



## **SANBI Biodiversity Series 5**

# **A plan for phylogenetic studies of southern African reptiles**

Proceedings of a workshop held at Kirstenbosch,  
February 2006

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## SANBI Biodiversity Series

The South African National Biodiversity Institute (SANBI) was established on 1 September 2004 through the signing into force of the National Environmental Management: Biodiversity Act (NEMBA) No.10 of 2004 by President Thabo Mbeki. The Act expands the mandate of the former National Botanical Institute to include responsibilities relating to the full diversity of South Africa's fauna and flora, and builds on the internationally respected programmes in conservation, research, education and visitor services developed by the National Botanical Institute and its predecessors over the past century.

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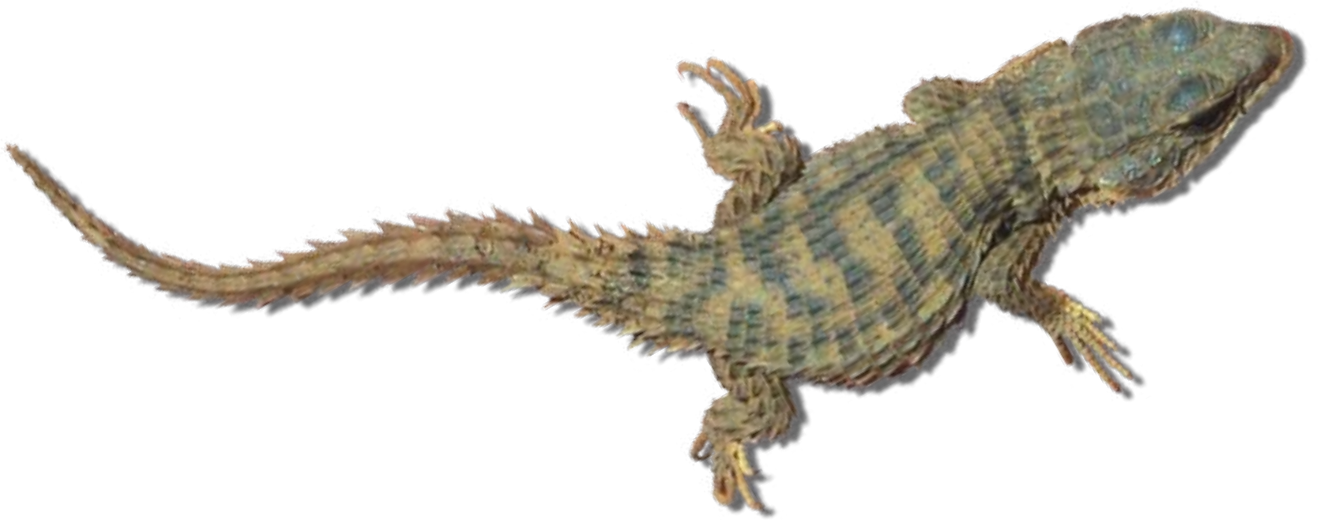
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# Introduction

The Southern African Reptile Conservation Assessment (SARCA) was launched in May 2005. Its primary aim is to produce a conservation assessment for the reptiles of South Africa, Lesotho and Swaziland within a four-year period (2005–2009). It has the distinction of being the first faunal project of the newly constituted South African National Biodiversity Institute (SANBI) which, in its former incarnation as the National Botanical Institute (NBI), was concerned only with plants.

SARCA was motivated principally by a clear need for an update of the South African Red List for reptiles which was last updated in 1988. However, projects of this kind aimed at being comprehensive in geographical and taxonomic scope, are confronted with a discipline's knowledge gaps. These gaps are particularly acute in southern Africa, where taxonomic studies in the last 20 years have revealed that the subcontinent is a global hotspot of reptile diversity. Inadequacies in the geographical sampling of reptiles are being addressed by a series of SARCA surveys in previously undersampled areas. However, this effort alone cannot specifically address the incomplete and sometimes problematic nature of the region's reptile alpha taxonomy (the description and naming of species). As conservation assessment and planning depend fundamentally on alpha taxonomy, it was soon apparent that SARCA would have to help initiate a programme to resolve the pressing taxonomic problems.

To this end, a workshop was organised to identify, list and prioritise all known taxonomic problems. In addition, the workshop participants would discuss, resolve and describe the methodological questions and the practicalities of methods and resources. This workshop was held from 22–24 February 2006, at SANBI's Biodiversity Research Building, Kirstenbosch, Cape Town. The event was funded by the South African National Research Foundation (NRF), facilitated by Renee le Roux and hosted by SANBI, with the particular assistance of Krystal Tolley.

The participants included Prof. Graham Alexander (University of the Witwatersrand), Mike Bates (National Museum, Bloemfontein), Prof. Aaron Bauer (University of Villanova, Pennsylvania), Dr Bill Branch (PE Museum), Marius Burger (ADU), Dr Michael Cunningham (University of the Free State), Dr Savel Daniels (University of Stellenbosch), James Harrison (ADU), Prof. Margaretha Hofmeyr (University of the Western Cape), Johan Marais (University of the Witwatersrand), Prof. Le Fras Mouton (University of Stellenbosch), Dr Krystal Tolley (SANBI), Andrew Turner (CapeNature) and rapporteurs Daniel Goedbloed (University of the Free State) and Lerina Kaars (University of the Free State, SANBI intern). Additional input was given during one session by Dr John Donaldson (SANBI) and Prof. Les Underhill (ADU). So, with few exceptions, the main researchers involved in the taxonomy of the region's reptiles were present, and contributed substantively to the proceedings of the workshop and to this report.

This report brings together, in a single document, a comprehensive set of guidelines for a whole section of southern Africa's biodiversity research, and should remain relevant for at least a decade. The herpetologists of the region congratulate the institutions, especially SANBI and NRF, that have had the vision and commitment to support this endeavour.

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# CHAPTER 1 Priorities for systematic studies on southern African reptiles

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Southern Africa has the richest reptile diversity in Africa (Bauer 1993; Branch 1999a), with a fauna that currently exceeds 520 species (Branch 1998; subsequent updates). Lizards form the dominant component of this rich fauna due, in part, to an exceptional radiation of geckos in the western arid region. Over 100 species of gecko are now known from the subcontinent, while the families Scincidae and Cordylidae are also well represented and the amphisbaenid diversity is the richest in Africa. Only one introduced reptile (*Rhamphotyphlops braminus*) has become established.

The current rate of species description shows little indication of reaching a plateau (Branch 1999a), even after 250 years of almost continuous study. This is evident in the increase in species numbers in recent decades (397 in Branch 1988; 480 in Branch 1998; 520+ in Branch unpubl. checklist). In addition to its diversity, the southern African reptile fauna also displays high endemism, particularly in lizards (mean 65.3%; Cordylidae 85.5%; Chamaeleonidae 95%). This endemism exceeds that of frogs and freshwater fish (50–60%) and is much greater than that of birds and mammals (<25%).

A directed programme of reptile surveys is a component of the Southern African Reptile Conservation Assessment (SARCA). The survey localities were selected by using a gap analysis of known reptile distributions, based on museum records in the major South African museums. The gap analysis identified areas with known reptile diversities, which were significantly lower than those predicted by an analysis of the distribution maps published in Branch (1998). In addition to collecting distribution data, the surveys may serve a useful ancillary function by collecting material for taxonomic revisions, as well as tissue for use in molecular studies. Moreover, they can be expected to uncover additional taxonomic novelties, as well as populations which do not fit easily into current hypotheses of species' distributions and diagnoses. To both direct

and optimise the taxonomic usefulness of these surveys, and the subsequent analysis of voucher material, it is necessary to review the taxonomic knowledge of the regional reptile fauna and to identify and highlight problematic taxa.

## Approach

A provisional list of genera in which cryptic taxa were known or suspected to be present, was prepared by the author. Problematic taxa included the following:

- species with subspecies (races) that have not been recently reviewed (see the chapter by Bauer in this volume for a discussion of species definitions and the subspecies concept in herpetology);
- species with disjunct ranges and geographically isolated populations, which may include cryptic taxa; and
- species with contiguous ranges, but with confusing morphological (including colouration) and/or habitat variation.

These were discussed at a workshop attended by invited researchers (see Introduction for list). Following discussion, the list was amended for oversights and new insights, and expanded to include details of proposed and ongoing research projects. Discussion then prioritised the identified problem taxa for attention (1–5, low-high) and the research funding required to resolve these problems (1–5). Problem taxa scored high if they were known to contain numerous new taxa, or had the potential to do so, based on the biological and distribution characteristics associated with high species richness. High scores for research funding were based on a lack of existing funding and a reasonable chance of obtaining essential study material. For the latter, the resolution of some taxonomic problems requires extralimital material that is currently not readily available (e.g. from Angola). Due to the interrelatedness of the reptile fauna of southern Africa, the analysis of problematic taxa was not limited to the SARCA region (South Africa, Lesotho and Swaziland).

## Results

Genera containing problematic taxa are summarised in Appendix 1. The scores for these





TABLE 1: Problematic taxa: a synopsis of genera, and known/possible species richness; priorities for research and funding needs; and the researchers currently working on, or interested in, the groups.

Family & genus	Spp. in sthrn Africa	Spp. in SARCA region	New spp. known un-described	New spp. expected	Problem taxa/populations	Research effort Score (1–5)	Score (1–5) Funding needed	Total score	Researcher(s): molecular	Researcher(s): morphology
<b>Lizards</b>										
<b>Gekkonidae</b>										
<i>Afroedura</i>	15	12	3	10	<i>pondolia</i> complex, <i>africanus</i> , <i>amatolica</i> complex	5	2	7	Whiting/Bauer	Bauer/Branch
<i>Afrogecko</i>	2	2	1	1	<i>Porphyrus</i>	2	1	3	Whitaker	Branch
<i>Chondrodactylus</i>	5	3	2	2	<i>anguifer</i> , <i>turneri</i>	2	1	3	Whiting/Bauer	Bauer/Branch
<i>Goggia</i>	8	8	?	?	<i>lineatus</i> ?	2	1	3	Whitaker	
<i>Hemidactylus</i>	4	1	?	?	<i>mercatorius/mabouia</i>	1	1	2	Whiting/Bauer	
<i>Lygodactylus</i>	12	8	2–3	2–3	rupicolous isolates ( <i>ocellatus</i> , <i>nigropunctatus</i> , <i>waterbergensis</i> )	3	2	5	Whiting/Bauer	Bauer/Branch
<i>Pachydactylus</i>	44	26	9	5	<i>marquensis</i> , <i>geijie</i> , <i>montanus</i> , <i>amoneus</i> , <i>maculatus</i>	3	1	4	Whiting/Bauer	Bauer/Branch
<i>Rhoptropus</i>	6	0	1	?	<i>bradfieldi</i> , <i>barnardi</i> , <i>biporosus</i>	2	1	3	Whiting/Bauer	Bauer
<b>Chamaeleonidae</b>										
<i>Bradypodion</i>	14	14	4	6	numerous isolates in KZN and escarpment forests	5	5	10	Tolley	Tilbury/Branch/Tolley
<b>Agamidae</b>										
<i>Agama</i>	11	7		1	<i>aculeata</i> , <i>knobelli</i>	2	2	4	Swart, Matthee	Fienling
<b>Lacertidae</b>										
<i>Ichnotropis</i>	3	2		1	<i>Capensis</i>	2	2	4		
<i>Merolepis</i>	7	4	1	2	<i>suborbitalis</i> , <i>knoxii</i>	3	2	5	Bauer	Bauer
<i>Nucras</i>	9	9	1	2	<i>tesselata</i> ( <i>elegans</i> , 'Var T', <i>lalandei</i> )	4	4	8	Bauer	Bauer/Branch
<i>Pedioplanis</i>	12	6	2	2–3	<i>burchelli</i> , <i>laticeps</i> , <i>namaquensis</i> , <i>lineocellata</i>	3	3	6	Makokha/Tolley/Bauer	Bauer
<i>Tropidosaura</i>	4	4		1	<i>burchelli</i> , <i>essexi</i> , <i>natalensis</i>	3	3	6	Cunningham	Branch
<b>Scincidae</b>										
<i>Acontias</i>	10	10	1	2	<i>breviceps</i> , <i>namaquensis</i> , <i>plumbeus</i>	3	1	4	Daniels	Heidemann
<i>Typhlosaurus</i>	9	8	1	1	<i>lineatus</i> , <i>aurantiacus</i>	2	2	4	Lamb/Bauer	Bauer
<i>Scelotes</i>	20	18	2–3	2–3	<i>caffer</i> , <i>limpopoensis</i>	3	2	5	Bauer/Whiting	Bauer
<i>Typhlacontias</i>	4	0	1	?	<i>Brevipes</i>	2	2	4	Whiting/Bauer	
<i>Panaspis</i>	2	2		1	<i>Wahlbergii</i>	2	1	3		
<i>Trachylepis</i>	24	14	1	1–2	<i>homalocephala</i> , <i>varia</i>	2	2	4	Whiting/Bauer	Bauer/Branch
<b>Cordylidae</b>										
<i>Chamaesaura</i>	3	3	?	?						
<i>Cordylus</i>	30	21	2	2–3	<i>warreni</i> , <i>minor</i> , <i>vittifer</i>	3	4	7	Bauer et al.	Mouton



<i>Pseudocordylus</i>	8	8	1	1-2	<i>melanotus, microlepidotus, capensis</i>		3	3	6	Mouton	Bates
<i>Platysaurus</i>	13	9		2-3	<i>intermedius, orientalis, pungweensis</i>		3	3	6	Keogh/Whiting	
<b>Gerrosauridae</b>											
<i>Gerrhosaurus</i>	7	5	1	?	<i>Multilineatus</i>		2	1	3		Broadley
<i>Tetradactylus</i>	5	5		?	<i>africanus, seps</i>		3	3	6		Branch (ftzsimonsi)
<b>Amphisbaenidae</b>											
<i>Chirindia</i>	2	1		1	<i>Langi</i>		2	2	4		
<i>Monopeltis</i>	8	5		1	<i>sphenorhynchus, infuscata</i>		2	2	4		
<i>Zygaspis</i>	5	2		1	<i>Vandami</i>		2	2	4		
<b>Snakes</b>											
<b>Typhlopidae</b>											
<i>Rhinotyphlops</i>	5	4		?	<i>Lalandei</i>		2	2	4		
<i>Typhlops</i>	2	2		?	<i>Bibroni</i>		2	2	4		
<b>Leptotyphlopidae</b>											
<i>Leptotyphlops</i>	12	9		1-2	<i>scutifrons, conjunctus, incognitus</i>		3	3	6	Daniels	Branch
<b>Atractaspididae</b>											
<i>Amblydipsas</i>	4	3		1	<i>Microphthalma</i>		2	2	4		
<i>Xenocalamus</i>	5	3		?	<i>Bicolour</i>		2	2	4		
<i>Homoroselaps</i>	2	2		?	<i>Lacteus</i>		1	2	3		Branch
<b>Colubridae (sl)</b>											
<i>Lamprophis</i>	6	6		2	<i>guttatus, 'mentalis', swazicus</i>		2	2	4	Kelly	Branch
<i>Lycodonomorphus</i>	4	3		?	<i>rufulus, laevisissimus</i>		2	2	4		
<i>Philothamnus</i>	5	4	1	?	<i>occidentalis, semivariegatus</i>		2	2	4		Alexander
<i>Tetescopus</i>	2	2	1	?	<i>Polystictus</i>		2	2	4		Haacke
<i>Dispholidus</i>	1	1		?	<i>Typus</i>		1	1	2		Broadley/Branch
<i>Psammophis</i>	13	11	1	?	<i>leightoni, crucifer, mossambicus</i>		2	2	4		Branch ( <i>crucifer</i> )
<i>Prosymna</i>	8	6		?	<i>sundevallii, bivittata</i>		1	1	2	Banach/Bauer	Bauer
<b>Elapidae</b>											
<i>Aspidelaps</i>	2	2		?	<i>Scutatus</i>		2	2	4		
<i>Elapsoidea</i>	4	3		?	<i>Sundevallii</i>		2	2	4		
<i>Hemachatus</i>	1	1		?	<i>Haemachatus</i>		1	1	2		
<i>Naja</i>	7	5		?	<i>Melanoleuca</i>		1	1	2	Wurster	Broadley
<b>Viperidae</b>											
<i>Bitis</i>	12	12		1-3	<i>atropos, rubida, peringueyi</i>		2	3	5	Joger/Cunningham	Branch
<b>Chelonians</b>											
<b>Testudidae</b>											
<i>Psammobates</i>	3	3		?	<i>Tentorius</i>		3	3	6	Daniels/Hofmeyr	Branch
<i>Homopus</i>	5	4		?	<i>areolatus, signatus</i>		3	3	6	Daniels/Hofmeyr	Branch/Hofmeyr
<b>TOTALS</b>	<b>409</b>	<b>303</b>	<b>31</b>	<b>55-65</b>							

genera, and the species within them requiring attention, are detailed in Table 1. Taxonomic problems exist in 50 genera containing 409 species, i.e. nearly 80% of southern African reptiles. Together they contain at least 31 known new species currently in various stages of formal description. In addition, these genera are expected to contain numerous (55–65) additional cryptic species. This supports the prediction that the reptile fauna of the subcontinent exceeds 600 species (Branch 1999a).

The genera containing known and expected cryptic taxa are not randomly distributed. It is expected that relatively few snake and tortoise species remain to be discovered. However, these groups have not been investigated as well as many lizard groups, and there are indications that some tortoises (e.g. *Homopus areolatus*, *Chersina angulata*) contain deeper genetic divergence than is reflected in the current morphological classification (S. Daniels & M. Hofmeyr pers. comm.). Similarly, the congruence between genes and morphology has not been assessed in many snakes, particularly fossorial groups (e.g. scolecophidians and atractaspidids) that may have low dispersal abilities.

Lizards are the most diverse group of South African reptiles (Bauer 1993) and are also the group in which relatively many new species have been described in recent years. Of the 71 new species described in the past 25 years (1980–2005), only eight were snakes and the remainder all lizards (Figure 1). Moreover, the

majority of new discoveries have had either rupicolous (38 species, 54%) or burrowing (23 species, 32%) habits (Figure 2). This supports Bauer's (1993) observation of the importance of substrate specificity in the cladogenesis of many lizard groups.

Geckos include the greatest number of known undescribed species (13), as well as the largest projected number of undiscovered cryptic taxa (20+). Most are rupicolous species in the genera *Afroedura*, *Pachydactylus* and *Lygodactylus*. Terrestrial lacertids, a dominant group in the western arid region, have previously been relatively neglected. This is reflected in a relatively high number of undescribed taxa: three known and eight expected. Although more fully studied, scincids and cordylids still contain significant numbers of new taxa, particularly in fossorial and rupicolous groups, respectively. Dwarf chameleons (*Bradypodion*) have recently been the focus of intense study (Tolley & Burger 2004; Tolley *et al.* 2004, 2006), with numerous taxonomic problems identified and currently under investigation (see Table 1 on page 2).

The priority genera are summarised in Table 2. The top five, in order, are: *Bradypodion*, *Nucras*, *Afroedura*, *Cordylus* and *Pedioplanis*. With the exception of *Nucras*, these genera are the subjects of current research. A number of other genera, suspected or known to have high cryptic diversity, require little additional funding because they are currently supported by overseas funding (e.g. *Pachydactylus*,

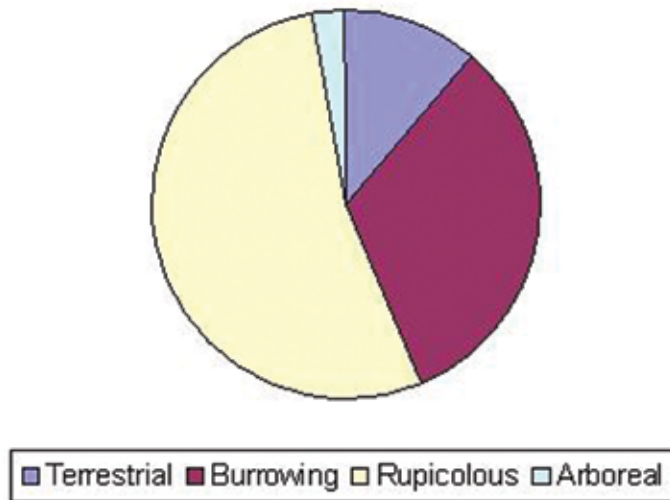
FIGURE 1: New species per taxonomic group described in the past 25 years.

**New species per taxonomic group (1980-2005)**



FIGURE 2: Habits of species described in the past 25 years.

**Life styles of new species (1980-2005)**



*Lygodactylus*, *Scelotes*; A. Bauer). *Afroedura* scored high for required research effort. It currently receives funding for sequencing (A. Bauer), but field work in South Africa to collect additional material requires further support.

Phylogenetic studies have shown that many lineages may have conservative morphologies despite significant underlying genetic divergence (e.g. *Pachydactylus*; Lamb & Bauer

2002). This suggests that more groups that have been, at least in part, intractable to traditional morphological analysis may benefit from complementary molecular studies (e.g. *Leptotyphlops*, *Bitis*, *Nucras*).

**Post-alpha**

The burgeoning increase in our knowledge of reptilian diversity in the subcontinent is due to a number of factors. Increases in funding and

TABLE 2: Summary of priority genera.

Genus	Research effort needed	Funding needed	Combined score	New species	
				currently undescribed	additional expected
<i>Bradypodion</i>	5	5	10	4	6
<i>Nucras</i>	4	4	8	1	2
<i>Afroedura</i>	5	2	7	3	10
<i>Cordylus</i>	3	4	7	2	2-3
<i>Pedioplanis</i>	3	3	6	2	2-3
<i>Tropidosaura</i>	3	3	6		1
<i>Platysaurus</i>	3	3	6		2-3
<i>Leptotyphlops</i>	3	3	6		1-2
<i>Psammobates</i>	3	3	6		?
<i>Homopus</i>	3	3	6		?
<i>Lygodactylus</i>	3	2	5		2-3
<i>Meroles</i>	3	2	5		2
<i>Scelotes</i>	3	2	5		2-3
<i>Pseudocordylus</i>	2	3	5	1	1-2
<i>Tetradactylus</i>	2	3	5	1	?
<i>Bitis</i>	2	3	5		1-3
<i>Acontias</i>	3	1	4	1	2
<i>Pachydactylus</i>	3	1	4	9	5





manpower, and an awareness of the necessity of field surveys, have resulted in collections from previously inaccessible or poorly surveyed regions. In addition, the increasing acceptance of evolutionary species concepts has resulted in the recognition of many allopatric species previously treated as races, e.g. within leaf-toed geckos (Branch *et al.* 1995; Bauer *et al.*, 1996, 1997; Good *et al.* 1996) and within the *Trachylepis striata* complex (Broadley 2000). The resulting taxonomic subdivision has resulted in numerous additional species, usually with relatively restricted distributions. Recent detailed taxonomic revisions have revealed the existence of threatened, previously overlooked species, e.g. the adders *Bitis albanica*, *B. armata* and *B. inornata* (Branch 1999b) and the Pygmy Wolf Snake *Lycophidion pygmaeum* (Broadley 1996), and highlighted the ongoing need for conservation efforts which are grounded in sound, up-to-date taxonomy.

Recent protocols for assessing conservation status (Mace & Lande 1991; Mace & Stuart 1994) have placed emphasis, in part, on the extent of occurrence and area of occupancy of threatened taxa. In this context, it is important to stress that over 30 South African reptiles have ultra-restricted distributions, i.e. are known from fewer than five quarter-degree grid cells (one cell is approx. 25 km square; see Branch 1999a for a list). Most of these species are found in small pockets of rocky or forested habitat in isolated escarpment mountains and may therefore be threatened by habitat loss. In addition, many of the new species currently awaiting description have restricted ranges and are therefore also of possible conservation concern.

It is opportune to emphasise the additional advantages that a sound taxonomic base will have for the future development of South African herpetological studies. Part of the SARCA initiative is to develop the tools—an atlas of distributions and a sound alpha taxonomy—required to assess the conservation status of the region's reptiles. These same tools, in conjunction with ongoing phylogenetic studies on evolutionary relationships, will allow novel biogeographic hypotheses to be formulated and tested.

Greater knowledge of reptile diversity and evolutionary relationships in the subcontinent will, in turn, allow the development of models of ecological processes and communities that are more relevant to Africa. Recent studies on the evolution of squamate venom systems

have emphasised the role of evolutionary 'tinkering', via the co-option and modification of existing biochemistry (Vidal 2002; Fry & Wüster 2004). An analogous approach can be applied to ecological modelling, in which the phylogenetic constraints and opportunities of African lineages (e.g. acontines, cordylids, atractaspidids, psammophines) can be assessed in the evolution of this unique reptilian heritage, rather than 'pigeon-holing' African systems into models based on studies on northern biota.

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## Appendix 1:

### Priorities for systematic studies on southern African reptiles

#### **SUBORDER: LACERTILIA**

#### **FAMILY: GEKKONIDAE**

***Afroedura*** Loveridge 1944

**Taxa:** Total: 15                      South Africa: 12                      Undescribed: 3 + 10?

**Last generic revision:** Loveridge 1947.

**Other taxonomic studies:** Haacke 1965; Onderstall 1984; Mouton & Mostert 1985; Jacobsen 1992a.

#### **Current studies:**

- A revision of the *karroica-halli* species complex has been completed; at least one new species is recognised (Bates & Branch in preparation).
- A new species from the Kouga Mts, eastern Cape Fold Mountains, has been identified (Branch in preparation).

#### **Remaining taxonomic problems:**

- A revision of the *A. pondolia* complex is essential. Jacobsen (1992a) signalled the presence of 17 taxa in the 'Transvaal', many (8+) of them representing new taxa that have yet to be described. Additional material and DNA samples for an assessment of these putative taxa are currently being collected (Bauer, Branch & Whiting ongoing).
- The taxonomic status of the northern Namibian population currently assigned to *A. cf. bogerti* (Branch 1998) needs resolution.
- The status of the three isolated races of *A. africana* recognised by Haacke (1965) need re-assessment (Branch & Bauer proposed).
- A number of species complexes have been proposed (Onderstall 1984; Jacobsen 1992a) and a molecular phylogeny of the genus is in preparation (Bauer, Branch & Whiting ongoing).

***Afrogecko*** Bauer, Good & Branch 1997

**Taxa:** Total: 2                      South Africa: 2                      Undescribed: 1?

**Last generic revision:** FitzSimons 1943; Loveridge 1947.

**Other taxonomic studies:** Haacke 1996; Bauer *et al.* 1997.

#### **Current studies:**

- Molecular studies have revealed significant genetic divergence in *A. porphyreus*, particularly in the Cape Peninsula (Whitaker unpub. obs.); eastern populations may be referable to *A. p. cronwrighti* (Whitaker & Branch); no further Namaqualand material has been obtained, and the status of *A. p. namaquensis* remains problematic.
- A molecular phylogeny of leaf-toed geckos and the relationships of the African genera is to be assessed (Bauer *et al.*).

#### **Remaining taxonomic problems:**

- Relationships of southern African species to *A. ansorgii* and an undescribed species (Haacke unpubl. obs.) from Angola.

***Chondrodactylus*** Peters 1864

**Taxa:** Total: 5                      South Africa: 3                      Undescribed: 2?

**Last generic revision:** morphology, Haacke 1976; genetics, Lamb & Bauer 2006.

**Other taxonomic studies:** Bauer & Lamb (2006) expanded the concept of the genus to accommodate a number of large-bodied species previously included in *Pachydactylus*.

#### **Current studies:**

- A broad-scale molecular study of *C. turneri* across its range is in preparation (Bauer & Lamb).
- Remaining taxonomic problems:
  - The status of *C. a. namibiensis* remains problematic. Bauer & Branch (2001) noted sympatry in the Richtersveld, and the races also show chromosomal differences (Branch unpubl. obs.).
  - The status of *laevigatus* and its affinities to *C. turneri* needs assessment.





**Goggia** Bauer, Good & Branch 1997**Taxa:** Total: 8 South Africa: 8 Undescribed: ?**Last generic revision:** FitzSimons 1943; Loveridge 1947**Other taxonomic studies:** Branch *et al.* 1995; Branch & Bauer 1997; Bauer *et al.* 1996; Good *et al.* 1997.**Current studies:**

- A detailed molecular phylogeny of the genus is underway (Whitaker in preparation).

**Remaining taxonomic problems:**

- A molecular phylogeny of leaf-toed geckos and the relationships of the African genera is to be assessed (Bauer *et al.*).

**Hemidactylus** Oken 1817**Taxa:** Total: 4 South Africa: 1 Undescribed: ?**Last generic revision:** Loveridge 1947.**Other taxonomic studies:** Broadley 1977; Vences *et al.* 2004; Carranza & Arnold 2006.**Current studies:**

- A phylogeny of African *Hemidactylus*, to supplement the study of Carranza & Arnold (2006), is planned (Bauer *et al.*).

**Remaining taxonomic problems:**

- The correct name for the southern African population of *H. mabouia* /*mercatorius* remains problematic (Vences *et al.* 2004; Carranza & Arnold 2006).
- Haacke (unpubl. obs.) noted the presence of *H. longicephalus* in northern Namibia. The status of this population remains unresolved.

**Lygodactylus** Gray 1864**Taxa:** Total: 12 South Africa: 8 Undescribed: 2–3?**Last generic revision:** Loveridge 1947; Pasteur 1965**Other taxonomic studies:** Jacobsen 1992, 1994a.**Current studies:** None.**Remaining taxonomic problems:**

The following problems are currently being assessed (Branch, Bauer, Whiting):

- Status of the races of *L. ocellatus* and *L. nigropunctatus*.
- Relationship of *L. angularis* and *L. gutturalis*, and northern montane isolates.
- Relationships and status of *L. capensis* and related taxa (e.g. *grotei*, *bradfieldi*).

**Pachydactylus** Wiegmann 1834**Taxa:** Total: 44 South Africa: 23 Undescribed: 9 + 5?**Last generic revision:** FitzSimons 1943; Loveridge 1947.**Other taxonomic studies:** Haacke 1966; McLachlan & Spence 1966, 1967; Broadley 1977b; Benyr 1995; Bauer & Branch 1995; Branch *et al.* 1996; Bauer 2000; Bauer & Lamb 2002; Lamb & Bauer 2000, 2002; Bauer *et al.* 2002.**Current studies:**

- The *Pachydactylus weberi-serval* complex was reviewed by Bauer *et al.* (2006a) with the description of eight new species and a further six being revived from synonymy.
- A new species from Augrabies has been described (Bauer *et al.* 2006b).

**Remaining taxonomic problems:**

The following problems are currently being assessed:

- Status of populations from the Cape Fold Mountains, Little Karoo and inland escarpment currently assigned to *P. geitjie* (Branch 1990; Branch & Bauer 1995), and their relationship to *P. monticolus* FitzSimons 1943 (Bauer & Branch in preparation).
- Status of *P. mariquensis latirostris* and populations in the Albany region, Eastern Cape (Bauer *et al.*).
- Status of the isolated population of *P. maculatus* on St Croix island, Algoa Bay, and the relationships of *P. maculatus* and *P. oculatus* (Bauer and Branch in preparation).



- Status of *P. montanus* around Onseepkaans (Bauer *et al.*).
- Status of additional populations assigned to the *P. serval-weberi* complex from Mt Uisib, Khumib River and Sossusvlei are under review (Bauer *et al.*).
- Status of *P. angolensis*, *P. katanganus*, and *P. amoenus* (Bauer *et al.*).
- Species variation within *P. punctatus* (Bauer *et al.*).

**Rhoptropus** Peters 1869

**Taxa:** Total: 6 South Africa: 0 Undescribed: 1 + ?

**Last generic revision:** FitzSimons 1943; Loveridge 1947.

**Other taxonomic studies:** Bauer & Good 1996; Röhl 1999; Lamb & Bauer 2001; Bauer & Lamb 2001.

**Current studies:**

- Detailed investigation of phylogenetic relationships within the genus using an expanding mitochondrial and nuclear gene data set (Bauer *et al.* in preparation).
- Additional taxa from northern Namibia (Bauer *et al.* in preparation).

**Remaining taxonomic problems:**

- Subspecies and also variation within *R. bradfieldi* (Bauer).

**FAMILY: CHAMAELEONIDAE**

**Bradypodion** Fitzinger 1843

**Taxa:** Total: 14 South Africa: 14 Undescribed: 7 + 3

**Last generic revision:** FitzSimons 1943.

**Other taxonomic studies:** Raw 1976, 1978; Bauer 1997; Tolley & Burger 2004; Tolley *et al.* 2004, 2006.

**Current studies:**

The following problems are currently being assessed:

- Several new taxa from the Cape Fold Mountains are currently being described (Branch, Tilbury, Tolley in preparation).
- Additional new taxa from KwaZulu-Natal and within the *transvaalense* complex (Tolley *et al.* in progress).

**Remaining taxonomic problems:**

- Problematic populations from Weza, Karkloof/Gilboa, Drakensberg/Sani pass), Jagersbos-Tsit-sikamma, Groot Winterhoek Nature Reserve, & Grootvadersbosch, Barberton, Elands Valley, Graskop, and Woodbush (Tolley or Townsend in progress).
- Conflict between morphological and genetic divergence within *B. melanocephalum/thamnobates* complex (Tolley *et al.* in progress).

**FAMILY: AGAMIDAE**

**Agama** Daudin 1802

**Taxa:** Total: 11 South Africa: 7 Undescribed: 1?

**Last generic revision:** No recent revision.

**Other taxonomic studies:** McLachlan 1981; Jacobsen 1990; Mouton & Herselman 1994; Matthee & Flemming 2002; Swart *et al.* 2004.

**Current studies:**

- Phylogenetic relationships among southern African Agama (Swart *et al.*).
- Phylogenetic studies of *A. atra* within the CFR have demonstrated divergent clades of unresolved taxonomic status (Swart *et al.*).

**Remaining taxonomic problems:**

- Although the specific status of *A. knobelli* has been supported (Matthee & Fleming 2002; Mouton & Herselman 1994), the extent of its distribution and the relationship between populations north and south of the Orange River remain unresolved.
- The taxonomy of the *A. armata* complex remains problematic, and status of the various taxa (e.g. *distanti*) requires further investigation.
- A phylogeny of African Agama is required.



**FAMILY: LACERTIDAE*****Ichnotropis*** Peters 1854**Taxa:** Total: 3                      South Africa: 2                      Undescribed: 1?**Last generic revision:** Laurent 1952.**Other taxonomic studies:** Broadley 1967.**Current studies:** None.**Remaining taxonomic problems:**

- The status of the isolated coastal population of *I. capensis* in KwaZulu-Natal should be assessed.
- The relationship between *I. capensis* and northern taxa (e.g. *bivittata*, *tanganicana*), including a possible new species in Angola (Branch unpubl. obs.), remains unresolved.

***Meroles*** Gray 1838**Taxa:** Total: 7                      South Africa: 4                      Undescribed: 1–2?**Last generic revision:** FitzSimons 1943.**Other taxonomic studies:** Haacke 1965; Arnold 1991; Branch 1994; Harris *et al.* 1998; Lamb & Bauer 2003.**Current studies:** None.**Remaining taxonomic problems:**

- Morphological and habitat divergence between *M. suborbitalis* populations in the vicinity of the lower Orange River require investigation.
- The problematic status of *M. knoxii perquensis* in southern Namibia, and possible genetic divergence between the populations in the western Little Karoo and west coast region require assessment.

***Nucras*** Gray 1838**Taxa:** Total: 9                      South Africa: 9                      Undescribed: 1 + 2?**Last generic revision:** Broadley 1972 (part).**Other taxonomic studies:** Jacobsen 1990; Branch & Bauer 1995.**Current studies:** None.**Remaining taxonomic problems:**

In addition to a molecular phylogeny of genus, the following specific problems need to be addressed:

- Status of *N. tessellata* varieties (*elegans*, Var 'T', etc; Broadley 1972).
- Status of the elongate *Nucras* recently discovered from the West coast (Mouton & Turner).
- Status of *N. holubi* isolate in northern Namibia.
- Status of *N. lalandei* isolates along the southern Cape coast (Agulhas, Mossel Bay) and along the northern escarpment.

***Pedioplanis*** Fitzinger 1843**Taxa:** Total: 12                      South Africa: 6                      Undescribed: 2 + 2–3?**Last generic revision:** None.**Other taxonomic studies:** Mayer & Berger-Dell'mour 1987; Berger-Dell'mour & Mayer 1989; Arnold 1991.**Current studies:**

The following problems are currently being assessed:

- Phylogeny for *Pedioplanis* is nearly completed (Makokha *et al.*).
- Phylogeography of *P. burchelli* has detected six clades (Makokha 2006); the status of these clades and their relationship(s) to *P. laticeps* require assessment.
- Presence of new taxa within *P. inornata*, *P. namaquensis* and *P. lineoocellata* (Makokha *et al.*).

**Remaining taxonomic problems:**

- Status of *P. l. pulchella* and Spergebeit isolates (Groblershoek: 2–3 taxa under *lineoocellata*).





**Tropidosaura** Fitzinger 1826

**Taxa:** Total: 4 South Africa: 4 Undescribed: 1?

**Last generic revision:** FitzSimons 1943.

**Other taxonomic studies:** Arnold 1989; Harris *et al.* 1998.

**Current studies:**

The following problems are currently being assessed (Branch & Cunningham, ongoing):

- Morphological revision of the genus and a molecular phylogeny.
- Phylogeography of montane isolates.
- Status of the races of *T. montana* and their relationship to *T. essexi*.

**Remaining taxonomic problems:**

- Availability and status of *T. burchelli* A. Smith 1849.

**FAMILY: SCINCIDAE**

**Acontias** Cuvier 1817

**Taxa:** Total: 10 South Africa: 9 Undescribed: 1 + 1-2?

**Last generic revision:** Broadley & Greer 1969.

**Other taxonomic studies:** Daniels *et al.* 2002, 2005.

**Current studies:**

The following problems are currently being assessed (Daniels *et al.* in preparation):

- Generic status of the two deep clades of small and large bodied forms.
- Status of isolates and races of *A. breviceps*, *lineatus* and *gracilicauda*.
- Status of *A. tasmani* and *A. orientalis*.
- Status of *A. percivali* isolates.

**Remaining taxonomic problems:**

- Status of the brown phase of *A. plumbeus* in Maputaland, and the southern (E. Cape) isolate of *A. plumbeus*.

**Typhlosaurus** Weigmann 1834

**Taxa:** Total: 9 South Africa: 8 Undescribed: 1 + 1?

**Last generic revision:** Broadley 1968.

**Other taxonomic studies:** Haacke 1986; Jacobsen 1987a; Broadley 1990a; Bates *et al.* 1998; Bauer *et al.* 2000.

**Current studies:**

The following problems are currently being assessed (Bauer *et al.*, in preparation):

- Phylogeny of *Typhlosaurus* has been completed (Lamb & Bauer).
- Elevation of *T. lineatus jappi* to a full species (Schneider & Bauer, in preparation).
- Status of isolates and races of *T. lineatus* and *T. cregoi*, and the insular races of *T. aurantiacus*.

**Remaining taxonomic problems: None.**

**Scelotes** Fitzinger 1826

**Taxa:** Total: 20 South Africa: 18 Undescribed: 2-3?

**Last generic revision:** De Witte & Laurent 1943.

**Other taxonomic studies:** Jacobsen 1987b; Broadley 1994; Whiting *et al.* 2003; Bauer *et al.* 2003.

**Current studies:**

- A phylogenetic investigation of African skinks (Whiting, Bauer & Branch) that addresses the monophyly of scincines, and some of the issues below.

**Remaining taxonomic problems:**

- Status of isolates of *S. caffer*.
- Status of races of *S. limpopoensis*.
- Status of southern Cape sand relicts.



**Typhlacontias** Bocage 1873**Taxa:** Total: 4 South Africa: 0 Undescribed: 1 + ?**Last generic revision:** Haacke 1997.**Other taxonomic studies:** Haacke 1964; Whiting *et al.* 2003.**Current studies:**

- Phylogeny and relationships to *Feylinia* (Whiting, Bauer, Branch).
- Description of a new species from Zambia (Broadley in preparation).

**Remaining taxonomic problems:**

- Status of isolates of *T. brevipes*.

**Panaspis** Cope 1868**Taxa:** Total: 2 South Africa: 2 Undescribed: 1?**Last generic revision:** None**Other taxonomic studies:** Broadley 1989; Jacobsen & Broadley 2000.**Current studies:** None.**Remaining taxonomic problems:**

- The status of the northern Namibian population currently assigned to *P. wahlbergii* requires assessment.

**Trachylepis** Fitzinger 1843**Taxa:** Total: 24 South Africa: 14 Undescribed: 1 + ?**Last generic revision:** None.**Other taxonomic studies:** Broadley 1960, 1969, 1974a, 1975a, 1977c, 2000; Broadley & Bauer 1999; Greer & Broadley 2000; Bauer 2003.**Current studies:**

- A broad phylogenetic investigation of African skinks (Whiting, Bauer, Branch) will also address some of the issues below.

**Remaining taxonomic problems:**

- Status of Transvaal *T. 'varia'* (Jacobsen 1990).
- Status of *T. homalocephala* races (*peringueyi*, *smithii*) and phylogeography of escarpment isolates.
- Status of the Namibian races of *T. sulcata*.
- Status of *T. variegata punctulata* and northern and western isolates.
- Status of *T. capensis* isolates.
- Generic status of *Trachylepis laevis*.

**FAMILY: CORDYLIDAE****Chamaesaura** Schneider 1801**Taxa:** Total: 3 South Africa: 3 Undescribed: ?**Last generic revision:** FitzSimons 1943; Loveridge 1944.**Other taxonomic studies:** Frost *et al.* 2001.**Current studies:** None.**Remaining taxonomic problems:**

- Status of the escarpment and Central African isolates of *C. anguina* and *C. macrolepis*.

**Cordylus** Laurenti 1768**Taxa:** Total: 30 South Africa: 21 Undescribed: 2 + 2-3 ?**Last generic revision:** FitzSimons 1943; Loveridge 1944.**Other taxonomic studies:** Mouton & van Wyk 1989, 1990, 1994; Frost *et al.* 2001.**Current studies:**

- A broad phylogenetic investigation of the Cordylidae (Whiting, Bauer, Mouton, Branch) will also address some of the issues below.



- Description of two new species in the *C. olefseni* complex and investigation of two other isolated populations (Mouton *et al.*).
- A revision of the *Cordylus warreni* complex (Bates & Cunningham; morphology and genetics).
- A revision of *Cordylus vittifer* (Bates & Cunningham; morphology and genetics).

**Remaining taxonomic problems:**

- Status of *C. cordylus* isolates.
- Phylogeography of *C. polyzonus*.
- Status of west coast melanistic *C. polyzonus* populations.
- Status of *C. minor* populations.
- Status of the *C. coeruleopunctatus* isolate in the Langeberg (Garcia Pass).

***Pseudocordylus*** A. Smith 1838

**Taxa:** Total: 8                      South Africa: 8                      Undescribed: 1 + 1-2?

**Last generic revision:** Loveridge 1944.

**Other taxonomic studies:** Broadley 1974b; Mouton & van Wyk 1995; Bates 2006.

**Current studies:**

- A detailed revision of the *P. melanotus* complex has been completed; the northern-most population of '*P. m. melanotus*' has been identified as a new species (Bates 2006).
- *Pseudocordylus* is paraphyletic and nested within *Cordylus* (Frost *et al.* 2001). An expanded molecular phylogeny of the family will allow resolution of the affinities (and thus naming) of the different *Pseudocordylus* clades (Whiting *et al.*).
- The taxonomy (Cunningham & Bates) and phylogeography (Cunningham) of the races of *P. microlepidotus* are being investigated.

**Remaining taxonomic problems:**

- Taxonomic status of the *P. capensis-robertsi* complex.

***Platysaurus*** A. Smith 1844

**Taxa:** Total: 13                      South Africa: 9                      Undescribed: 2-3 ?

**Last generic revision:** Broadley 1978.

**Other taxonomic studies:** Broadley 1974a, 1976; Jacobsen 1994b; Branch & Whiting 1997; Scott *et al.* 2003.

**Current studies:**

- Expanded molecular phylogenies of the genus (Keogh *et al.*) and family (Whiting *et al.*) are in preparation, and will address some of the problems below.

**Remaining taxonomic problems:**

- Status of the races of *P. intermedius*, *P. orientalis*, *P. pungweensis*, etc.

**FAMILY: GERRHOSAURIDAE**

***Gerrhosaurus*** Gray 1865

**Taxa:** Total: 7                      South Africa: 5                      Undescribed: 1 ?

**Last generic revision:** Loveridge 1942.

**Other taxonomic studies:** FitzSimons 1943; Broadley 1986; Lamb *et al.* 2003; Locketto 2002.

**Current studies:**

- The taxonomic status of *G. multilineatus* races is under review (Broadley).

**Remaining taxonomic problems:**

- Taxonomic status of *G. validus maltzahni*.

***Tetradactylus*** Merrem 1820

**Taxa:** Total: 5                      South Africa: 5                      Undescribed: ?

**Last generic revision:** Loveridge 1942.

**Other taxonomic studies:** Berger-Dell'mour 1985; Branch 1990b; Bates 1996; Lamb *et al.* 2003; Salvidio *et al.* 2004.





**Current studies:**

- Validation of *T. fitzsimonsi* as a full species, and its relationship to *T. africanus* and *T. boulengeri* from DCR (Branch).
- A morphological analysis of the genus (Bates).

**Remaining taxonomic problems:**

- A molecular phylogeny is required, including an assessment of *Paratetradactylus*.
- Status of isolates of *T. seps* (*laevicauda*) and *T. tetradactylus* (*bilineatus*) in the Eastern Cape (Branch 1990b) should be re-assessed.

**FAMILY: AMPHISBAENIDAE*****Chirindia*** Boulenger 1907**Taxa:** Total: 2                  South Africa: 1                  Undescribed: 1?**Last generic revision:** Loveridge 1941.**Other taxonomic studies:** Broadley & Gans 1978a; Jacobsen 1984.**Current studies:** None.**Remaining taxonomic problems:**

- Taxonomic status of *C. langi occidentalis*.

***Monopeltis*** A. Smith 1848**Taxa:** Total: 8                  South Africa: 5                  Undescribed: 1?**Last generic revision:** Loveridge 1941.**Other taxonomic studies:** Gans & Broadley 1974; Broadley, Gans & Visser 1976; Broadley 1997b; Gans 2005.**Current studies:** None.**Remaining taxonomic problems:**

- Status of *M. sphenorhynchus* races.
- Status of *M. infuscata* (Bates).

***Zygaspis*** Cope 1885**Taxa:** Total: 5                  South Africa: 2                  Undescribed: 1?**Last generic revision:** Loveridge 1941.**Other taxonomic studies:** Broadley & Gans 1969, 1978b; Broadley & Broadley 1997.**Current studies:** None.**Remaining taxonomic problems:**

- A molecular phylogeny of the small African amphisbaenians is required.
- Taxonomic status of *Z. vandami* races.

**SUBORDER: SERPENTES****INFRAORDER: SCOLECOPHIDIA****FAMILY: TYPHLOPIDAE****SUBFAMILY: TYPHLOPINAE*****Rhinotyphlops*** Fitzinger 1843**Taxa:** Total: 5                  South Africa: 4                  Undescribed: ?**Last generic revision:** Roux-Esteve 1974.**Other taxonomic studies:** Broadley & Wallach 2000.**Current studies:**

- The monophyly and generic status of African typhlopids is under review (Wallach & Broadley in preparation).

**Remaining taxonomic problems:**

- The taxonomic status of the central Namibian population of *R. lalandei* should be assessed.







**Typhlops** Oppel 1811

**Taxa:** Total: 2 South Africa: 2 Undescribed: ?

**Last generic revision:** Roux-Esteve 1974.

**Other taxonomic studies:** Broadley & Wallach 2000.

**Current studies:**

- The monophyly and generic status of African typhlopids is under review (Wallach & Broadley in preparation).

**Remaining taxonomic problems:**

- The taxonomic status of the eastern Zimbabwe *T. bibronii* isolate should be assessed.

**FAMILY: LEPTOTYPHLOPIDAE**

**Leptotyphlops** Fitzinger 1843

**Taxa:** Total: 12 South Africa: 9 Undescribed: ?

**Last generic revision:** No pan-African revision.

**Other taxonomic studies:** Broadley & Watson 1976; Broadley & Wallach 1996; Broadley & Wallach 1997; Broadley & Broadley 1999.

**Current studies:** None.

**Remaining taxonomic problems:**

- A phylogeny of African species and relationships to New World populations is required.
- The taxonomic status of *L. conjunctus-incognitus* complex.
- The taxonomic status of *L. sylvicolous* forest isolates.
- The relationship of *L. nigricans-jacobseni* complex.

**CAENOPHIDIA**

**FAMILY: ATRACTASPIDIDAE**

**Amblyodipsas** Peters 1849

**Taxa:** Total: 4 South Africa: 3 Undescribed: 1 ?

**Last generic revision:** Broadley 1971.

**Other taxonomic studies:** Jacobsen 1986.

**Current studies:** None.

**Remaining taxonomic problems:**

- Status of *A. microphthalma nigra*.

**Xenocalamus** Günther 1868

**Taxa:** Total: 5 South Africa: 3 Undescribed: ?

**Last generic revision:** Broadley 1971a.

**Other taxonomic studies:** Bates 1991.

**Current studies:** None.

**Remaining taxonomic problems:**

- Status of *X. bicolor* races.

**Homoroselaps** Jan 1858

**Taxa:** Total: 2 South Africa: 2 Undescribed: ?

**Last generic revision:** None.

**Other taxonomic studies:** None.

**Current studies:**

- Geographical variation in *H. lacteus* and its taxonomic status (Branch).

**Remaining taxonomic problems:** None.

**FAMILY: COLUBRIDAE (sensu lato)**

**Lamprophis** Fitzinger 1843

**Taxa:** Total: 6 South Africa: 6 Undescribed: 1?

**Last generic revision:** Pan-African, none; southern African, Broadley 1990.

**Other taxonomic studies:** Roux-Estève & Guibe 1965; Thorpe & McCarthy 1978; Hughes 1997.

**Current studies:**

- Description of new genus for *swazicus* (Kelly and Branch).
- Status of *L. capensis-mentalis* (Kelly).
- A molecular phylogeny of the genus and related genera (Kelly).

**Remaining taxonomic problems:**

- Status of *L. guttatus* populations.

***Lycodonomorphus*** Fitzinger 1843

**Taxa:** Total: 4                      South Africa: 3                      Undescribed: 1 ?

**Last generic revision:** Loveridge 1958.

**Other taxonomic studies:** Broadley 1967b; Raw 1973; Haagner & Branch 1994.

**Current studies:**

- Phylogeny and monophyly of *Lycodonomorphus* (Kelly).

**Remaining taxonomic problems:**

- Status of isolated populations of *L. rufulus* and *L. obscuriventris*.
- Status of *L. laevissimus* races and populations from different drainage systems.

***Philothamnus*** A. Smith 1847

**Taxa:** Total: 5                      South Africa: 4                      Undescribed: 1 + ?

**Last generic revision:** Loveridge 1958.

**Other taxonomic studies:** Broadley 1959, 1966a; Hughes 1985.

**Current studies:** None.

**Remaining taxonomic problems:**

- Status of *P. natalensis occidentalis*.
- Status of western arid population of *P. semivariatus*.

***Telescopus*** Wagler 1830

**Taxa:** Total: 2                      South Africa: 2                      Undescribed: 1 + ?

**Last generic revision:** Pan-African, none.

**Other taxonomic studies:** None.

**Current studies:**

- Description of new Namibian species (Haacke).

**Remaining taxonomic problems:**

- Status of *T. semiannulatus polystictus*.

***Dispholidus*** Duvernoy 1832

**Taxa:** Total: 1                      South Africa: 1                      Undescribed: 1 ?

**Last generic revision:** Laurent 1952; Broadley & Wallach 2002.

**Other taxonomic studies:** None.

**Current studies:**

- Status of Cape population (Broadley *et al.*).

**Remaining taxonomic problems:**

- Relationship of southern African populations to northern races (Laurent 1952).

***Psammophis*** Boie 1825

**Taxa:** Total: 13                      South Africa: 11                      Undescribed: 1 + ?

**Last generic revision:** Brändstatter 1995, 1996; southern Africa, Broadley 2002.

**Other taxonomic studies:** Broadley 1966, 1975b, 1977d, 2002; Hughes 1999; Kelly 2005.

**Current studies:**

- A molecular phylogeny of the Psammophinae has been completed (Kelly).



- Genetic divergence within the *P. mossambicus-philippsi* complex has been studied and shown to be in conflict with the current taxonomic arrangement (Kelly).
- Molecular divergence between taxa within the *P. leightoni* complex (Kelly) is in conflict with their recent elevation to full species (Broadley 2002).

**Remaining taxonomic problems:**

- A possible high-altitude cryptic species of *P. crucifer* has been discovered (Branch).

***Prosymna*** Gray 1849

**Taxa:** Total: 8                      South Africa: 6                      Undescribed: ?

**Last generic revision:** Broadley 1980.

**Other taxonomic studies:** Broadley 1965, 1995.

**Current studies:**

- Phylogeny and phylogenetic relationships (Banach & Bauer).

**Remaining taxonomic problems:**

- Status of isolated populations of *sundevallii* and *bivittata* in western arid region.

**FAMILY: ELAPIDAE**

***Aspidelaps*** A. Smith 1849

**Taxa:** Total: 2                      South Africa: 2                      Undescribed: ?

**Last generic revision:** Broadley & Baldwin 2006.

**Other taxonomic studies:** Broadley 1968b.

**Current studies:** None.

**Remaining taxonomic problems:**

- Both *A. scutatus* and *A. lubricus* have extensive ranges with races of problematic status that would benefit from molecular studies (Broadley & Baldwin 2006).

***Elapsoidea*** Bocage 1866

**Taxa:** Total: 4                      South Africa: 3                      Undescribed: ?

**Last generic revision:** Broadley 1971b.

**Other taxonomic studies:** Broadley 1998.

**Current studies:** None.

**Remaining taxonomic problems:**

- Status of *E. sundevallii* races.

***Hemachatus*** Fleming 1822

**Taxa:** Total: 1                      South Africa: 1                      Undescribed: ?

**Last generic revision:** None.

**Other taxonomic studies:** None.

**Current studies:** None.

**Remaining taxonomic problems:**

- The taxonomic status of striped populations in the Western and Eastern Cape provinces, Kwa-Zulu-Natal and Zimbabwe.
- The uniform, large Highveld form.

***Naja*** Laurenti 1768

**Taxa:** Total: 7                      South Africa: 5                      Undescribed: ?

**Last generic revision:** Broadley 1968a

**Other taxonomic studies:** Broadley 1974b, 1995; Wüster & Broadley 2003.

**Current studies:**

- Revision of African spitting cobras (Wüster, Broadley *et al.*).
- Revision of *N. melanoleuca* complex (Wüster, Broadley *et al.*).

**Remaining taxonomic problems:** None.





**FAMILY: VIPERIDAE****Bitis** Gray 1842**Taxa:** Total: 12 South Africa: 11 Undescribed: 1–3?**Last generic revision:** None.**Other taxonomic studies:** Haacke 1975; Branch 1999b.**Current studies:**

- Taxonomic status of De Hell population of *B. rubida* (Branch).
- Taxonomic status of *B. atropos* isolates (Branch).

**Remaining taxonomic problems:**

- Phylogeography of *B. caudalis* and *B. arietans*.
- Taxonomic status of *B. peringueyi* populations from northern and southern dune seas.
- Phylogeny of genus.
- Applicability of *Calaechidna* for southern dwarf species.

**ORDER: CHELONIA****SUBORDER: CRYPTODIRA****FAMILY: TESTUDINIDAE****Homopus** Dumeril & Bibron 1835**Taxa:** Total: 5 South Africa: 4 Undescribed: ?**Last generic revision:** Loveridge & Williams 1957.**Other taxonomic studies:** Cooper & Boycott 1990; Branch 1992.**Current studies:**

- Description of new Namibian species (*'bergeri'*) (Branch 2006, submitted).
- Phylogeography of *H. areolatus* (Daniels, Hofmeyr).

**Remaining taxonomic problems:**

- Phylogeography of *H. femoralis*.
- Phylogeny and generic division.

**Psammobates** Fitzinger 1835**Taxa:** Total: 3 South Africa: 3 Undescribed: ?**Last generic revision:** Loveridge & Williams 1957.**Other taxonomic studies:** Broadley 1997a,b.**Current studies:** None.**Remaining taxonomic problems:**

- Status of *P. tentorius* races (Daniels, Hofmeyr, Branch).

**SUBORDER: PLEURODIRA****FAMILY: PELOMEDUSIDAE****SUBFAMILY: PELOMEDUSINAE****Pelomedusa** Wagler 1830**Taxa:** Total: 1 South Africa: 1 Undescribed: ?**Last generic revision:** Loveridge 1941.**Other taxonomic studies:** Bour 1982.**Current studies:** None.**Remaining taxonomic problems:**

- Status of *P. olivacea* and *P. nigra* (Bour 1982).



## CHAPTER 2 Taxonomic units relevant to conservation planning



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### Species as the units of conservation concern

A crucial component of any conservation assessment is the establishment of a consensus as to what lineage within the hierarchically structured genealogy of a given taxon constitutes the minimally relevant conservation unit. Although it is often the case that one or more infraspecific lineages (populations, demes, etc.) may be of regional conservation concern because of localised threats and/or vulnerability due to isolation, there are several reasons for considering the described species, rather than any less-inclusive clades, as the units of conservation concern with respect to the reptiles of South Africa.

In the discipline of herpetology, the rank category of subspecies has never been employed as extensively as it has in other fields, such as ornithology. Indeed, there has been a near uniform rejection of the subspecies in modern herpetology as a result of arguments that most or all of the previously described subspecies represent either 'pattern classes' (groups identified by their common possession of superficial features) that do not reflect evolutionary units, or valid species as recognised by either of the two dominant species concepts employed by herpetologists (see below; Frost *et al.* 1992; Grismer *et al.* 1994; Grismer 1999). From a pragmatic viewpoint, unnamed infraspecific lineages, i.e. those identified by phylogenetic analysis but not formally described, are difficult to manage because their spatial limits are often vague and because conservation-relevant legislation must be based on names that are uniformly recognised and applied by the scientific community to unambiguously identifiable units of evolutionary significance.

### Species concepts and species delimitation

How then should species be delimited, and what is the relationship between genetic studies and the alpha taxonomy of the organisms concerned? There has been much recent

interest in the topic of species delimitation and its relationship to species concepts (Wiens & Servedio 2000; Brown & Diesmos 2001; Wiens & Penkrot 2002; Ferguson 2002; Hebert *et al.* 2003; Sites & Marshall 2003, 2004; Blaxter 2004; Watson 2005). The dominant species concepts employed in herpetology today are lineage-based (Frost & Hillis 1990; Mayden 1997; de Queiroz 1998) in that they focus on species as historical entities or evolutionary units. Although numerous iterations of such species concepts have been proposed, the two best-known and most often employed are the evolutionary species concept and the phylogenetic species concept. An evolutionary species is 'a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate' (Wiley 1981), whereas a phylogenetic species is 'a ... cluster of organisms that is diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent' (Cracraft 1989).

In practice, we are chiefly concerned not as much with the species concepts themselves, but with the properties that such lineages express and that permit us to infer species boundaries (Otte & Endler 1989; Ereshefsky 1992; Howard & Berlocher 1998; Watson 2005). A variety of operational criteria for identifying species boundaries have been proposed (Sites & Marshall 2003, 2004). Such criteria may be either tree-based or character-based. Tree-based criteria identify taxa as separate lineages (branches) on phylogenetic trees, generated from genetic or other data sets. Character-based criteria rely on the identification of synapomorphies—usually morphological—that are indicative or diagnostic of independently evolving lineages (Wiens & Penkrot 2002). Although the correspondence is not exact, these two categories of criteria may be regarded as compatible with the evolutionary and phylogenetic species concepts, respectively.

Wiens and Penkrot (2002) found significant discordance between tree- and character-based methods in their analysis of North American phrynosomatid lizards of the genus *Sceloporus*. In such cases they favoured



the species limits suggested by data from mitochondrial DNA, arguing that some taxa exhibit high levels of within-species phenotypic variation and relatively low between-species differentiation, and that such circumstances represented a 'worst-case scenario' for morphologically based (character-based) species delimitation. In these cases, differentiation in haplotype (lineage sorting) may occur faster than in diagnostic morphological characters, providing a more accurate picture of lineage boundaries. However, numerous studies have found congruence between character-based and mtDNA tree-based approaches with respect to species boundaries (e.g. Hollingsworth 1998). We expect, therefore, that even morphologically conservative groups of South African reptiles will, upon careful study, yield diagnostic morphological features to support the recognition of their constituent species-level taxa.

### Relationship between tree- and character-based species delimitation

Ideally, DNA-sequence-derived, tree-based species delimitations and morphological character-based species delimitations should provide reciprocal illumination and, in combination, should yield the most robust hypotheses on species boundaries. Phylogenetic studies based on mitochondrial and, when possible, nuclear DNA sequence data, should be used to generate trees depicting nested sets of lineages. All lineages that are not, at this moment, engaged in reproduction, immigration or emigration with respect to other lineages, may be considered independently evolving units under some version of the evolutionary species concept.

Clearly, taken to its extreme, this interpretation reduces to absurdity, as all branches in a phylogenetic tree could be thought of as at least incipient species. Unfortunately, there are no precise guidelines for identifying the amount of genetic differentiation indicative of specific status. In practice, comparisons may be made with the minimum differentiation of sequence divergence for a given gene between currently recognised, morphologically distinct sister species within the genus/clade of interest. However, such points of reference may be lacking in the case of groups that include cryptic taxa which have yet to be taxonomically evaluated, as is presumed to be the case for a number of the South African reptile taxa of high priority for genetic study. Furthermore, such comparisons must be limited to variation in the same portion of the same gene. Even then, in the

case of mitochondrial DNA, the patterns generated by a single gene may result in a gene tree that differs from the true species tree.

The erection of one or more trees (= hypotheses of relationships) is the goal of phylogenetics, and to the extent that the assumptions of methods of tree building and optimisation are met, this systematic procedure may be viewed as relatively objective. Such hypotheses are also testable through the addition of more data. However, phylogenetic data are not automatically translatable into statements about species boundaries and therefore cannot, alone, identify the units of conservation concern.

Phylogenetic or phylogeographic study has to be paired with taxonomic study in order to provide a rational basis for the recognition of certain identified clades as species. In particular, such taxonomic work will identify the diagnosable features that constitute character-based criteria for specific recognition. This work, which is typically morphological, uses the taxonomist's particular knowledge of a group to identify the characters and degree of differentiation that, in the light of intra- and interspecific variation, are likely to be indicative of lineage independence. The taxonomist's knowledge base also includes the nomenclatural history of the group under study, permitting the correct application of names to the entities revealed through the combination of tree- and character-based approaches to species delimitation. Although distribution patterns alone should not be used in constructing hypotheses of species boundaries, geographic concordance (as reflected by allopatry) with both the tree- and character-based species limits, is generally indicative of lineage independence and, therefore, corroborative of the taxonomic decisions based on tree- and character-based delimitations (Bergmann & Russell 2006). This points to the relevance of the SARCA database in helping to resolve taxonomic issues.

### Recommendations

We propose a pluralistic procedure—the combination of molecular phylogenetics and morphology-based systematic approaches, corroborated by other data (e.g. geographic or ecological) where possible—for the establishment of a stable alpha-level taxonomy for the reptiles of South Africa. The evolutionary lineages detected by the phylogenetic analysis of genetic data should be studied in an informed taxonomic context that would permit the recognition of diagnosable species which could be used as the basis for meaningful conservation





assessment. Infra-specific clades (populations, demes, etc.) may be of legitimate conservation concern at a local or regional level. Information about such threatened or vulnerable units should be included in conservation assessments, although not prioritised at a national level. As the subspecific rank is not generally considered to reflect evolutionary history, subspecies among South African reptiles should be seen as evidence that further phylogenetic and/or taxonomic research is required.

Currently, within the South African herpetological community, there are a small number of herpetologists who are trained in molecular phylogenetics and/or phylogeography, and who can identify independently evolving lineages. However, there is an even more acute lack of trained taxonomists who can competently deal with the character-based aspects of the problem of species recognition and the resulting nomenclatural issues. Therefore, we advocate that molecular systematists should partner with reptile taxonomists who can identify chiefly morphological diagnostic features and who have the knowledge base to describe new taxa formally, placing them in the context of existing taxonomic literature and ensuring that scientific names are correctly applied.

Only in this combination can genetic data be 'translated' into a format that can be easily understood and employed by the various users of biodiversity data. Though such a combination of areas of expertise provides a short-term solution to the most pressing issues in South African reptile alpha taxonomy, it will ultimately be necessary to build national capacity by training museum staff, molecular systematists and others, in taxonomic procedure. To this end, it is recommended that an initial workshop on practical taxonomy and nomenclature should be held in conjunction with the Herpetological Association of Africa meeting in November 2006.

## Summary

- Species are the units relevant to conservation planning.
- Intraspecific units may be important on a local or regional scale.
- Subspecies are typically not used in herpetology; their use reflects insufficient systematic data.
- Species concepts in herpetology are lineage-based.
- Species delimitation involves the identifica-

tion of independent lineages (tree-based approaches) and the identification of the diagnostic features of such lineages (character-based approaches).

- Genetic approaches alone can identify lineages but are usually not sufficient to determine which clades or lineages should be recognised as species.
- Genetic approaches should be combined with morphologically based systematic approaches to stabilise the alpha taxonomy of South African reptiles.
- Molecular systematists should partner with taxonomists to generate results that would be useful to the consumers of biodiversity data.
- Taxonomic training is a necessary capacity-building step for progress in the systematics and conservation of reptiles in South Africa.
- It is recommended that a workshop on practical taxonomy and nomenclature in herpetology should be convened in November 2006.

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## CHAPTER 3 Mismatches between morphology and genetics

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There are cases where there is an apparent mismatch between the results of morphological and genetic analyses. This discussion offers possible solutions to these cases of discord.

In most instances, when morphological and genetic measures are compared, there is a high degree of congruence in the delineation of taxa, and the relationships between these taxa. However, there are other cases where the results of genetic measures differ substantively from the results of morphological analyses. In fact, there may be little association between molecular rates of change and morphological rates of change (Bromham *et al.* 2002). There are four possible scenarios for the relationship between these two types of data:

1. *High morphological resolution but low genetic resolution*: although taxa appear to be phenotypically well-defined, there is little or no detectable differentiation in the analysed genes. This may result from several possible causes, including phenotypic plasticity or rapid morphological divergence owing to strong selective pressures. Taxa that show morphological divergence, but have no apparent genetic divergence, are most appropriately termed morphotypes.
2. *Low morphological resolution but high genetic resolution*: here genetic isolation results in genetic differentiation, but these differences are not reflected in the phenotype. Taxa that are genetically well-defined but morphologically indistinguishable are referred to as cryptic species.
3. *High levels of morphological and genetic resolution, with low levels of concordance between the two data streams*: the boundaries of morphologically well-defined taxa may not agree with those of genetically defined taxa. This situation may arise as a result of the use of inappropriate morphological characters (e.g. characters may be analogous).

4. *High levels of morphological and genetic resolution with high levels of concordance*: the taxa are well-defined and the boundaries defined by morphology and genetics are in agreement. This is an ideal situation since the phenotype can be used to identify genetically delineated taxa in the field.

Of the categories listed above, the fourth is the most common. However, clades within certain taxa may show characteristics of scenarios 1 to 3. Where there is discord between morphology and genetics, which of the data streams should carry more weight? The workshop delegates strongly supported the idea that there is no requirement for the phenotypes of two species to be distinguishable. There are many examples, worldwide, of taxa that have been genetically isolated for long periods of time—usually, but not necessarily, through geographic isolation—that are genetically well-defined, but nevertheless morphologically indistinguishable. The delegates were of the opinion that, if such genetic differentiation made geographic sense, i.e. the genetically defined clades map on the ground in a nonrandom pattern, then the taxa should be defined as good, albeit cryptic, species.

In this regard, the dwarf chameleons of the genus *Bradypodion* are noteworthy as they often show strong and complex discord between genetic and morphological patterns. Several other clades are likely to show similar discordance, e.g. *Acontias*, *Bitis*, *Leptotyphlops* and *Pedioplanis*. In fact, there appear to be instances where scenarios 1 and 2 apply variously to different clades within a genus. For example, the obvious morphological differences between *Bradypodion melanocephalum* and *B. thamnobates* are not supported by any measured genetic divergence (scenario 1), whereas the populations of *B. damaranum* in the Grootvadersbosch Nature Reserve, Langeberg Mountains, closely resemble those in Knysna Forest to the east, but are different genetically (scenario 2). There are several possible explanations for these apparent mismatches:

- *B. melanocephalum* and *B. thamnobates* occur in different habitats. Morphological differences may represent little more than



the expression of phenotypic plasticity, or conversely, rapid morphological diversification. This hypothesis is eminently testable using a 'swapping' experimental protocol, or by raising young from the two species under the two different types of environmental conditions.

- Current sampling regimes may simply be inadequate, so that patterns of genetic variation are not detected. This could be remedied with the collection and analysis of more specimens.
- The genetic markers used may not provide sufficient resolution for the problem at hand. Though there is a suite of acceptable markers which suffice for detecting lineages that have undergone historical separation, recently diverged lineages may require additional, more sensitive markers.
- Reticulation in the evolutionary history of any of the *Bradypodion* clades may have resulted in a mismatch between the pattern shown by certain genes and certain morphological traits. The relative importance of reticulation could be teased out by using the sequences of several nuclear genes for the construction of phylogenies, or by sequencing linked genes (e.g. mitochondrial genes). Reticulation should result in discordance between the patterns shown in various gene sequences, and may reveal concordance between certain genes and phenotypic characteristics.
- Apparent differences in morphology may be due, in part, to bias in the sampling regime. For example, the individuals of some forest species of *Bradypodion* are difficult to collect when they are perched high in the canopy. However, juveniles appear to be more likely to move out of forest patches into surrounding ecotones, where they are relatively low to the ground, easily observed and therefore easily collected. Certain populations may be diagnosed as being morphologically distinct because all the specimens collected from one population are juveniles. This source of bias can be overcome by careful measurement of the ecology and life history of *Bradypodion* species. Similar sampling biases are likely to hold for other taxonomic groups.
- *B. damaranum* populations have been separated for a considerable time and have drifted apart genetically, but the lack of habitat differences has resulted in morphological stasis.

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## CHAPTER 4 Methods, techniques and protocols for phylogenetic studies on southern African reptiles

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The purpose of this discussion is to outline basic technical approaches for the molecular systematics of South African reptiles, with special attention to issues arising from SARCA (Southern African Reptile Conservation Assessment). We specifically address the collection and storage of tissue samples for genetic analysis, and the laboratory approaches and analytical methods that will provide data of suitable resolution.

### Phylogeny and taxonomy

A broader aim in this research programme is to integrate molecular phylogenetic studies with taxonomy. The initial intent of these studies is to identify and describe species lineages, and secondly, to infer relationships among these lineages in order to understand their distribution and evolution, and thereby make a contribution to taxonomy and conservation. As a policy, the phylogeneticist should be prepared either to carry out morphological descriptive work, or to enlist the collaboration of taxonomists. The benefit of this approach is that it links phylogenetic studies with the naming of the actual entities used in conservation, land-use planning and legislation, and thereby extends the impact of these studies beyond transitory scientific publications. A further requirement for this linkage is that each phylogenetic lineage must be associated with sequenced voucher specimens, with accurate collection details cross-referenced in both genetic and taxonomic databases.

### Collection methods and preservation

In most lizards and other reptiles, tail tips provide suitable tissue for DNA extraction. In some cases, tail clipping destroys or renders

useless taxonomically important morphological features (e.g. subcaudal scales in snakes and legless lizards, such as *Acontias*). For these taxa, liver tissue or scale clips can be sampled, before fixing specimens in formalin. Tissue samples should be preserved in 96% ethanol, in pre-numbered 1.5–2.0ml lock-top or gasket-top tubes. For small species (e.g. *Leptotyphlops*), the entire specimen should be stored in 80% alcohol. Our strategy of collecting small tissue samples in the field is preferable to the preservation of whole specimens in alcohol, because the latter approach gives lower DNA yields and may reduce specimen quality. Care should be taken not to overload the ethanol preservative with tissue, as this can result in incomplete preservation and the degradation of DNA. The size of the sample should not exceed 10% of the volume of preservative in the tube.

Tubes should be labelled both with marker pen on the tube lid, and with a numbered label inside the tube. Particular care should be taken to avoid spillage of alcohol over the external label and leakage of ink into the tube. Tubes carrying samples should be kept separately from fresh tubes.

### Storage and curation

DNA tissue samples collected for SARCA will be stored for the short term (i.e. for the next five years) at the Molecular Systematics Laboratory facility at the South African National Biodiversity Institute (SANBI), Kirstenbosch Research Centre, Cape Town. Tissue samples will be placed in fresh 96% ethanol (with an air lock in each tube), given an additional printed tape label around the tube, and housed in a minus-40 °C chest freezer. This freezer will be provided by SANBI, pending a proposal and final approval from the Executive Committee for its purchase. Sample tubes will be placed in DNA sample boxes ( $\pm$  70 tubes per box) which are labelled with the sample numbers. These sample numbers will be cross-referenced to specimen data within the SARCA tissue sample database (see below). Boxes will be organised into removable tower units for easy access. Tower units will be labelled with the box numbers.

Subsamples of tissues in the reptile tissue bank (see database section) will be freely



available to SARCA co-investigators and collaborators for a period of five years (2007–2011). These parties will not be charged any handling levy for accessing the tissues, but researchers will be expected to cover the cost of postage for shipping samples. A Memorandum of Understanding between SARCA and SANBI has to be drawn up to the satisfaction of both parties, detailing the daily administration of the tissue bank, the management and curation of the collection, and the management of the associated database (to be drafted by KAT). SANBI will take responsibility for the management of collections, with a portion of the Molecular Systematics Laboratory Manager's time to be directed to this duty.

After the initial five-year period, the tissue samples will be available to any interested party. In the interim, samples from nontarget groups may be requested by researchers not involved with SARCA. The distribution of such tissues will be monitored by the SARCA genetics task team, including the SANBI Molecular Systematics Laboratory Senior Scientist.

### Databasing

A reptile tissue database is to be set up at SANBI to house the records for SARCA tissue samples going into freezer storage. This database will be in Microsoft Access format and contain information about the field number, voucher specimen number and place of lodging, point locality, locality description, and the collector. Each tissue sample deposited in the animal tissue bank will also be assigned an accession number, and tissues will be stored sequentially in a minus-40°C freezer, according to accession number. Corresponding vouchers will be deposited at South African museums according to SARCA procedures for vouchering.

The database will be restricted to the SANBI Molecular Systematics Laboratory Senior Scientist, the SARCA Project Co-ordinator and Project Herpetologist, SARCA co-investigators and SARCA collaborators, for an initial five-year period (2007–2011). The database will be made available online (password-restricted) to these parties for the same duration. After five years, the database will be made publicly available, allowing other researchers to request tissues from the DNA bank. SANBI will take responsibility for the database, with a portion of the duties of the Molecular Systematics Laboratory Manager directed to entering data, managing the database and addressing the requests from SARCA project co-investigators and collaborators.

### Lab protocols

Laboratory protocols should follow established, standard techniques for DNA extraction, PCR and sequencing. The exact methods will vary according to taxon and according to laboratory. In many cases, kit extractions will be used (e.g. the Qiagen DNA tissue extraction kit) to produce high-quality, high-yield extracts which will provide enough DNA template for numerous amplifications. Alternative protocols are phenol-chloroform or Chelex extractions. PCR should follow the standard approaches that have been successfully used for reptiles (e.g. Lamb & Bauer 2003; Daniels *et al.* 2004; Tolley *et al.* 2006), and these protocols will vary according to the gene targeted. Temperature gradient machines, or adjustable ramp-time machines, are useful for the amplification of nuclear genes where slower ramping times may be needed for adequate strand extension. Big Dye cycle sequencing can be carried out in  $1/8$  standard reactions, and cost-saving  $1/16$  reactions could be used for more robust PCR amplifications. Fragment visualisation using automated sequencing machines will follow the differing procedures in the laboratories involved.

### Targeted genes

Many recent molecular systematic studies on reptiles (e.g. Macey *et al.* 1998; Townsend & Larson 2002) have adopted a standard set of gene fragments for the construction of phylogenetic trees including the full sequence of the mitochondrial protein-coding gene ND2, part of the mitochondrial large subunit ribosomal RNA gene, 16s (3' section) and part of the nuclear coding gene RAG-I. These genes complement one another by accessing the elevated substitution rates of mitochondrial DNA, the predictable pattern of molecular evolution at coding genes, and the structural stability of ribosomal genes. In addition, these genes access at least two independent paths of inheritance through the genealogy of each species: one for the mitochondrial genes inherited as a single nonrecombining unit, and at least one for RAG-1 which is encoded on a chromosome in the cell nucleus and is subject to recombination between homologous chromosomes with different histories. In combination, these gene fragments allow the identification of lineages and their systematic relationships across the range of time-scales and speciation rates encountered in most extant vertebrate genera or subgenera, and have proved a reliable suite of markers for phylogenetic studies (e.g. Tolley *et al.* 2004, 2006). We recommend that studies of reptiles in southern Africa should adopt





these three genes to produce sequence-data sets that could be compared with the existing DNA sequence data from reptiles.

All sequence data must be accessioned into the GenBank international DNA sequence database (<http://www.ncbi.nih.gov/>). To date, there are 38 778 squamate (lizards, snakes and amphisbaenians) sequences in the GenBank, including 2 829 from ND2, 3 927 from 16s and 112 RAG-I sequences, indicating the wealth of comparative background data available for these genes (figures for chelonians are 27 ND2, 276 16s, and 27 RAG-1 sequences). All other commonly sequenced fragments in squamates are mitochondrial DNA segments such as Cytochrome *b* with 6 641 entries, the small subunit RNA gene 12s with 4 039, or COI (Cytochrome Oxidase I), with 971 sequence entries. (These data were gathered from 'Entrez Nucleotide'—at the web page above—using search terms in the format: squamata[ORGN] AND ND2.)

Several authors have recently advocated the use of 'DNA barcodes' consisting of COI sequences to assign specimens to described taxa and to discover unrecognised species (Hebert *et al.* 2003; Hebert *et al.* 2004). Though we agree with the principle of using DNA sequences to assist in specimen identification and in discovering cryptic lineages, we do not believe that COI is the most appropriate gene for this purpose in amphibians and reptiles. Within vertebrates, COI has a similar rate of silent substitutions (changes that do not affect expression of the gene) to the other 12 mitochondrial protein-coding genes, including ND2, but COI has a more highly constrained amino-acid sequence, and therefore few expressed differences (Zardoya & Meyer 1996). In addition, as the sequences flanking COI are variable, this limits the potential for designing 'universal' primers for PCR amplification and sequencing. Consequently, there is a high rate of primer failure and new COI primers continually have to be designed to accommodate a broader taxonomic range and improved sampling within lineages.

These objections apply equally to the extensively sequenced Cytochrome *b* gene which has a highly conserved expressed sequence and considerable variation within flanking sequences. By contrast, ND2 has the highest frequency of expressed changes among mitochondrial genes (Zardoya & Meyer 1996) and this boosts information from the abundant silent substitutions. ND2 is flanked by several highly conserved tRNA genes (in particular

tRNA-Methionine, tMET and tRNA-Tryptophan, tTRP) which are well-suited to primer design. Similarly, the availability of the 'universal' primers, 16sar and 16sbr (Cunningham *et al.* 1992) allows the easy amplification of the 3' half of 16s across taxonomic classes and even phyla, resulting in an extensive comparative database for this gene. This 16s fragment has proved useful in detecting deeply divergent but phenotypically cryptic lineages of herpetofauna, a commonly encountered situation (Vences *et al.* 2005). This same 16s fragment is often insufficient, however, to resolve recent divergences among phenotypically distinct taxa (such as in some *Bradypodion*).

The well-sequenced 12s gene shows a similar pattern of evolution to 16s but the most frequently sequenced fragment is only around 340bp long, so it is an inefficient use of resources (each sequence run is a single cost unit and a single run can give over 600bp of high-quality sequence data). Considered together with these deficiencies, the relatively meagre database of squamate COI sequences makes this gene a low priority in molecular systematic and taxonomic studies of the southern African herpetofauna.

## Sampling

The number of individuals to be sequenced depends on the taxonomic group to be studied. In some cases, previous work has been carried out, and additional work can build upon this (e.g. *Pedioplanis*; Sakwa pers. comm.) so that a relatively small number of samples are required to fill remaining sampling gaps (e.g. 50 individuals). Other groups, with relatively few species (e.g. *Afrogecko*), or a limited geographic distribution (e.g. *Cordylus coeruleopunctatus*), will warrant the analysis of a smaller number of samples ( $\pm 50$  individuals). In more taxonomically complex groups (e.g. *Bradypodion*, *Afroedura*), or widespread and poorly known groups (e.g. *Nucras*), a larger number of samples will be necessary ( $\pm 100$  individuals).

A fraction of the individual samples should be sequenced in both directions to ensure that data are free of amplification errors. We recommend that both strands should be sequenced from at least one representative of each taxonomically significant lineage identified. For ND2, amplification can be carried out for the entire gene region of approximately 1 200bp, but sequencing must be carried out in two overlapping fragments ( $\pm 700$ – $900$ bp each), due to the limitations of capillary fragment analysis. We recommend that for





phylogenetic/taxonomic studies, the entire ND2 gene ( $\pm 1\ 200\text{bp}$ ) should be sequenced from representatives of each lineage, but within these lineages the 5' section ( $\pm 700\text{bp}$ ) of ND2, adjacent to tTRP, suffices. Reaction failure is, unfortunately, an inherent part of any DNA sequencing study. Accordingly, a fraction of the total expected reactions must be taken into account when building budgets and planning laboratory work. A reasonable maximum expected rate of reaction failure would be  $\pm 10\%$ .

The total number of sequencing reactions will depend upon the above, but can be estimated as follows:

- 50 individuals, three genes (ND2 in two fragments) = 200 sequence reactions, plus 30% in both directions, plus 10% margin = 286 sequence reactions;
- 75 individuals, three genes (ND2 in two fragments) = 300 reactions, plus 30% in both directions, plus 10% margin = 429 reactions;
- 100 individuals, three genes (ND2 in two fragments) = 400 reactions, plus 30% in both directions, plus 10% margin = 572 reactions.

### Analyses and interpretation

In actively speciating groups, slowly evolving genes may not resolve their evolutionary relationships or allow the identification of taxonomically significant units (suggested by phenotypic variation or patterns at other genes). These groups should be considered on a case-by-case basis to assess whether there is sufficient diversity for identifying lineages. A related and common problem occurs when recently evolved species share gene variants inherited from a common ancestor, resulting in discrepancies among genes and between genes and phenotype. In these cases, the reduced population size of mitochondrial DNA, due to maternal inheritance, will result in a more rapid sorting of variants and a greater discrimination among sister taxa at mitochondrial genes. By contrast, where hybridisation is a possibility, especially among closely related and sympatric taxa, analyses of nuclear DNA genetic variation are essential to assess the extent and significance of genetic interchange among these lineages. Mitochondrial genes can support this assessment (e.g. through analyses of cytonuclear disequilibrium), but these sequences are inadequate for *discovering* such patterns, as mitochondrial DNA has a uni-parental mode of inheritance. The reten-

tion of ancestral variation, hybridisation and differences in resolution among data sources are distinct possibilities which may be difficult to distinguish. These problems reflect the processes of lineage sorting and adaptive divergence that generate new species. In some cases there will not be any simple resolution of recently evolved taxa, despite observable phenotypic differences among populations.

Data analysis should proceed according to currently accepted techniques, subject to peer review in the publication process. We strongly encourage the exploration of novel methods, such as coalescent approaches, particularly where these are aimed at delimiting taxonomically significant lineages. Suitable methods of phylogenetic inference include maximum likelihood, Bayesian algorithms and parsimony. Standard computer programs for these analyses are PAUP (Swofford 2002), MrBayes 3.1.0 (Huelsenbeck & Ronquist 2001), although there are numerous alternative computer programs and methods which may be appropriate. Because data sets will include a combination of several genes, it will be necessary to investigate the potential for conflict among independent nuclear and mitochondrial data partitions, and between sequence sites evolving under different molecular constraints (silent versus expressed sites, protein-coding versus ribosomal sites), to determine whether the same lineages are consistently identified across gene partitions and analytical methods. In addition, model-based approaches should investigate the fit of alternative models to the data and the impact of model selection on the identification of lineages and their relationships. This may include partitioning a data set to allow model parameters to vary according to partition.

### Future considerations

#### Long-term storage of tissue

This discussion deals primarily with the short-term storage of reptile tissue samples (i.e. over the next five years). However, the issue of long-term storage is recognised as highly relevant. We recommend that SANBI and SARCA should investigate possibilities of collaborating with tissue banks either nationally (SA BioBank) or internationally.

#### Barcoding

There are a number of barcoding initiatives, many of which are being directed through the Consortium for the Barcoding of Life (CBOL). Contributing to the barcoding database was not recognised as an immediate goal for



reptile systematics in South Africa. Instead of constructing a database for CBOL, which would not be especially useful for reptile systematics, it was decided that the best available DNA fragments should be chosen for resolving taxonomic problems. Although barcoding would not be the immediate goal, its usefulness was recognised, and it was suggested that once units important for conservation (e.g. species) had been identified, additional funding could be sought to construct a barcode database for these units. This would allow SARCA eventually to fit within the broader CBOL framework.

### Phylogenetic diversity

The genetic data gathered during SARCA will allow analyses of geographic variation in phylogenetic diversity (PD) across the entire reptile fauna of the region. This would entail constructing a matrix of gene sequences from across the region, building phylogenetic trees from these data, and in this way generate PD values for individual grid cells, according to lineage distributions. This measure of evolutionary diversity could then be compared with maps of species diversity.

### Reptile e-collection

We recognise that, emanating from SARCA, an online searchable database for South African reptiles should ultimately be constructed. Such a database should contain species accounts, photos, museum voucher information, DNA sample information and possibly also DNA barcode information. The database would essentially be an electronic collection of reptiles for the dissemination of web-based information. Although this is beyond the scope of the present project, it is recommended that it should be a goal for the future.

### Recommendations

1. Molecular systematics studies should be extended to include the formal description and morphological characterisation of the taxa that are discovered.
2. Collectors of reptile tissues for genetic analysis should follow the standard protocol outlined above, including preservation, data collection and curation.
3. A Memorandum of Understanding should be drawn up between SARCA and SANBI, concerning the establishment of a herpetological tissue collection at the SANBI Molecular Systematics Laboratory, Kirstenbosch. This agreement should cover the facilities and labour required for this

collection, the curation of the collection, the associated database and access to the collection.

4. A set of two mitochondrial DNA fragments (the 3' end of 16S rDNA and the entire ND2 coding sequence) and a nuclear DNA fragment (part of the RAG-1 gene) should be used as the standard molecular toolbox for herpetological systematics in southern Africa. Sequences of these standard fragments should be obtained from each lineage requiring taxonomic description, to allow comparisons across taxa. This recommendation, however, should not inhibit the exploration of other gene fragments or phylogeographic studies based on a subset of these genes.

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## CHAPTER 5 A sampling and implementation strategy for phylogenetic studies on southern African reptiles

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In his landmark study of northern South Africa (the former Transvaal), Jacobsen (1989) commented: 'It is evident that we are still in the alpha stage of herpetological taxonomy.' Despite the publication of field guides, regional checklists and taxonomic revisions over the past 17 years, Jacobsen's statement remains true today. We are unable to say how many reptile species occur in southern Africa and our estimates are, at best, educated guesses based on rates of species discovery and observed variation within problematic groups (see Chapter 1 of this report). This knowledge gap contrasts with an increasing emphasis on surveys and the mapping of biodiversity (e.g. Harrison *et al.* 1997; Driver *et al.* 2004; Minter *et al.* 2004) and on the development of landscape plans intended to achieve ecologically sustainable and socially equitable development (Stewart 2000; Cowling & Pressey 2003; Everson & Morris 2006).

Incomplete taxonomic knowledge impedes our understanding of southern African biodiversity and its global context. Taxonomic uncertainty also reduces the effectiveness of land-use planning and, in the worst cases, plans based on inadequate taxonomy allow the extinction of unrecognised species of global significance (Daugherty *et al.* 1990).

We do not believe, however, that this gap in taxonomic knowledge is inevitable or insurmountable. In many, if not most, cases the recognition and description of new species is limited by sampling or by difficulty in interpreting observed variation. New tools, in particular DNA sequencing, along with increasing survey effort, allow a reinterpretation of this variation and promise accelerated taxonomic description (see Chapter 4).

This report outlines a three-year programme of sampling, DNA-sequence analyses and species descriptions, aimed at achieving a complete, or near-complete, inventory of reptile species in South Africa, Lesotho and Swaziland in the medium-term future. This programme will boost herpetofaunal knowledge beyond the 'alpha stage' to a new focus on the processes affecting species relationships and distribution—the primary information needed for landscape and biodiversity conservation planning. This concluding chapter covers geographic priorities for sampling and the people, resources and funding required for implementing the programme.

We use the general term 'problematic taxa' here to refer to the groups, such as subspecies, species or clusters of related species, that require investigation and description. These include those that vary morphologically or ecologically among areas and habitats, such as *Afroedura langi* (see Jacobsen 1989), as well as others discovered in studies of genetic variation, which suggest the presence of divergent lineages within what are currently recognised as single, cohesive species (such as in *Cordylus oelofseni*; Daniels *et al.* 2004). (See Chapter 1.)

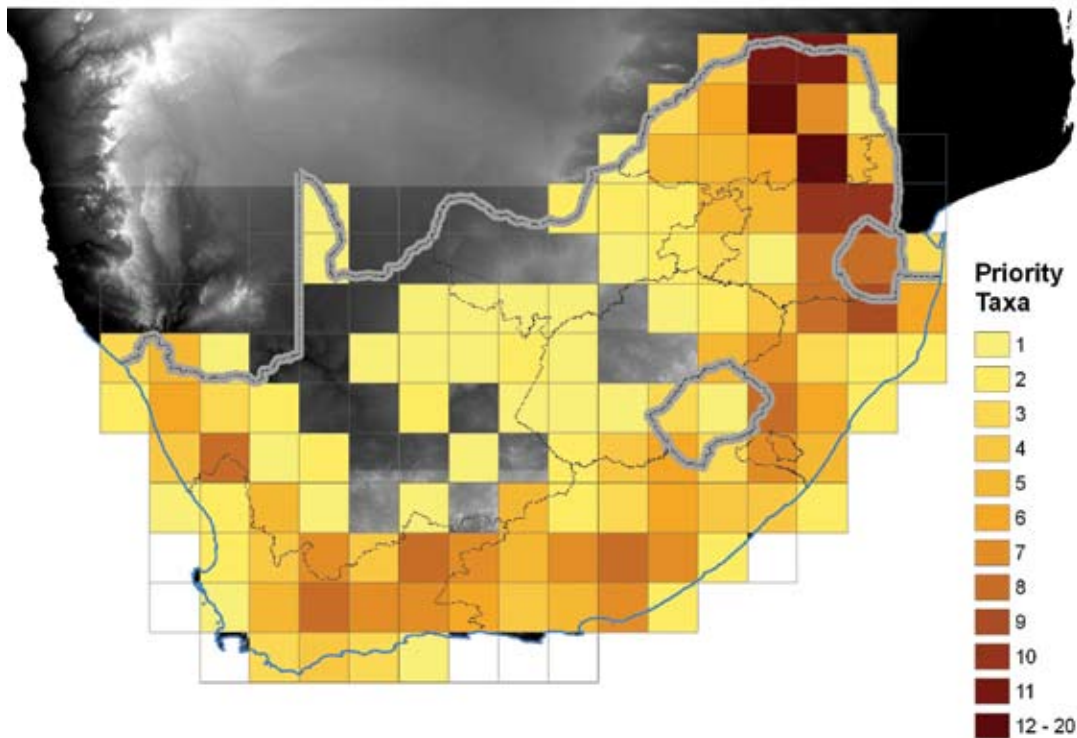
### Geographic sampling to address taxonomic priorities

The non-availability of samples and specimens from recognised problematic taxa is the major impediment to species resolution and description assisted by DNA-sequencing. As taxonomy is inherently a comparative process, sampling must aim for comprehensive coverage across the biogeographic areas in which problematic groups and their better-known relatives occur. SARCA has completed a preliminary gap analysis, based on currently recognised species, to determine the priority areas for mapping reptile species diversity across South Africa, Lesotho and Swaziland. Of the top 100 grid cells identified in that analysis, 84 were in the Nama Karoo or arid savanna biomes, mostly in the Northern Cape and North West provinces (B. Erasmus, unpubl. data).

Subsequent surveys, which included collection of DNA samples, have encountered considerable species diversity in these areas and



FIGURE 1: Priority one-degree grid cells, based on numbers of priority taxa.



dramatic range extensions for some species (<http://www.reptiles.sanbi.org/>). This confirms that the arid interior of South Africa has been underrepresented in previous surveys and requires further survey effort. However, the distribution of taxonomically problematic groups may not match that of undersampled grid cells, as the latter tend to be in extensive and relatively homogeneous habitats with few locally endemic species. In addition, even in well-surveyed areas, few previous studies collected tissue samples for DNA analysis or attempted to collect specimens from a full range of life stages. Studies such as Jacobsen's (1989) survey of the Transvaal and Raw's (2001) study of *Bradypodion* uncovered taxonomic problems, but were unable to resolve these, owing to developmental variation among individuals and a lack of genetic data on relationships among populations. For these reasons, a separate analysis is required to define survey priorities for taxonomic inventory and description.

An initial attempt at assigning sampling priorities for achieving taxonomic resolution is shown in Figures 1 and 2. These maps were created by overlaying the distributions of known problem taxa (given in Chapter 1), mapped on a one-degree grid, excluding the areas from which there are existing genetic samples and specimens. The underlying distributional data were extracted from published

reviews and taxonomic studies (De Waal 1978; Jacobsen 1989; Mouton & van Wyk 1994; Branch & Bauer 1995; Bates 1996; Bauer & Branch 2003; Bourquin 2004; Daniels *et al.* 2004, 2005), supplemented with our own field records and information from Branch (1998). Associated with these maps is a database of priority taxa and their distribution across degree cells and local biogeographic areas. This database may be updated over time to correct inaccuracies in distributional knowledge and to vary taxon priorities according to ongoing research.

Local biogeographic areas were defined subjectively for each taxon, based on the range boundaries, geographic barriers and priority populations suggested at the workshop. These areas specify a scale of sampling redundancy, within which populations are likely to be cohesive taxonomic units. Taxa sampled in one degree cell should be down-weighted across other cells in the same biogeographic region during reanalyses of priorities. In wide-ranging taxa, these biogeographic areas represent regional populations. For example, Figure 3 defines the populations of *Chersina angulata* that require sampling in the Eastern Cape, Lower Karoo, Agulhas plain and the arid North West. In highly fragmented taxa, such as the dwarf chameleons, *Bradypodion* spp., biogeographic areas are defined at a finer scale, with 18 of these areas across the eastern half







FIGURE 2: Priority one-degree grid cells, weighted by summed taxon priority values.

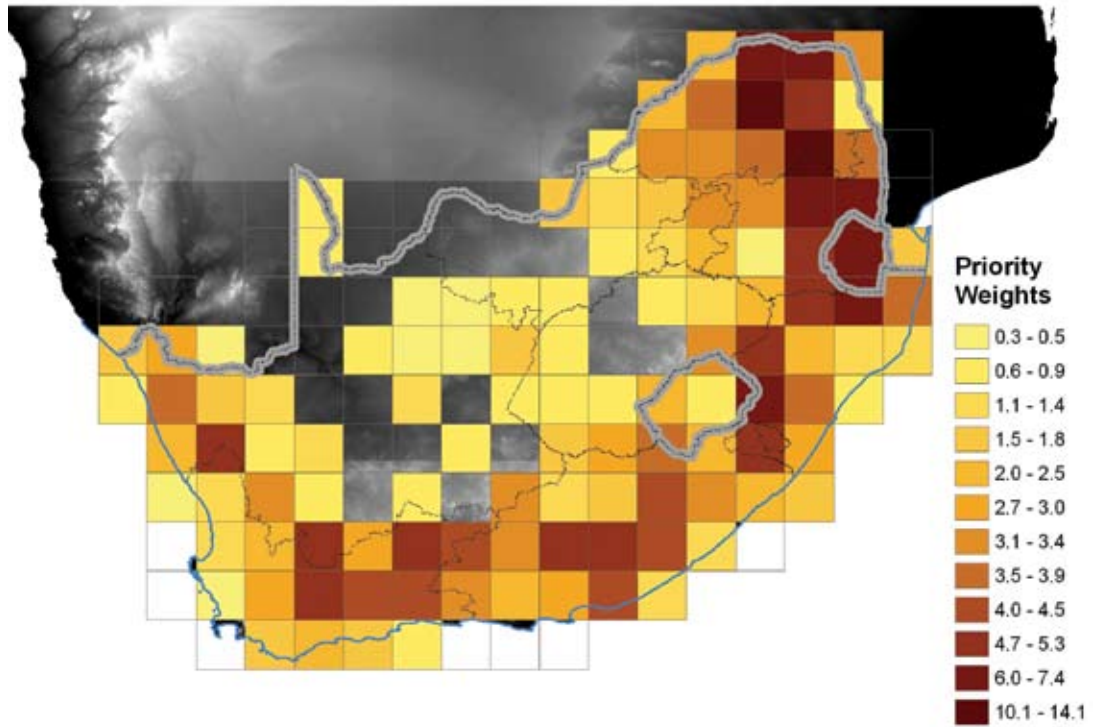


FIGURE 3: Priority areas for sampling individual taxa: *Chersina angulata*.

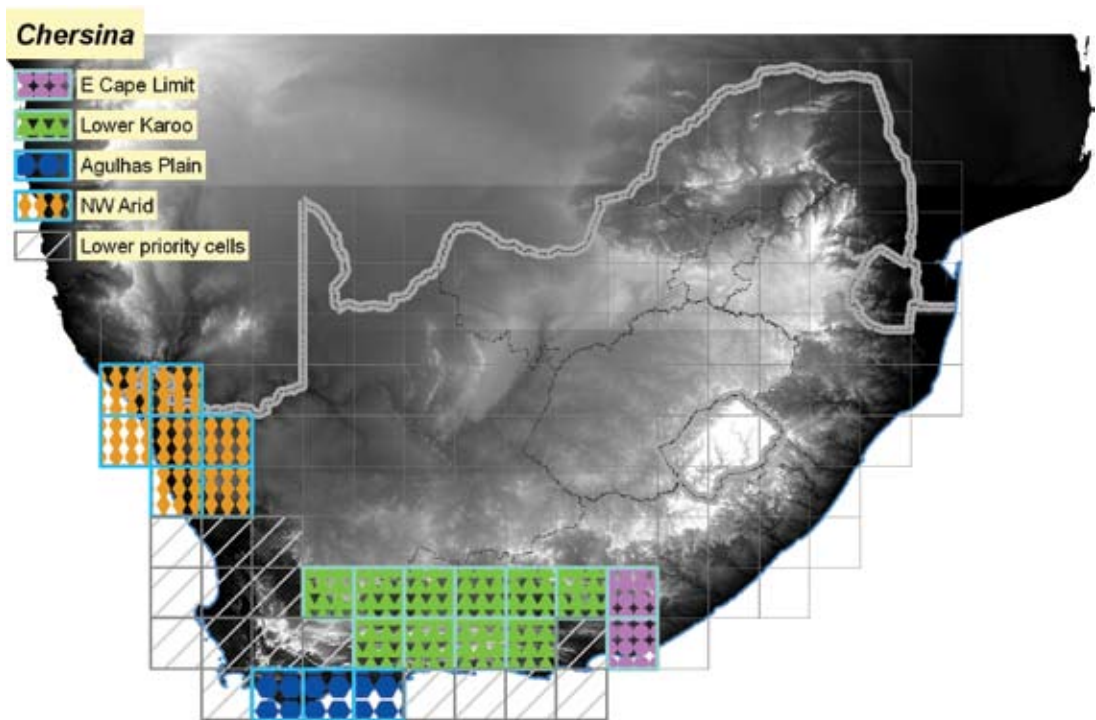
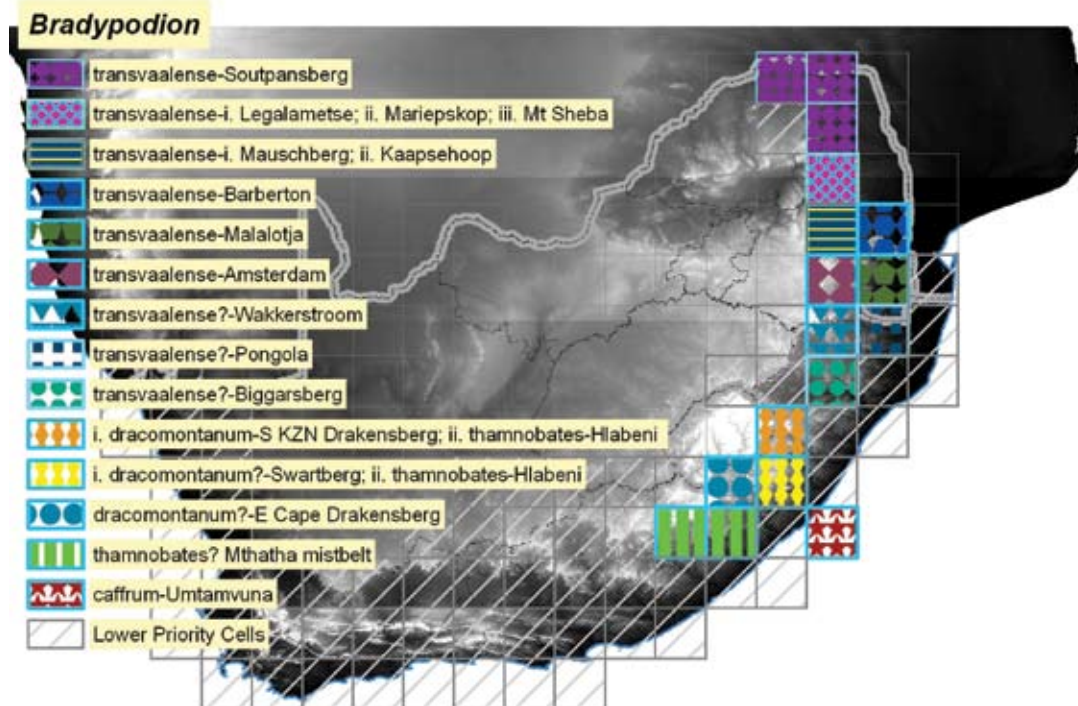




FIGURE 4: Priority areas for sampling individual taxa: *Bradypodion* spp.

of the study area (Figure 4). The definition of biogeographic areas does not affect the initial assessment of priorities in Figure 2, which is based simply on the occurrence of taxa within degree grid cells.

The results shown here suggest that between 0 and 20 problematic taxa occur in any particular grid cell within the study area. The top 25 grid cells in terms of the occurrence of these taxa are shown in Table 1 (see page 44). The 10 highest-ranked grid cells are from the relatively well-surveyed eastern escarpment areas, with the top six cells located along the north-eastern escarpment which was surveyed in Jacobsen's (1989) study. Other high-ranking cells are distributed around the inland escarpment, from the Amathole Mountains to Namaqualand, along the inland Cape Fold Mountains and in the arid north-west, bordering Namibia.

Figure 2 and Table 2 show the top 20 priority sampling areas for the taxonomic resolution of reptile species in South Africa, Lesotho and Swaziland, based on the workshop assessment of problematic taxa and their relative priority for systematic research (see Chapter 1). Figure 2 differs from Figure 1 in that the score for each grid cell is the sum of the priority weightings for the taxa occurring in that cell (higher-priority cells have a higher total weight). The weighted data show a similar pat-

tern to Figure 1, with only slight differences in the order of priority cells.

The distribution of priority degree grid cells for taxonomic sampling contrasts strikingly with the results from the SARCA gap analysis, in that the arid interior plateau is given a low priority and the highest priorities for taxonomic survey are assigned to the surrounding escarpment. Both analyses assign relatively low priority to the coastal periphery, despite the relatively high diversity and the ongoing discovery of new species in these areas (e.g. Bauer *et al.* 2003). Inadequate collections from some areas may contribute to the discrepancy between these analyses, as most new species are discovered, or recognised, through comparisons of existing samples and museum specimens. The overall pattern, however, is unlikely to be an artefact of incomplete sampling and, as suggested above, there are good reasons that surveys targeting deficits between known and expected diversity may differ from geographic priorities for addressing taxonomic problems.

Many problematic groups comprise a series of isolated populations scattered across naturally fragmented habitats, such as rocky outcrops, mountain ranges or forest patches. These species, their patchy habitats and the barriers separating populations are particularly associated with the escarpment areas identified in



TABLE 1: Degree grid cells (DGC) with the most problem taxa. The cells shown include seven or more problem taxa.

DGC	Area	Province or country	Problem taxa
2430	NE Escarpment	Limpopo / Mpumalanga	20
2329	Haenertsburg	Limpopo	16
2229	NW Soutpansberg	Limpopo	11
2230	NE Soutpansberg	Limpopo	11
2531	Barberton	Mpumalanga	10
2530	Sabie–Nelspruit	Mpumalanga	10
2731	Pongola	KwaZulu-Natal / Swaziland	9
2631	Mbabane	Swaziland	8
2929	Underberg	KwaZulu-Natal	8
2730	Wakkerstroom	Mpumalanga / KwaZulu-Natal	8
3320	Western Little Karoo	Western Cape	8
3222	Beaufort West	Western Cape / Northern Cape	8
2630	Amsterdam	Mpumalanga / Swaziland	8
3226	Winterberg	Eastern Cape	8
3018	Kamiesberge	Northern Cape	8
3029	Kokstad	KwaZulu-Natal / Eastern Cape	7
2330	Tzaneen	Limpopo	7
3220	Roggeveldberge	Northern Cape / Western Cape	7
2829	Van Rheenen	Free State / KwaZulu-Natal	7
3225	Bankberg	Eastern Cape	7
3223	Kamdeboo	Eastern Cape / Western Cape	7
3326	Grahamstown	Eastern Cape	7
3322	Eastern Little Karoo	Western Cape	7
3227	Amathole	Eastern Cape	7
3321	Central Little Karoo	Western Cape	7

Figures 1 and 2. For example, the highest-priority cell (DGC 2430) straddles a biogeographic barrier, the Olifants River valley, separating sections of the north-eastern escarpment in Mpumalanga and Limpopo Provinces. By itself, the current SARCA survey strategy will be insufficient for a taxonomic resolution of these groups; a modified survey programme is required to achieve a complete inventory of species.

### Implementation

The sampling of all known problematic groups across all the regions in which they occur would require around 250 taxon-per-site collections. (For example, Figure 2 summarises results from 239 combinations of taxa and biogeographic areas, distributed across 115 degree grid cells; approximately half of these fall in the top 20 priority degree grid cells.) Even within priority cells it is unlikely that optimal sampling can be achieved, because some taxa are rarely encountered. The approach advocated here is that of targeted surveys of all reptile taxa occurring within the 20 highest priority degree grid cells, over the next two years. This taxonomic sampling will be conducted by the SARCA field team and project

collaborators, and will be co-ordinated with the existing diversity-oriented survey programme. Based on previous SARCA surveys, this will require a 10-day trip to each priority area, costing around R10 000 per trip (total cost of R200 000 for 20 surveys, excluding wages and vehicle hire).

Supplementary collecting for particular taxa will be conducted by associated research groups using additional funding sources (for taxon- or region-specific projects). Attendance at the workshop showed that this initiative and SARCA already have the support of most professional herpetologists in the region. Any other research groups conducting systematic studies of the southern African herpetofauna will be contacted to facilitate an exchange of locality data and samples. Samples of lower-priority taxa, collected through these various sources, will allow the discovery of additional taxonomically problematic groups. The ongoing evaluation of taxon and geographic priorities, every three to six months, will be required to achieve sufficient coverage of all taxa. These priority weightings can be used to measure the progress made with sampling, by summing the weightings of all taxa collected for each population.





TABLE 2: Highest-priority degree grid cells (DGC) for taxonomic sampling. (Weightings for individual taxa vary from 0–1.)

Rank	DGC	Area	Province or country	Weighted score
1	2430	NE Escarpment	Limpopo / Mpumalanga	14.1
2	2329	Haenertsburg	Limpopo	10.1
3	2531	Barberton	Mpumalanga	7.4
4	2229	NW Soutpansberg	Limpopo	7.3
4	2230	NE Soutpansberg	Limpopo	7.3
4	2530	Sabie—Nelspruit	Mpumalanga	7.3
7	2731	Pongola	KwaZulu-Natal / Swaziland	6.5
8	2631	Mbabane	Swaziland	6.2
9	2929	Underberg	KwaZulu-Natal	6.0
10	3029	Kokstad	KwaZulu-Natal	5.3
11	2730	Wakkerstroom	Mpumalanga / KwaZulu-Natal	5.2
11	3320	Western Little Karoo	Western Cape	5.2
13	3222	Beaufort West	Western Cape / Northern Cape	5.1
14	2630	Amsterdam	Mpumalanga / Swaziland	4.9
15	3226	Winterberg	Eastern Cape	4.8
15	2330	Tzaneen	Limpopo	4.8
15	3220	Roggeveldberge	Northern Cape / Western Cape	4.8
18	3018	Kamiesberge	Northern Cape	4.7
18	2829	Van Rheenen	Free State / KwaZulu-Natal	4.7
18	3225	Bankberg	Eastern Cape	4.7

Ideally, DNA sequences and voucher specimens should be obtained from an average of at least two individuals of each taxon, from each local biogeographic area, to allow basic comparisons of variation within and between areas. In this way, with optimal sampling, about 500 samples would require sequence analysis to address the known problems. The ongoing analysis of other specimens and sequences will discover further taxonomic anomalies and potential cryptic species which should be explored. Therefore, as a conservative estimate, the total number of samples requiring DNA sequencing to achieve a complete species inventory of the reptile fauna would be 1 000 individuals, sparsely distributed across taxa and biogeographic regions. However, an application for funding should probably not attempt to cover the ideal scenario, but rather an initial series of analyses which would address a significant proportion of the known problems. At the workshop, this was estimated to be an analysis of about 460 individuals from approximately 60 taxa in 18 priority genera. (See Chapters 1 and 4.) Not all of the taxa identified in Chapter 1 of this report would be adequately sampled, but about half would be, and for the remainder it would become clearer which taxa require additional sampling and analysis.

Following the approach suggested in Chapter 4, this translates into some 2 640 sequencing reactions (sequencing 16S, ND2 and RAG-1 gene fragments, with allowance for some bi-

directional sequencing and a 10% margin for reaction failure). At current rates, this will cost R396 000 (at R150 per sequencing reaction), including preparation costs, but excluding student bursaries or wages for laboratory assistance.

A substantial proportion—approximately half—of this required funding has already been awarded to workshop participants for taxonomic projects on particular groups (notably to A.M. Bauer for the systematic resolution of gekkonids and lacertids). A further R198 000 will be required to cover the sequencing of the balance of the taxa (see Table 3).

The sequencing and sequence analysis will largely be done by students working on particular problematic taxa. This project can accommodate four M.Sc. students over the next three years, with supervision spread among project collaborators at different institutions (R240 000 in grantholder-linked student bursaries). Additional sampling and sequencing will be needed for analyses of phylogeography (the structuring of genealogical relationships across landscapes, within species or among closely related species) to reveal the timescale of isolation separating populations and the location of historical refugia resulting from past climate change. Similarly, the modelling of species' potential distributions, based on the locality data generated here, would allow an investigation of the ecological factors limiting species distribution, the identification of





TABLE 3: Three-year budget summary.

Activity	Leaders	Cost
Surveys and sampling of taxonomic priorities	SARCA project team (M. Burger, J.A. Harrison)	R200 000
DNA sequencing of priority taxa	SARCA genetics team (see Chapter 4); University of Villanova laboratory (A.M. Bauer)	R396 000 (approx. half as co-funding from USA research grant)
Specimen comparisons and collaboration	W.R. Branch (PE Museum), M.F. Bates (National Museum), A.M. Bauer (University of Villanova)	R75 000
Publication costs for taxonomic revisions, e.g. page charges	W.R. Branch (PE Museum), M.F. Bates (National Museum), A.M. Bauer (University of Villanova)	R10 000
Student bursaries	Project collaborators (SANBI, UWC, SU, UFS, UCT)	R240 000
TOTAL		R921 000

possible isolated populations and predictions of species' responses to ongoing climatic changes. These related analyses are relevant to this project, in particular to the discovery of isolated populations and unrecognised species, and are particularly suited to postgraduate student projects.

Some phylogeographic analysis will be possible with the data generated here, for groups with many small, isolated and phenotypically variable populations (such as *Bradypodion*). Preliminary modelling could also be investigated as a student project to generate hypotheses of distribution for newly discovered species lineages. More detailed studies of these aspects should be conducted by associates or other research groups, using other funding sources.

Finally, these surveys will enlarge South African museum collections, making these more representative of the complete herpetofauna. At the same time, these new specimens and discoveries from associated DNA-sequence analysis will substantially increase the need for comparative morphological analysis, much of which is likely to be borne by museum-based researchers. This will require visits to other collections to examine types and other material, and visits to collaborators at different institutions to discuss variation in DNA sequences and morphological variation in voucher specimens. As an initial impetus to species description over the next three years, this programme should budget for local and international research visits to institutions to allow synergistic interpretation of results from morphological and molecular analyses (total R75 000).

A summary of all costs associated with the project appears in Table 3. The stated

amounts were used in a funding application to the South African National Research Foundation (NRF) in April 2006. The budget assumes significant co-funding from a USA National Science Foundation (NSF) research grant held by Prof. Aaron Bauer at the University of Villanova, USA.

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