New Data on a Sand-Shuttling Eye-Popping Lizard *)

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ABSTRACT
Some thirty years elapsed since the discovery of A. makarikarica, before it was observed that it displayed a peculiar sand-shuttling behaviour.

In this paper it is reported that it practices a kind of eye-popping as well. The possibility of an underlying hydraulic mechanism is discussed. A very peculiar distribution pattern in Southern Africa is recorded, together with new distribution records along the Etosha Pan. The lecture is illustrated by colour slides.

INTRODUCTION
The occurrence of A. makarikarica in South West Africa was recorded by Steyn, Finkelday and Buys (1963). The same preliminary paper described its curious sand-ducking behaviour, similar to that shown by Phrynocephalus nejdensis, an agamid lizard of the Arabian Desert.

Agama makarikarica was originally described as a subspecies of the hispida group by V. FitzSimons (1932), who noticed that A. makarikarica is associated with pans. Hughes (pers. comm.) strongly suggested that it be accorded full specific status on account of its small earhole and other morphological characters setting it apart from the A. hispida group. This was subsequently done by Broadley.

In South West Africa, the lizard was known only from the Ondangua vicinity and from the Namutoni area. In spite of considerable field work during the years 1962 — 1965 the lizard was not found elsewhere in South West Africa.

**DISTRIBUTION**
It was therefore with some surprise that the authors observed near Okondeka at the western end of the Etosha Pan, a lizard that clearly showed the peculiar wriggling behaviour typical of A. makarikarica when shuttling in the sand. This was at the beginning of October, 1966.

Closer investigation in the area visited, bordering on the southern half of the pan, revealed that A. makarikarica is present from Okondeka in the west to the Namutoni area in the east. It is remarkable, however, that it is present only along a band six to ten miles wide along the border of the pan (Fig. 1). Beyond this, A. makarikarica is replaced by A. hispida aculeata, for no reason obvious without further study. Also the two species appear to be mutually exclusive, at least in the area which could be investigated to the south, east and west of the Etosha Pan.

On working through the material in the Transvaal Museum collection, Hughes (pers. conn.) found some years ago that A. makarikarica was present in S.W. Africa, but was mistaken for Agama hispida aculeata. It is also present at Bothaville in the O.F.S.

Some of the distribution results presented here are thus in fact quite old, but have never been published.

**MATERIAL**
a) One adult from Fort Namutoni, S.W.A. collected by J. Breyer, 1919.
b) 2 adult, 4 juvenile specimens and 3 baby lizards, from Bothaville, O.F.S. collected by A. Roberts, June, 1920.
c) 1 adult, 2 baby lizards, from Itota Dune, 45 miles S. of Ondongua, S.W.A. Collected by V. FitzSimons, June, 1937.
d) 1 juvenile, from Farm Okosongomingo, Waterberg Dist., S.W.A. Collected by V. FitzSimons, May, 1937.
e) 1 adult, from 75 mls. N. of Namutoni, S.W.A. Collected by V. FitzSimons, May, 1937.
f) 1 baby lizard, from Western edge of Etosha Pan. Collected by V. FitzSimons, June, 1937.
g) 1 adult from Ohopoho, Kaokoveld, Collected by W. Giess, May, 1959.
h) 3 adults, 1 juvenile specimen, from Okondeka area, Etosha Pan, S.W.A. Collected by W. J. Steyn, October, 1966. (Two of these were kept alive in Pretoria up to January, 1967).

Material a—h above is in the Transvaal Museum collection.

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EYE-POPPING BEHAVIOUR

With the permission of the authorities, collecting was done, and a number of live specimens were taken home. Stopping over near Otjiwarongo at the farm of Mr. and Mrs. Nico Oelofse, Mr. Oelofse drew attention to a peculiar movement of the eyes. Upon closer study, this was disclosed to be a partial eye-protrusion, literally an eye-popping event (Plate 1). The process begins as a kind of “screwing up” of the eyes. The eye-slit is then almost closed while the eye-ball within the lids is gradually protruded, reaching a maximal protrusion as shown in Plate 1.

The eye is not closed, and there is no sign that the lids are stressed, or the eye-ball compressed, in any way. Both eyes are protruded simultaneously.

Duration of the phenomenon was usually between 5 and 10 seconds, after which the eye-balls recede slowly. The eye-ball can also be retracted independently of the eye-lid, so that some slight space is left between the lids and the eye (Plate 2). Initially during captivity the behaviour was displayed fairly frequently. At Otjiwarongo, 6 of 14 lizards were seen to display this behaviour during the course of an hour of constant observation. The behaviour was observed less frequently afterwards in the Transvaal Museum, where they were watched by the herpetologist Mr. W. D. Haacke. He did not see the behaviour before the animals had been in his laboratory for some weeks, and then it occurred only at infrequent intervals.

DISCUSSION

These lizards do not thrive in captivity. Under these conditions they usually die after some months. Possibly the conditions of captivity have an adverse effect on behaviour characteristics of these animals. It was noticed earlier that the sand-shuttling behaviour also petered out under laboratory conditions in Windhoek, though not disappearing completely.

It is not yet possible to explain the mechanism underlying the eye protrusion phenomenon. The following factors could play a role and should be investigated.
Some members of the North American genus *Phrynosoma* show similar sand-shuttling behaviour to that of *Agama makarikarica*. It is interesting to note that some *Phrynosoma* species actually squirt blood out of their eyes as a means of protection. This suggests the possibility of hydraulic mechanisms operating in the eye region of some lizards. Withdrawal of the eye-ball independently of the lid, however, minimizes the chances that the underlying mechanism is purely hydraulic.

In *Agama makarikarica* it is possible to protrude the eye-balls artificially by application of pressure under the jaw. It should therefore be investigated whether contracting muscles between the skull base and skull roof could produce the effect. The action of the tongue is a further factor that was suggested. The meaning of this behaviour is equally obscure at present. One may perhaps be permitted to put forward a speculative idea on this issue. The sand-ducking behaviour is probably protective. The animals do not submerge completely, and it is a fair guess that eye-protection may allow better vision when the animal is partly submergered. (In their natural surroundings, the mechanical nature of the coarse sand and grit on a hard surface makes it mostly impossible to submerge completely). The eye lid may also act as a kind of “lens hood” when the eye-ball is withdrawn, such as is the case in Plate 2. The glare on the white pan surface and surroundings is intense.

The eye-lids of *Phrynocephalus nejdensis* are said to protect the eyes against sand. The eye lids (Plates 4a, 4b, 4c) in *Agama makarikarica* closely resemble those of *Phrynocephalus nejdensis*.

The eye-protrusion could possibly also help to throw off sand grains from the eye region, particularly when the lizard is maximally submergered, such as in Plate 5. In that figure, the eyes are protruded. During protrusion the eye region is cleared of sand by the bulging eye lids, so that vision becomes possible without exposing the head.

It is well-known that some agamids such as *Draco volans* have display devices to render them “bigger than life-size” to enemies, and as a threatening device. The eye-protrusion behaviour of *Agama makarikarica* could be of this nature also: The body in Plate 1 is in a threat posture as was described for *A. a. agama*, but the mouth is closed.

The ear-hole deserves note. In *Phrynocephalus nejdensis* (and others in that genus) no external ear hole is visible. In *Agama makarikarica* the ear hole is much smaller than in other *Agama* species.
It may therefore be suggested that the reduction or closure of the external ear hole is an adaptation to keep sand out of the ears in both genera as they both practise sand-shuttling.

The peculiar distribution pattern is perhaps the biggest problem remaining to be solved. Apart from an apparently discontinuous pattern over South West Africa, Botswana, and the Orange Free State, there is the peculiar marginal distribution along the Etosha Pan.

The taxonomical position with regard to the 3 main population areas is also not clear. In spite of considerable assistance with the supply of live specimens for study, the sand-shuttling behaviour so typical of the South West African specimens was so far not observed in members of the other populations. Also, some gular and dorsal colour markings are rather constantly different in the South West African specimens. Gular markings in Agama a. agama and in other reptiles have been found to be individually characteristic and constant. The presence of black gular patches in the S.W.A. population may therefore be of taxonomic significance, and will be specifically dealt with in a further study now under way.

In conclusion it may be said that this ordinary looking lizard presents a number of extraordinary aspects for study. This study is now well under way and will establish a new subspecies of Agama makarikarica as well as include a slow motion picture analysis of its sand-ducker behaviour.

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Plate 3. Agama makarikarica and right, top, Agama anchietae. The small specimen is sinking into the sand. Eyes not protruded.
Plates 4a, b & c. *Agama makarikarica*, eye-lids of injected specimen. In 4a the serrated edge of the lower lid is clearly seen. Fig. 4b shows the upper lid from below. Fig. 4c shows arrangement of scales at the posterior junction of the eye-lid. Note the pigmentation of the inner elongated scales. (Photographs Dr. L. Schuitze and Mr. D. Goode.)

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Plate 5. *Agama makarikarica*: Maximal submersion with the eyes protruded. By permission of the Editor of Cimbebasia.

Figure 2. The distribution of *Agama makarikarica* in Southern Africa (1967).