REPTILE SYSTEMATIC STUDIES IN SOUTHERN AFRICA: A BRIEF HISTORY AND OVERVIEW

By

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SUMMARY

Southern Africa has the richest reptile diversity in Africa, with a fauna that currently exceeds 490 species. Present rates of discovery, which for lizards are still comparable to those in the early phases of exploration, indicate that the fauna may approach, if not exceed, 600 species. Lizards form the dominant component (60.9%) of the reptile fauna. The 578 recognised taxa (species and subspecies) were described by 101 authors, of which 12 authors were responsible for 12 or more taxa and together named 68.9% of the total taxa. The five most productive authors were, in order: A. Smith, W. Peters, D. Broadley, J. Hewitt, and V. FitzSimons. The contributions of these authors, the growth in herpetological studies in the last 25 years, and the importance of regional surveys in the development of biogeographic models, are summarised. Over 50 species of reptile have very restricted distributions (less than 3 quarter-degree grid squares) and may be of conservation concern. Despite national rhetoric evincing concern for the biodiversity crisis, there has been a recent decline in herpetological posts and manpower.

INTRODUCTION

The Cape Floristic Kingdom is justifiably famous for the wealth of its plant diversity, especially in the Fynbos and Nama Succulent Karoo biomes. Less well-known, or even locally appreciated, are the riches of the reptile fauna. It is now evident that South Africa has the richest reptile diversity in Africa, due, in part, to the exceptional radiation of geckos in the western arid regions, and cordylids in the escarpment mountains (summarised in Branch, 1998a). This richness was first noted by Bauer (1993), even though his figures significantly underestimated the region's true diversity (e.g. he recorded 293 reptile species in South Africa, whereas 351 species are now known). Currently (May 1999) the reptile fauna for southern Africa comprises 491 species (578 taxa) in 116 genera and 23 families (Branch, 1998a; plus subsequent updates). Lizards form the dominant component of the reptile fauna (299 species, 60.9% of the total; Figure 1), followed by snakes (146 species, 29.7%), with lesser contributions by chelonians (28 species, 5.7%) and amphisbaenians (17 species, 3.5%). There is also a single crocodilian (0.2%). Despite their relatively low numbers, land tortoise (Testudinidae) diversity within the region is significant, comprising 14 of the 42 living species (33.3%) and 5 of the 11 genera (45.5%) (Branch, 1998a; Iverson, 1992). Within lizards, geckos predominate (91 species, 30.4% of lizard fauna), followed by skinks (69 species, 23.1%), cordylids (55 species, 18.4%) and lacertids (37 species, 12.4%). Endemicity in all lizard families, with the exception of the depauperate, conservative and wide-ranging varanids is high (mean 65.3%), especially within the Cordylidae (85.5%) and Chamaeleonidae (95%) (Branch, 1998b and in prep.).

A graph of the cumulative rate of species description (Figure 2) shows little indication of reaching a plateau, indicating that the herpetofaunal diversity of the subcontinent remains poorly

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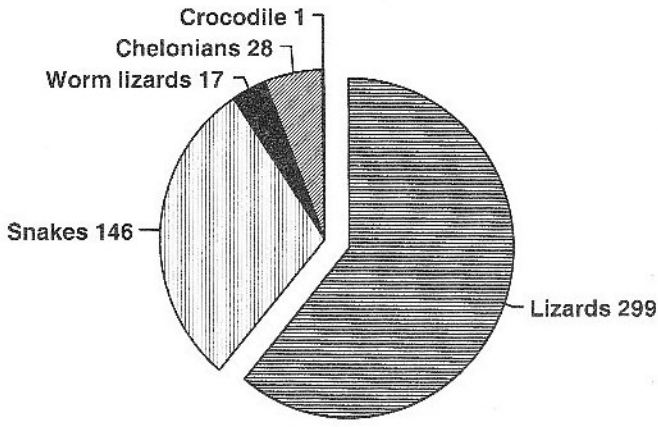

Figure 1. Composition of the southern African reptile fauna

documented. This is demonstrated by the inclusion of 83 new species in a recent revision of the subcontinent's reptiles (Branch, 1998a), compared with the previous review ten years earlier (Branch, 1988a). This is a rate of discovery of a new species approximately every 41 days, and new species continue to be described at a rate similar to that by Andrew Smith, 150 years ago.

Many of these new discoveries are cryptic species, particularly among lizards. Whilst some have been discovered by the utilisation of modern genetic analysis (e.g. *Goggia braacki*, Good *et al.*, 1996), others are obvious (morphologically) taxonomic novelties, discovered as a result of field work in poorly surveyed areas (e.g. *Afroedura hawaquensis* in the southwestern Cape fold mountains, Mouton & Mostert, 1985; *Montaspis gilvomaculata* from the Drakensberg escarpment, Bourquin, 1991; *Goggia gemmula* from the Richtersveld, Bauer *et al.*, 1996).

Descriptions of many other taxonomic novelties await publication, including new species of skink (*Mabuya*, N. Province, Jacobsen in prep.), gecko (*Afroedura*, Kaokoveld, Griffin in prep.; N. Province, Jacobsen in prep.; Free State, Bates & Branch in prep.; and Eastern Cape, Branch in prep.), and chameleon (*Bradypodion*, Branch in prep.). In addition, a number of

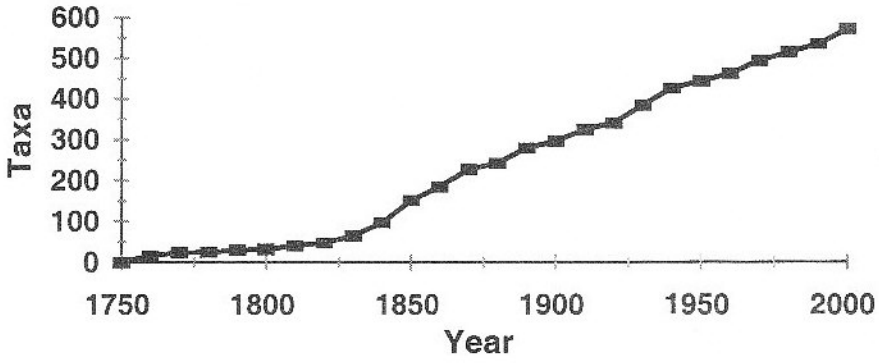

Figure 2. Cumulative rate of description of the southern African reptile fauna.

Table 1. Comparative reptile diversity for selected African countries.

Country	Area (1000 km^2)	Total[1]	Chelonia	Crocodylia	Lacertilia[2]	Serpentes	Diversity index[3]
Southern Africa	3060	491	28	1	316	146	1.60
Sudan	2506	115	8	1	43	63	0.46
Zaire	2345	290	17	3	93	166	1.23
Algeria	2381	81	3	0	53	25	0.34
Libya	1760	56	3	0	32	21	0.31
South Africa	1221	409	26	1	259	123	3.35

[1] Currently recognised species; data taken from Bauer (1993), updated from Branch (1998a), Broadley (1998), Poynton (1998), Schleich *et al.* (1996).
[2] Including Lacertilia and Amphisbaenia.
[3] Total reptile diversity/10 000 km^2.

genera (e.g. *Meroles* and *Pedioplanis*, Lacertidae; *Acontias*, Scincidae; *Pachydactylus* (in part), Gekkonidae; *Bradypodion*, Chamaeleonidae) require modern taxonomic revisions that can also be expected to reveal greater taxonomic diversity.

It is probable that gecko diversity in the subcontinent will soon exceed 100 species, and that the total reptile diversity will easily exceed 550 species. This is indicated by the recent discovery of numerous cryptic species (*Cordylus*, Mouton & van Wyk,1990, 1994; geckos, Branch *et al.*, 1995a, 1996; *Leptotyphlops*, Broadley & Wallach, 1997a,b), some of which cannot be morphologically differentiated (e.g. *Goggia braacki*, Good *et al.*, 1996). In addition, the increasing application of evolutionary species concepts can be expected to result in the recognition and naming of many allopatric populations, whilst modern surveys of even well-developed regions, e.g. the Little Karoo (Branch & Bauer, 1995), continue to reveal numerous new distribution records and taxonomic novelties. Given these factors, the reptile diversity of the subcontinent may eventually exceed even 600 species.

In comparison, Zaire, the second-largest country in Africa and of almost equal size to the subcontinent, has a total herpetofauna of 522 species (Broadley, 1998; Poynton, 1998), only 290 of which are reptiles. In fact, southern Africa has a greater number of gecko species than the total lizard fauna of Zaire (Broadley, 1998). Conversely, the amphibian fauna of Zaire (232 species, Poynton, 1998) easily exceeds that of the subcontinent (132 species). That the southern African reptile diversity is not simply proportional to size and the influence of arid habitats is evident from comparison with Sudan, Algeria and Libya (Schleich *et al.*, 1996), large African countries with extensive arid habitats, but which are herpetologically depauperate, particularly for lizards (Table 1). It is evident that other factors, such as the great antiquity of the Namib region (Ward & Colbett, 1990), have played a part in developing this exceptional reptile diversity.

SYSTEMATIC HISTORY

A total of 101 authors have been individually or jointly involved in the description of the 578 currently recognised species and subspecies of southern African reptiles. Most authors (44) have been involved in the description of only a single taxon. However, 12 authors have been involved in the description of ten or more taxa, including (in order): Andrew Smith, Wilhelm Peters, Donald Broadley, John Hewitt, Vivian FitzSimons, George Boulenger, José Bocage, Carl

Table 2. Main authors of Southern African reptile species and subspecies[1].

Author	Period[2]	Snakes	Lizards	Worm Lizards	Chelonia	Total taxa
A. Smith	1828–1849	24	37	1	2	64
W. Peters	1844–1882	20	30	2	1	53
D. Broadley	1958–present	19	25	6	0	51
J. Hewitt	1909–1938	1	43	0	3	47
V. FitzSimons	1930–1964	5	37	2	1	45
G. Boulenger	1882–1920	10	26	2	2	40
J. Bocage	1866–1896	12	10	1	0	23
C. Linnaeus	1754–1766	9	7	0	5	21
J. Gray	1830–1865	0	13	0	2	15
N. Jacobsen	1984–present	1	12	1	0	14
A. Günther	1860–1893	13	0	0	0	13
W. Haacke	1964–present	1	11	0	0	12

[1] Currently valid taxa.
[2] Between first and last descriptions.

Linnaeus, John Gray, Niels Jacobsen, Albert Günther, and Wulf Haacke. Together they are responsible for describing 68.9% of the total taxa (Table 2). Most of these authors have worked alone, whilst others have collaborated with only one (Boulenger, Jacobsen and Haacke) or two (Hewitt) other workers. Don Broadley is a notable exception, having published with numerous other co-authors (9). Modern descriptions (post-1985) are increasingly multi-authored, reflecting the increasing application of traditional morphological and biochemical techniques.

A graph of the chronology of the description of currently recognised species (Figure 3) shows a series of pulses. These peaks, which may almost be considered the equivalent of nomenclatural punctuated equilibria, reflect the active years of the principal researchers. It is logical and informative to review the history of systematic studies on the subcontinent's reptiles within the context of these eras, highlighting the individual interests and, in some cases, their differing taxonomic approaches.

The Linnaean era

Early collections were little used in scientific study until Carolus Linnaeus (1707–1778) and others began the first serious attempts to identify logical order in the diversity of life, and the birth of systematics formally dates from the publication of the tenth edition of the *Systema Naturae* by Linnaeus (1758–1759) (Mayr, 1969; Ford & Simmons, 1997). Linnaeus (1754–1766) described 21 South African reptiles. Many originated in the Cape, although some were mistakenly believed to have been collected elsewhere, e.g. the geometric tortoise (*Testudo geometrica* = *Psammobates geometricus*) from "Asia" and the berg adder (*Vipera atropos* = *Bitis atropos*) from "America". Others, particularly the sea turtles, are wide-ranging species, known to Linnaeus from elsewhere. Linnaeus once wrote that: "There is no place in the world with so many rare plants, animals, insects and other wonders of Nature as Africa, and it seems to have been concentrated to the Cape" (Hanström, 1955). He was so impressed with life's diversity in the Cape that eight of his pupils visited the region (Brink, 1955).

In the remaining years of the 18th century and the early years of the 19th century a number of other authors embraced Linnaean nomenclature and applied names to several species first

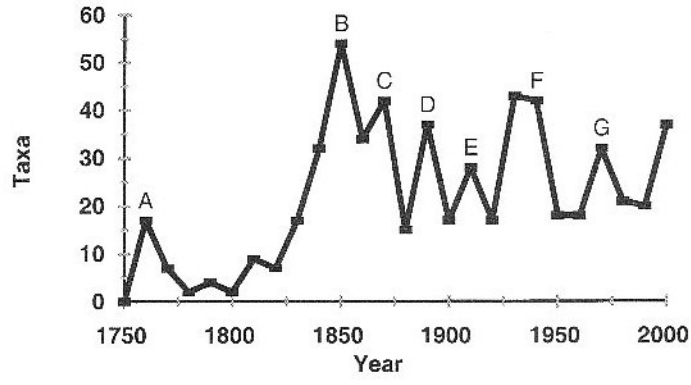

Figure 3. Chronology of the description of reptile taxa: (**A**) C. Linnaeus, (**B**) A. Smith, (**C**) W. Peters, (**D**) G. Boulenger, (**E**) J. Hewitt, (**F**) V. FitzSimons, (**G**) D. Broadley.

described in earlier, non-taxonomic works; e.g. Daudin's (*Vipera cornuta* 1803) and Cuvier's (*Vipera lophophrys* 1829) were formal descriptions of the many-horned adder (*Bitis cornuta*), and based on the brief mention of a horned serpent encountered and described in Paterson's journal of his travels in southern Africa (Paterson, 1789). During the 60 years (1768–1826) after Linnaeus's seminal work the rate of species description was low, with only another 31 currently valid species being described in the period, most by Daudin (1803).

Two early field naturalists

Andrew Smith

Andrew Smith is the true father of South African zoology, and his extensive travels in the subcontinent are well documented (Kirby, 1965). He arrived in the Cape in 1821 as a medical surgeon to the British military garrison. Much of his time (1821–1837) in Africa, however, was spent exploring the frontier, conducting scientific investigations and conferring with native tribes on behalf of the British government. Whilst at the Cape he founded and became the first Superintendent of the South African Museum. During his life he described 173 southern African vertebrate species, in recognition of which Charles Darwin successfully proposed his election as a Fellow of the Royal Society in 1857.

Smith's major collections were made during several extended expeditions, including trips to Namaqualand and southern Namibia (1828–1829), to Zululand (1832) where he met the Zulu king Dingane, and to "Central Africa" (then the northern provinces of South Africa!) from 1834–1836. His first publication based on his collections involved discussion of several new snakes and appeared in the *Edinburgh New Philosophical Journal* (Smith, 1826). Others of his early descriptions appeared in a newspaper, the *South African Commercial Advertiser* (Smith, 1828). At this time the total described herpetofauna of southern Africa comprised only 53 taxa, only a small fraction (7.4 %) of the 720 taxa currently recognised. His subsequent studies were to drastically increase this number.

On his return to London in 1837, Smith worked on the large collections he amassed during his expeditions. These formed the basis of his monumental *Illustrations of the Zoology of South*

Africa, published in 28 parts over the period 1838–1849. The herpetology section contained 78 outstanding plates by G.H. Ford, who accompanied Smith on his 1834–1836 expedition. This was one of the first monographic reviews of a regional fauna, and it is now a rare work commanding high prices. Most of Ford's zoological drawings were retained by Smith and on his death returned to the artist, who presented them to Albert Günther. They were purchased by the University of Witwatersrand in 1936. Many of his earlier names were ignored by Smith when he published his *Illustrations*, and it is likely that he considered these names as nomenclatorially invalid. However, they have subsequently been accepted by the International Commission for Zoological Nomenclature (Opinion 1278, Bull. Zool. Nomen. 41, 1984), and some were available for recently recognised taxa, e.g. *Bufo pantherinus* (Brooke, 1992), and *Bitis armata* (Branch, 1999a).

Smith remains responsible for describing the greatest number of reptile species currently recognised in southern African (64 species, comprising 24 snakes, 37 lizards, one amphisbaenian and two chelonians). With the exception of William Burchell's (1822) description of *Vipera inflata* (an excellent name for the puff adder which unfortunately is a junior synonym of Merrem's *arietans*), Smith was the first describer familiar with the South African herpetofauna in the field. In some respects, it is perplexing to see how many rare and inconspicuous species Smith described (e.g. *Bradypodion taeniabronchum, Gerrhosaurus typicus, Scelotes inornatus*, and *S. capensis*) whilst failing to collect other wide-ranging (e.g. *Mabuya variegata*) or (at least now) common species in the regions he worked (e.g. *Afroedura karroica, Bradypodion karroicum, Pachydactylus serval*, etc.).

Much of the material that typifies Smith's names returned with him to Britain, and is now mainly incorporated into the Natural History Museum (London) collection. Other material is still retained in the Royal Scottish Museum (Edinburgh). Smith's species descriptions were based on a single or few specimens, and he did not specify types or identify the specimen(s) upon which his descriptions were based. FitzSimons (1937) briefly details the fate of Smith's collections, and notes that many of his descriptions appear composite, making the identification or designation of types very difficult. He attempted to link surviving specimens in both the Natural History Museum (London) and Royal Scottish Museum (Edinburgh) with Smith's descriptions, but with only limited success. However, even where he could fit specimens with Smith's descriptions, FitzSimons (1937) unfortunately did not designate lectotypes, nor did he give the catalogue numbers of the specimens he could match to descriptions. Tragically, his work is now of limited use as it must be repeated by any new worker investigating Smith's material. In some cases lectotypes for Smith's species have been subsequently designated (e.g. *Nucras tessellata*, Broadley, 1972; *Scelotes inornatus*, Broadley, 1994), whilst for other species for which Smith's specimens are lost, or from which it is impossible to identify type(s), neotypes have been designated (e.g. *Bitis armata*, Branch, 1999a). Ulber (1999) provides a useful annotated Table of Contents for the Reptilia volume of Smith's *Illustrations*, and notes the existence of a poorly known errata slip (1849) which stabilises the correct spelling of certain names.

Despite his prominence as the "Father" of zoology in South Africa, Smith's name is celebrated by only two reptile taxa, neither currently valid: *Testudo smithi* Boulenger 1886 (= *Psammobates tentorius*), and *Euprepis smithii* Gray 1845 (= *Mabuya homalocephala*).

Wilhelm Peters

Only recently has the contribution of Wilhelm Peters to the early growth of southern African herpetology been fully acknowledged (Bauer *et al.*, 1995). Neglect stemmed, in part, from the obscure publications in which his work appeared and the fact that most were published in

German. His travels were also mainly peripheral to the subcontinent, occurring in the inhospitable and poorly settled regions of the Zambezi Delta and coastal northern Mozambique. Many of the species he described are characteristic of the Indian Ocean coastal belt and it was only much later, during the latter half of the 20th century, that surveys in southern Mozambique and Maputaland (Bruton & Haacke, 1980) revealed their presence in the subcontinent.

Peters travelled extensively in Mozambique and Madagascar (1842–1848), publishing the first descriptions of a new fish (*Ctenopoma multispinis*), lizard (*Tropidolepisma striatum* = *Mabuya striata*) and frog (*Dactylethra Muelleri* = *Xenopus muelleri*) whilst still in the field (Peters, 1844). Many years later, as part of the established scientific community in Berlin, the results of his Mozambique expeditions were reported in a series of monographic treatments in the *Naturwissenschaftliche Reise nach Mossambique*. Mammals (1852) and freshwater fish (1868) appeared first, followed (after a long delay) by the final part on the herpetofauna (Peters, 1882). To this day it remains as the only summary of the Mozambique herpetofauna and, as with Smith's *Illustrations*, its age and the exceptional quality of the hand-coloured plates make it a rare and much-sought collector's item.

Peters was an accomplished mammalogist and ichthyologist and also published widely on a variety of invertebrate groups. However, he was principally a herpetologist and described nearly 650 reptile and amphibian taxa (Bauer *et al.*, 1995), with major contributions for colubrid snakes (describing 118 species) and skinks (111 species). Except for Andrew Smith, Peters described the second-highest number (53) of valid taxa for southern African reptiles, including 30 lizards, 20 snakes, 2 amphisbaenians and a terrapin. He also named 12 amphibians from the subcontinent. Despite this the names of few local species commemorate him, but include *Rhinotyphlops schlegelii petersi* and *Xenopus laevis petersi*.

The excellent publication of Bauer *et al.* (1995) provides a detailed biography of Peters, an extensive review of his scientific contributions, and a complete facsimile collection of all his herpetological publications.

George Boulenger

Born in Belgium, Boulenger (1858–1937) was the leading taxonomic herpetologist of his time, and published over 900 scientific papers, most on herpetology (Adler, 1989). His monumental nine-volume *Catalogues*, detailing the batrachian (1882), lizard (1885–1887), chelonian (1889), and snake (1893–1896) collections of the British Museum, were then the most detailed overviews of world herpetology, and they remain baseline references for even modern taxonomic revisions. He described a total of 40 southern African reptile species and subspecies (including 26 lizards, 10 snakes, 2 chelonians, 2 amphisbaenians) as well as 15 amphibians from the subcontinent. Many of his new species were based on material collected by early travellers (e.g. ffolliot Darling, Ansorge, Grant and Neave), or forwarded to him for identification by Peringuey and Sclater of the South African Museum. Although most of his papers dealt with the description of miscellaneous new species as they arrived at the British Museum, he did in the later part of his career undertake generic revisions, including the lacertid genera *Nucras* (Boulenger, 1917) and *Eremias* (Boulenger, 1918), as well as southern African agamas (Boulenger & Power, 1921). The names of few local species commemorate him, but do include the tortoise, *Homopus boulengeri*, and skink, *Mabuya boulengeri*. Other African reptiles include *Elapsoidea boulengeri* Boettger 1895 and *Boulengerina* Dollo 1886, a genus of aquatic cobras from central Africa.

John Hewitt

Born in Sheffield, England, John Hewitt initially served as Curator of the Sarawak Museum in

Malaysia, before coming to South Africa as the Assistant for Lower Vertebrates at the Transvaal Museum, Pretoria (1909–1910). He soon left, however, to take up the position of Director of the Albany Museum, Grahamstown (1910–1958). Here he was to remain for the rest of his life, dying in 1961, a few years after his retirement.

As was typical of the age, Hewitt was a "Jack-of-all-Trades", and yet Master of many. He published over 160 papers, but few monographs or popular works. In addition to 47 papers on herpetology (1905–1938), he published on topics as diverse as arachnology (33 papers, 1909–1935), ornithology (9 papers, 1913–1948), mammalogy (3 papers, 1913–1927), and archaeology and prehistory (21 papers, 1912–1955). His remaining papers covered subjects such as animal distributions, the Albany Museum, biographies, evolution, as well as 22 papers on various topics whilst based in Sarawak.

Like Boulenger, Hewitt (1880–1961) was a museum-based systematist, and there is little evidence that he undertook much field work. Although Adler (1989) states that Hewitt accompanied Paul Methuen on a trip to Madagascar in 1911, in fact he only identified the material that Methuen brought back. A number of new taxa were described in the reports on the reptiles (five species or varieties, Methuen & Hewitt, 1913a) and amphibians (five species and one genus, Methuen & Hewitt, 1913b), of which two reptiles and four frogs are still valid (Glaws & Vences, 1994).

Hewitt had an exceptional "taxonomist's eye", and described numerous cryptic species, often on the basis of very few specimens. With the exception of tortoises (see below), few of his numerous new taxa have been subsequently invalidated. Unfortunately, Hewitt was less than rigorous with typification of his new taxa, and the number of individuals, and the place of deposition and catalogue numbers of his type material is often confused (e.g. *Afroedura karroica* complex, Bates & Branch, 1999). As was also common practice at the time, he regularly exchanged type material with other institutions, particularly Arthur Loveridge (Museum of Comparative Zoology, Harvard), Vivian FitzSimons (Transvaal Museum) and Gladwyn Noble (American Museum of Natural History, New York). As "types" were more desirable in exchanges than other material, Hewitt often exchanged topotypic material, some of which had been collected subsequent to the cotype material used in the descriptions. This, in some cases, has been mistakenly incorporated and labelled as type material in these collections (e.g. *Cordylus tasmani* Power, Branch, 1999b), even though they have no nomenclatural standing.

In the latter part of his tenure as Director at the Albany Museum, Hewitt's taxonomic rigour was strained by the great morphological variability displayed by the rich chelonian fauna of southern Africa. He described numerous new taxa, particularly among the ornately patterned tent tortoises. Within *Chersinella* (now *Psammobates*) he recognised no less than 27 species and subspecies, many occurring in sympatry or within close proximity to one another. Apart from one enthusiastic amateur (Archer, 1968, 1973), this diversity was rejected by most subsequent workers and the great monographic review of African chelonians by Loveridge & Williams (1957) reduced the complexity considerably, leaving only three species: *P. geometrica, P. oculiferus* and *P. tentorius* (the latter with three poorly defined subspecies, *tentorius, trimeni and verroxii*, whose ranges overlapped considerably; see Greig and Borchet, 1976). It should be stressed, however, that Loveridge and Williams were unfamiliar with southern African tortoises in the field and that a modern taxonomic appraisal of morphological variability within the *Psammobates tentorius* complex is urgently required (Cunningham & Branch, in prep.).

Despite his chelonian confusion, Hewitt remains the fourth most prolific describer of valid southern African reptiles (47 taxa), particularly of lizards, of which he described 43 taxa. He also described a single snake species (*Bitis albanica*), but only three of his many "new" chelonian species and subspecies are still recognised. He also erected a number of new reptile gen-

era (of which two are still valid), including *Basutosaura* (= *Tropidosaura*), *Megachersine* (= *Geochelone*, Loveridge & Williams, 1957), *Narudasia, Neotestudo* (= *Chersina*, Loveridge & Williams, 1957), *Pseudacontias* (Madagascan; = *Paracontias* Mocquard, Brygoo, 1980), *Pseudomopus* (currently a synonym of *Homopus*, but possible representing a valid genus; Branch in prep.), *Rhoptropella* (= *Phelsuma*,), and *Scelotes*. He is also responsible for naming the greatest number (19) of southern African amphibians, as well as the amphibian genera *Anhydrophryne, Arthroleptella, Microbatrachus* (= *Microbatrachella*), *Microphryne* (Madagascan) and *Natalobatrachus*.

Hewitt was the first southern African herpetologist to attempt to compile zoological subregions within southern Africa based on the composition and distribution of the fauna. His initial study involved only lizards, and he identified distinctive western and eastern sub-regions (Hewitt, 1910). However, he stressed that not all species were restricted to either of these sub-regions, and that in the north both merged into adjacent regions. His list of characteristic lizards of the western arid region includes the radiation of lacertids in the genera *Eremias* (= *Pedioplanis* and *Heliobolus*) and *Scaptira* (= *Meroles*, including *Aporosaura*), the gekkonid genera *Ptenopus, Palmatogecko, Chondrodactylus, Rhoptropus* and *Colopus*, and species such as *Chamaeleo namaquensis* and *Typhlosaurus lineatus*. He noted (Hewitt, 1910) that "the most characteristic elements of the western sub-region show many structural adaptations for a deserticolous habitat." Although he recognised no specific Cape region, he did note that the Limpopo River formed a northern barrier for some species, including *Mabuia trivittata* (= *Mabuya capensis*), *Pseudocordylus microlepidotus* (then containing *P. melanotus*) and *Chamaesaura aenea*, whilst species such as *Agama kirkii* were not found south of the river.

As Poynton (1987) has noted, Hewitt (1923) incorporated a phylogenetic component into his zoogeographic observations with his observation of "the great number of apparently primitive forms in the Cape fauna, especially that of the west". However, Hewitt's assessment of primitive characters was subjective and not formulated within a modern phylogenetic approach, rooted in monophyly, outgroup analysis and character polarisation. Moreover, his use of the term "primitive" appears to contain a hierarchical assessment of grade (ability), rather than a simple reflection of ancestral distance. This is reflected in statements such as: "early stocks of lizards, whose descendants remain as the various serpentiform genera, were pushed to the coastal belt by the recent lizards which now dominate Southern Africa" (Hewitt, 1923). Throughout much of this discussion serpentiform species are often termed "degenerate" and their movement underground seen as a retreat from "dominant", fully limbed forms. It is also true that Hewitt was a dispersalist, believing in successive waves of dominant tropical species invading the subcontinent, pushing the more primitive forms southwards to the coastal regions.

His administrative duties, especially after the disastrous fire that destroyed the Albany Museum in 1941, curtailed his herpetological career, and his popular summary of the Eastern Cape vertebrate fauna (Hewitt, 1937) was one of his last contributions to southern African herpetology. During his lengthy career, Hewitt described 153 taxa, including four varieties (roughly equivalent to races), 67 subspecies, 69 species and 13 genera. Of these, one genus and 10 other taxa were Madagascan. With changing species concepts (Frost & Hillis, 1990) and taxonomic refinements, the use of varietal and subspecific categories is in decline. Currently 62 (47.7%) of Hewitt's 130 non-generic herpetological taxa are still considered valid. His massive contributions to reptile systematics were only belatedly recognised with the descriptions of *Heleophryne hewitti* Boycott 1988 and *Phyllodactylus hewitti* (= *Goggia hewitti*, Branch *et al.*, 1995a), although earlier FitzSimons (1947) had named a small frog (*Arthroleptella hewitti*) in his honour.

FitzSimons and his sons

Frederick William FitzSimons became the Director of the Port Elizabeth Museum in 1906, and soon afterwards opened the first snake park in Africa. He published the first popular books on South African snakes (FitzSimons, 1910, 1912), and was the first to detail the toxic nature of boomslang venom (FitzSimons, 1909). These were not minor moments, as the snake park was only the second in the world, and his books were the first on African snakes and some of the first in the world to adopt a popularist theme. They were also the first summaries of the subcontinent's snake fauna. He also did pioneering work on the production of antivenoms for the treatment of snakebite. Although FitzSimons never described any new taxa, he was the first to record in a local newspaper, the *Eastern Cape Herald*, the presence of the red-lipped snake (*Crotaphopeltis hotamboeia*) in the Eastern Cape; hence the origin of one of the popular names (Herald snake) for the species. His name is commemorated in the snake lizard *Tetradactylus africanus fitzsimonsi* Hewitt 1915 (= *Tetradactylus fitzsimonsi*).

FitzSimons had two sons, Vivian and Desmond, both of whom continued their father's herpetological interests. Desmond, the younger son (1906–1963), worked with his father at the Port Elizabeth Snake Park, where from 1933–1937 he was an honorary assistant working on the development of antivenoms. In 1939, in company with his mother, he established the FitzSimons Snake Park in Durban, where he milked thousands of snakes. He became the leading distributor of antivenoms in South Africa, and supplied much of the antivenom used during the Second World War. In his later life he prepared most of the line drawings and photographs for his brother's *Field Guide to the Snakes of South Africa* (FitzSimons, 1970). He made no direct contributions to the systematics of the subcontinent's reptiles, although he did discover the first specimens of the forest cobra in Zululand (FitzSimons, 1947), a species then previously known only as far south as Malawi.

Following the award of an M.Sc. from Rhodes University in 1923, Vivian FitzSimons (1901–1975) became the Curator of Lower Vertebrates, and later the Director, of the Transvaal Museum in Pretoria. Despite curating fish as well reptiles and amphibians, FitzSimons showed little systematic interest in fish, and the substantial part of his publication output concerned systematic herpetology. In none of his papers or monographs did FitzSimons attempt any form of overview of assemblages or affinities within the southern African herpetofauna, and he appears to have been uninterested in either their evolution or biogeography. He was the first native South African to undertake active field work, and he was a member of the Vernay–Lang Kalahari Expedition in 1930, and the Southern Rhodesia Expedition in 1937. Between 1929–1941 he produced a dozen systematic papers in the *Annals of the Transvaal Museum*, describing numerous new species of reptiles and amphibians. These culminated in his major monograph on *The Lizards of South Africa* (FitzSimons, 1943), a thesis for which he was award a D.Sc. from the University of the Witwatersrand in 1942. Following his appointment as Director of the Museum in 1947 he concentrated more on snake systematics, although he continued to describe new lizards, frogs and a fish. His latter studies again culminated in a monographic treatment, this time of the region's snakes (FitzSimons, 1962). This publication, which continues to form the definitive text on the subcontinent's snake fauna, was completely revised by Don Broadley and republished as *FitzSimons' Snakes of Southern Africa* (Broadley, 1990a).

During his lengthy career, FitzSimons described numerous taxa (96), including 37 subspecies and 58 species but only one genus (*Angolosaurus*). His studies were basically restricted to the subcontinent, and he described few extralimital species (e.g. *Phelsuma astovei* from the Indian Ocean and *Ablepharus anselli* from Zambia). Despite the relatively unknown fauna he studied, only 50% of his descriptions are still valid (Table 2); 36 of 57 lizards (63.2%), five of

11 snakes (45.5%), two of seven amphisbaenians (28.6%), and one of three chelonians (33.3%). He seemed to have had a particularly poor eye for frogs, as only four of the 18 (22.2%) amphibian species he described are still valid. He even redescribed Boulenger's species *Strongylopus hymenopus* twice in different genera, first as *Phrynobatrachus lawrencei* in 1947 and then as *Rana draconensis* in the following year!

Numerous reptiles and amphibians commemorate his name, including: the legless skinks *Fitzsimonsia* Witte and Laurent 1943 (= *Typhlacontias*), *Scelotes fitzsimonsi* Broadley 1994, and *Typhlosaurus aurantiacus fitzsimonsi* Broadley 1868, the gecko *Pachydactylus laevigatus fitzsimonsi* Loveridge 1947 (= *Pachydactylus fitzsimonsi*), the flat lizard *Platysaurus guttatus fitzsimonsi* Loveridge 1944 (= *Platysaurus orientalis fitzsimonsi*), the plated lizard *Gerrhosaurus flavigularis fitzsimonsi* Loveridge 1942 (= *G. flavigularis*), and the snakes *Elapsoidea sundevallii fitzsimonsi* Loveridge 1944 and *Lycodonomorphus laevissimus fitzsimonsi* Raw 1973 (= *Lycodonomorphus laevissimus*).

Arthur Loveridge and Donald Broadley

During the period 1925–1957 Arthur Loveridge was the most prolific African herpetologist. On his retirement, this mantle transferred to Don Broadley, who remains, without doubt, Africa's premier living herpetologist. In fascinating symmetry, Broadley's early history mirrors that of his mentor, Arthur Loveridge. Both were born in England, first became interested in reptiles as teenagers, published short natural history notes on British snakes, and the early education of each was affected by world wars. Loveridge was appointed in 1914 to the post of Curator at the new Museum in Kenya. His early army service in East Africa was punctuated with herpetological collecting, and after the end of hostilities he became a game warden in Tanganyika (Tanzania). However, he continued to collect reptiles and amphibians, many of which he had difficulty identifying. Following a fortuitous meeting with Thomas Barbour, then Assistant Curator of Herpetology at the Museum of Comparative Zoology (MCZ), Harvard University, Loveridge forwarded his collections to Harvard. Later (1924), he was invited to Harvard (at Barbour's personal expense) to replace him at the MCZ. There Loveridge blossomed, undertaking a series of five year-long expeditions to East Africa. The reports of the immense collections he amassed formed the basis for his definitive monographic reviews of African lizard families and many snake groups (for fuller details and references see Adler, 1989).

Numerous species names honour Loveridge; among the African herpetological examples are the amphibians *Arthroleptis loveridgei* de Witte 1933 (= *Schoutedenella loveridgei*) and *Rana loveridgei* Laurent 1954 (= *Ptychadena porosissima*), the amphisbaenid genus *Loveridgea* Vanzolini 1951, the snake *Elapsoidea sundevallii loveridgei* Parker 1949 (= *E. loveridgei loveridgei*), and the gecko *Afroedura transvaalica loveridgei* Broadley 1963 (= *A. loveridgei*).

Shortly before Loveridge retired from MCZ to St Helena in 1957, Don Broadley was demobbed after conscripted service in the Royal Air Force. The latter stages and aftermath of the Second World War had severely curtailed Broadley's education, but his interest in herpetology led him, like Loveridge 40 years earlier, to apply to become Curator at the Corydon Museum in Nairobi, but the post was unavailable. Instead, in October 1954, he accepted a Town Planning post in Salisbury, Rhodesia (Harare, Zimbabwe). Within a few years he moved to the Roads Department and a field station near Bulawayo. His constant travels in the field soon unearthed (literally in many cases) numerous reptiles, many of which were not easily identified. The standard monograph on lizards (FitzSimons, 1943) only patchily covered the region north of the Limpopo River, especially for tropical species that only just extended south of the Zambezi River. Loveridge's reports on his East African collections were therefore more useful. Shortly after he had contacted Loveridge, the first of Broadley's numerous scientific publications began

to appear; they included a review of the snakes of Rhodesia that appeared in the MCZ *Bulletin* (Broadley, 1959).

During the next 40 years Broadley published over 200 detailed scientific papers of African herpetology (see Branch, 1997 for a detailed bibliography). Within them are the descriptions of 84 new African taxa, including 4 genera (and subgenera), 41 species and 39 subspecies. Of these 51 (19 snakes, 25 lizards, and 6 amphisbaenians) are valid southern African reptile taxa (Fig. 3; Table 1). All but two remain valid, although the status of several others has changed, being subsequently validated as full species. Recent papers have been increasingly synthetic and monographic in nature. In collaboration with Professor J.C. Poynton a five-part synopsis of the amphibians of the Zambeziaca region (Zimbabwe, Botswana, Malawi, Zambia and Mozambique) was prepared (Poynton & Broadley, 1985, 1986, 1987, 1988, 1991), whilst Fitz-Simons' classic monograph on southern African snakes was fully revised (Broadley, 1990a). Checklists with keys have been published for Zambia (Broadley, 1971, 1973), Zimbabwe (Broadley, 1988), and Tanzania (Broadley & Howell, 1991).

In recognition of the extent and quality of his contributions, Broadley received the first Herpetological Association of Africa "Exceptional Contribution to African Herpetology Award" (Branch, 1991a). A special issue of the *African Journal of Herpetology* (volume 46(2), 1997) was dedicated to him in the year of his 65th birthday (Branch, 1997). In addition, numerous African reptiles and amphibians have been named in his honour, including: *Acontias plumbeus broadleyi* FitzSimons 1956 (= *A. percivali occidentalis*, Broadley & 1969), *Hyperolius marmoratus broadleyi* Poynton 1963 (= *H. swynnertoni broadleyi*); *Nothophryne broadleyi* Poynton 1963, *Hemisus guineensis broadleyi* Laurent 1972, *Ptychadena broadleyi* Stevens 1972, *Leptopelis broadleyi* Poynton 1985, *Pelusios broadleyi* Bour 1986, *Lygodactylus broadleyi* Pasteur 1995, *Elapsoidea broadleyi* Jakobsen 1996, *Leptotyphlops broadleyi* Wallach & Hahn 1997, *Platysaurus broadleyi* Branch & Whiting 1997, and *Atheris broadleyi* Lawson 1999.

The last 25 years

Interest in the southern African reptile fauna is reflected in the increasing number of authors publishing new descriptions and undertaking taxonomic studies. Much of this has been driven by the growth of university involvement in systematic studies, and the increase in funding stimulated by concern over the biodiversity crisis (e.g. Anon, 1994; Cotterill, 1995). The changing political climate has also lessened the isolation of South African scientists, resulting in burgeoning international collaboration. The latter has prompted the increasing application of molecular studies and modern cladistic analysis of phylogenetic relationships. Mirroring the increased depth of modern systematic analysis has been an increasing tendency for researchers to specialise in specific groups; e.g. the Cordylid working group based in Stellenbosch (see Mouton & Van Wyk, 1997, and references therein) and studies on the Gekkonidae by Prof. A. Bauer (Villanova University) and his co-workers (e.g. Bauer *et al.*, 1997).

A large proportion of local herpetologists currently active in the subcontinent were nurtured by Prof. J.C. Poynton, via the far-sighted accelerated M.Sc. programme initiated at the University of Natal. Emphasising regional surveys and systematic reviews, the students under Poynton's supervision undertook detailed studies, e.g. Broadley (1964, 1966), Jacobsen (1989), Lambiris (1988), Bates (1992) and Boycott (1993). Both directly, via their publications, and indirectly, via the large collections from poorly known areas that they amassed, their studies have been instrumental in the renaissance in herpetology in the subcontinent.

Regional focus has also been evident in individual studies in the karroid and western arid regions (e.g. Haacke, 1984; Auerbach, 1987; Branch & Braack, 1989; Bauer *et al.*, 1993;

Branch, 1994), in the eastern subtropical zone (e.g. Bruton & Haacke, 1980; Broadley, 1990b, 1992), and Cape fold mountains (e.g. Mouton *et al.*, 1987; Branch, 1990; Branch & Bauer, 1995). The work of Jacobsen (1989) in the northern provinces of South Africa (the old Transvaal) resulted in the discovery of numerous new taxonomic novelties (e.g. Jacobsen 1992, 1994, 1997; Jacobsen & Newbery, 1989).

Phylogenetic studies on southern African reptiles are still in their infancy, with only a few groups being the subject of modern systematic analysis. Phylogenies have been proposed for only a few groups, most notably the Lacertidae (Arnold, 1989), the lacertid genera *Pedioplanis* and *Meroles* (Arnold, 1991), southern African gekkonid genera (Bauer 1990; Joger 1985), and leaf-toed geckos (Bauer *et al.*, 1997). A number of others are under study (e.g. Cordylidae, Mouton *et al.*, in prep.; *Platysaurus*, Whiting & Keogh in prep.; *Pachydactylus* and related genera, Bauer *et al.*, in prep.; and *Bradypodion*, Branch *et al.*, in prep.).

Biogeography

Recent zoogeographic studies on the herpetofauna have also been led by Poynton. He initially developed Hewitt's ideas with amphibians, noting a specific Cape Temperate fauna that passed through an abrupt transition to a Tropical fauna (Poynton, 1962). In a general paper on the region's herpetofauna, Poynton & Broadley (1978) elaborated this concept further, but made little comment on Hewitt's proposal of a western, desert-adapted lizard fauna. Further refinement of zoogeographical sub-regions followed Bruton & Haacke's (1980) review of the Maputaland herpetofauna. This introduced additional sub-categories, including Eastern and Western Tropical Transitional and Temperate Transitional, as well as Tropical Wide-Ranging and Tropical East Coast Littoral sub-divisions. This introduced a new flexibility, assigning species rather than geographical areas to categories, thus accommodating individual variation in species distributions. It is an approach that has been used in numerous regional surveys (e.g. Haacke, 1984; Bates, 1992; Branch & Bauer, 1995).

The formulation of subjective zoogeographic subregions, much like Acocks' (1975) veld types, has descriptive value but gives little insight into the evolutionary processes or vicariant events that may have shaped reptile diversity. Indeed Crowe's (1990) objective demonstration of high species diversity of amphibians along the eastern and southern seaboard and depauperate lizard diversity in the central region seem to reflect little more than the distribution of the dominant ecological factors for both groups, i.e. rainfall for amphibians, and rock for lizards.

Attempts to integrate reptile distributional data with phylogenetic hypotheses are in their infancy. Mouton & Oelofsen (1988) proposed a model to explain the speciation and distribution of melanistic geographical isolates in the *Cordylus cordylus* complex in the south-western Cape. They proposed vicariant splitting of a warm-adapted ancestral population during the last glacial period (20–18 000 years BP), local adaptation of a melanistic isolate, subsequent fragmentation of its range (leading to the speciation of *C. niger* and *C. oelofseni*), and re-invasion of valleys and coastal regions by the warm-adapted *C. cordylus* following amelioration of the climate (10–5 000 years BP). As attractive as this model appears, the various isolates when subsequently tested by allozyme studies have proved to have much greater genetic distances than predicted (Brody *et al.*, 1993). However, it is entirely possible that the general scenario is correct, but occurred earlier, perhaps piecemeal, during previous glacial cycles.

Although Arnold (1991) has proposed detailed phylogenies for southern African *Pedioplanis* and *Meroles* (including *Aporosaura*), and has demonstrated in *Meroles*, at least, a progressive adaptation to sandy habitats, it has not been easy to translate the current distributions of the species into a series of hypothesised vicariant events.

Branch (1990) has briefly summarised some of the processes likely to have generated

geographical isolates, and thus promoted speciation in the southern African herpetofauna. He noted that fluctuations in the extent of the southern coastal plain caused by sea-level changes associated with Glacial Maxima, and the climatic changes associated with these marine transgressions, can be expected to affect adjacent montane populations. The current, almost mutually exclusive, distributions of *Cordylus coeruleopunctatus* and *C. cordylus* in the southern Cape coastal region represents a situation analogous to that hypothesised by Mouton & Oelofson (1988) for melanistic cordylids in the southwestern Cape. These events have also affected other species in the region, including isolates on the offshore islands (Branch, 1991b), and may be responsible for the disjunct coastal populations of *Lycophidion capense, Gerrhosaurus flavigularis* and *Nucras lalandei*. In addition, the speciation of various disjunct and putative sister taxa, including *Bufo pardalis–pantherinus, Hyperolius semidiscus–horstockii, Afrixalus knysnae–brachycnemis*, and *Bitis armata–albanica*, may have resulted from such vicariant events affecting coastal populations. The recent description of the Cunene racer (*Coluber zebrinus*) from Northern Namibia (Broadley & Schätti, 1997), a genus with obvious Palearctic affinities previously only known as far south as southeast Kenya, may add reptilian support to the proposed transient "arid corridor" linking the Horn of Africa and the southwest arid region (Balinsky, 1962).

More recently, the development of computerised geographical information software has stimulated attempts to define southern African patterns of distributions, species richness and endemism (e.g. vertebrates, Crowe, 1990; snakes, Lombard *et al.*, 1995; chelonians, Branch *et al.*, 1995b). However, the results of these studies have not been combined with phylogenetic hypotheses to reveal possible vicariant scenarios that may have generated the observed diversity, but rather have been used to guide and objectify conservation and land-use management, etc.

Conservation

The high endemicity displayed by southern African reptiles is reflected in many of their restricted distributions, and this may have important conservation consequences for these taxa. Very restricted distributions, i.e. species known from less than five quarter-degree squares (one QDS = approximately 25 km square), are common in southern African reptiles, particularly among rupicolous and forest-dwelling forms. Currently ten species of Southern African *Cordylus* (*aridus, cloetei, imkeae, minor, niger, namaquensis, lawrenci, campbelli, pustulatus*, and *rhodesianus*) have such limited distributions. Most are restricted to the southern and western regions of the subcontinent. Similar restricted distributions are also displayed by many other lizards, including the cordylids (*Pseudocordylus nebulosus, Platysaurus monotropis, P. relictus, P. intermedius inopinus*, and *P. i. parvus*), chameleons (e.g. *Bradypodion kentanicum, B. taeniabronchum, Rhampholeon marshalli*, and *R. gorongosae*), geckos (*Cryptactites peringueyi, Goggia braacki, G. gemmula, Afrogecko swartbergensis, Afroedura major, Homopholis mulleri, Lygodactylus bernardi, L. graniticolus, L. methueni, L. waterbergensis, Pachydactylus oreophilus, P. sansteyni*, and *P. tsodiloensis*), fossorial skinks (e.g., *Typhlosaurus lineatus richardi, T. lomii, Acontophiops lineatus, Acontias poecilus, Scelotes limpopoensis albiventris, S. inornatus, S. vestigifer*, and *S. insularis*), and a few lacertids (*Australolacerta rupicola, Pedioplanis husabensis*, and *P. rubens*). Very restricted distributions are not as evident in snakes, but do occur in the taxa *Bitis inornata, B. albanica, Leptotyphlops pungwensis, L. telloi, Aparallactus nigriceps, Lycophidion semiannule, L. nanum, L. pygmaeum, Coluber* sp., and *Montaspis gilvomaculatus*. Despite the intensity of publicity and conservation attention directed towards endangered birds and mammals in southern Africa, no endemic birds and few small mammals have such restricted ranges.

It is now over a decade since the appearance of the last revision of the South African Red Data book for Reptiles and Amphibians (SA RDB, Branch, 1988b). No comparable Red Data Book of threatened reptiles is available for the adjacent countries of southern Africa. In addition to the numerous taxonomic novelties discovered in southern Africa during the last decade, other well-known species are now known to have more restricted distributions or are subject to increased environmental threats. At least 53 South African reptile species have very restricted distributions (see above), and yet their possible conservation plight remains sadly neglected. It is obvious that many of these species urgently require conservation attention, and a modern reappraisal of the SA RDB for Reptiles and Amphibians is essential. For example, the Albany adder (*Bitis albanica*) is known from only eight specimens and is severely threatened by habitat destruction (Branch, 1999a). It appears to be one of the most endangered vertebrates in Africa, and yet its threatened status remains neglected and almost unknown.

The future of reptile systematics in southern Africa

Despite recurrent pleas for the importance of systematic studies (e.g. Crowe *et al.*, 1989; Cracraft, 1995; Davis, 1996), herpetological manpower in southern Africa declines, with the recent loss of senior herpetological posts at South African Museum (1991), State Museum, Windhoek (1990), National Museum, Bloemfontein (1997), Transvaal Museum (1999), Transvaal Nature Conservation (1996), Eastern Cape Nature Conservation (1997) and KwaZulu-Natal Parks Board (1997). No new appointments at these, or other national museums or nature conservation bodies, have refilled these vacated posts. Technical assistant posts at other institutions, e.g. Port Elizabeth Museum, have also been frozen for many years. Aside from the direct problem of curtailed curation and research on these existing collections, the lack of manpower also has longer-term consequences. There is a critical lack of training for the next generation of herpetological curators, and the national heritage of historical collections, amassed at great cost and labour, are in danger of deteriorating through neglect.

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