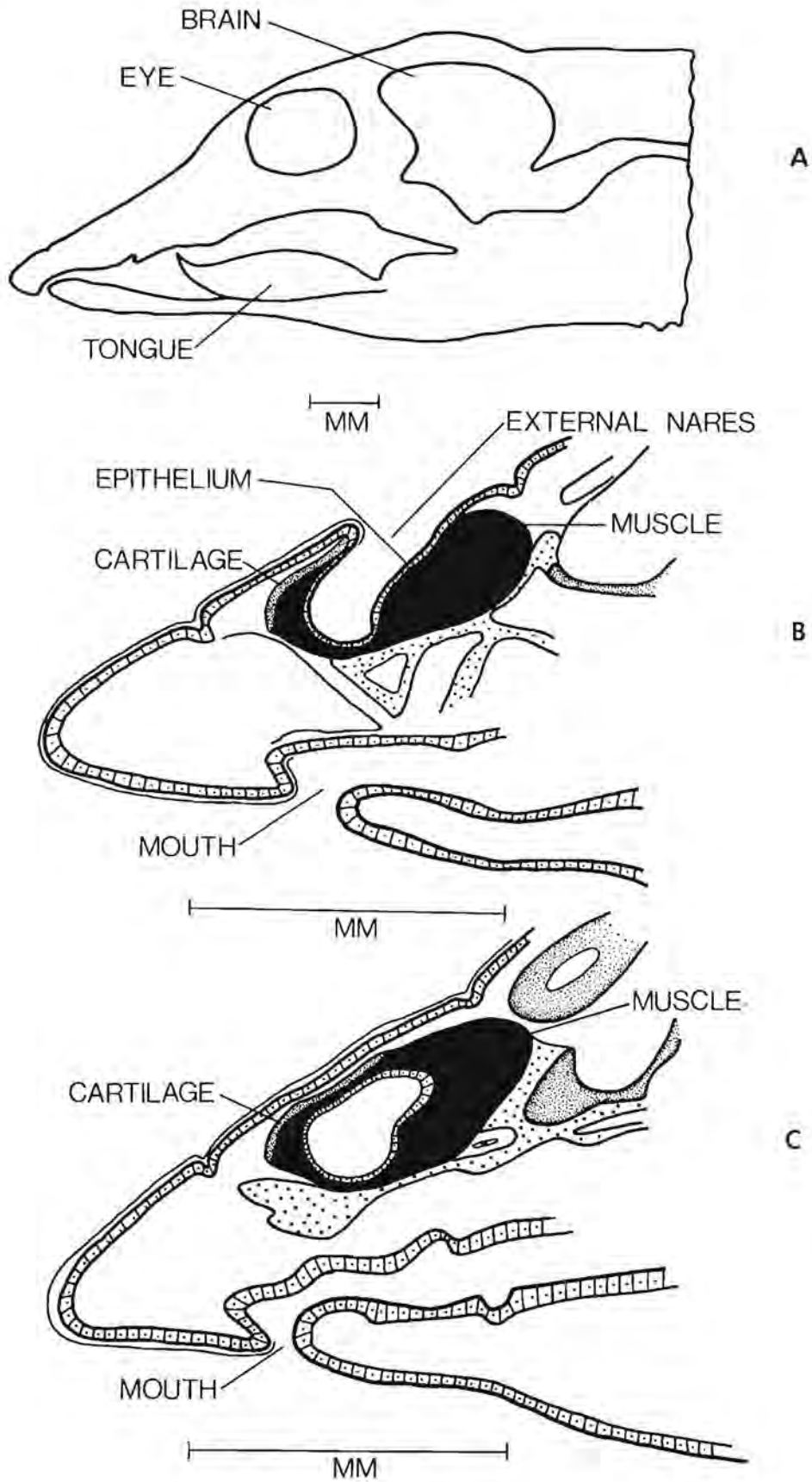


Figure 10. (A) Sagittal section through skull of *Aporosaura anchietae* showing shovel-like form of snout. (B) Shows how external nares open in a posterior direction and the presence of a cartilagenous nasal flap. (C) This section is lateral to B and shows how the cartilage flap is attached to the well developed muscle.

REFERENCES

- Bentley, P. J. and Blumer, W. F. C., 1962. Uptake of water by the lizard, *Moloch horridus*. *Nature* 194: 699.
- Brain, C. K., 1962. Observations on the temperature tolerance of lizards in the central Namib desert, South West Africa. *Cimbebasia* 4: 1.
- Bustard, H. R., 1967. Gekkonid lizards adapt fat storage to desert environments. *Science* 158: 1197.
- Carpenter, C. C., 1967. Aggression and social structure in iguanid lizards, p. 87 in "Lizard Ecology: A Symposium" ed. by W. W. Milstead, Univ. of Missouri Press, Columbia, Missouri.
- Cowles, R. B., 1956. Notes on natural history of a South African agamid lizard. *Herpetologica* 12: 297.
- Fitzsimons, V. F. M., 1943. The lizards of South Africa. Transvaal Museum Memoir No. 1, Pretoria, South Africa.
- Gross, W. J., 1954. Osmotic responses in the sipunculid *Dendrostomum zosteriolum*. *J. Exp. Biol.* 31: 402.
- Hamilton, W. I. and Coetzee, C. G., 1969. Thermoregulatory behaviour of the vegetarian lizard *Angolosaurus skoogi* on the vegetationless northern Namib desert dunes. *Scient. Pap. Namib Desert Res. Stn.* 47: 95.
- Hoesch, W., 1960. Über die Tierwelt im Gebiet der Südwestafrikanischen Wanderdünen. *Natur und Volk* 90: 252.
- Holm, E., 1970. The effect of light and temperature upon the endogenous and activity rhythms of the sand-diving Namib Desert lizard *Aporosaura anchietae*. (In preparation).
- Khalil, F. and Abdel-Messeih, G., 1959. The storage of extra water by various tissues of *Varanus griseus* Daud. *Z. Vergleich Physiol.* 42: 415.
- Khalil, F. and Abdel-Messeih, G., 1961. Effect of water deficit and water excess on the composition of blood of *Varanus griseus* Daud. *Z. Vergleich. Physiol.* 45: 82.
- Koch, C., 1961. Some aspects of abundant life in the vegetationless sand of the Namib Desert dunes. *Scient. Pap. Namib Desert Res. Stn.* 1.
- Logan, R. F., 1960. Central Namib Desert. *Nat. Acad. Sci. — Nat. Res. Council, Publ.* 758.
- Mayhew, W. W., 1968. Biology of Desert Amphibians and Reptiles. Chapter 6 in "Desert Biology" ed. by G. W. Brown, Academic Press, New York.
- Meigs, P., 1966. Geography of coastal deserts. *Arid Zone Research*, 28. Unesco, Paris.
- Mertens, R., 1955. Die Amphibien und Reptilien Südwestafrikas. *Abh. Senckenb. Naturf. Ges.* 490: 1-172.
- Norris, K. S. and Dawson, W. R., 1964. Observations on the water economy and electrolyte excretion of chuckwalla (*Lacertilia, Sauromalus*). *Copeia* p. 638.
- *Porter, W., 1966. Solar radiation through the body wall of living vertebrates with emphasis on desert reptiles. Ph. D. Thesis, Univ. of California, Los Angeles, California. (Cited by Mayhew, 1968 above).
- Schmidt-Nielsen, K., 1964. "Desert Animals, physiological problems of heat and water". Oxford Univ. Press, London.
- Schulze, B. R., 1969. The climate of Gobabeb. *Scient. Pap. Namib Desert Res. Stn.* 38: 5.
- *Tercafs, R. R., 1963. Phenomenon of permeability of reptile skin. *Arch. Intern. Physiol. Biochim.* 71: 318.
- Warburg, M. R., 1966. On the water economy of several Australian geckos, agamids and skinks. *Copeia* p. 230.
- * Not seen in the original