African Herp News

## Newsletter of the Herpetological Association of Africa



Number 50

**APRIL 2010** 

## ARTICLES

### RECENT STUDIES ON THE EVOLUTION OF AFRICAN SNAKES AND CHELONIANS: A PERSONAL PERSPECTIVE

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Many of the recent systematic studies on Southern African reptiles have been reviewed elsewhere (Branch & Bauer 2010). I refer readers to that review for a more detailed presentation of recent systematic methodology and the resultant taxonomic insights and updates. In this less formal presentation, and as retirement looms and I enter my dotage, it seems opportune to review the changing paradigm in systematic research as illustrated by some of my recent collaborative studies on African snakes and chelonians. There is not space to document all the literature dealing with these changes; again I refer interested readers to the review above.

Modern systematics places emphasis on revealing patterns of relationship among groups. Such patterns are figuratively represented as trees or cladograms. Monophyly, the property of a clade (group) that consists of an ancestor and all its descendants, is the *sine qua non* of modern systematics, and all modern classifications comprises hypotheses of nested groups exhibiting monophyly (phylogenies). Biochemical adjuncts to traditional taxonomy have proliferated since the middle of the last century. However, detailed genomic analysis linked with increasingly sophisticated computer processing of sequence data, is a phenomenon of the 21<sup>st</sup> century. These recent technological advances have allowed a more objective assessment of phylogenetic relationships.

It has become increasingly obvious that species may result from different mechanisms and histories, and there is increasing use of evolutionary and phylogenetic species to reflect hypotheses about the boundaries of past and present gene transfer within evolutionary lineages of Life's diversity. The burgeoning discipline of 'Evo-Devo' (the interface between development and evolution; see Carroll 2005 for a popular review) has demonstrated how quickly drastic morphological change can occur by modulation of the activity of genes that govern embryonic development. Many findings of molecular phylogenies conflict with historical ideas of relationships previously based solely or largely on morphological analysis. The conflict between earlier classifications based on morphotypic species definitions, and modern molecular phylogenies becomes particularly evident with generic hierarchies. Earlier classifications that highlighted unique morphologies led to the creation of monotypic genera for extreme morphotypes. This is the case with the web-footed gecko (previously *Palmatogecko rangei*) which despite its bizarre morphology is now known to be closely related to thick-toed geckos (*Pachydactylus*), to which it has since been transferred. Conversely, the emphasis on morphology resulted in a lack of appreciation of deep evolutionary divergences that may be obscured by the selective maintenance of conservative morphologies. This again can be illustrated with a local example; many of the geographically isolated populations of leaf-toed geckos previously placed in the cosmopolitan genus *Phyllo-dactylus* are now assigned to different families of gekkotan lizards (e.g. African *Gog-gia* to the Gekkonidae, and New World *Phyllodactylus* to the Phyllodactylidae). As we have become aware of the extent of cryptic (in a morphological sense) diversity, there has been a burgeoning description of new species, genera, and higher categories, or the revival from synonymy.

#### Chelonia

My forays into chelonian biology have been opportunistic, often anecdotal and sadly superficial. Despite a few early forays (e.g. Branch 1984, Burger & Branch 1994) I have not given the group the effort and attention it deserves. However, for the last 15 years this has not been necessary as the detailed studies of Retha Hofmeyr and Victor Loehr, along with their students and colleagues, have brought a modern approach to the study of tortoise biology in the subcontinent. My work has simply resolved some taxonomic issues, i.e. the description of a new dwarf tortoise (Homopus solus Branch 2007) from Namibia, and to present a general overview of chelonian diversity and biology in sub-Saharan Africa (Branch 2008). However, I continue to be intrigued by the impact of avian predation on tortoises. I published a number of early studies on chelonian predation by Kelp Gulls (Branch & Els 1990) and Pale Chanting Goshawk (Malan & Branch 1992), and with Chris and Tilda Stuart I am currently looking at chelonian predation by White-necked raven in the Karoo. I am also involved with Uwe Fritz (Dresden) and others in assessing phylogeography and species boundaries within the Marsh terrapin (Pelomedusa subrufa) and Hinge-back tortoises (Kinixys sp.). The former has been particularly exciting, revealing deep genetic structure and possibly numerous cryptic species within this Pan-African species

#### Snakes

#### Higher Order Relationships

When I first started as a herpetologist at Port Elizabeth Museum in 1979 the landscape of snake systematics was very different. The 'Colubridae' existed as a massive (over 2500 species) and unwieldy assemblage of 'advanced' snakes. The family was little more than a rag bag for snakes that didn't have other specialized features such as erectile (Viperidae) or fixed (Elapidae) front fangs. Due to the simplified anatomy that attends a serpentine life style, snakes do not possess many external or internal features that allow confident classification of monophyletic groups. Similar problems have dogged the classification of other serpentine squamates, including worm lizards (amphisbaenians) and even grass lizards (*Chamaesaura*).

The first snake classification I became familiar with had basically existed since the time of Boulenger (1858-1937), and it displayed a preoccupation with dentition using snake teeth as key features in assigning snakes to certain families. Now, with the genius of hindsight, it is difficult to appreciate why such strange snakes as 'mole vipers' (*Atractaspis*), as they were then known, were classified for so long as a viper, despite their completely un-viperid appearance and life style. Even their fang erection mechanism is completely different from that of true vipers. My early studies on hemipenes, chromosomes and the serotaxonomy of African snakes were all stimulated by the desire to address the systematic affinities of *Atractaspis*, as they were to tackle other taxonomic problems. Now different hypotheses of snake relationships appear almost monthly, and in bewildering diversity. I detail below some of the general and more specific problems in snake systematics with which I have recently been involved.

#### Scolecophidian Snakes

In recent years I have collaborated with Blair Hedges (Penn State University, USA), Nicolas Vidal (Paris, France) and Steve Donnellan (Adelaide, South Australia), along with other co-workers, on a broad assessment of higher level relationships within primitive scolecophidians snakes. We have constructed a molecular dataset for scolecophidians with detailed sampling within the largest family, Typhlopidae (blindsnakes).

The results (Vidal et al. 2010) show that scolecophidians have had a long Gondwanan history, and that initial diversification followed separation of East and West Gondwana ~150 million years ago (Myr ago). Monophyly of the Anomalepididae and Leptotyphlopidae is confirmed, but deeper than expected divergence occurs within the Typhlopidae. The major recent clades of blind snakes diverged between 63 (78–49) and 59 (74–46) Myr ago, just after the end-Cretaceous extinctions, and subsequent diversification of clades during the Cenozoic parallels that of their primary food sources—ants and termites.

Previous detailed morphological studies, particularly those of Don Broadley and Van Wallach (Broadley & Broadley 1999, Broadley & Wallach 1997a, b), were believed to have resolved much of the species diversity within African thread snakes (Leptotyphlopidae). However, evolutionary relationships within the family remained almost completely unknown. The family is relatively large (nearly 120 species) and has a mainly Gondwanan distribution. For many years it comprised a single massive genus (*Leptotyphlops*), with only one other monotypic West African genus (*Rhinoleptus koniagui*). Solny Adalsteinsson was the lead researcher on a molecular phylogeny of leptotyphlopids (Adalsteinsson *et al.* 2009) that revealed deep genetic divergence between morphologically very conservative lineages. A new classification of the family proposed massive higher order readjustment, with the recognition of two subfamilies, the Epictinae (New World and Africa) and Leptotyphlopinae (Africa, Arabia, and Southwest Asia). Three tribes were recognized within the latter subfamily, of which two

(Myriopholini and Leptotyphlopini) occur in southern Africa. Most southern African species were retained in a reduced *Leptotyphlops*, but a number were transferred to new genera including *Myriopholis longicaudus, Namibiana occidentalis* and *N. gracilor*. An additional finding of this initial study was evidence of an unusually large number of undescribed species. More than a dozen have been provisionally identified, particularly within the *Leptotyphlops scutifrons-conjunctus-incognitus* species complex. For other scolecophidians a large molecular dataset of all major lineages was assembled, and our results (Vidal et al. 2010) demonstrated that scolecophidians have had a long Gondwanan history, and that their initial diversification followed the separation of East and West Gondwana approximately 150 Ma. The earliest blindsnake lineages, representing two new families, were distributed on the palaeolandmass of Indigascar (India + Madagascar). Later evolution involved several oceanic dispersals, including westwards across the Atlantic.

#### Viperidae

The taxonomic status and phylogenetic relationships of the radiation of small adders (*Bitis*) of the subcontinent remain complicated. When describing *Bitis rubida* (Branch 1997) I specifically restricted the type locality to the Cederberg population, being aware that there existed confusing morphological variation in other populations, particularly from the Little Karoo (Branch 1999). Studies of variation within different populations of the Red Adder (*B. rubida*) and the Berg Adder (*Bitis atropos*), as well as phylogenetic relationships between all small *Bitis*, are currently underway. In conjunction with Chris Kelly (Rhodes University), Wolfgang Wüster and Axel Barlow (Bangor University, Wales) we have been accumulating tissues for molecular analysis and traditional morphological data in order to address these various problems. Studies of the four isolated populations of *B. atropos*, using molecular and morphological analysis, have already demonstrated that some of these populations should be treated as separate species, and that genetic divergence of populations within the Cape Fold mountains also indicate the possible presence of cryptic taxa (Branch & Kelly 2008; Kelly et al. 2009a). The formal description of these new species is in preparation.

In the introduction I discussed increasing awareness that morphology can change very rapidly and obscure evolutionary relationships. A good example is the recent description of a dwarf, terrestrial forest viper, *Atheris mabuensis*, from northern Mozambique (Branch & Bayliss 2009). Previously the bizarre fat, terrestrial Usambara viper (*Adenorhinus barbouri*) was placed in a monotypic genus when, in fact, it is genetically closely-related to arboreal forest vipers (*Atheris*) and has been formally transferred to that genus (Branch & Bayliss 2009). The new Mozambique species represents a terrestrial habitat shift within the genus that may have preceded the rapid morphological adaptations displayed by *A. barbouri*.

#### The African Snake Radiation

Recently I have collaborated on several molecular studies designed to investigate

phylogenetic relationships within the African snake radiation, as well as studies on a number of more restricted groups within this radiation. In the first (Nagy et al. 2005), a spectrum of 49 snakes from a broad variety of families was investigated. The results identified a number of interesting groupings, particularly the monophyly of a number of informal groups discussed earlier by Charles Bogert (Bogert 1940) and Monique Bourgeois (Bourgeois 1968), i.e. the Atractaspidinae, Psammophiinae, Lamprophiinae, and Pseudoxyrhophiinae (although these are not always the names they used).

The removal of Atractaspis from the Viperidae to a new family (earlier the Atractaspidae, but now more correctly Atractaspididae or Atractaspidinae, depending on the hierarchy adopted – see below) led to conflicting common names for the group (burrowing asps, stiletto snakes, side-stabbing snakes), and also to a search for their close relatives. Sam McDowell (McDowell 1968) first indicated that dwarf garter snakes (now harlequin snakes, Homoroselaps, and then placed in the genus Elaps) were wrongly placed within the family Elapidae. His detailed morphological studies indicated that they were better grouped with a suite of other African burrowing snakes, including *Atractaspis*, the Natal Black Snake (Macrelaps), purple-gloss snakes (Amblyodipsas), centipede-eaters (Aparallactus), quill-snouted snakes (Xenocalamus), and several other small snakes from the central and west African tropical forests. However, the status of harlequin snakes as atractaspidids or elapids see-sawed for sometime, depending upon whether authorities placed emphasis on cranial anatomy or venom gland morphology (Underwood & Kochva 1993). In the last iteration of my field guide (Branch 1998) harlequin snakes were still grouped with elapids. However, Nagy et al. (2005) subsequently confirmed that harlequin snakes (*Homoroselaps*) were not elapids, despite their front fangs and venom, and that McDowell (1968) was correct in suggesting that they are most closely related to Atractaspis and other African burrowing snakes.

The clades Psammophiinae, Lamprophiinae, and Pseudoxyrhophiinae all group with atractaspidids and elapids, and have subsequently been placed in a superfamily Elapoidea. They are not closely related to other African 'back-fanged' snakes such as eggeaters (*Dasypeltis*), twig snakes (*Thelotornis*), boomslang (*Dispholidus*), herald snakes (*Crotaphopeltis*), tiger snakes (*Telescopus*), green snakes (*Philothamnus*), etc, which are all colubrids (in a now more restricted clade). Neither are they related to marsh snakes (*Natriciteres*) or swamp snakes (*Limnophis*), which are African representatives of the mainly Eurasian and Neotropical water snakes (Natricidae).

The psammophiine genera (*Dipsina, Hemirhagerrhis, Malpolon, Mimophis, Psammophis, Psammophylax,* and *Rhamphiophis*) are distributed throughout Africa including Madagascar, the Middle East, south-central Asia, and southern Europe (Branch 1998). Their monophyly is well supported by morphological and molecular data, and the studies of Chris Kelly and colleagues have done much to resolve evolutionary relationships within the group, including the transfer of *Dromophis* into the synonymy of *Psammophis* (Kelly et al. 2008). The Pseudoxyrhophiinae includes numerous endemic Malagasy snake genera, as well as a number of species found in the Comoros. Surprisingly, a number of problematic genera from continental Africa (*Duberria, Amplorhinus* and possibly

*Montaspis*), whose evolutionary relationships were previously obscure, were found to associate with this clade (Vidal et al. 2008).

The Lamprophinae (sensu Vidal *et al.* 2008), an assemblage of African snakes equivalent to the Lamprophidae of Kelly et al. (2009b), includes a basic division between wolf snakes and their relatives (*Lycophidion, Hormonotus, Mehelya* and *Gonionotophis*) and house snakes and their relatives (*Pseudoboodon, Bothrolycus, Bothrophthalmus, Lamprophis* and *Lycodonomorphus*).

Generic and species boundaries within these clades are problematic, and a number of generic re-arrangements and descriptions of cryptic taxa are to be proposed (Kelly et al. in prep.). The relationships of a number of unusual snakes, such as shovel-snouts (*Prosymna*), Western keeled snake (*Pythonodipsas carinata*) and mole snake (*Pseudaspis cana*), sometimes placed in additional families (Prosymnidae and Pseudaspididae, Kelly et al. 2009b), I consider still unresolved.

There are different, and somewhat conflicting, classifications of Elapoid snakes, and these reflect different hypotheses of relationships among the snakes studied. I am coauthor on conflicting treatments of Elapoid classification, that either recognize an inclusive Lamprophiidae containing varying numbers of subfamilies (e.g. Atractaspidinae, Psammophiinae, Lamprophiinae, and Pseudoxyrhophiinae; Vidal *et al*, 2008, 2009), or that threats these subfamilies as full families, each of equivalent status to the Elapidae (e.g. Kelly et al., 2008, 2009b). My apparent schizophrenia simply reflects differences among myself and my colleagues as to the hierarchical level to be placed on the major branches of the different phylogenies. These differ in their fine structuring and statistical support, and the different classifications are affected by both the number and variety of genes sequenced and the diversity of taxa sampled. It must be stressed that classifications are not 'cast in stone', but rather reflect consensus and usage, and only time will tell which of these various hypotheses, if any, serve the herpetological communities' needs.

#### 'Colubridae'

There have been few studies on African Colubridae *sensu stricto*, and phylogenetic relationships within non-elapoid African snake groups remain poorly known. Bourgeois (1968) erected a subfamily Philothamninae, but this has not yet been assessed by molecular data and its status even as a tribe (Philothamini) remains problematic. Green snake tissues were incorporated into a molecular assessment of the status of green snakes from São Tomé and adjacent islands in the Gulf of Guinea (Jesus et al. 2009). The study revealed that the insular species *Philothamnus girardi* and *Philothamnus thomensis* should be consider as distinct sister species. They form a monophyletic unit that indicates a single colonization event of one island (probably São Tomé), followed by dispersal to Annobon. In addition, *Hapsidophrys principis* from Príncipe was also shown to be a valid species and sister to mainland *H. smaragdina*. Eli Greenbaum (University of Texas at El Paso, USA) and I are currently accumulating tissues from *Philothamnus* and related genera in order to resolve their phylogeny.

#### **Final comments**

This brief review is personal and idiosyncratic. These are exciting times in reptile systematics, with numerous individuals and groups publishing cutting-edge research. The phylogenies and proposed new classifications are bound to be unstable, and some will be discarded and others modified as a greater diversity of taxa and markers are incorporated. These hypotheses of relationship will be further impacted as herpetologists address the challenge of developing a full squamate classification. That snakes are a subset of lizards is uncontested. The nomenclatural problem is to reshuffle the familial and suprafamilial hierarchies of both snakes and lizards in a manner that reflects systematic truth, and yet causes the least disruption to familiar names and arrangements. It will not be easy!

#### ACKNOWLEDGEMENTS

Bayworld, the small provincial museum at which I'm based, does not have gene sequencing equipment, nor am I competent to undertake such studies. Thus the great majority of the laboratory work for the studies that I detail above was undertaken by colleagues, as reflected in the fact that I am a junior author on most of the resultant publications. I prefer to view this relationship as more symbiotic than parasitic....To all I acknowledge my debt, and give my thanks for friendship and collaboration.

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# THE SOUTHERN AFRICAN REPTILE CONSERVATION ASSESSMENT, 2005-2009

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#### INTRODUCTION

In the more than twenty years that have elapsed since the publication of the last Red Data Book of Reptiles of South Africa (Branch 1988) there have been substantial improvements in our understanding of reptile diversity, distribution and threats. For example, between 1988 and 2006, there was a 25% increase in the number of recognized reptile species, with an average of six new species described per year (Branch et al. 2006). Over the past two decades the distribution ranges of several reptile species have been considerably altered by the transformation of land for agriculture, urban development