

# THE STATUS OF HERPETOLOGY IN SOUTHERN AFRICA

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## ABSTRACT

The major developments in southern African herpetology during the last decade are reviewed and first consideration is given to the taxonomic work which is essential to provide a sound foundation for subsequent zoogeographical, ecological and ethological research. With the passage of time there will be a gradual shift in emphasis from traditional taxonomic studies to projects based upon living animals both in the field and in the laboratory.

This seems an opportune time to review the major developments in southern African herpetology during the last decade and to make a few suggestions on areas where further research could be particularly fruitful.

Sound taxonomy must provide the basis for all zoogeographical, ecological and ethological studies on the herpetofauna of southern Africa. Van Dijk (1971a) and Poynton (1972) have drawn attention to the danger of a distribution pattern being seriously distorted by the plotting of localities for misidentified specimens. In this respect full generic revisions which are pan-African in scope are of prime importance. I will now review the position with regard to the various groups of reptiles and amphibians.

The Testudinata of southern Africa will repay further systematic study. Although the African Pleurodira were revised by Loveridge (1941) and the Cryptodira by Loveridge & Williams (1957), these studies were based on the literature and the limited amount of material available in American museums. Subsequently Laurent (1956, 1964, 1965) has made important contributions to our understanding of the central African forms, but a reappraisal of the tortoises and terrapins of southern Africa is long overdue. The many subspecies of *Pelomedusa subrufa* and *Kinixys belliana* recognized by Hewitt have all subsequently been placed in synonymy, but their status should be re-examined when adequate material can be assembled.

Passing on to the lizards, we may first consider the Gekkonidae. Wulf Haacke is in the process of publishing his M.Sc. thesis on the burrowing geckos of the genera *Ptenopus*, *Palmatogecko*, *Kaokogecko*, *Colopus* and *Chondrodactylus* (Haacke 1975). He is also revising the genus *Rhoptropus*. David Onderstall is working on the eastern forms of *Afroedura*. Probably the genus most in need of revision is *Pachydactylus*, with its numerous species in the south-west arid: there are many points of disagreement between the findings of FitzSimons (1943) and Loveridge (1947).

The important study on the genus *Lygodactylus* by Pasteur (1964) has greatly improved our understanding of these dwarf geckos, but the status of the form *bradfieldi* in relation to *L. capensis* requires further investigation.

The main problems with regard to the Agamidae concern the relationship of *Agama*

*planiceps* to *A. agama* and the number of recognizable sub-species of *Agama hispida* (if any); there appears to be little doubt that *Agama makarikarika* is a good species. However, I would like to see someone with access to an electron microscope follow up the study on the dermal sense organs of Nigerian species of *Agama* by Grandison (1968).

The genus *Chamaeleo* was last reviewed by Hillenius (1959), but subsequently Klaver (1973) published a useful review of the variation in chameleon lung anatomy. Lynn Raw is at present having a fresh look at the problematic South African *Chamaeleo pumilus* group.

The African Scincidae present many taxonomic problems. Recent revisionary studies include a new subfamilial classification (Greer 1970a), a redefinition of the genera of Scincinae (Greer 1970b), and revisions of the genera *Typhlosaurus* (Broadley 1968b) and *Acontias* (Broadley & Greer 1969). The generic assignment of the various African 'snake-eyed skinks' is still *sub judice*. The genera still sorely in need of revision are *Scelotes* and *Mabuya*. I have recently reviewed the *Mabuya maculilabris* group (Broadley 1974a) and the *M. lacertiformis* complex (Broadley 1975b), while in Australia David Horton is preparing a review of the genus *Mabuya* throughout its entire range. The *Mabuya striata* complex remains the most formidable assemblage still to be unravelled. Wulf Haacke is working on the genus *Typhlacontias* and the south-east African populations of *Cryptoblepharus boutonii*.

Although the family Cordylidae was revised by Loveridge (Gerrhosaurinae 1942; Cordylinae 1944), his studies were based on the literature and somewhat meagre material in the Museum of Comparative Zoology. The genus *Cordylus* is in need of revision, preferably by a herpetologist based in the Cape Province, where most of the problem forms occur. My own M.Sc. thesis on the genus *Platysaurus* (Broadley 1964) has still to be revised for publication.

As far as the family Lacertidae is concerned, the most urgent need is for additional material of the two isolated southern African species of *Lacerta*, both of which are known only from the unique types: *L. australis* from Ceres in the south-western Cape and *L. rupicola* from Lake Fundusi in the Soutpansberg. Despite my recent review of *Nucras* (Broadley 1972), this genus still remains the most problematic.

The suborder Amphisbaenia has recently been subjected to intensive study. The genus *Zygaspis* (excluding *violacea*) was revised by Saiff (1970) and a full revision of the southern African forms of *Monopeltis* and *Dalophia* by Carl Gans, John Visser and myself has been completed. Only *Zygaspis violacea* and the southern forms of *Chirindia* remain to be examined.

The taxonomy of the Scolecophidia has long been in the doldrums, so the admirable revision of the African Typhlopidae by Rolande Roux-Estève (1974) will be universally welcomed. Her decision to divide the African species into two genera will perhaps be less enthusiastically received. The African representatives of the genus *Leptotyphlops* have received little attention since the publication of Boulenger's catalogue in 1893, although the classification of the New World species is well advanced. At Umtali Museum a review of the genus in south-east Africa is nearing completion. Scale counts for over 800 specimens have been tabulated. John Visser is investigating the anatomy of *Typhlops* and *Leptotyphlops*.

The classification of the higher snakes (Caenophidia) remains one of the major problems in herpetology, the study of Underwood (1967) serving to stimulate interest in the problem. Bourgeois (1968) examined the cranial osteology of many African caenophidian snakes and she was the first to propose the removal of the genus *Atractaspis* from the Viperidae to the Aparal-

lactinae. McDowell (1968) proposed the transfer of the genus *Elaps* (for which he used the name *Homorelaps* Boulenger) from the Elapidae to the Aparallactinae, but this move was opposed by Kochva & Wollberg (1970). The continuing studies of Dr W. R. Branch on serum proteins, karyotypes and hemipenal morphology should help to clarify the systematic position of such 'problem genera'.

Among the Colubridae the tribe which perhaps presents the most problems, because of its very simple hemipenal morphology, is the Psammophini. *Rhamphiophis acutus* has been revised (Broadley 1971c) and a review of *Psammophylax* is nearing completion. I have recently reviewed the species *Psammophis leightoni* and *P. notostictus* (Broadley 1975a) and a re-examination of the *Psammophis sibilans* complex is well advanced.

The re-examination of the genus *Lycophidion* by Laurent (1968) covered very little material from southern Africa and I have in hand a revision of the southern forms. The variation in *Lycodonomorphus laevis* has recently been reviewed by Lynn Raw (1973), the other south-east African forms having been investigated earlier (Broadley 1967). The genus *Natriciteres* has also been reviewed (Broadley 1966a).

The relationships of the genus *Prosymna* remain obscure. The genus was revised by Loveridge (1958) and the *Prosymna sundevallii* group was subsequently revised by Broadley (1965), but the species *P. ambigua* still requires re-examination. Unfortunately little material is available from the critical northern parts of the species range.

The fossorial colubrids belonging to the genera *Amblyodipsas* and *Xenocalamus* have recently been revised (Broadley 1971b) and I have in hand a review of the genus *Thelotornis*. A revision of the widespread genus *Dispholidus* would be useful. The lack of a green phase in the south-west Cape suggests some racial divergence in this area.

In the family Elapidae, the genus *Elapsoidea* has recently been revised (Broadley 1971a) and considerable progress made with the genus *Naja* (Broadley 1968a, 1974b). Variation in *Aspidelaps scutatus* has been analysed (Broadley 1968c): a similar study of *Aspidelaps lubricus* might prove interesting.

Garth Underwood is examining the relationships of species of Viperinae at the British Museum and the affinities of *superciliaris* again seem to be uncertain. Wulf Haacke has been working on the small *Bitis* species of the south-west arid.

In respect of the Amphibia, we may conveniently examine the progress made subsequent to John Poynton's revision of the Amphibia of Southern Africa (1964). A major development was the provision of systematic keys to southern African anuran tadpoles (Van Dijk 1966, 1971c).

Studies on African species of *Bufo* continue in the Netherlands (Hulselmans 1970) and at the University of Texas (Tandy & Keith 1972). Alan Channing has described the tadpoles of several species.

A synopsis and key to the southern African species of *Ptychadena* was published by Poynton (1970). A revision of the genus *Hemisus* was undertaken by Laurent (1972) and Schiøtz has published revisions of the *Hyperolius viridiflavus* superspecies (1971) and the eastern forms of *Afrixalus* (1974); he has another paper on East African forms of *Leptopelis* and *Hyperolius* in press.

At the Queen Victoria Museum, Charles Parry is investigating the status of *Pyxicephalus*

*edulis* Peters and the variation in the tadpoles of Rhodesian frogs.

The study of zoogeography in southern Africa was greatly stimulated by the symposium on this subject organized by the Zoological Society of Southern Africa at Port Elizabeth in 1961. As a basis for zoogeographical studies on the herpetofauna of southern Africa we have distribution maps for the snakes (FitzSimons 1962) and the amphibians (Poynton 1964). John Greig has been mapping the distribution of tortoises, but we still have no distribution maps for the lizards, with the exception of some groups that have recently been revised. I am doubtful whether it is now worthwhile to prepare distribution maps using the locality data from 'Lizards of South Africa' (FitzSimons 1943) because so much additional material is now available. Distribution maps for the reptiles of the Kruger National Park have already been published by Pienaar (1966). At the Transvaal Museum, Wulf Haacke has assembled huge collections from the western Cape Province, South West Africa and southern Angola. At the National Museum, Bloemfontein, Schalk de Waal is preparing his Ph.D. thesis on the Sauria and Serpentes of the Orange Free State and has collected more than 4 000 specimens from 220 localities. Lynn Raw has assembled important collections of the reptiles of Natal and James Culverwell is working on the distribution of reptiles in Swaziland. Mike Bruton has made good collections in Tongaland and these will be reported on jointly with Wulf Haacke.

My own Ph.D. thesis on the herpetology on south-east Africa (Broadley 1966b) was basically a zoogeographical study. I am revising the reptile section for publication during 1976–77. The area covered includes Botswana, Rhodesia, Zambia, Malawi and Moçambique; a check list and keys to the reptiles and amphibians of Zambia has already been published (Broadley 1971d).

In the United States, Bailey (1960) established a concept which he termed Effective Temperature (abbreviated to ET) and Stuckenberg (1969) used Bailey's formula to produce an ET map of southern Africa. As on Poynton's maps the limit of a tropical climate is defined as a mean temperature of 18°C for the coldest month of the year and theoretically any locality with an ET of 18°C should have mean daily temperatures higher than 18°C throughout the year. In contrast, a locality with an ET of 15°C would be expected to have mean daily temperatures above 15°C on only 214 days of the year. Stuckenberg observed that 'A close correlation is demonstrated between the distribution of snakes and the ET zones. A causal relationship is considered to exist because of physiological and behavioural adaptations of snakes to temperature factors. Most tropical species are excluded by the 15°C ET isoline, whereas most South African endemic species do not range beyond the 16°C isoline. Frogs show similar correlations.'

At the same symposium, a paper by Poynton & Bass (1970) examined the possible factors limiting the distribution of tropical amphibians in KwaZulu: these were geology, topography and water types; rainfall and evaporation; seasonality; temperature; physical history of the area; vegetation; predators and prey and competition between tropical and non-tropical species (the 'friction zone' effect). They considered that the distribution of tropical amphibians seems to be most closely related to temperature and the frequency of optimal breeding nights.

Many of the ecological and ethological studies on reptiles have been concerned with endangered species or those of economic importance, as with the work undertaken on marine turtles by George Hughes (*e.g.* Hughes 1974a; 1974b) and others, and extensive work on crocodiles carried out in Natal by Tony Pooley and in Rhodesia by David Blake and John Loveridge.

Field studies on North American reptiles have been in progress for at least 35 years and Robert Bustard has recently published some very nice field studies of Australian lizards. The first major study on a 'common or garden' African reptile was 'The Life of the Rainbow Lizard' by Vernon Harris (1964). This book stimulated the launching of field studies on local lizards by the Department of Herpetology at Umtali Museum. Mike Bruton has made ecological studies of *Agama atra* at Grahamstown. Nils Jacobsen is carrying out field studies on lizards in the northern Transvaal. Wulf Haacke has done a lot of work on the ecology and behaviour of his burrowing geckos, and in the case of *Ptenopus* he has had to consider an additional feature – the call (Haacke 1969). Burrage (1973) made a comparative study of the ecology and behaviour of *Chamaeleo p. pumilus* and *C. namaquensis*.

Many herpetologists have investigated the life histories of southern African amphibians, the first comprehensive treatment being 'The frogs of South Africa' (Wager 1965). 'The Amphibians of Malawi' by Margaret Stewart (1967) followed and a study of the reproductive ecology of amphibians of the Transvaal highveld was published by Balinsky (1969). Van Dijk (1971b, 1972) has investigated the ecology and behaviour of anuran tadpoles. John Visser has taken a particular interest in the life history of *Heleophryne*.

In Rhodesia John Loveridge has investigated the behaviour and physiological adaptations used by *Chiromantis* to avoid desiccation (Loveridge 1970) and is now extending this study to other treefrogs. When one considers laboratory studies on amphibians, it seems that there is more literature on *Xenopus laevis* than any other lower vertebrate, but I will not attempt to review this field.

The future will undoubtedly see a gradual shift in emphasis from taxonomic and zoogeographical studies towards investigation of ecological, ethological and physiological problems.

#### REFERENCES

- BAILEY, H. P. 1960. A method of determining the warmth and temperateness of climate. *Geogr. Annlr* 42:1–16.
- BALINSKY, B. I. 1969. The reproductive ecology of amphibians of the Transvaal Highveld. *Zool. afr.* 4:37–93.
- BOURGEOIS, M. 1968. Contribution a la morphologie comparée du crane des ophidiens de l'Afrique Centrale. *Publs Univ. off. Congo* 18:1–293.
- BROADLEY, D. G. 1964. A monographic study of the cordylid lizard genus *Platysaurus*. M.Sc. thesis, Univ. Natal, Pietermaritzburg.
- BROADLEY, D. G. 1965. A revision of the *Prosymna sundevallii* group (Serpentes: Colubridae). *Arnoldia* (Rhodesia), 2(5):1–6.
- BROADLEY, D. G. 1966a. A review of the genus *Natriciteres* Loveridge (Serpentes: Colubridae). *Arnoldia* (Rhodesia), 2(35):1–11.
- BROADLEY, D. G. 1966b. The herpetology of South-East Africa. Ph.D. thesis, Univ. Natal, Pietermaritzburg.
- BROADLEY, D. G. 1967. A review of the genus *Lycodonomorphus* Fitzinger (Serpentes: Colubridae) in south eastern Africa, with a key to the genus. *Arnoldia* (Rhodesia), 3(16):1–9.

- BROADLEY, D. G. 1968a. A review of the African cobras of the genus *Naja* (Serpentes: Elapinae). *Arnoldia* (Rhodesia), 3(29):1-14.
- BROADLEY, D. G. 1968b. A revision of the African genus *Typhlosaurus* Wiegmann (Sauria: Scincidae). *Arnoldia* (Rhodesia), 3(36):1-20.
- BROADLEY, D. G. 1968c. A revision of *Aspidelaps scutatus* (A. Smith) (Serpentes: Elapinae). *Arnoldia* (Rhodesia), 4(2):1-9.
- BROADLEY, D. G. 1971a. A revision of the African snake genus *Elapsoidea* Bocage (Elapidae). *Occ. Pap. natn. Mus. Rhod. B.*, 4:577-626.
- BROADLEY, D. G. 1971b. A revision of the African snake genera *Amblyodipsas* and *Xenocalamus* (Colubridae). *Occ. Pap. natn. Mus. Rhod. B.*, 4:629-697.
- BROADLEY, D. G. 1971c. A revision of *Rhamphiophis acutus* (Günther) with the description of a new sub-species from Zambia (Serpentes: Colubridae). *Arnoldia* (Rhodesia), 5(8):1-8.
- BROADLEY, D. G. 1971d. The reptiles and amphibians of Zambia. *Puku*, 6:1-143.
- BROADLEY, D. G. 1972. A review of the *Nucras tessellata* group (Sauria: Lacertidae) *Arnoldia*, (Rhodesia), 5(20):1-36.
- BROADLEY, D. G. 1974a. A review of the *Mabuya maculilabris* group in south-eastern Africa (Sauria: Scincidae). *Arnoldia* (Rhodesia), 6(23):1-10.
- BROADLEY, D. G. 1974b. A review of the cobras of the *Naja nigricollis* complex in south-western Africa (Serpentes: Elapidae). *Cimbebasia* (A), 2:155-162.
- BROADLEY, D. G. 1975a. A review of *Psammophis leightoni* and *P. notostictus* in southern Africa (Serpentes: Colubridae). *Arnoldia* (Rhodesia), 7(13): 1-17.
- BROADLEY, D. G. 1975b. A review of the *Mabuya lacertiformis* complex in southern Africa (Sauria: Scincidae). *Arnoldia* (Rhodesia), 7(18):1-16.
- BROADLEY, D. G. & GREER, A. E. 1969. A revision of the genus *Acontias* Cuvier (Sauria: Scincidae). *Arnoldia* (Rhodesia), 4(26):1-29.
- BURRAGE, B. R. 1973. Comparative ecology and behaviour of *Chamaeleo pumilus pumilus* (Gmelin) and *C. namaquensis* A. Smith (Sauria: Chamaeleonidae). *Ann. S. Afr. Mus.* 61: 1-158.
- FITZSIMONS, V. F. M. 1943. The lizards of South Africa. *Transv. Mus. Mem.* 1:1-528.
- FITZSIMONS, V. F. M. 1962. *Snakes of southern Africa*. Cape Town/Johannesburg: Purnell.
- GRANDISON, A. G. C. 1968. Nigerian lizards of the genus *Agama* (Sauria: Agamidae). *Bull. Br. Mus. nat. Hist. (Zool.)* 17:67-90.
- GREER, A. E. 1970a. A subfamilial classification of scincid lizards. *Bull. Mus. comp. Zool. Harv.* 139:151-183.
- GREER, A. E. 1970b. The systematics and evolution of the subsaharan Africa, Seychelles and Mauritius scincine scincid lizards. *Bull. Mus. comp. Zool. Harv.* 140:1-23.
- HAACKE, W. D. 1969. The call of the barking geckos (Gekkonidae: Reptilia). *Scient. Pap. Namib Des. Res. Stn*, 46:83-93.
- HAACKE, W. D. 1975. The burrowing geckos of southern Africa, 1. (Reptilia: Gekkonidae). *Ann. Transv. Mus.* 29:197-243.
- HARRIS, V. A. 1964. *The life of the rainbow lizard*. London: Hutchinson.
- HILLENUS, D. 1959. The differentiation within the genus *Chamaeleo* Laurenti 1768. *Beaufortia*, 8(89):1-92.

- HUGHES, G. R. 1974a. The sea turtles of South-East Africa. 1. Status, morphology and distributions. *Investl Rep. Oceanogr. Res. Inst. Durban*, 35:1-144.
- HUGHES, G. R. 1974b. The sea turtles of South-East Africa. II. The biology of the Tongaland loggerhead turtle *Caretta caretta* L., with comments on the leatherback turtle *Dermochelys coriacea* L. and the green turtle *Chelonia mydas* L. in the study region. *Investl Rep. Oceanogr. Res. Inst. Durban*, 36:1-96.
- HULSELMANS, J. L. J. 1970. Preliminary notes on African Bufonidae. *Revue Zool. Bot. afr.* 81: 149-155.
- KLAVER, CH. J. J. 1973. Lung-anatomy: aid in chameleon taxonomy. *Beaufortia*, 20(269):155-177.
- KOCHVA, E. & WOLLBERG, M. 1970. The salivary glands of Aparallactinae (Colubridae) and the venom glands of *Elaps* (Elapidae) in relation to the taxonomic status of this genus. *J. Linn. Soc. (Zool.)*, 49:217-224.
- LAURENT, R. F. 1956. Contribution à l'herpétologie de la région des grands lacs de l'Afrique Centrale. *Annls Mus. r. Congo Belge Sér. 8 vo. Sci. Zool.* 48:1-390.
- LAURENT, R. F. 1964. Reptiles et Amphibiens de l'Angola. *Publicões cult. Co. Diam. Angola* 67:1-165.
- LAURENT, R. F. 1965. A contribution to the knowledge of the genus *Pehusios* (Wagler). *Annls Mus. r. Afr. cent. Sér. 8 vo. Sci. Zool.* 135:1-33.
- LAURENT, R. F. 1968. A re-examination of the snake genus *Lycophidion* Duméril and Bibron. *Bull. Mus. comp. Zool. Harv.* 136:461-482.
- LAURENT, R. F. 1972. Tentative revision of the genus *Hemisis* Gunther. *Annls Mus. r. Afr. cent. Sér. 8 vo. Sci. Zool.* 194:1-67.
- LOVERIDGE, A. 1941. Revision of the African terrapin of the family Pelomedusidae. *Bull. Mus. comp. Zool. Harv.* 88:465-524.
- LOVERIDGE, A. 1942. Revision of the African lizards of the family Gerrhosauridae. *Bull. Mus. comp. Zool. Harv.* 89:483-543.
- LOVERIDGE, A. 1944. Revision of the African lizards of the family Cordylidae. *Bull. Mus. comp. Zool. Harv.* 95:1-118.
- LOVERIDGE, A. 1947. Revision of the African lizards of the family Gekkonidae. *Bull. Mus. comp. Zool. Harv.* 98:1-469.
- LOVERIDGE, A. 1958. Revision of five African snake genera. *Bull. Mus. comp. Zool. Harv.* 119: 1-198.
- LOVERIDGE, J. P. 1970. Observations on nitrogen excretion and water relations of *Chiro-mantis xerampelina* (Amphibia, Anura). *Arnoldia* (Rhodesia), 5(1):1-6.
- LOVERIDGE, A. & WILLIAMS, E. E. 1957. Revision of the African tortoises and turtles of the sub-order Cryptodira. *Bull. Mus. comp. Zool. Harv.* 115:161-557.
- MCDOWELL, S. B. 1968. Affinities of the snakes usually called *Elaps lacteus* and *E. dorsalis*. *J. Linn. Soc. (Zool.)* 47:561-578.
- PASTEUR, G. 1964. Recherches sur l'évolution des Lygodactyles, lézards Afro-Malgaches actuels. *Trav. Inst. scient. chérif. zool.* 29:1-132.
- PIENAAR, U. DE V. 1966. *The reptiles of the Kruger National Park*. Pretoria: National Parks Board of Trustees.

- POYNTON, J. C. 1964. The Amphibia of Southern Africa: a faunal study. *Ann. Natal Mus.* 17: 1–334.
- POYNTON, J. C. 1970. Guide to the Ptychadena (Amphibia: Ranidae) of the southern third of Africa. *Ann. Natal Mus.* 20:365–375.
- POYNTON, J. C. 1972. Note on a confusion between ecology and zoogeography. *Zool. afr.* 7: 471–472.
- POYNTON, J. C. & BASS, A. J. 1970. Environment and amphibian distribution in Zululand. *Zool. afr.* 5:41–48.
- RAW, L. R. G. 1973. A review of the dusky-bellied water snake *Lycodonomorphus laevisimus* (Günther), with descriptions of two new sub-species. *Ann. Natal Mus.* 21:713–718.
- ROUX-ESTÈVE, R. 1974. Revision systématique des Typhlopidae d’Afrique. Reptilia–Serpentes. *Mém. Mus. natn. Hist. nat. Paris*, (A) 87:1–313.
- SAIFF, E. I. 1970. Geographical variation in the genus *Zygaspis* (Amphisbaenia: Reptilia). *Herpetologica*, 26:86–119.
- SCHIØTZ, A. 1971. The superspecies *Hyperolius viridiflavus* (Anura). *Vidensk. Meddr dansk naturh. Foren.* 134:21–76.
- SCHIØTZ, A. 1974. Revision of the genus *Afrixalus* (Anura) in eastern Africa. *Vidensk. Meddr dansk naturh. Foren.* 137:9–18.
- STEWART, M. M. 1967. *Amphibians of Malawi*. State University of New York Press.
- STUCKENBERG, B. R. 1969. Effective temperature as an ecological factor in Southern Africa. *Zool. afr.* 4:145–197.
- TANDY, M. & KEITH, R. 1972. *Bufo* of Africa. In *Evolution in the genus Bufo*, ed. Blair, W. F.
- UNDERWOOD, G. 1967. *A contribution to the classification of snakes*. London: British Museum (Nat. Hist.)
- VAN DIJK, D. E. 1966. Systematic and field keys to the families, genera and described species of Southern African anuran tadpoles. *Ann. Natal Mus.* 18:231–286.
- VAN DIJK, D. E. 1971a. The zoocartographic approach to anuran ecology. *Zool. afr.* 6:85–118.
- VAN DIJK, D. E. 1971b. Anuran ecology in relation particularly to oviposition and development out of water. *Zool. afr.* 6:119–132.
- VAN DIJK, D. E. 1971c. A further contribution to the systematics of Southern African anuran tadpoles – the genus *Bufo*. *Ann. Natal Mus.* 21:71–76.
- VAN DIJK, D. E. 1972. The behaviour of southern African anuran tadpoles with particular reference to their ecology and related external morphological features. *Zool. afr.* 7:49–55.
- WAGER, V. A. 1965. *The frogs of South Africa*. Cape Town/Johannesburg: Purnell.