



Snakes of Angola: An annotated checklist

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Abstract.—The first annotated checklist for over 120 years is presented of the snakes of Angola, Africa. It details the snakes currently recorded from Angola (including the Cabinda enclave), and summarizes the literature documenting their description, provenance, and often tortuous taxonomic history. The species are assigned, with comment where appropriate, to higher taxonomic groupings based on modern snake phylogenetic studies, and the need or potential for further studies are noted. In 1895 José Vicente Barboza du Bocage recorded 71 snakes in his monographic treatment of the Angolan herpetofauna, and subsequently Monard (1937) added 10 additional species. This review documents the 122 snakes currently recorded from Angola, and lists a further seven that have been recorded in close proximity to the Angolan border and which can be expected to occur in Angola, albeit marginally. Cryptic diversity identified in taxa such as the *Boaedon capensis-fuliginosus-lineatus* complex and *Philothamnus semivariegatus* complex indicate more species can be expected. Relative to southern Africa, the Angolan snake fauna contains a higher proportion of colubrid snakes, enhanced particularly by diverse arboreal species of the Congo Basin. There are relatively few endemic snakes (5.4%), and most inhabit the mesic grasslands of the escarpment and adjacent highlands. None are obviously threatened, although records of the endemic Angolan adder (*Bitis heraldica*) remain scarce and the species may require directed surveys to assess its conservation status.

Resumo.—Este trabalho apresenta a primeira lista comentada de cobras de Angola, África. Esta lista enumera as espécies atualmente registradas em Angola (incluindo o enclave de Cabinda) e resume a bibliografia que documenta a sua descrição, origem, e história taxonómica, muitas vezes sinuosa. As espécies são atribuídas, com comentários quando se justifica, a grupos taxonómicos superiores, com base em estudos filogenéticos recentes, e a necessidade ou potencial para mais estudos é também referida. Em 1895, José Vicente Barboza du Bocage registou 71 espécies de cobras no seu estudo monográfico da herpetofauna angolana. Mais tarde, Monard (1937) adicionou 10 espécies. Esta revisão documenta as 122 espécies atualmente registradas para Angola, e lista outras sete que foram também encontradas perto das fronteiras angolanas e cuja ocorrência em Angola, embora de modo marginal, pode ser expectável. A diversidade críptica identificada em táxons como o complexo *Boaedon capensis-fuliginosus-lineatus* e o complexo *Philothamnus semivariegatus* indicam que mais espécies podem ser esperadas. Comparativamente com a África Austral, a fauna de cobras de Angola tem uma maior proporção de colubrídeos, aumentada particularmente por diversas espécies arborícolas da Bacia do Congo. Há relativamente poucas (5,4%) espécies endémicas, e a maioria ocupa as pastagens de altitude da escarpa e o planalto adjacente. Nenhuma espécie se encontra ameaçada de forma evidente, embora os registos da víbora angolana endémica (*Bitis heraldica*) continuem a ser escassos, e a espécie possa requerer levantamentos dirigidos para que o seu estatuto de conservação seja avaliado.

Keywords. Bocage, taxonomy, Africa, diversity, endemism, conservation

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Introduction

The need for national summaries of biodiversity and the selection of suitable areas for protection are of increasing urgency in the face of exploding human populations and their demand for natural resources. However, biodiversity surveys in Angola were severely curtailed in the post-colonial era, and for nearly 60 years studies on

Angolan biodiversity remained almost quiescent. Reptile studies were particularly curtailed and as a consequence knowledge of the status and distribution of many Angolan snake species remains poorly known. This is understandable as the last monographic review was published over 120 years ago (Bocage 1895). Nearly 50 years later Monard (1937) prepared an updated overview incorporating new material (Monard 1931), but overlooked a

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number of regional reports (e.g., Schmidt 1933; Parker 1936), and many others have subsequently appeared (e.g., Mertens 1938; Bogert 1940; Hellmich 1957a; 1957b; FitzSimons 1959). Summaries of snakes in the collection of the Museu do Dundo in extreme north-east Angola (Laurent 1950, 1954; Tys van den Audenaerde 1967) added numerous records of snakes from the Congo Basin. Others were added by Laurent (1964), who also described the extensive collections of reptiles from northeast and southwest Angola collected by António Barros de Machado, then Director of the Museu do Dundo. In the last 10 years increasing access to Angola, coupled with awareness of the urgent need to document the remaining wildlife and to revitalize the Angolan protected area network, has led to increasing numbers of herpetological surveys (Huntley 2009; Ceriaco et al. 2014, 2016; Ernst et al. 2014; Huntley 2015; Conradie et al. 2016, 2017; Conradie and Branch 2017; Branch 2018) and the concomitant discovery of new species (amphibians - Conradie et al. 2012a, 2013; reptiles - Conradie et al. 2012b; Stanley et al. 2016; Branch et al. 2017). Regional (Branch et al. 2012; Ceriaco et al. 2014a, 2016a; Baptista et al. 2018a) and even national (Oliveira 2017) summaries are increasingly appearing, and this checklist forms part of these developments.

All these publications included important taxonomic insights and new records of Angolan snakes, but usually listed only generalized localities for the species with little discussion of habitat associations, although Parker (1936), Monard (1937), and Hellmich (1957b) attempted to place the herpetofauna within an early biogeographic framework. Most, however, were working with museum collections, many collected by explorers or local people and with little habitat insight or even detailed locality data. These deficiencies all limit their usefulness in constructing biogeographic patterns, or in gaining insight into the conservation of the listed species. At the outset it is important to stress aspects of Bocage's (1895) monograph, particularly with respect to its coverage and the taxonomic milieu in which it was written. His work summarizes nearly 30 years of study on the Angolan herpetofauna, but also includes discussion of some species from the adjacent Congo area, particularly between the Congo River mouth and the Bight. His discussions include material from Cabinda Province (formerly Portuguese Congo), which was established as a protectorate of Angola in 1885, but only fully incorporated into Angola by the mid-1920s.

Although Bocage described many new genera and species from Angola, many were subsequently synonymized under other names. In part, this was because his papers before the mid-1880s were during the early stages of his development as a taxonomist, and he was not as familiar with the peripheral literature. More importantly he was not based at a major European museum such as those in London, Paris, or Berlin, and Portugal was also no longer a dominant colonial power. Albert Günther and George Boulenger at the British Museum were fa-

miliar with a cosmopolitan herpetofauna rather than just African, and perhaps were less impressed by novelty than Bocage. Certainly, Bocage deferred to Boulenger's judgement when the latter synonymized many of Bocage's new taxa, often without comment in his publications and his monumental catalogue of snakes (Boulenger 1883–1886). Bocage did, however, continue to discuss variation within Boulenger's composite species and subsequently, as modern taxonomy developed new tools and insight into evolutionary relationships, some of Bocage's names were revived (e.g., *Afrotyphlops angolensis* from *Typhlops punctatus* and *Phliothamnus angolensis* from *P. irregularis*). In some of his species accounts Bocage used varieties (var.), e.g., *Typhlops punctatus* var. *lineolatus*, which in many respects is an outdated equivalent of subspecies. The latter itself has been under criticism as lineage-based species definitions become increasingly prevalent (Frost and Hillis 1990) and the subspecies concept considered by many redundant. Acceptance of this in the modern taxonomic approach is reflected in recent revisions in which no new subspecies of southern African snakes have been described in the last 40 years, and many earlier subspecies proposed in particular by Laurent and Broadley in the 1960s–1980s have been either rejected or raised to full species. Many of the 'varieties' Bocage noted have subsequently been re-assessed, some rejected, some becoming full species.

The online Reptile Database (Uetz et al. 2018) has revolutionized public access to biodiversity documentation. It provides a wealth of information for every currently recognized reptile species, summarizing details of the original description, locality of type material, generalized synonymies, relevant literature, etc. It is a 'home base' for systematic studies and the generation of regional checklists. Understandably, however, it is not without problems. A search on Reptile Database (Uetz et al. 2018) currently generates a list of 267 Angolan reptiles, including 122 snakes. Unfortunately, it is inaccurate in a number of respects, as some species are included that are unknown from the country: e.g., *Calabaria reinhardti*, *Aparallactus guentheri*, and *Hemirhagerrhis nototania*, and even the South American *Micrurus bogerti* and Madagascan *Compsophis boulengeri*. Other species are duplicated and listed under historical and current assignments: e.g., *Atheris ansiolepis* (= *Atheris squamigera*) and *Bitis peringueyi* (= *Bitis heraldica*).

As a first small step towards a modern synthesis of the Angolan herpetofauna an up-to-date annotated checklist of the snakes of Angola is summarized below. It builds on the summaries in Bocage (1895) and Monard (1937), and on a modern electronic database (Uetz et al. 2018), but includes details of taxonomic changes, literature conflicts, and new discoveries. It does not fully cover the historical literature, or directly re-assess the identification of historical museum material. It also makes no attempt to map the distributions of Angolan snakes, as other initiatives are currently involved in these tasks (Marques et al. 2014). Instead it serves as a working document for Afri-

can and Angolan researchers, established and new, who want to understand the diversity of Angolan snakes and the development of our knowledge of them. The checklist details the 122 snakes currently recorded from Angola (including the Cabinda enclave), and summarizes the literature documenting their description, provenance, and often tortuous taxonomic history. The species are assigned, with comment where appropriate, to higher taxonomic groupings based on modern snake phylogenetic studies, and the need or potential for further studies are noted. For the historical literature authors of only original records are noted, and historical place names have been updated to their modern name or spelling at the first occurrence and the updated name subsequently used. Additional new snake distribution records for Angola will be published elsewhere (Branch et al., in prep.). Gazetteer of most historic Angolan place names mentioned in early faunal accounts is included in Crawford-Cabral and Mesquitella (1989).

Comments on the Checklist

The higher-level taxonomy adopted in the checklist reflects recent developments in our understanding of phylogenetic relationships of African snakes. Recent taxonomic insights into higher nomenclatural categories are included in the introductory text to the various sections below, and many are updated versions of those presented elsewhere for South African snakes (Branch and Bauer 2014). Vidal et al. (2009) summarized increasing understanding of the early history and phylogenetic relationships of snakes. At the outset it should be stressed that snakes are a subset of lizards but that this is rarely reflected in current taxonomic hierarchies where snakes are afforded similar subordinal status (Serpentes) to that of all other lizards (Sauria). This historical anomaly is slowly being addressed and a suitable nomenclatural hierarchy developed that addresses these relationships and their attendant complexity (e.g., Pyron et al. 2013). It has become increasingly evident that snakes originated on West Gondwana, that part of the supercontinent comprising South America and Africa. Among extant lineages, the deepest divergencies are found between what have been termed the Amerophidia and Afrophidia (Vidal et al. 2009). The monophyly of this division has been supported in subsequent molecular phylogenies (e.g., Reynolds et al. 2014), and also reproductive anatomy (Seigel et al. 2011), but awaits full acceptance (Hisang et al. 2015). The division occurred 106 (116–97) Ma, probably in association with continental breakup. Most (~85%) living snakes are afrophidians and are now globally distributed, having initially dispersed out of Africa through Laurasia or on the ‘Indian raft’. Most basal afrophidian families (Henophidia) diverged in the Cretaceous (104–70 Ma), while advanced afrophidian families (Caenophidia) diverged in the early Cenozoic, 63–33 Ma (Vidal et al. 2009).

The ~3,500 living snakes display an evolutionary trend

of increasing gape size, from fossorial scolecophidians (locally represented by the blind snakes, Typhlopidae, and thread snakes, Leptotyphlopidae) to ecologically diverse alethinophidians, large-mouthed lineages that feed and swallow large prey (also more descriptively called macrostomatans). Among the latter, the Henophidia (pythons and relatives) comprise relictual lineages scattered throughout tropical and subtropical regions, and including all but one of the world’s largest (>5 m) snakes. The Caenophidia comprise the great majority of living snakes (~2,700 spp.), divided among numerous families, and including all the venomous species.

The use of subspecies (previously races or varieties) has been declining in the 21st Century (Uetz and Stylianou 2018), and no snake subspecies have been described in greater southern Africa (the subcontinent and all the countries immediately bordering to the north) since two South Africa races of *Lycodonomorphus laevis* (Raw 1973).

SCOLECOPHIDIA

Blind snakes (Typhlopidae) and thread snakes (Leptotyphlopidae) and their non-African relatives are ancient lineages. Due to their burrowing life style they are morphologically conservative and have thus been a source of great taxonomic confusion in studies based on traditional morphology. Fortunately, recent detailed morphological studies by Broadley and Wallach on both African families (Broadly and Watson 1976; Broadley and Broadley 1999; Broadley and Wallach 2007a, b, 2009) has brought relative stability to species boundaries in both. However, modern molecular phylogenies have not only revealed the antiquity of these lineages, but also deep divergences between them (Adalsteinsson et al. 2009; Hedges et al. 2014; Pyron and Wallach 2014; Nagy et al. 2015). As a consequence, higher taxonomic relationships within scolecophidians have been in upheaval with numerous new genera, and the shuffling of species between these as taxon sampling increases. In leptotyphlopids numerous cryptic species have been signaled (Adalsteinsson et al. 2009), and studies on Australian typhlopids have shown similar diversity (Martin et al. 2013). Despite the current taxonomic upheaval, deeper insight into both phylogenetic relationships and biogeographic patterns continue to emerge (Vidal et al. 2010; Nagy et al. 2015), with scolecophidians believed to undergo an initial diversification following the separation of East and West Gondwana and isolation on Indigascar, the combined India and Madagascar (Vidal et al. 2010). Studies on Angolan scolecophidians are in their infancy and it is likely that further taxonomic diversity awaits discovery. Western arid leptotyphlopids of Southern African were placed in the genus *Namibiana* by Adalsteinsson et al. (2009), whilst Broadley and Wallach (2009) placed most Angolan typhlopids in the new genus *Afrotiphlops*, as well as reviving *Letheobia* for the majority of the small, pink, attenuate forms.

Family: Leptotyphlopidae

Shaba Thread Snake

Leptotyphlops kafubi (Boulenger 1919)

Glauconia kafubi Boulenger, 1919. Descriptions d'Ophidiens et d'un Batracien nouveaux de Congo. *Rev. Zool. Afr.*, Bruxelles 7(2): 186.

Revived from synonymy of *Leptotyphlops nigricans* by Broadley and Broadley (1999). Unknown from Angola by Bocage (1895), but subsequently recorded by Laurent (1964, as *Leptotyphlops emini emini*) from Lagoa Calundo and Luisavo Falls (= Quedas do Luisavo). No fresh material has been recorded.

Peter's Thread Snake

Leptotyphlops scutifrons (Peters 1854)

Stenostoma scutifrons Peters, 1854. Diagnosen neuer Batrachier, welche zusammen mit der früher (24 Juli und 17 August) gegebenen Übersicht der Schlangen und Eidechsen mitgeteilt werden. *Ber. Bekanntmach. Geeignet. Verhandl. Königl.-Preuss. Akad. Wiss.*, Berlin 1854: 621.

Bocage's (1895) records from Catumbela and Novo Redondo (=Sumbe) were reassigned to *Nambiana latifrons* (Broadley and Broadley 1999). Bocage's (1895) material from Duque de Braganca (= Calandula), Huila, Biballa (= Bibala), Capangombe, Caconda and Cahata, and Ferreira's (1904) from Cazengo and Zembe were destroyed and their current assignment remains problematic. The presence of this species in Angola is currently confirmed by only a single specimen from Chitau, north of Kuito (Broadley and Broadley 1999), however, Adalsteinsson et al. (2009) demonstrated that numerous cryptic lineages are currently subsumed under *L. scutifrons* (type locality Sena, Mozambique), and it is unlikely that Angolan material is conspecific with Mozambique material.

Damara Thread Snake

Namibiana labialis (Sternfeld 1908)

Glauconia labialis Sternfeld, 1908. Neue und ungenügend bekannte afrikanische Schlangen. *S. Ber. Ges. Naturforsch. Freunde Berlin* 4: 92.

The first Angolan specimen was collected in May 1954 by Dr Charles Koch at Miranda, Cunene Province, Angola (1614Dd, 16°47'S, 14°57'E). This was documented by Broadley and Broadley (1999), but overlooked in subsequent reviews of the region (Ceriaco et al. 2016a). No other Angolan material has been recorded. Adalsteinsson et al. (2009) placed the species and others in the new genus *Namibiana*.

Benguela Thread Snake

Namibiana latifrons (Sternfeld 1908)

Glauconia latifrons Sternfeld, 1908. Neue und ungenügend bekannte afrikanische Schlangen. *S. Ber. Ges. Naturforsch. Freunde Berlin* 4: 94.

This species has caused confusion, and continues to be mis-assigned to *L. scutifrons* (Ceriaco et al. 2016a). Sternfeld (1908) noted that material identified as *Glauconia scutifrons* by Boulenger was different from Peters (1854) type for the species, and therefore proposed the new name *Glauconia latifrons* for this material. Unfortunately, he gave no type locality. Broadley and Watson (1976) noted that Boulenger's knowledge of *scutifrons* was based solely on two specimens from Benguela, identified as such by Peters (1865). To stabilize the situation, they designated the Benguela material as the types of *Leptotyphlops latifrons*, and also reassigned Bocage's (1895) records of *Stenosoma scutifrons* from Catumbela and N'Gunza (= Novo Redondo) to *L. latifrons*. The species is endemic to the coastal region of southwestern Angola.

Angolan Beaked Thread Snake

Namibiana rostrata (Bocage 1886)

Stenostoma rostratum Bocage, 1886. Typhlopiens nouveaux de la Faune africaine. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 11: 173.

The only specimen known to Bocage (1886) was his type of *Stenosoma rostrata* sent by Anchieta from "Humbe, sur les bords du Cunene." Broadley and Broadley (1999) noted additional material, including another thread snake collected in May 1954 by Dr Charles Koch at Vane e Lombe, Namibe Province, Angola (1513Ad, 15°30'S, 13°30'E), two from west of Huila, and a problematic record from "Luanda." Many old specimens were listed from the home base of the collector, rather than from where they were actually collected. Fresh material from Luanda is required to confirm if the species extends as far north.

Family: Typhlopidae

Angolan Blind Snake

Afrotyphlops angolensis (Bocage 1866)

Onychocephalus angolensis Bocage, 1866. Lista dos reptis das possessões portuguesas d'África occidental que existem no Museu Lisboa. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 1: 46, 65.

First described by Bocage (1866a) as *Onychocephalus angolensis* nov. sp.?, but without a diagnosis and therefore a *nomen nudum*. It was soon correctly described by Bocage (1866b) from "districto do Duque de Bragança,

situado na latitude de Loanda, porém umas 75 leguas para o interior, portuguesas Africa occidental.” He confusingly treated it as *Typhlops conigicus* (Boettger 1887) in his monograph (Bocage 1895) even though his own name had priority. Parker (1936, as *T. punctatus intermedius*) recorded it from Congulu and Quirimbo, and Laurent (1954, finally as *T. angolensis*) from Dondo. Laurent (1964) described Dundo material as the subspecies *T. angolensis adolfi*, but this is no longer recognized (Broadley and Wallach 2009).

Angolan Giant Blind Snake

Afrotyphlops anomalus (Bocage 1873)

Onychocephalus anomalus Bocage, 1873. Reptiles nouveaux de l'intérieur de Mossamedes. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 4: 248.

Described by Bocage (1873a) from “Huilla, l'intérieur de Mossamedes,” (= Huilla, Huila Province, not “Moçamedes [= Namibe]” as recorded by Ceriaco et al. 2016a). Other localities are given in Bocage (1895) and Monard (1937). Broadley and Wallach (2009) discussed the varied taxonomic history of the species and placed it in a new genus (*Megatyphlops*) that was itself subsequently subsumed within the current genus (Hedges et al. 2014). The species appears to occur on the high plateau and has recently been recorded at Lubango and other inland localities.

Blotched Blind Snake

Afrotyphlops congestus (Duméril and Bibron 1844)

Onychocephalus congestus Duméril and Bibron, 1844. *Erpetologie Générale ou Histoire Naturelle Complete des Reptiles*. Vol. 6. *Libr. Encyclopédique Roret*, Paris: 334.

A northern Congo Basin species that extends south to Cabinda, and is known only from the type of *Typhlops* (*Onychocephalus*) *crassatus* Peters, 1881 collected at “Chinchoxo” (= Lândana, Cabinda). Its complicated taxonomic history is reviewed by Broadley and Wallach (2009).

Lined Blind Snake

Afrotyphlops lineolatus (Jan 1864)

Typhlops (*Ophthalmidion*) *lineolatus* Jan, 1864. *Iconographie générale des ophiidiens*. 9. Livraison. J.B. Bailière et Fils, Paris: 24.

First recorded from Angola by Bocage (1893) when he described *Typhlops boulengeri* (type-locality “Quindumbo, dans l'intérieur de Benguela, Angola”). Later corrected to *Typhlops punctatus lineolata* (Bocage 1895), and described again as *Typhlops bocagei* by Fer-

reira (1904) from “Cabicula, Bom Jesus (margens do Quanza).” Additional material was noted from Cazengo (Ferreira 1903), Rio Luinha (Ferreira 1906), and Dundo Laurent (1954, 1964). Broadley and Wallach (2009) designated a lectotype (BMNH 1946.1.11.18) for *T. boulengeri* Bocage, 1893. Ceriaco et al. (2014b) noted a syntype (MHNFCP 017434) from Angola donated to the Porto museum from Lisbon, and confirmed the identity of the specimen. However, Bocage’s original material from “Quindumbo” (= Chindumbo – Crawford-Cabral and Mesquitela 1989) is now lost, and a range extending to Benguela Province does not conform to the species’ known habitat (forest) and distribution (Broadley and Wallach 2009). The only other Angolan localities given for the species by Broadley and Wallach (2009) are Cazengo (Ferreira 1903) and Rio Luinha (Ferreira 1906), both in Cuanza Norte Province. Bocage’s (1893) Chindumbo locality should be treated with caution unless confirmed by new material. Ceriaco et al. (2014b) signaled the possible rediscovered of one of the syntypes of *Typhlops bocagei* Ferreira, 1904, but have not subsequently discussed its significance with respect to its current taxonomic status.

Schmidt’s Blind Snake

Afrotyphlops schmidti (Laurent 1956)

Typhlops schmidti Laurent, 1956. Laurent RF. 1956. Contribution à l’herpetologie de la région des Grandes Lacs de l’Afrique centrale. *Ann. Mus. Roy. Congo Belge* (Sci. Zool.) 48: 71.

Described from “Nyunzu, Terr. D’Albertville,” Democratic Republic of the Congo (DRC) (Laurent 1956), the species is mainly restricted to southern DRC and adjacent northern Zambia, with only two records for Angola; Calundo and Cazombo, Moxico Province (Laurent 1964).

Schlegel’s Blind Snake

Afrotyphlops schlegelii (Bianconi 1847)

Typhlops [sic] *schlegelii* Bianconi, 1849. Lettera al Dottore Filippo de-Filippi, Professore di Zoologia a Torino sopra alcune nuove specie di rettili del Mozambico. *Nuovi Ann. Sci. Nat.*, Bologna (ser. 2) 10: 106.

All country records are restricted to localities above the escarpment in southwest Angola. Bocage was confused by this species and described it as a new species on three different occasions: *Onychocephalus petersii* described from “Biballa” (= Bibala, Namibe Province) (Bocage 1873a), *Typhlops* (*Onychocephalus*) *humbo* described from Quissange (Bocage 1886), and *Typhlops hottentotus* from “Humbe” (Bocage 1893). Broadley and Wallach (2009) discuss this taxonomic confusion and summarize recent records.



Fig. 1. *Afrotrophlops mucroso*, Lungue Bungue River, Moxico Province (Photo: Werner Conradie).

Giant Blind Snake

Afrotrophlops mucroso (Peters 1854)

Onychocephalus mucroso Peters, 1854. Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgeteilt werden. *Ber. Bekanntmach. Geeignet. Verhandl. Königl.-Preuss. Akad. Wiss.*, Berlin 1854: 621.

A sister species to the previous species and long considered an eastern subspecies. Broadley and Wallach (2009) map five localities in northwest Angola but give no voucher details. Laurent (1964) listed *Typhlops schlegeli mucroso* from Chicapa, Calonda and Camissombo in Lunda Province, and these may be the source (in part) of these records. It extends further south in the poorly surveyed eastern region of the country (Fig. 1.; Conradie April 2018).

Leopoldville Beaked Blind Snake

Letheobia praeocularis (Stejneger 1894)

Typhlops praeocularis Stejneger, 1894. Description of a new species of blind snake (Typhlopidae) from the Congo Free State. *Proc. US Natl. Mus.* 16: 709.

Known in Angola from a single record from Dundo (Laurent 1964, as *Typhlops praeocularis lundensis*). Roux-Esteve (1974) rejected the race *lundensis* and transferred the species to *Rhinotyphlops*. Binomials were retained by Broadley and Wallach (2007), who transferred the species again to *Letheobia*.

HENOPHIDIA

Family: Pythonidae

Pythons form part of the Henophidia, along with boas and their relatives. They are restricted to the Old World with about 40 species in eight genera, most within Australasia and with only four in Africa, three of which occur in Angola. The Calabar Burrowing Python (*Calabaria reinhardtii*) is no longer included within the Pythonidae as it has greater affinities with boas, and is placed in a monotypic subfamily (Calabariinae) within an enlarged Boidae (Pyron et al. 2014). It is restricted to forest habitat in West Africa and the Congo Basin, but is unknown from Angola, although it may extend south into Cabinda.

Namib Dwarf Python

Python anchietae (Bocage 1887)

Python anchietae Bocage, 1887. Sur un Python nouveau d'Afrique. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 12: 87.

Bocage (1887a) described the dwarf python from "Catumbella" (= Catumbela, Benguela Province). Additional Angolan specimens are noted from Hanha (Bogert 1940) and 18 km from Lobito to Hanha (Laurent 1964). During field work in Angola (1974), Wulf Haacke collected the only record from the inland plateau at Viriambundo, Huila Province (15°33'S, 14°03'E, 1,288 m a.s.l.). Restricted mainly to the coastal plain of southwest Angola, with a more extensive distribution in northern Namibia.

Southern African Python

Python natalensis (Smith 1840)

Python natalensis Smith, 1840. Illustrations of the Zoology of South Africa, Reptilia. Smith, Elder, and Co., London: 3, pl. 9.

Angolan pythons examined by Bocage (1895) were mostly from southern Angola and conformed to *P. natalensis*. He thus referred them to *P. natalensis*, but he was cautious whether they were "a species apart or... a simple variety of *P. Sebae*". For most of the 20th Century African pythons were treated as a monotypic *P. sebae*, although Monard (1931) noted that his material from Ebanga, Chimporo and Vila da Ponte (= Cuvango) had the characteristics of *natalensis*. Broadley (1984) revived *P. s. natalensis* as a subspecies for southern populations, to which he referred material from Bocage (1895), Bogert (1940), and Monard (1937). He considered the Kwanza River to be the northern boundary for the species in the west. Later he raised *P. s. natalensis* to a full species (Broadley 1999).



Fig. 2. *Python natalensis*, bottom of Leba Pass, Namibe Province.

Northern African Python

Python sebae (Gmelin 1789)

Coluber Sebae Gmelin in Linnaeus, 1789. *Caroli a Linné Systema naturae*. 13. ed., Tom 1 Pars 3. G. E. Beer, Lipsiae: 1118.

Bocage (1895) did not refer any Angolan pythons to *P. sebae*. Broadley (1984), however, considered the species to enter northern Angola, reaching as far south as Ambriz on the coast. Both Laurent (1954, 1964) and Tys van den Audenaerde (1967) recorded pythons from Dundo, which Broadley (1984) also referred to *P. sebae*. Broadley (1984) showed that scalation features overlapped considerably between *sebae* and *natalensis*, and that the most distinctive features between the putative taxa were the extent of scale fragmentation on the crown of the head and head color pattern. There are no Angolan localities where parapatry occurs between the two taxa (Broadley 1984).



Fig. 3. *Python sebae*, Cabesa da Cobra, Soyo (Photo: Warren Klein).

CAENOPHIDIA

Within Africa most snakes are part of the Caenophidian radiation, i.e., the ‘higher’ snakes, and include a suite of snake families that comprise the Colubroidea. Knowledge of snake relationships has changed drastically in the new millennium, fuelled by developments in genetic sequencing, computer assessment and modeling of relationships, and increasing gene and taxon sampling. Numerous new arrangements and higher taxonomic categories have been proposed, and increasing consensus is being reached. Branch and Bauer (2014) gave a summary with an African perspective, but this has been modified by recent phylogenetic updates (e.g., Hsiang et al. 2015; Figueroa et al. 2016). The concept of the Colubroidea proposed by Vidal et al. (2007, 2010), which is restricted to a clade of snakes that is sister to the Elapoidea (Elapidae + Lamprophiidae) of Kelly et al. (2008) is maintained. It includes various families previously treated as subfamilies within a more inclusive Colubridae (e.g., Natricidae and other non-African families), and the Colubroidea is therefore equivalent to previous usage of the Colubridae. Pyron et al. (2011) give fuller discussion and a conflicting treatment. A major difference between conflicting arrangements is that basal caenophidian lineages such as the Viperidae are included, along with other diverse snakes, within the Colubroidea of Pyron et al. (2011), but not

within the restricted usage of Vidal et al. (2007, 2010). The families Natricidae and Colubridae, the latter including the recently recognized subfamily Grayinae (Pyron et al. 2011), are the only representatives of the Colubroidea in Angola. It should be stressed, however, that the higher-level relationships of snakes remain unsettled, and understanding of the snake tree of life remains incomplete (Figueroa et al. 2016) and that the arrangement adopted here is likely to change again.

Family: Colubridae

Relationships within the African colubrid radiation remain unresolved. Based on cranial features Bourgeois (1968) recognized a subfamily Boiginae that included the genera *Boiga* (restricted now to Asia as the two African species were transferred to *Toxicodryas*), *Telescopus*, *Crotaphopeltis*, and *Dipsadoboa*. Subsequent molecular data (Gravlund 2001; Kelly et al. 2003; Figueroa et al. 2016) also support the inclusion of *Dasypeltis* within the Boiginae. Bourgeois (1968) erected two other subfamilies: the Dispholidinae including diverse tree snakes of the genera *Thrasops*, *Rhamnophis*, *Dispholidus*, *Thelotornis* and *Xyelodontophis* (the latter now synonymized with *Thelotornis*, Eimermacher 2012); and the Philothamninae, including the genera *Philothamnus* and *Hapsidophrys*. The latter has not been supported by molecular data although Figueroa et al. (2016) found these genera were sister to Bourgeois Dispholidinae. Broadley and Wallach (2002) recognized Bourgeois subfamily as the tribe Dispholidini, and the diverse colubrids treated as subfamilies by Bourgeois (1968) are perhaps best treated as tribes (Boigini, Dispholidini) within the Colubridae. Relatively few African colubrids have been included in phylogenies, usually with only single species representatives of the diverse genera, and fuller resolution of their relationships await fuller taxon sampling.

Subfamily: Colubrinae

White-lipped Snake

Crotaphopeltis hotamboeia (Laurenti 1768)

Coronella hotamboeia Laurenti, 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austracorum, quod autoritate et consensu. Vienna, Joan. Thomae: 58.

Bocage (1895) considered the species (as *Crotaphopeltis rufescens*) to be common throughout much of Angola, and most recent surveys (e.g., Parker 1936; Hellmich 1957; Ceriaco et al. 2016b; Conradie et al. 2016, 2017) confirm this, although it appears rare in northeast Angola (Laurent 1950).

Barotse Water Snake

Crotaphopeltis barotseensis (Broadley 1968)

Crotaphopeltis barotseensis Broadley, 1968. A new species of *Crotaphopeltis* (Serpentes: Colubridae) from Barotseland, Zambia. *Fieldiana. Zoology* 51(10): 136.

A poorly known snake, still known in Zambia only from the type locality (Kalabo). All other records are restricted to the Okavango Delta (Rasmussen 1997), with the exception of the first records for Angola collected during the National Geographic Okavango Wilderness Project survey of the headwaters of the Cuito River (Conradie et al. 2017; Conradie and Branch 2017).



Fig. 4. *Crotaphopeltis barotseensis*, Lake Saliakembo, Cuando Cubango (Photo: Werner Conradie).

Confusing Egg-Eater

Dasylepis confusa (Trape and Mané 2006)

Dasylepis confusa Trape and Mané, 2006. Le genre *Dasylepis* Wagler (Serpentes : Colubridae) en Afrique de l'Ouest: description de trois espèces et d'une sous-espèce nouvelles. *Bull. Soc. Herp.*, France 119: 28.



Fig. 5. *Dasylepis confusa*, Cuanavale River Source, Cuando Cubango (Photo: Werner Conradie).

This recently described species was described from Senegal, with disjunct records as far east as Cameroon, West Africa (Trape and Mané 2006). Bates (2013) recorded additional material, and extended the range as far south as Gabon, but Bates et al. (2012) and Bates and Broadley (2018) noted that *D. confusa* extends in to Angola. Recent material collected during the NGOWP surveys (Conradie

et al. 2017; Conradie and Branch 2017) conform to this species, as does the illustration of *D. scabra* from Cagandala in Ceriaco et al. (2016b) as it has the '5L' color pattern (Gans 1959) that Trape and Mané (2006) refer to *D. confusa*. Further studies are required to resolve the species' distribution in Angola and further south.

Palm Egg-Eater

Dasypeltis palmarum (Leach 1818)

Coluber palmarum Leach, 1818. in Tuckey, Narrative of an expedition to explore the river Zaire, usually called the Congo, in South Africa, in 1816. London, J. Murray: 408.

Bocage (1895) listed uniform-colored egg-eaters, which he referred to var. *palmarum* from Ambaca, Catumbela, Dombe (= Dombe Grande), Quissange and Quindumbo, and also from Lândana in Cabinda (Peters 1877). Bocage (1897) later listed "Dous exemplares da var. *palmarum*" in material collected by Achietae at Hanha, and Boulenger (1905) referred material from Punga Andonga (= Pungo Andongo) to *D. scabra* var. *palmarum*. Laurent (1964) also recorded a uniform colored snake from Dundo that may well have been *D. palmarum*. Various *Dasypeltis* species with blotched patterns occasionally have uniform-colored individuals, e.g., *D. scabra* (Branch 1998), *D. atra* and *D. medici* Spawls et al. (2018), and the status of uniform-colored Angolan egg-eaters and their assignment to *D. palmarum* needs further study.



Fig. 6. *Dasypeltis palmarum*, Soyo (Photo: Warren Klein).

Rhombic Egg-Eater

Dasypeltis scabra (Linnaeus 1758)

Coluber scaber Linnaeus, 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiæ. 10th Edition: 223.*

Bocage (1895) considered egg-eaters to comprise a "single species of the genus *Dasypeltis*" and with "several varieties more or less distinct in their colors" occurring in Angola. However, as his material was destroyed in the Lisbon fire

it is now difficult to assign his records to the diverse species now recognized or recently described. Subsequent authors, e.g., Parker (1936), Laurent (1954, 1964), Tys van den Audenaerde (1967), Ceriaco et al. (2016) have reported new Angolan material (but see *D. confusa* and *D. plamarum*). Bates and Broadley (2018) elevated *D. loveridgei* Mertens 1954 to a full species based on Namibian material, but whether it extends into southern Angola remains uncertain.

Shreve's Tree Snake

Dipsadoboa shrevei (Loveridge 1932)

Crotaphopeltis shrevei Loveridge, 1932. New opisthoglyphous snakes of the genera *Crotaphopeltis* and *Trimerorhinus* from Angola and Kenya Colony. *Proc. Biol. Soc. Washington* 45: 83.

Described by Loveridge (1932) as *Crotaphopeltis schrevei*, on a single specimen from "Missao de Dondi, Bella Vista" (Missão do Dondi, Huambo, 12°32'S, 16°15'E). Only two other Angolan specimens are known (Chitau, Schmidt 1933; Lagoa Calundo, Moxico Province, Laurent 1964). It is more common in northern Zambia, extending into southeastern DRC. Tanzanian records (Rasmussen 1986; Spawls et al. 2018) from Arusha usually refer to as *D. s. kageleri* are particularly problematic, which possibly deserves specific status (Branch et al. submitted).

Punctate Boomslang

Dispholidus typus punctatus (Laurent 1955)

Dispholidus typus punctatus Laurent, 1955. Diagnoses préliminaires des quelques Serpents venimeux. *Rev. Zool. Bot. Afr.* 51: 129.

Bocage first recorded the boomslang (as *Bucephalus capensis*) in Angola from Dondo, and later (Bocage 1895) noted that the species was very abundant in the highlands, but absent from the coastal region. He listed numerous localities, and others are given by Laurent (1950, 1954, 1964), Tys van den Audenaerde (1967), Peters (1881), Loveridge (1936), Bogert (1940), Manaças (1973, 1981), Ceriaco et al. (2016b), etc. Boomslang display both ontogenetic and sexual dimorphic color change, compounded by regional color phases. This has resulted in numerous taxonomic names, treated by various authors as synonyms, species or subspecies. Males of the most widespread color form in Angola have a dark body with numerous yellow blotches, and were referred to *Dispholidus typus punctatus* based on material from Dundo by Laurent (1954). In a molecular phylogeny of the Boomslang, Eimemacher (2012) identified at least four separate clades that he concluded represented distinct species, including *D. viridis* from southern Africa, north and west of the Great Escarpment, and *D. punctatus* from Angola, northern Zambia and adjacent DRC, but deferred taxonomic revival of these species pending clarification of additional putative new taxa

in East Africa.

Green Boomslang

Dispholidus typus viridis (Smith 1838)

Bucephalus viridis Smith, 1838. Illustration Zoology of South Africa pl. 3.

Bocage (1882) referred material from Caconda to *Bucephalus capensis*, var. *viridis* Smith 1838. Later, however, he noted a green boomslang only from Humbe (Bocage 1895), with other color forms, particularly punctate, occurring at other localities, but also at Humbe. *Dispholidus typus viridis* was recently revived by Broadley and Blaylock (2003), following a molecular phylogeny of the genus (Eimemacher 2012).

Emerald Snake

Hapsidophrys smaragdina (Schlegel 1837)

Dendrophis smaragdina Schlegel, 1837. Essai sur la physiologie des serpens. Partie Descriptive. La Haye (J. Kips, J. HZ. et W. P. van Stockum): 237.

It was known to Bocage (1895) only from Cabinda (Lândana). Subsequently, Ferreira (1903) recorded the first Angolan specimen from N'Dalla-Tando (= N'Dalatando) and Hellmich (1957) added a large series from Piri-Dembos (= Piri). Laurent (1954, 1964) and Tys van den Audenaerde (1967) recorded the first records from northeast Angola (Dundo).

Angolan Green Snake

Philothamnus angolensis (Bocage 1882)

Philothamnus angolensis Bocage, 1882. Notice sur les espèces du genre "*Philothamnus*" qui se trouvent au Muséum de Lisbonne. *Jorn. Sc. Lisb.* 9(33): 7.

Most Angolan material has been referred to *Chlorophis* (= *Philothamnus*) *irregularis*: e.g., Peters (1881), Bocage (1895), Ferreira (1903), Parker (1936), Monard (1937), Bogert (1940), Hellmich (1957), and Laurent (1964). Although Hughes (1985) resolved confusion concerning the content of *Philothamnus irregularis* and restricted this name to West African populations, reviving Bocage's *P. angolensis* for southern populations, this has sometimes been overlooked (e.g., Ceriaco et al 2014; Ceriaco et al. 2016b).

Striped Green Snake

Philothamnus dorsalis (Bocage 1866)

Leptophis dorsalis Bocage, 1866. Lista dos reptis das possessões portuguesas d' Africa occidental que existem no Museu Lisboa. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 1: 48.

When naming *Leptophis dorsalis* Bocage (1866) gave the

ill-defined type locality “Molembo, Afrique occidentale,” which he later emended (Bocage 1882) to “Molembo de la Côte de Loango au nord du Zaire” (= Malembo, Cabinda Prov., ext. NW Angola, 05°20’S, 12°11’E). He later (Bocage 1895) listed a number of Angolan localities (Rio Dande, Loanda, Benguela, Catumbela, and Pungo-Andongo). Those south of the Kwanza River are likely to have been confused with *P. ornatus* (e.g., Catumbela), or their origin given as the collector’s home base (e.g., Benguela). Additional material was recorded (often as *P. semivariiegatus dorsalis*, Loveridge 1958) from Dondo and Libolo (= Calulo) (Hellmich 1957).



Fig. 7. *Philothamnus dorsalis*, Soyo (Photo: Warren Klein).

Emerald Green Snake

Philothamnus heterodermus (Hallowell 1857)

Chlorophis heterodermus Hallowell, 1857. Notes of a collection of reptiles from the Gaboon country, West Africa, recently presented to the Academy of Natural Sciences of Philadelphia, by Dr. Henry A. Ford. *Proc. Acad. Nat. Sci. Philadelphia* 9: 54.

Bocage (1895) knew *Philothamnus herterodermus* only from the Congo, but it was subsequently recorded for Angola from: Congulu (= Fazenda Congulo, Parker (1936), Piri (Hellmich 1957b), Dundo (Tys van den Audenaerde 1967), and Capanda Dam (Ceriaco et al. 2014).

Slender Green Snake

Philothamnus heterolepidotus (Günther 1863)

Ahaetulla heterolepidota Günther, 1863. On some species of tree-snakes (*Ahaetulla*). *Ann. Mag. Nat. Hist.* (3) 11: 286.

This elegant species was known from Angola to Bocage (1866, 1879, 1882, 1887b), and by 1895 he knew it from varied localities (Dondo, Duque de Braganca, Quibala, Caconda and Cassange). Additional records include Muita River, Cameia, Moxico and Dundo (Laurent 1950, 1954, 1964; Tys van den Audenaerde 1967).

Southeastern Green Snake

Philothamnus hoplogaster (Günther 1863)

Ahaetulla hoplogaster Günther, 1863. On some species of tree-snakes (*Ahaetulla*). *Ann. Mag. Nat. Hist.* (3) 11: 284.

Bocage (1895) did not include *P. hoplogaster* in his monograph, but listed material that he had earlier (Bocage 1887b) referred to *P. hoplogaster* from St Salvador du Congo (= M’banza-Kongo) as *P. irregularis*. The status of this specimen remains unresolved. Laurent (1964) listed Angolan material from Dundo, Alto Chicapa and Camissombo, but whether this material is correctly identified also remains unknown. Loveridge (1958) did not list the species from Angola or discuss any material from the country. In contrast, Hughes (1985) mapped seven Angolan records (without M’banza-Kongo), but cited no authority for these records. A snake from north of Saurimo, Lunda Sul Province shows genetic monophyly with *P. hoplogaster* but deep divergence (Englebrecht et al. 2018). This is provisionally referred to this species, but is being investigated further. .

Günther’s Green Snake

Philothamnus nitidus (Günther 1863)

Ahaetulla nitida Günther, 1863. On some species of tree-snakes (*Ahaetulla*). *Ann. Mag. Nat. Hist.* (3) 11: 286.

The only Angolan records are from Dundo (Laurent 1964; Tys van den Audenaerde 1967). Loveridge (1958) treated *P. nitidus* and *P. dorsalis* (see above) as subspecies of *P. semivariiegatus*, but Laurent (1960) revived *P. nitidus* as a valid species and described DRC material as a new race, *P. n. loveridgei*, that Hughes (1985) continued to recognize. However, a molecular phylogeny of the genus (Englebrecht et al. 2018) confirmed specific status of *P. nitidus* but only intra-specific divergence between the two putative subspecies. We therefore reject *P. n. loveridgei* and *P. nitidus* reverts to binomials.

Ornate Green Snake

Philothamnus ornatus (Bocage 1872)

Philothamnus ornatus Bocage, 1872. Diagnoses de quelques espèces nouvelles de Reptiles d’Afrique occidentale. *Jorn. Sci. Lisbon* 4: 80.

Bocage (1872) described his new species on three specimens “from Cacheu, on the coast of Guinea, the other two collected at Huilla by Mr. d’Anchieta” and was therefore probably composite, with the Guinea specimens referable to *P. dorsalis*, which also has a dorsal stripe. Nomenclatural problems were avoided when Bogert (1940) restricted the type locality to Huilla (= Huila), and discussed another specimen from Huambo. Additional material was recorded from Bela Vista (Hellmich 1957), and obtained during the National Geographic Okavango

Wilderness Project survey of the headwaters of the Cuito River (Conradie et al. 2016, 2017).

Spotted Bush Snake

Philothamnus semivariiegatus (Smith 1840)

Dendrophis (Philothamnus) semivariiegata Smith, 1840. Illustrations of the zoology of South Africa, Reptilia. Smith, Elder, and Co., London, 2.

Bocage (1882b) first described *Philothamnus smithii*, based on diverse material from Portuguese Guinea and Angola. He was cautious referring southern Angolan material from Capangombe and Maconjo to his new species, but on coloration considered Angolan material from Catumbela, Huila and Humbe to be similar to material from Bissau. He later (Bocage 1895) referred all Angolan material to *P. semivariiegatus*. Loveridge (1958) restricted the name *P. smithii* to Portuguese Guinea, and Trape and Baldé (2014) revived *smithii* as a West African subspecies of *P. semivariiegatus*, extending from Guinea to Niger (Trape and Mané 2015). They noted that “Molecular studies suggest that this taxon could deserve full species status.” Subsequent Angolan material from Dundo was referred to *P. semivariiegatus* (Laurent 1954, 1964). Recent Angolan material, including some included in a recent molecular phylogeny of the genus (Englebrect et al. 2018), confirmed cryptic diversity within *P. semivariiegatus*.



Fig. 8. *Philothamnus semivariiegatus*, Humpata, Huila.

Large-eyed Green Treesnake

Rhamnophis aethiopissa (Günther 1862)

Rhamnophis aethiopissa Günther, 1862. On new species of snakes in the collection of the British Museum. *Ann. Mag. Nat. Hist.* (3) 9: 129.

In his monograph Bocage (1895) did not consider *Rhamnophis aethiopissa* Günther described from “West Africa,” as it was then unknown from either Congo or Angola. It is a rare arboreal snake of closed canopy forest, and the first Angolan recorded was from Piri (Hellmich 1957).

Hook-nosed Snake

Scaphiophis albopunctatus (Peters 1870)

Scaphiophis albopunctatus Peters, 1870. Eine Mitteilung über neue Amphibien (*Hemidactylus*, *Urosaura*, *Tropidolepisma*, *Geophis*, *Uriechis*, *Scaphiophis*, *Hoplocephlaus*, *Rana*, *Entomogossus*, *Cystignathus*, *Hylodes*, *Arthroleptis*, *Phyllobates*, *Cophomantis*) des Königlich-zoologischen Museums. *Monatsber. Akad. Wiss.*, Berlin 1870: 644.

Bocage (1895) did not know this eastern savannah species from Angola. The only Angolan record is from Mui-ta River (Laurent 1950).

Damara Tiger Snake

Telescopus finkeldeyi (Haacke 2013)

Telescopus finkeldeyi Haacke, 2013. Description of a new Tiger Snake (Colubridae, *Telescopus*) from south-western Africa. *Zootaxa* 3737(3): 281.

A recently described species (Haacke 2013) mainly restricted to Damaraland, Namibia, entering the southwest arid region of Angola. Haacke (2013) recorded a single Angolan record from just north of Namibé and an additional record from Espinheira (Fig. 19.; Branch December 2012).



Fig. 9. *Telescopus finkeldeyi*, Espinheira, Namibe.

Western Tiger Snake

Telescopus semiannulatus polystictus (Mertens 1954)

Telescopus semiannulatus polystictus Mertens, 1954. Neue Schlangenrassen aus Südwest- und Südafrika. *Zool. Anz.* 152: 215.

Bocage (1895) noted that this snake (as *Crotaphopeltis semiannulatus*) was rare in Angola, and was known to him only from Gambos, Humbe, and Quissange. Additional specimens were recorded from Calulo (Hellmich 1957) and recently from coastal Namibe. All these specimens are referred to the western subspecies *T. s. polystictus*, which probably deserves specific status.



Fig. 10. *Telescopus semiannulatus polystictus*, Lucira, Namibe.

Oates' Vine Snake

Thelotornis capensis oatesi (Günther 1881)

Dryiophis oatesi Günther, 1881. In Oates, Matabeleland and the Victoria Falls. London.

Bocage (1895) discussed this species under the name *Dryiophis kirtlandii* var. *oatesi*, and knew that it was “frequently seen in the highlands of Angola to the south of the Kwuanza.” Additional material has been recorded (as *Thelotornis capensis*) from Hanha (Bogert 1940), Chitado (Hellmich 1957), Alto Chicapa (Laurent 1964), and Longa (Conradie et al 2016). Loveridge (1953) revived *oatesii* as a subspecies of *T. kirtlandii*, later transferred to the southern species *T. capensis* by Broadley (1979a).

Forest Vine Snake

Thelotornis kirtlandii (Hallowell 1844)

Leptophis kirtlandii Hallowell, 1844. Descriptions of new species of African reptiles. *Proc. Acad. Nat. Sci. Philadelphia* 1844: 62.

Known to Bocage (1895) in Angola only from Calandula. Subsequent material recorded from Caconda and Quirimbo (Parker 1936), Piri-Dembos (Hellmich 1957); Dundo (Laurent 1964; Tys van den Audenaerde 1967) and Ile Bena-Mai, Rio Luachimo (Laurent 1954).



Fig. 11. *Thelotornis kirtlandii*, Soyo (Photo: Warren Klein).

Yellow-throated Treesnake

Thrasops flavigularis (Hallowell 1852)

Dendrophis flavigularis Hallowell, 1852. On a new genus and two new species of African serpents. *Proc. Acad. Nat. Sci. Philadelphia* 1852: 205.

Bocage (1895) knew the species in Angola only from Cabinda (Lândana), although it was subsequently recorded from Piri (Hellmich 1957).

Jackson's Treesnake

Thrasops jacksoni (Günther 1895)

Thrasops jacksonii Günther, 1895. Notice of Reptiles and Batrachians collected in the eastern half of tropical Africa. *Ann. Mag. Nat. Hist.* (6) 15: 528.

Bocage (1895) did not know the species from Angola, although it was subsequently recorded from Dundo (Tys van den Audenaerde 1967). Broadley and Wallach (2002) reviewed the genus, and did not include Angola in the range of *T. jacksoni*, although in their map they plot a locality at Calandula. The recent discovery of the species in Gabon (Carlino and Pauwels 2013) and also from Soyo, Angola (Fig. 12. Klein April 2011) indicates that the species may occur in sympatry with *T. flavigularis* in the forests of Cabinda and even northwestern Angola. The status of both species in the region needs confirmation.



Fig. 12. *Thrasops jacksoni*, Soyo (Photo: Warren Klein).

Blanding's Treesnake

Toxicodryas blandingii (Hallowell 1844)

Dipsas blandingii Hallowell, 1844. Description of new species of African reptiles. *Proc. Acad. Nat. Sci. Philadelphia* 1844: 170.

This large, nocturnal snake has been recorded infrequently from Angola. Bocage (1895) had no records for Angola and the first documented record for the country was based on a specimen from Congola (Parker 1936).

Subsequently Hellmich (1957) recorded material from Piri and Laurent (1964) from Dundo.

Powdered Treesnake

Toxicodryas pulverulenta (Fischer 1856)

Dipsas pulverulenta Fischer, 1856. Neue Schlangen des Hamburgischen Naturhistorischen Museums. *Abhandl. Nat. Ver. Hamburg* 3(4): 81.

As with Blanding's Tree Snake, Bocage (1895) knew of no Angolan material, and again Parker (1936) and Hellmich (1957) recorded this species from Congulu and Piri, respectively. No additional material is known.

Subfamily: Grayinae

Ornate Water Snake

Grayia ornata (Bocage 1866)

Macrophis ornatus Bocage, 1866. Reptiles nouveaux ou peu connus recueillis dans les possessions portugaises de l'Afrique occidentale, que se trouvent au Muséum de Lisbonne. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 1: 47.

Bocage (1866) described *Macrophis ornatus* by from Duque de Braganca (= Calandula), and it was transferred to *Grayia* by Sternfeld (1917). Little additional material has been recorded: Dundo (Laurent 1954, 1964), Lagoa Carumbo (Branch and Conradie 2015).



Fig. 13. *Grayia ornata*, Lagoa Carumba, Lunde Norte.

Smith's Water Snake

Grayia smithii (Leach 1818)

Coluber smythii Leach, 1818. In Tuckey: Narrative of an expedition to explore the river Zaire, usually called the Congo, in South Africa, in 1816. London, J. Murray: 409.

Bocage (1866) described *Grayia triangularis* based on "l'exemplaire d'Angola, recueilli à Rio Dande par M. Banyures." He continued to use this name in his mono-

graph, although it was soon synonymized with *G. smithii* by Günther (1895). Bocage (1895) noted that it must be rare and confined to north of the Kwanza. The few subsequent specimens confirm its rarity: Cambondo (Ferreira 1904), Dundo and Luachimo River (Laurent 1964).

Thollon's Water Snake

Grayia tholloni (Mocquard 1897)

Grayia tholloni Mocquard, 1897. Sur une collection de Reptiles recueillis par M. Haug, à Lambaréné. *Bull. Soc. Philom.*, Paris (8) 9: 11.

Bocage (1895) had no records for Angola and the only documented record for the country remains Laurent's (1964) record from Rio Muita, Lunda Norte.

Family: Natricidae

The Natricidae is a recent coloniser of Africa, and has a relatively low diversity in sub-Saharan Africa with only five genera (*Afronatrix*, *Heliophis*, *Hydraethops*, *Limnophis*, and *Natriciteres*) and 11 species. All are semiaquatic, feeding on frogs and fish.

Bangweulu Swamp Snake

Limnophis bangweolicus (Mertens 1936)

Helicops bangweolicus Mertens, 1936. Eine neue Natter der Gattung *Helicops* aus Inner-Afrika. *Zoologischer Anzeiger* 114: 284.

Mertens' (1936) species *L. bangweolicus* was described from Lake Bangweulu, northern Zambia, and treated as a synonym of Günther's *L. bicolor* by de Witte (1953). It was revived as a subspecies by Laurent (1964), who found snakes referable to both taxa in northeast Angola, recording *L. bicolor bangweolicus* from Calundo, Moxico. Broadley (1991a) found the species in close proximity in the Ikelenge pedicle in northwest Zambia, and suggested that the two races should be treated as full species. This was supported by additional material from the region (Haagner et al. 2000), which also supported a dietary difference between the two species. Conradie et al (2016, 2017) record additional material in the Angolan Okavango catchment.

Striped Swamp Snake

Limnophis bicolor (Günther 1865)

Limnophis bicolor Günther, 1865. Fourth account of new Species of Snakes in the Collection of the British Museum. *Ann. Mag. Nat. Hist.* (3) 15: 97.

Günther (1865) described *Limnophis bicolor* based on two specimens sent by Bayão in 1864 from Calandula. Bocage (1866, 1879) discussed additional specimens

sent by Anchieta from Huila, Caconda, Quindumbo, and Cahata, and Boulenger (1893) transferred the species to *Helicops*. Bocage (1895) discussed the species (as *Helicops bicolor*) and noted that it was found only on the high plateau. Later specimens were recorded from Hanha (Bocage 1896) and numerous localities on the southern high plateau (Monard 1931, 1937), and Bela Vista (Hellmich 1957). After reassessing the taxonomic status of *L. bicolor* (see above), Laurent (1964) recorded specimens of *L. b. bicolor* from Alto Chilo and Alto Chicapa. Branch and Conradie (2015) recorded the species around Lagoa Carumba, Lunda Norté, where it was commonly caught in fish traps.



Fig. 14. *Limnophis bicolor*, Lagoa Carumba, Lunde Norte.

Western Forest Marsh Snake

Natriciteres bipostocularis (Broadley 1962)

Natriciteres variegata bipostocularis Broadley, 1962. Serpentes, Colubridae, *Natriciteres olivacea bipostocularis* n. subsp. *Occ. Pap. Nat. Mus. South. Rhodesia* 3 (26B): 785.

The status of Marsh snakes in Angola remains problematic. Although Bocage listed two species, *Natriciteres fuliginoides* and *N. olivaceus*, in his monograph, only the latter was known to him from Angola, based on Peter's (1882) record from Malanje and Anchieta's record from Punga Andongo (also noted by Boulenger 1905). Later records included Dondo (Hellmich (1957) and Dundo and Muita (Laurent 1950, 1954). Subsequently, Broadley (1966a) referred Peter's Malanje record and another from Bela Vista (Hellmich 1956, as *Natriciteres olivacea uluguruensis*) to *N. variegata bipostocularis*, which was described from northeastern Zambia and extended west through Katanga to the highlands of central Angola (Broadley 1966b). It is now treated as a full species (Broadley et al. 2003). There remains a large disjunction between the main range of *N. bipostocularis* in Zambia and DRC and the isolated records in western Angola, although the eastern regions of the country remain poorly surveyed.

Olive Marsh Snake

Natriciteres olivacea (Peters 1854)

Coronella olivacea Peters, 1854. Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgeteilt werden. *Ber. Bekanntmach. Geeignet. Verhandl. Königl.-Preuss. Akad. Wiss.*, Berlin 1854: 622.

Bocage (1895) knew this small marsh snake (as *Mizodon olivaceus*) from relatively few localities, e.g., Pungo-Andongo and Malange (= Malanje), and considered that its range south was limited by the Kwanza River. Additional material includes: "Angola," a specimen from the Vernay Lang Angola expedition without further details (Bogert 1840), Dundo and Muita (Laurent 1954), and Dondo (Hellmich 1957).

Family: Lamprophiidae

Early molecular studies helped clarify interfamilial relationships within advanced snakes (Vidal and Hedges 2002a; Kelly et al. 2003; Lawson et al. 2005; Vidal et al. 2007), and highlighted the existence of a major clade (Elapoidea, Vidal et al. 2007) that included elapids (cobras, mambas, sea snakes, etc.) and a large and diverse radiation of mostly African and Malagasy snakes. The latter radiation has been treated as the Lamprophiidae (Vidal et al. 2009). Pyron et al. (2011) noted that they considered "the most difficult aspect of higher-level colubroid taxonomy to be Lamprophiidae, the assemblage of mostly African snakes related to Elapidae." The Lamprophiidae envisaged by Vidal et al. (2007) initially included only four subfamilies: the Psammophiinae, Atractaspidinae, Lamprophiinae, and Pseudoxyrhophiinae. Kelly et al. (2008) treated these as full families, and also proposed the additional families Prosymnidae and Pseudaspidae. Subsequent studies (e.g., Pyron et al. 2011; Figueroa et al. 2016) have basically retained these groupings as subfamilies (but with additional, sometimes non-African members of various subfamilies). The Pseudoxyrhophiinae include numerous Malagasy genera with a number of species also found in the Comoros Islands. Surprisingly, the African genera *Duberria*, *Amplorhinus* (and probably *Montaspis*) are also included in this subfamily, but none occur in Angola.

Subfamily: Atractaspidinae

The atractaspidines are sometimes raised to a full family (Figueroa et al. 2016), with a reduced Atractaspidinae containing only *Atractaspis* and South African *Homoroselaps*, and all other genera placed in a new subfamily, the Aparallacinae. This arrangement is not adopted here, where the Atractaspidinae is retained within the Lamprophiidae and contains all genera traditionally placed in that group. A suite of genera have usually been assigned to the atractaspidines (*Amblyodipsas*, *Aparallactus*, *Atractaspis*, *Brachyophis*, *Chilorhinophis*, *Elapotinus*, *Homoroselaps*, *Hypoptophis*, *Macrelaps*,

Poecilopholis, *Polemon*, *Xenocalamus*), which are distributed broadly in Africa but with a limited occurrence of some genera in the Middle East. The monophyly of atractaspidines is well supported by both morphological (McDowell 1968; Underwood and Kochva 1993; Zaher 1999) and molecular data (Nagy et al. 2005; Vidal and Hedges 2007; Portillo et al. 2018). Figueroa et al. (2016) proposed that *Xenocalamus* be synonymized with *Amblyodipsas*, but based this on very limited taxon sampling of these genera. A more comprehensive molecular analysis of the subfamily (Portillo et al. 2018) included 158 individuals from six of eight aparallactine genera, and revealed numerous cryptic taxa, as well as the need for a number of generic readjustments to retain monophyletic clades that continue to include generic status for both *Xenocalamus* and *Amblyodipsas*, but with adjusted species content.

Bibron's Burrowing Asp

Atractaspis bibronii (Smith 1849)

Atractaspis bibronii Smith, 1849. Illustrations of the Zoology of South Africa. 3 (Reptiles). Smith, Elder, and Co., London: 51.

Bocage (1895) knew the species from Catumbela, Benguela and Dombe Grande, the only places from which Anchieta sent material, and on this basis noted that "cette espèce, qui paraît affectionner en Angola la zone littorale." Additional material (as *Atractaspis bibroni rostrata*) was recorded from Dundo (Laurent 1950, 1954, 1964; Tys van den Audenaerde 1967).

Congo Burrowing Asp

Atractaspis congica (Peters 1877)

Atractaspis congica Peters, 1877. Übersicht der Amphibien aus Chinchoxo (Westafrika), welche von der Africanischen Gesellschaft dem Berliner zoologischen Museum übergeben sind. Monatsber. königl. Akad. Wiss. Berlin. 1877 (October): 616.

Bocage (1873) did not recognize the first Angolan record sent to him from Huilla by Anchieta, as a new species and mistakenly referred it to *Atractaspis aterrima*. Peters (1877) described the species a few years later from Lândana, Cabinda. He later (Peters 1881) record another specimen from Cuango. Bocage (1895) concluded that the species lived in the highlands of the interior, as he had received material from Quibula, Quindumbo, Galanga, Caconda, and Huila from Anchieta. Later additions included: Cazengo (Ferreira 1904), Calandula, Golungo Alto (Boulenger 1905), Bimbe (Monard 1937), Entre Rios, Piri, Bela Vista, Alto Cubal (Hellmich 1957), Alto Cuilo (as *A. c. congica*), and Calundo, Moxico (*A. c. orientalis*) (Laurent 1964), and show that it has a wider distribution than known to Bocage (1895). The status of Laurent's subspecies of *A. congica*, e.g., *A. c. orientalis*

Laurent, 1945 from Katanga and northern Zambia, and *A. c. lelupi* Laurent, 1950 from Katanga remain problematic, although Wallach et al. (2014) treated *A. lelupi* as a full species.



Fig. 15. *Atractaspis congica*, Soyo (Photo: Warren Klein).

Southern Reticulate Burrowing Asp

Atractaspis reticulata heterochilus (Boulenger 1901)

Atractaspis heterochilus Boulenger, 1901. Matériaux pour la faune du Congo. Batraciens et reptiles nouveaux. *Ann. Mus. Congo Belge, Zool.* (sect. C. ser. 1) 2: 13.

Hellmich's (1957) record of *A. reticulata heterochilus* from Piri-Dembos (= Piri) is the only record of this species from Angola, and needs re-examination to confirm it is not misidentified. The race is recorded from Cameroon to Gabon and so may extend through Cabinda further south.

Subfamily: Aparallactinae

Common Purple-glossed Snake

Amblyodipsas polylepis (Bocage 1873)

Calamelaps polylepis Bocage, 1873. *Mélanges erpétologiques*. II. Sur quelques reptiles et batraciens nouveaux, rares ou peu connus d'Afrique occidentale. *Jorn. Acad. Sci.*, Lisboa 4: 216.

Bocage's (1873) description of *Calamelaps polylepis* was based on a snake from Dondo, and later material was added from Quissange and Humbe (Bocage 1895), Cabicula (Ferreira 1904), and Cazengo (Boulenger 1905). Broadley (1971a) when revising the genus added no further Angolan material, but recognized an East African race (*A. p. hildebrandtii*) whose status has not been reassessed.

Kalahari Purple-glossed Snake

Amblyodipsas ventrimaculata (Roux 1907)

Rhinocalamus ventrimaculata Roux, 1907. Sur quelques Reptiles sud-africains. *Rev. suisse Zool.* 15: 78.

The presence of this Kalahari species was first recorded in Angola from material collected during NGOWP surveys (Conradie et al. 2017; Conradie and Branch 2017) and from Bicular National Park (Baptista et al., in prep.).



Fig. 16. *Amblyodipsas ventrimaculata*, Cuito River Source, Cuando Cubango (Photo: Werner Conradie).

Cape Centipede Eater

Aparallactus capensis (Smith 1849)

Aparallactus capensis Smith, 1849. Illustrations of the Zoology of South Africa. 3 (Reptiles). Smith, Elder, and Co., London, 16.

Bocage (1895) recorded the species (as *Urechis capensis*) from Sumbe, Bibala and Gambos, but discussed variation among this small sample (5 specimens). Boulenger (1895) considered Bocage's material to be composite and referred some to *A. guentheri* and the others to two new species, *A. bocagii* and *A. punctatolineatus*, but confusingly without allocating to which of Bocage's specimens/localities these names applied! The type localities for these new species therefore by default became simply 'Angola'. Loveridge (1944) revised the genus and assigned Bocage's Quindumbo specimen to true *A. c. capensis*, and his other material from Bibala, Gambos and Sumbe to *A. c. bocagii*. Boulenger's *A. punctatolineatus* was relegated to the synonymy of *A. c. capensis* by Loveridge (1944), but treated as a subspecies, *A. capensis punctatolineatus*, by De Witte and Laurent (1947). Laurent (1954) recorded *A. c. punctatolineatus* from Dundo and Sombo, and Broadley (1961) continued to recognize *A. c. punctatolineatus* as a northwestern race. However, after discussing in detail morphological variation in all subspecies Broadley (1966a) rejected them all and later formally returned *A. capensis* to binomials (Broadley 1983). However, a recent molecular phylogeny of the Aparallactinae (Portillo et al. 2018) noted deep divergence between various *A. capensis* populations, for which some of Boulenger's names may be available. Branch and McCarthy (1992) recorded a specimen near Cuito Cuanavale with a blunt head and low labials counts, but that was otherwise typical for *A. capensis*. Apart from this specimen, no recent

material has been collected and the status of Angolan *A. capensis*, particularly western *bocagii* (currently in the synonymy of *A. capensis*), is unresolved.

Wilson's burrowing snake

Hypoptophis wilsoni (Boulenger 1908)

Hypoptophis wilsoni Boulenger, 1908. Description of three new snakes from Africa. *Ann. Mag. Nat. Hist.* (8) 2: 93.

It is known in Angola from only a single record of *H. wilsoni katangae* from Dundo (Laurent 1964). De Witte and Laurent (1947) differentiated *H. w. katangae* from typical *H. w. wilsoni* by its lower ventral and subcaudal counts and nasal condition. Broadley (1966a) noted that Zambian material was intermediate between the two poorly defined races and subsequently reverted to binomials (Broadley 1998a; Broadley et al. 2003). No recent material has been available for genetic assessment.

Collared Snake-Eater

Polemon collaris (Peters 1881)

Microsoma collare Peters, 1881. Zwei neue von Herrn Major von Mechow während seiner letzten Expedition nach West-Afrika entdeckte Schlangen und eine Übersicht der von ihm mitgebrachten herpetologischen Sammlung. *Sitzungsber. Ges. naturf. Freunde*, Berlin 1881(9): 148.

Peters (1881) described *Microsoma collare* from "Macange, Cuango, West-Afrika." However, Peters (1881) interchanged the spellings Macange and Malange frequently in the paper, and Crawford-Cabral and Mesquitella (1989) listed Malange as a variant of Malanje. Wallach et al. (2014) corrected the type locality to Malanje, Malanje Province, northern Angola (9°33'S, 16°20'E). Crawford-Cabral and Mesquitella (1989), who prepared a summary of all published records of Angolan terrestrial vertebrates (1784–1974), do not discuss any of Peters' reptile publications, and also list "Macanje" as a version of Maconge, Moçamedes (= Namibe Province, 15°01'S, 13°12'E). However, this cannot refer to Peters' locality as *Polemon collaris* is a forest species. Bocage (1887b) referred a specimen from Cazengo to this species, and later two from Quindumbo (Bocage 1895). Additional material was noted from Gulango Alto (Ferreira 1904), Entre Rios and Bela Vista (Hellmich 1957 - as *Miodon gabonensis*, then a senior synonym of *M. collaris*, which was later revalidated as a full species, Bogert 194). A recent specimen, confirmed by genetic monophyly (Portillo et al. 2018) was collected from northeast Angola.

Bi-colored Quill-snouted Snake

Xenocalamus bicolor machadoi (Laurent 1954)

Xenocalamus bicolor machadoi Laurent, 1954. Reptiles et batraciens de la région de Dundo (Angola) (Deuxième note). Companhia de Diamantes de Angola (Diamang), Serviços Culturais, Publicações Culturais, No. 2: 45.

First recorded from Angola by Boulenger (1905) on a specimen from between Benguela and Bihé (= Bié Province) collected by Anchieta, but mistakenly assigned to *Xenocalamus mechowii*, Peters. Laurent (1954) described *Xenocalamus bicolor machadoi* from Dundo, including Boulenger's (1905) material. Broadley (1971a) reviewed the genus and recognized four subspecies in *X. bicolor* and two in *X. mechowii* (see below). Genetic material is required to re-assess the status of these races.

Elongate Quill-snouted Snake

Xenocalamus mechowii (Peters 1881)

Xenocalamus mechowii Peters, 1881. Zwei neue von Herrn Major von Mechow während seiner letzten Expedition nach West-Afrika entdeckte Schlangen und eine Übersicht der von ihm mitgebrachten herpetologischen Sammlung. *Sitzungsber. Ges. naturf. Freunde*, Berlin 1881(9): 147.

Described by Peters (1881) from "Macange, West-Afrika." Wallach et al. (2014) corrected the type locality to Malanje (see above). Bocage (1895) overlooked Peters (1881) description and did not discuss the genus in Angola. Witte and Laurent (1947) described *X. m. inornatus* from northern Namibia, and Laurent (1954) noted the second Angolan specimen of *X. m. mechowii* from Sombo. Broadley (1971a) continued to recognize both subspecies, but had no additional Angolan material. Branch and McCarthy (1992) recorded the first Angolan record of the southern race from near Lupire. The status of the *X. mechowii* subspecies has not been genetically assessed.

Subfamily: Lamprophiinae

This assemblage of African snakes (equivalent to the Lamprophiidae of Kelly et al. 2008) includes a basic division between wolf snakes and their relatives (*Lycophidion*, *Chamaelycus*, *Hormonotus*, *Mehelya*, *Gonionotophis*, *Limaformosa*, etc.) and house snakes and their relatives (*Boaedon*, *Bothrophthalmus*, *Lycodonomorphus*, etc.). Kelly et al. (2011a) restricted *Lamprophis* for a group of four South African snakes, and revived *Boaedon* for all other African house snakes (albeit that not all taxa had been assessed). In addition, numerous additional cryptic taxa within southern *Boaedon* populations were identified, but not described pending further studies. The presence of paraphyletic genera within file snakes was also identified (Kelly et al. 2011a), but the inclusion of *Mehelya* within *Gonionotophis* to maintain generic monophyly was premature. Fuller taxon sampling has resulted in the revival of *Mehelya* (but with reduced content), the description of two new genera (*Limafor-*

mosa and *Gracililima*), and reduced content for *Gonionotophis*, now restricted to the majority of the dwarf file snake species (Broadley et al. 2018). Unresolved, although the subject of ongoing investigation, are species boundaries and phylogenetic relationships within house snakes (*Boaedon*) and their aquatic relatives (*Lycodonomorphus*).

House Snake

Boaedon capensis-fuliginosus-lineatus complex (Boie 1827)

Resolution of the taxonomic status of these house snakes remains one of the most persistent and challenging problems in African herpetology (e.g., Roux-Esteve and Guibe 1965; Thorpe and McCarthy 1978; Hughes 1997). Numerous studies have juggled the nomenclature, with various names and generic assignments proposed, as well as new species described (Greenbaum et al. 2015; Trape and Medannikov 2016). Kelly et al. (2011a) resolved most generic affiliations although adjustments have occurred (Greenbaum et al. 2015) or are probably required (*Lycodonomorphus* (?) *subtaeniatus*, see below). *Lamprophis* is now restricted to a few South African endemics, with all other names/species by genetic monophyly or default being transferred to *Boaedon*. House snakes are common throughout Angola, but none were included in the above studies, and neither were many other African populations or even putative species (e.g., *mentalis*, *erlangeri*, *arabicus*, *bedriagae*, etc.), and the status of all remains unresolved. The names *Alopecion variegatum* Bocage, 1867 and *Boaedon lineatus* var. *angolensis* Bocage, 1895, currently considered synonyms of *B. lineatus*, remain unresolved. In addition, the Coastal House Snake (*B. littoralis*) recently described (Trape and Mediannikov 2016) from the coastal region of southern Gabon and Republic of Congo, may extend at least into Cabinda. It is probable that many different house snake species currently occur in Angola, but their distributions and diagnostic features, as well as the allocation of existing names and description of new species, are under investigation (Hallermann et al., in prep.). In addition, it is likely that a number of species from adjacent regions, e.g. *B. radfordi*, are likely to enter the northern forested habitats.



Fig. 17. *Boaedon capensis-fuliginosus-lineatus* complex, near Menongue, Cuando Cubango.

Olive House Snake

Boaedon olivaceus (Dumeril 1856)

Holuropholis olivaceus Duméril, 1856. Note sur les reptiles du Gabon. *Revue et Magasin de Zoologie Pure et Appliquée*, Paris (2) 8: 466.

Bocage (1895) specifically stated that he knew of no Angolan material. It was subsequently recorded from Dundo (Laurent 1954; Tys van den Audenaerde 1967), but the recent description of a sister species, *B. radfordii*, from the Albertine Rift (Greenbaum et al. 2015), means that the relationship of Dundo material to this new species requires assessment.

Red-Black Striped House Snake

Bothrophthalmus lineatus (Peters 1863)

Elaphis (Bothrophthalmus) lineatus Peters, 1863. Über einige neue oder weniger bekannte Schlangenarten des zoologischen Museums zu Berlin. *Monatsb. Königl. Akad. Wiss.*, Berlin 1863: 287.

Not known to Bocage (1895) from Angola, although it was subsequently recorded from Dundo (Laurent 1950, 1954, 1964; Tys van den Audenaerde 1967). This remains the only Angolan locality. Plain western populations, previously known as *B. l. brunnaeus*, are now treated as a full species (Pauwels et al. 2006), and may extend south to Cabinda.

Parker's Banded Snake

Chamaelycus parkeri (Angel 1934)

Oophilositum parkeri Amgel, 1934. Remarques sur le genre *Oophilositum* Parker (Colubridé aglyphe) et description d'une espèce nouvelle. *Bull. Soc. Zool.*, France 59: 417.

Parker (1936) recorded *Oophilositum parkeri* from Fazenda Congulu, and this remains the only known Angolan material. The species was transferred to *Chamaelycus* by de Witte (1963). Parker's (1936) material creates a significant disjunction in the species' range, which elsewhere is restricted to DRC and Congo Brazzaville (Trape and Roux-Estève 1995).

Yellow Forest Snake

Hormonotus modestus (Duméril, Bibron and Duméril 1854)

Lamprophis modestus Duméril, Bibron and Duméril, 1854. *Erpétologie générale ou Histoire Naturelle complète des Reptiles*. Vol. 7 (partie 1). Paris, 429.

A characteristic species of the Congo forest known from Angola from a single specimen from scarp forest habitat at Congula (Parker 1936).

Brussaux's Dwarf File Snake

Gonionotophis brusseauii (Mocquard 1889)

Gonionotus brussexi Mocquard, 1889. Sur une collection de reptiles du Congo. *Bull. Soc. Philomath.*, Paris (8) 1: 146.

This small file snake was not known to Bocage (1895) from Angola. Laurent (1954) documented the only Angolan record from Dundo.

Common File Snake

Limaformosa capensis (Smith 1847)

Heterolepis capensis Smith, 1847. *Illustrations of the zoology of South Africa, Reptilia*. Smith, Elder, and Co., London: 55.

Bocage (1895) did not know this species from Angola. Monard (1937) signalled the first record (as *Mehelya capensis capensis*) from Huambo, and additional material was recorded from Rio des Ganguelles (Angel 1923), 'Rives du la Calundo', 105 km E Luso, Moxico (Laurent 1964), and 14 km north Mapupa (Branch and McCarthy 1992). Despite Laurent's records, Haacke (1981) and Broadley (1983) continued to exclude Angola from the range of *M. capensis*. The few known records are all restricted to the eastern regions of Angola. In a molecular analysis Kelly et al. (2011a) showed that *Gonionotophis brussexi* (Mocquard 1889; type species) was nested within *Mehelya*, and as the former generic name had priority, the latter and all other file snakes were placed in *Gonionotophis*. Lanza and Broadley (2016) also reassessed northern populations related to *G. capensis*, with the revival of *G. chanleri* and *G. savorgnani* as full species. Moreover, a more recent phylogeny with greater taxon sampling confirmed monophyletic clades within *Gonionotophis sensu lato*, and led to the revival of *Mehelya* (but restricted to *M. poensis*, *M. stenophthalmus*, *G. egbensis*, *G. gabouensis* (Trape and Mané 2005), and *G. laurenti*); a more traditional content for *Gonionotophis* (including the dwarf species *G. brussexi*, *G. grantii* and provisionally *G. klingi*); the description of a new genus, *Gracililima* for *G. nyassae*; and a new genus *Limaformosa* for the remaining file snakes of the *G. capensis* complex (Broadley et al. 2018).

Savorgan's File Snake

Limaformosa savorgani (Mocquard 1887)

Heterolepis Savorgnani Mocquard, 1887. Du genre *Heterolepis* et des espèces qui le composent, dont trois nouvelles. *Bull. Soc. Philom.*, Paris (7) 11: 27.

Bocage knew no file snakes from Angola and reported only *Heterolepis bicarinatus* from the Congo (Bocage 1866). He later (Bocage 1895) corrected this identification to *H. guirali*. Loveridge (1939) undertook the last revision of file snakes and placed *H. guirali* in the synon-

omy of *Mehelya capensis savorgani*. Lanza and Broadley (2016) revived *M. savorgani* as a full species, and included northern Angola in the species' range, but examined no Angolan material or gave citations for Angolan localities. It was recently transferred to a new genus by Broadley et al. (2018).



Fig. 18. *Limaformosa savorgani*, Soyo (Photo: Warren Klein).

Vernay's File Snake

Limaformosa vernayi (Bogert 1940)

Mehelya vernayi Bogert, 1940. Herpetological results of the Vernay Angola Expedition. I. Snakes, including an arrangement of the African Colubridae. *Bull. Amer. Mus. Nat. Hist.* 77: 28.

This poorly known file snake was described from Hanha by Bogert (1940). Haacke (1981) reviewed file snakes in the western arid region, and noted few additional records (<10) for northern Namibia, but no new material from Angola. It was recently transferred to a new genus by Broadley et al. (2018).



Fig. 19. *Mehelya poensis*, Lagoa Carumba, Lunde Norte.

Equatorial File Snake

Mehelya poensis (Smith 1849)

Heterolepis poensis Smith, 1849. Illustrations of the zoology of South Africa, Reptilia. Smith, Elder, and Co., London: 55.

Bocage (1895) did not discuss *M. poensis* from either

Angola or the Congo region. Its presence in Angola was first signaled from Cabicula (Cazengo) (Ferreira 1904). Additional material was recorded from Piri (Hellmich 1957); Dundo (Laurent 1950), Muita River (Tys van den Audenaerde 1967), and Lagoa Carumbo (Branch and Conradie 2015). Recently placed in an expanded *Goni-notophis* (Kelly et al 2011a), but now returned to a reduced *Mehelya* (Broadley et al. 2018).

White-bellied Water Snake

Lycodonormorphus (?) *subtaeniatus* (Laurent 1954)

Lycodonormorphus subtaeniatus Laurent, 1954. Reptiles et batraciens de la région de Dundo (Angola) (Deuxième note). Companhia de Diamantes de Angola (Diamang), Serviços Culturais, Publicações Culturais, No. 23: 38.

Laurent (1954) described *Lycodonormorphus subtaeniatus* based on a specimen from Keseki (DRC) and a series of 12 paratypes, including four from Dundo, which remain the only Angolan material. At the same time Laurent (1954) also described the subspecies *L. s. upembae* from Nyonga (DRC). The type series for both taxa included material previously identified as *Boaedon*, i.e., *B. virgatus* and *B. lineatus*, respectively (Laurent 1952; De Witte 1933). It was thus not unexpected that when preparing a molecular phylogeny of house snakes of the description of their new species *B. radfordii*, Greenbaum et al. (2015) found *L. s. upembae* embedded within *Boaedon*, to which it was transferred. No new material was available to assess the generic relationships of *L. subtaeniatus*, but the current placement within *Lycodonormorphus* is problematic and its relationship to *B. virgatus* with which has previously been confused should be investigated.

Hellmich's Wolf Snake

Lycophidion hellmichi (Laurent 1964)

Lycophidion hellmichi Laurent, 1964. Reptiles et batraciens de l'Angola (troisième note). Companhia de Diamantes de Angola (Diamang), Serviços Culturais, Museu do Dundo (Angola), No. 67: 95.

Laurent (1964) described *Lycophidion hellmichi* from "Kapolopopo, desert de Mossamedes," and included the *L. c. capense* (Hellmich 1957, Entre Rios) in the synonym, which was the first record of the species in Angola. He later (Laurent 1968) assigned a number of Namibian specimens to *L. hellmichi*, which Broadley (1991b) later realized were a new species, *L. namibianum*. The only remaining Namibian specimen of *L. hellmichi* is from the Kaokoveld (Broadley 1991b), and Broadley (1996) recorded another Angolan specimen from Quis-sange. It therefore appears to be known from only three specimens.

Flat Wolf Snake

Lycophidion laterale (Hallowell 1857)

Lycophidion laterale Hallowell, 1857. Notes of a collection of reptiles from the Gaboon country, West Africa, recently presented to the Academy of Natural Sciences of Philadelphia, by Dr. Henry A. Ford. *Proc. Acad. Nat. Sci. Philadelphia* 9: 58.

A dwarf West African species, ranging from Ivory Coast to Uganda, and south to Angola. It was known to Bocage (1866, 1895) only from Molemo (Cabinda), but later recorded from north of the Kwanza River (Ferreira 1903) and from N'Dalatando (Monard 1937).

Speckled Wolf Snake

Lycophidion meleagre (Boulenger 1893)

Lycophidium meleagris Boulenger, 1893. Catalogue of the snakes in the British Museum (Nat. Hist.) I. London (Taylor and Francis): 337.

A small wolf snake described from Ambriz and Ambrizete (= N'zeto) in coastal northern Angola (Boulenger, 1893). These remained the only material known to Bocage (1895). Additional material was recorded from Cabiri (Ferreira 1904), Libolo-Luati (= Calulo) (Hellmich 1957), Landana (Cabinda) and Luanda (Broadley 1996). Specimens referred to this species have been recorded over 3,000 km away in coastal northern Tanzania (Broadley 1996), thus creating a considerable zoogeographic anomaly. The assignment of the Tanzanian material needs to be tested for genetic monophyly.

Spotted Wolf Snake

Lycophidion multimaculatum (Boettger 1888)

Lycophidion capense multimaculata Boettger, 1888. Materialien zur Fauna des unteren Congo. II. Reptilien und Batrachier. *Ber. Senck. Ges.* 1887: 67.

Bocage (1895) referred Angolan material to two forms of *L. capense*, one from the Congo (St. Salvador), Cabinda and Calandula (that may be referable to *L. meleagris*) and wolf snakes from the southern parts of Angola (Galanga, inland from Namibe, Caconda) that he referred to var. *multimaculata* (Boettger). Additional records are recorded as *L. capense* from Malanje (Peters 1881), Entre-Rios, and Piri (Hellmich 1957); and as *L. c. multimaculatum* from Dundo, Alto Cuilo, Cazombo, Macondo, Calonda (Laurent 1964). Broadley (1991b) reviewed Namibian wolf snakes, describing *L. namibianum* (see below), and raised *L. multimaculatum* to a full species, recording it as far south as the Caprivi. Branch and McCarthy (1992) recorded the species from Cuito Cuanavale. Broadley (1996) reviewed all the Angolan species, mapped their distributions, and no longer considered *L. capense* to occur in the country.

Namib Wolf Snake

Lycophidion namibianum (Broadley 1991)

Lycophidion namibianum Broadley, 1991. A review of the Namibian snakes of the genus *Lycophidion* (Serpentes: Colubridae), with the description of a new endemic species. *Annals Transvaal Mus.* 35 (14): 210.

This attractive wolf snake was described by Broadley (1991b) from northern Namibia, and included many Namibian specimens previously confused with Laurent's *L. hellmichi* (Broadley 1991). The only Angola record was collected at Espinheira (Branch et al., in prep.).



Fig. 20. *Lycophidion namibianum*, Espinheira, Namibe.

Ornate Wolf Snake

Lycophidion ornatum (Parker 1936)

Lycophidion ornatum Parker, 1936. Dr. Karl Jordan's expedition to South-West Africa and Angola: Herpetological collections. *Novit. Zool.* (London) 40: 122.

Described from two specimens from scarp forest at Fazenda Congulu (Parker 1936), which remain the only known Angolan records. Elsewhere it extends through DRC to south Sudan (Broadley 1996).

Subfamily: Psammophiinae

The psammophiine genera (*Dipsina*, *Hemirhagerhis*, *Malpolon*, *Psammophis*, *Psammophylax*, *Rhamphiophis*) are distributed throughout Africa, the Middle East, south-central Asia, and southern Europe (Branch 1998; Kelly et al. 2008), with *Mimophis* restricted to Madagascar. Their monophyly is supported by morphological and molecular data (Cadle 1994; Brandstätter 1996; Zaher 1999; Vidal and Hedges 2002a; Kelly et al. 2008). Two recent genera have been synonymized: *Dromophis* with *Psammophis* (Kelly et al. 2008) and *Rhagerhis* with *Malpolon* (Figueroa et al. 2016). Figueroa et al. (2016) consider Asian *Psammodynastes* to also be part of the Psammophiidae, but this species has a bifurcate, heavily ornamented hemipenis (see Fig. 17 in Zaher 1999) that contrasts with the well established synapomorphy of

the simple, tubular and unadorned hemipenes of psammophines. We therefore continue to exclude *Psammodynastes* from the Psammophidae.

Viperine Rock Snake

Hemirhagerrhis viperina (Bocage 1873)

Psammophylax viperinus Bocage 1873. Bocage JVB. 1873. Melanges erpetologiques. II. Sur quelques reptiles et batraciens nouveaux, rares ou peu connus d'Afrique occidentale. *Jorn. Acad. Sci.*, Lisboa 4: 222.

Bocage (1873) described *Psammophylax viperinus* from Dombe Grande, and later added further Anchieta material from Humbe, Maconjo, and Capangombe (Bocage 1895), but deferred to Boulenger in treating this material as *Psammophylax nototaenia*. Bogert (1940) added new records from the Vernay Lang Angola expedition from Hanha, Huambo, and Munhino, and revived it as a subspecies, *H. nototaenia vipernua*, for all Angolan material. Laurent (1964) recorded a specimen from Humpata. Broadley (2000) revived *H. viperina* again as a full species, and noted no *H. nototaenia* from Angola.

Angolan Sand Snake

Psammophis angolensis (Bocage 1872)

Amphiophis angolensis Bocage, 1872. Diagnoses de quelques espèces nouvelles de Reptiles d'Afrique occidentale. *Jorn. Sci.*, Lisbon 4: 82.

This dwarf psammophine was described by Bocage (1872) from “Dondo, (intérieur d'Angola).” Wallach et al. (2014) discuss confusion over the correct location of Bocage's type locality “Dondo,” which has been presented in various forms; e.g., Danda, Loanda Distr. (Loveridge 1940; Broadley 1962), Donda, Loanda Distr. (FitzSimons 1962; Auerbach 1987), and Dondo, Luanda Distr. (Crawford-Cabral and Mesquitela 1989). They note that it was correctly located by Loveridge (1957) and Hellmich (1957a) as Dondo, north bank of Kwanza River, SW Cuanza Norte Distr., NW Angola (09°41'S, 14°26'E, elevation 50 m). Additional material was noted (Bocage 1895) from Caconda, Quindumbo, Humbe, Sumbe, Pungo-Andongo and Ambrizette (=N'Zeto), and later from Dundo, Cameia, and Lagoa Calundo (Laurent 1964).

Ansorge's Sand Snake

Psammophis ansorgii (Boulenger 1905)

Psammophis ansorgii Boulenger, 1905. A list of the batrachians and reptiles collected by Dr. W. J. Ansorge in Angola with descriptions of new species. *Ann. Mag. Nat. Hist.* (7) 16: 113.

Boulenger (1905) described *Psammophis ansorgii* on a snake collected by Anchieta between “Benguella to Bihe, Angola.” Hellmich (1957) recorded the species from

Bela Vista, but of his seven specimens, five were just heads. However, this new material allowed him to note that the preocular was, at most, only in narrow contact with the frontal, and he therefore removed the species from the synonymy of *P. jallae*, where it had been placed by Loveridge (1940). This was followed by Broadley (1977, 2002), who noted no new material. Branch et al. (2018a) discussed new material and phylogenetic relationships, and noted that it is one of the few snakes endemic to Angola.



Fig. 21. *Psammophis ansorgii*, Tundavala, Huila (Photo: Ninda Baptista).

Jalla's Sand Snake

Psammophis jallae (Peracca 1896)

Psammophis jallae Peracca, 1896. Retili et Anfibi raccolti a Kazungula e sulla strada da Kazungula a Buluwaio dal Rev. Luigi Jalla, Missionario Valdese nell' alto Zambese. *Boll. Mus. Zool. Comp. Anat. Univ. Torino* 11(255): 2.

Loveridge (1940) removed *P. jallae* from the synonymy of *P. crucifer*, and Broadley (1977, 2002) discussed additional material, although noting that it remained known from Angola only from the type of *Psammophis rohani* Angel, 1921 (Lumuna River). A second Angolan record was noted by Conradie et al. (2017).

Leopard Sand Snake

Psammophis leopardinus (Bocage 1887)

Psammophis sibilans var. *leopardinus* Bocage 1887. Melanges erpetologiques. I. Reptiles et Batraciens du Congo. II. Reptiles de Dahomey. III. Reptiles de l'Ile du Prince. IV. Reptiles et Batraciens de Quissange (Benguella) envoyés par M. J. d'Anchieta. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 11: 206.

Bocage (1887b) was confronted with diverse color patterns and scalation in sand snakes, and like many subsequent researchers (Boulenger 1895; Loveridge 1940; Broadley 1977, 2002) found it difficult to resolve species boundaries. As was customary at the time he used varieties to characterize intraspecific grouping. Some of these have subsequently been demonstrated, both morphologically (Broadley 1977, 2002) and genetically (Kelly et al.

2008) to be valid species. One such is this species, first described by Bocage (1887) as a variety of *P. sibilans* (now restricted to North Africa), eventually as a western subspecies of *P. brevirostris* (Broadley, 1977), before being raised to a full species (Broadley 2002). The latter lists numerous localities for western Angola, including the type locality Catumbela.

Namib Sand Snake

Psammophis namibensis (Broadley 1975)

Psammophis leightoni namibensis Broadley, 1975. A review of *Psammophis leightoni* and *Psammophis notostictus* in southern Africa (Serpentes: Colubridae). *Arnoldia* 7 (13): 9.

Some early Bocage *Psammophis* material from Mossamedes (= Namibe, MBL 1809) and Rio Curoca (MBL 1810) was studied by Broadley before the Lisbon fire. He assigned them to a new taxon, described initially as a western arid subspecies (Broadley 1975) of *P. leightoni*, but later treated as a full species, *P. namibensis* (Broadley 2002). Additional material, collected by Haacke from Cunene Forde 15 km NE, Iona Res, Foz do Cunene and Pico de Acevedo, was also assigned to this species (Broadley 2002). It has a much greater distribution in the western arid region, through Namibia to South Africa.

Karoo Sand Snake

Psammophis notostictus (Peters 1867)

Psammophis moniliger var. *notostictus* Peters 1867. Peters, Wilhem Carl Hartwig 1867. Über eine Sammlung von Flederthieren und Amphibien aus Otjimbingue in Südwestafrika, welche Hr. Missionär Hahn dem zoologischen Museum zugesandt hat. Monatsber. königl. Akad. Wiss., Berlin 1867 (April): 237.

Bocage (1887) described *Psammophis sibilans*, var. nova. *stenocephalus* from “l’intérieur de Mossamedes” (= Rio Curoca), but this was later synonymized with *P. notostictus* by Broadley (1977) and in Angola is known from only a few localities in Namibe Province, but extending south to the Karoo of South Africa. Broadley (2002) noted material from Rio Sau Nicolau (= Rio Bentiba), and Ceriaco et al. (2016a) from Espinheira and Pico de Azevedo.

Mozambique Grass Snake

Psammophis mossambicus (Peters 1882)

Psammophis sibilans var. *mossambica* Peters 1882. Naturwissenschaftliche Reise nach Mossambique auf Befehl seiner Majestät es Königs Friedrich Wilhelm IV. in den Jahren 1842 bis 1848 ausgeführt von Wilhelm C. Peters. Zoologie III. Amphibien. Berlin (Reimer), 122.

The large sand snakes of the *Psammophis sibilans-philippisi-mossambicus* complex have remained a recurrent taxonomic problem among African snakes for over 100 years; see discussion and shifting nomenclature in Bocage (1887, 1895), Boulenger (1895), Loveridge (1940), Broadley (1977, 2002), Hughes (1999), and Brandstätter (1995, 1996). Most Angolan *Psammophis* have previously been included in varied taxa within this complex. Broadley (2002) lists numerous localities for this species, which is widespread in savannah and secondary habitats in Angola. Whether all Angolan large sand snakes are referable to *P. mossambicus*, or whether northwest populations have affinities with West African *P. philippisi*, requires fresh material and genetic assessment.

Western Strip-bellied Sand Snake

Psammophis subtaeniatus (Peters 1882)

Psammophis sibilans var. *subtaeniata* Peters 1882. Naturwissenschaftliche Reise nach Mossambique auf Befehl seiner Majestät es Königs Friedrich Wilhelm IV. in den Jahren 1842 bis 1848 ausgeführt von Wilhelm C. Peters. Zoologie III. Amphibien. Berlin (Reimer), 121.

Bocage (1895) recognized five forms of *Psammophis sibilans* (vars. A–E), of which var. A he contrasted with Peters’ var. *subtaeniata*. He noted that his specimens from Rio Bengo, Catumbela, Bibala, Maconjo, Humbe and Cunene, all collected by Anchieta, looked like var. *subtaeniata*. Broadley (2002) list numerous localities for *P. subtaeniatus* in Angola, including many from the Lisbon Museum subsequently lost in the fire. The species is restricted to the semi-arid scrubland and mopane woodland, above and below the escarpment in southwest Angola. Broadley (2002) includes *Psammophis bocagii* Boulenger, 1895 as a synonym.

Western Sand Snake

Psammophis trigrammus (Günther 1865)

Psammophis trigrammus Günther, 1865. Fourth account of new Species of Snakes in the Collection of the British Museum. *Ann. Mag. Nat. Hist.* (3) 15: 95.

For many years this snake was known only from the type locality (“São Nicolau, Mossamedes”). Bocage (1887) seemed to consider it distinct, but only as a variety of *Psammophis sibilans* and not identical to the other varieties he described at the time (e.g., *stenocephalus* and *leopardinus*). Later he seems to have overlooked the species as he did not discuss it in his monograph (Bocage 1895). This may be why Monard (1937) also overlooked it, as its taxonomic status has never been challenged. Broadley (2002) plotted the limited extension into southwest Angola.

Zambezi Sand Snake

Psammophis zambiensis (Hughes and Wade 2000)

Psammophis zambiensis Hughes, 2000. On the African leopard whip snake, *Psammophis leopardinus* Bocage, 1887 (Serpentes, Colubridae), with the description of a new species from Zambia. *Bull. nat. Hist. Mus. Lond (Zool.)* 68(2): 75.

Only recently described (Hughes and Wade 2002), the species was first reported from Angola during the NGOWP surveys in the headwater region of the Angolan Okavango catchment (Conradie et al. 2017; Conradie and Branch 2017).



Fig. 22. *Psammophis zambiensis*, Cuanavale River Source, Cuando Cubango (Photo: Werner Conradie).

Striped Beaked Skaapstekker

Psammophylax acutus (Günther 1888)

Psammophylax acutus Günther, 1888. Contribution to the knowledge of snakes of tropical Africa. *Ann. Mag. Nat. Hist.* (6) 1: 327.

First recorded from Angola by Bocage (1873) from material sent by Capello and Ivens from Cassange (= Baixa de Cassange). Unfortunately he misidentified it as *Rhagerhis tritaeniata* and later, after Günther (1888) had described it as a new species on a specimen from Pungo Andongo, apologized to the collectors (Bocage 1895) and noted more specimens from Caconda and Huila. Additional material was noted from Benguela to Bié (Boulenger 1905), Bela Vista (Hellmich 1957), Alto Chicapa, Alto Cuilo, and Dundo (Laurent 1964). Broadley (1971c) revised the species, which was later transferred to *Psammophylax* (Kelly et al. 2008).

Huila Skaapstekker

Psammophylax ocellatus (Bocage 1873)

Psammophylax ocellatus Bocage 1873. Melanges herpétologiques. II. Sur quelques reptiles et batraciens nouveaux, rares ou peu connus d'Afrique occidentale. *Jorn. Acad. Sci., Lisboa* 4: 221.

Bocage (1873) described *Psammophylax ocellatus* on the basis of an adult snake from “l'intérieur de Mossamedes (Gambos).” Additional material was recorded (as *P. rhombeatus*) from Humbe (Bocage 1895; Boulenger 1896) and Tundavala (Baptista et al. 2018a). Broadley (1977) reviewed the Angolan material and revived *P. r. ocellatus* as a northern subspecies. Branch et al. (2018a) extending the known range to the Chela escarpment region and also validated *P. ocellatus* as a full species.



Fig. 23. *Psammophylax ocellatus*, Humpata, Huila.

Striped Skaapstekker

Psammophylax tritaeniatus (Günther 1868)

Rhagerhis tritaeniatus Günther, 1868. Sixth account of new species of snakes in the collection of the British Museum. *Ann. Mag. Nat. Hist.* (4) 1: 423.

First recorded from Dondo by Bocage (1873), and later from the Rio Kwanza, Quissange, Cahata, Quindumho, Caconda, Huila, Gambos, and Humbe by Bocage (1895), who noted it was one of the most common and widespread snakes on the highlands of Angola. Additional records from Cuvango, Mupanda, Vila da Ponte (= Cuvango) (Monard 1937), Capelongo (Bogert 1940), Alto Cubal (Hellmich 1957), Cazombo, Forte Roçadas (Laurent 1964), and Calombe (Manaças, 1973). Broadley (1977) reviewed the genus.

Subfamily: Prosymninae

A small subfamily containing only the African genus *Prosymna*, which currently includes 16 species. It is well-differentiated genetically (Kelly et al. 2008) and morphologically (Broadley 1980). They are small terrestrial snakes with an exclusive diet of reptile eggs (Broadley 1979b).

Zambezi Shovel-snout Snake

Prosymna ambigua (Bocage 1873)

Prosymna ambiguus Bocage, 1873. *Melanges erpetologiques*. II. Sur quelques reptiles et batraciens nouveaux, rares ou peu connus d'Afrique occidentale. *Jorn. Acad. Sci.*, Lisboa 4: 218.

Bocage (1873) described *Prosymna ambiguus* on a small juvenile from Calandula, which remained the only Angolan specimen known to him (Bocage 1895). Laurent (1954) reviewed *Prosymna ambigua* and described three new subspecies, including *P. a. brevis* based on an extensive series from Dundo and Sombe, and Sandoa in DRC. This subspecies was subsequently synonymized by Broadley (1980) with typical *P. a. ambigua*, who continued to recognize *P. a. bocagii* Boulenger, 1897 for a northern race in the Congo basin. Recent material was collected from Cangandala (Ceriaco et al. 2016b).



Fig. 24. *Prosymna ambigua*, 20 km W Lola, Namibe.

Angola Shovel-snout Snake
Prosymna angolensis (Boulenger 1915)

Prosymna angolensis Boulenger, 1915. A list of the snakes of the Belgian and Portuguese Congo, northern Rhodesia, and Angola. *Proc. Zool. Soc.*, London 1915: 208.

Boulenger (1915) gave a terse description of *Prosymna angolensis*, noting only that he referred snakes discussed by Bocage as *Prosymna frontalis* (1895, p. 98, pl., fig. 2) to his new species and gave the type locality simply as "Angola." Loveridge 1958 cleared up the mess and designated "Huila, 15°5'S, 13°30'E, Angola" as the type locality. Broadley (1980) assigned Bocage's inland *frontalis* material from Bibala, Caconda, and Maconjo to *P. angolensis*, as well other material, including an unusual coastal record (Mossamedes) that may be either a misidentified *P. frontalis* or the locality of the collector rather than that of the specimen. Additional records from Bela Vista (Hellmich 1957), and southeast Angola (Conradie et al. 2017; Conradie and Branch 2017), and all indicate that it is a species of the escarpment foothills and inland plateau.

South-west Shovel-snout Snake
Prosymna frontalis (Peters 1867)

Temnorhynchus frontalis Peters, 1867. Über eine Sammlung von Flederthieren und Amphibien aus Otjimbingue in Südwestafrika, welche Hr. Missionär Hahn dem zoologischen Museum zugesandt hat. *Monatsber. königl. Akad. Wiss. Berlin*. 1867 (April): 236.



Fig. 25. *Prosymna frontalis*, Espinheira, Namibe.

Peters (1867) described *Temnorhynchus frontalis* from "Otjimbingue, Südwestafrika" (= Otjimbingwe, SE Erongo Distr., cen. Namibia), and Bocage (1882) noted the first record of the species in Angola, based on material collected by Anchieta from Bibala and Mossamedes. He later referred inland material sent by Anchieta from Quiassange, Quibula, Quindumbo, Caconda, Huila, Maconjo and Bibala to this species (Bocage 1895), but records above the escarpment were incorporated into Boulenger's (1915) description of *P. angolensis*. This restricted *P. frontalis* to the arid habitats below the escarpment in southwest Angola.



Fig. 26. *Prosymna visseri*, Espinheira, Namibe.

Visser's Shovel-snout Snake
Prosymna visseri (FitzSimons 1959)

Prosymna visseri FitzSimons, 1959. Some new reptiles from southern Africa and southern Angola. *Annals Transvaal Mus.* 23: 406.

Prosymna visseri was one of the first new reptiles that Charles Koch collected incidentally whilst researching the tenebrionid beetle fauna of the Angolan Namib region. Described by FitzSimons (1959) from Caraculo, Haacke collected several others during his field work in

southwest Angola, but the species was known from only three specimens at the time of Broadley's (1980) revision. It was later described from Namibia (McLachlan 1987), from where all subsequent specimens have come (Bauer et al. 2000). All Angolan records are from arid habitats in the coastal southwest, but the species extends further inland in the Kaokoveld, Namibia.

Subfamily: Pseudaspinae

This small subfamily currently includes only two species in monotypic genera. Although Pyron et al. (2011) expanded the content of Pseudaspidinae to include African *Bufo* and Asian *Psammodynastes*, this was not supported by Figueroa et al. (2016), who rather associated the latter with the Psammophiinae (but see above).

Mole Snake

Pseudaspis cana (Linnaeus 1758)

Coluber canus Linnaeus, 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiæ. 10th Edition: 221.

First recorded from Angola by Bocage (1882) when describing a new genus and species *Ophirhina anchietae* from Caconda, in the interior of Benguela. Bocage soon realized that his 'new' species was already known, and discussed further material in his monograph (Bocage 1895) as *Pseudaspis cana*. Monard (1937) recorded material from Cuvango and Sanguéve, and Bogert (1940) from Mombolo.



Fig. 27. *Pythonodipsas carinata*, Baba, Namibe.

Western-keeled Snake

Pythonodipsas carinata (Günther 1868)

Pythonodipsas carinata Günther 1868. Sixth account of new species of snakes in the collection of the British Museum. *Ann. Mag. Nat. Hist.* (4) 1: 426.

First collected in September 1956 in Angola by Koch from Cima, Rio Giraul, Mossamedes and included in an updated map for the species (Branch et al. 1997), but

without locality details. FitzSimons (1962) and Broadley (1983) both utilized Koch's record in species maps and noted the distribution to include southern Angola.

Family: Elapidae

The taxonomy of African elapids has changed considerably in recent years, particularly among cobras (*Naja*), although the generic relationships of allied species have also been affected and numerous new species have been described (Broadley 1968, 1995; Broadley and Wüster 2004; Wüster and Broadley 2003, 2007; Wallach et al. 2009; Ceriaco et al. 2017; Wüster et al. 2018). Water cobras (*Boulengerina*) were demonstrated to be closely related to the Forest Cobra (*Naja melanoleuca*) and therefore synonymized with *Naja* (Nagy et al. 2005; Wüster et al. 2007). Wallach et al. (2009) proposed four subgenera within *Naja*, with the subgenus *Naja* restricted to Asia, and with the three other subgenera used for African cobras, and Angolan species assigned to various subgenera: i.e., *Naja* (*Boulengerina*) *melanoleuca*, *N.* (*Uraeus*) *anchietae*, *N.* (*Afronaja*) *mossambica*, *N.* (*Afronaja*) *nigricollis*, and *N.* (*Afronaja*) *n. nigricincta*. Moreover, a recent revisions of forest cobras (Ceriaco et al. 2017; Wüster et al. 2018) recognize a suite of five species, with typical *N.* (*B.*) *melanoleuca* entering northern Angola and the revived *N.* (*B.*) *subfulva* occurring in central Angola.



Fig. 28. *Aspidelaps lubricus cowlesi*, 70 km N Namibe, Namibe.

Coral Shield Cobra

Aspidelaps lubricus cowlesi (Bogert 1940)

Aspidelaps lubricus cowlesi Bogert, 1940. Herpetological results of the Vernay Angola Expedition. I. Snakes, including an arrangement of the African Colubridae. *Bull. Amer. Mus. Nat. Hist.* 77: 94.

Bogert (1940) described *Aspidelaps lubricus cowlesi* from a snake collected from Munhino (101 km east of Namibe, via railroad). Originally considered endemic to Angola, Mertens (1971) extended its range into the Kaokoveld. Broadley and Baldwin (2006) relegated it to the

synonymy of the northern Namibia subspecies *A. l. infuscatus*, citing intermediates between *A. l. cowlesi* and *A. l. infuscatus*. Unusually they still presented an account for *A. l. cowlesi* even though synonymizing it. Moreover, no morphological data was presented to show that even *A. l. infuscata* was a valid taxon, or a molecular data presented to support the new taxonomic arrangement.



Fig. 29. *Dendroaspis jamesoni*, Gabela, Cuanza Sul.

Jameson's Mamba

Dendroaspis jamesoni (Traill 1843)

Elaps jamesoni Traill, 1843. Description of the *Elaps jamesoni*, a new species of serpent from Demerara. *Edinburgh New. Phil. J.* 34 (67): 53.

The identification of historical records of Angolan mambas is complicated by confusion between green and black mambas in the early literature. Prior to 1946 the Black Mamba (*D. polylepis*) was considered a juvenile of the southern Green Mamba (*D. angusticeps*), and recognition of the Black mamba as a separate species was only confirmed by FitzSimons (1946). Bocage (1888) discussed the identification of mambas, reducing the number of species then known from seven to three, whilst also describing a new, overlooked species from Angola, *D. neglectus* (hence the unusual name). He gave detailed scale counts of the material he examined, and also presented a diagnostic key to the species recognized. From this it is evident that he applied the existing names wrongly: His *D. jamesoni* is now identified as *D. viridis*; his *D. angusticeps* is really *D. polylepis*; and his new species *D. neglectus* was already known as *D. jamesoni*. This arrangement continued to be reflected in his monograph (1895), where two species of mamba were correctly considered to occur in Angola, both unfortunately incorrectly named. *Dendroaspis jamesoni* has been recorded from Pungo-Andonga (the type of *Dendroaspis welwitschii* Günther, 1865, which Bocage considered a synonym of his own *D. neglectus* even though Günther's name had priority). As *D. neglectus* it was recorded from north of the Kwanza River (Bocage 1888) and from N'Dalatando (Ferreira 1903); and recorded correctly as *Dendroaspis jamesoni jamesoni* from Piri, Bela Vista (Hellmich 1957) and Dundo (Laurent 1954), although the status of the

eastern subspecies *D. j. kaimosae* needs genetic assessment. Recent material was discussed by Vaz Pinto and Branch (2015).

Black Mamba

Dendroaspis polylepis (Günther 1864)

Dendroaspis polylepis Günther, 1864. Report on a collection of reptiles and fishes made by Dr. Kirk in the Zambesi and Nyassa Regions. *Proc. Zool. Soc.*, London 1864: 310.

All early records (up to 1946) from Angola were discussed under *D. angusticeps* (Peters 1881; Bocage 1888, 1895; Monard 1937; Bogert 1940), until *D. polylepis* was shown to be a valid species (FitzSimons 1946). The species is nowhere common, but is relatively well-known in the central and southern regions. Bocage (1895) recorded it from the "hauts-plateaux de l'intérieur d'Angola," although Bogert (1940) recorded it from Hanha.

Günther's Garter Snake

Elapsoidea guentherii (Bocage 1866)

Elapsoidea guentherii Bocage, 1866. Lista dos reptis das possessões portuguesas d'Africa occidental que existem no Museu Lisboa. *Jorn. Sci. Math. Phys. Nat.*, Lisboa 1: 50.

Bocage (1866) described both the genus and species *Elapsoidea guentherii* in one of his first herpetological papers. The description was based on material sent by Anchieta from Cabinda, and led to the long association between these two icons of Angolan herpetology. Another adult from Bissau was included in the description, and to avoid confusion Parker (1949) later restricted the type locality to Cabinda. Additional material was discussed by Bocage (1895), Loveridge (1936), Bogert (1940), Hellmich (1957), Laurent (1964), and Broadley (1971b) who summarized its range from the northern parts of Angola, through Zambia to Zimbabwe.

Angolan Garter Snake

Elapsoidea semiannulata semiannulata (Bocage 1882)

Elapsoidea semi-annulata Bocage, 1882. Reptiles rares ou nouveaux d'Angola. *Journ. Sci.*, Lisboa 8(32): 303.

After describing the previous species, Bocage (1882) described *Elapsoidea semiannulata* from additional material from Caconda, but in his monograph (Bocage 1895) treated his new species as *E. guentheri* var. *semiannulata*. Laurent (1964) described *Elapsoidea decosteri huilensis* from Humpata, which was relegated to the synonym of *E. s. semiannulata* by (Broadley 1971b). However, Broadley (1971b) also treated a species described by Werner (1897) from Ghana as a northern race, *Elapsoidea semiannulata moebiusi*, that extended to Gabon but was unrecorded from Cabinda or northern Angola. All of

Bocage's northern localities (1866, 1895, 1897) were restricted to Bissau, but Broadley (1998) reassessed some of Laurent's Congo-Kinshasa material and reassigned it to *E. s. moebiusi*. Although Broadley (1998) described the range of *E. s. moebiusi* as extending into northern Angola, he neither mapped nor noted any localities supporting this claim. His closest locality was a poorly defined "Bas Congo" (Broadley 1998), and the race remains unknown from Angola, including Cabinda. Haacke and Finkeldey (1967) recorded the first record of *E. s. semiannulata* from southern Africa. Broadley (1971b) summarized and mapped the species in Angola, and recognized *E. s. boulengeri* Boettger, 1895, from Mozambique as an eastern race, which he later raised to a full species (Broadley 1998). This is unrecorded from Angola, although known from adjacent regions in Namibia and Zambia, and parapatry between *E. s. semiannulata* and *E. boulengeri* occurs in the Caprivi area.

Anchieta's Cobra

Naja (Uraeus) anchietae (Bocage 1879)

Naja anchietae Bocage, 1879. Reptiles et batraciens nouveaux d'Angola. *J. Acad. Sci.*, Lisbon 7: 89.

As with the previous species, Bocage (1879) also described *Naja anchietae* from snakes sent from Caconda. Mertens (1937) relegated it to a subspecies of the Egyptian Cobra (*N. haje anchietae*), Broadley (1995) referred southern populations of *N. haje* to the Snouted Cobra (*N. annulifera*), retaining *N. a. anchietae* as a western race. Finally, Broadley and Wüster (2004) revalidated Bocage's original name. Angolan specimens have thus been described under various names. Broadley and Wüster (2004) refer Bocage's (1895) *N. haje* material to *N. anchietae*. Known records were summarized and mapped in Broadley (1995) and Broadley and Wüster (2004), and its range was extended north to Capanda Dam by Ceriaco et al. (2014a).



Fig. 30. *Naja annulata*, Lagoa Carumbo, Lunde Norte.

Banded Water Cobra

Naja (Boulengerina) annulata (Peters, 1876)

Naja annulata Buchholz and Peters in Peters, 1876. Eine zweite Mittheilung über die von Hrn. Professor Dr. R. Buchholz in Westafrika gesammelten Amphibien. Monatsber. königl. Akad. Wiss. Berlin 1876 (February): 119.

Bocage (1985) mentioned *Naja annulata* from the Congo, but knew of no Angolan records. The first and only record for the country came from Lagoa Carumbo region (Branch and Conradie 2012). Wüster et al. (2018) noted that *Aspidelaps bocagei* Sauvage, 1884 (type locality: Gabon and Majumba) is not a synonym of *N. melanoleuca*, as recorded by various authors, but instead of *Naja annulata*.



Fig. 31. *Naja melanoleuca*, Soyo (Photo: Warren Klein).

Central African Forest Cobra

Naja (Boulengerina) melanoleuca (Hallowell 1857)

Naja haje var. *melanoleuca* Hallowell 1857. Notes of a collection of reptiles from the Gaboon country, West Africa, recently presented to the Academy of Natural Sciences of Philadelphia, by Dr. Henry A. Ford. *Proc. Acad. Nat. Sci. Philadelphia* 9: 61.

Bocage (1895) had a very different understanding of species boundaries within African cobras compared with modern nomenclature, but the loss of so much of his material has made assignment of his records to modern species difficult. Much of his cobra material was grouped as varieties under the spitting cobra *N. nigricollis*, e.g., *Naja nigricollis* var. *melanoleuca*. Fortunately, Broadley (1974) examined this material before it was destroyed in the Lisbon Museum fire (1978) and corrected the identity of the individual specimens of which none was referable to true *Naja melanoleuca* (Hallowell). To stabilize taxonomy Broadley (1974) designated MBL 1972 from "Caconda" as the lectotype of Bocage's (1895) *Naja nigricollis* var. *melanoleuca*, and treated it as a synonym of *N. nigricollis*. Whether Bocage knew true forest cobras from Angola remains debatable, but subsequent records confirming its presence are from Pungo Andongo (Boulenger 1905), Piri, Calulo, Sangeunge (Hellmich 1957), Dundo (Laurent 1954, 1964) and Soyo (Wüster et al. 2018). Genetic material from the latter validated

the presence of true *N. melanoleuca* in northwest Angola (Wüster et al. 2018). Laurent (1964) considered that true *N. melanoleuca* in northeast Angola was probably confined to forest galleries with *N. subfulva* living in secondary forests and the intervening savannas.

Brown Forest Cobra

Naja (Boulengerina) subfulva (Laurent 1955)

Naja melanoleuca subfulva Laurent, 1955. Diagnoses préliminaires des quelques Serpents venimeux. *Rev. Zool. Bot. Afr.* 51: 127–139.

The taxonomic status of the different populations of the forest cobra has long been problematic. Don Broadley (in litt., July 2013), in conjunction with Wolfgang Wüster and colleagues, recognized at least six species-level taxa within the forest cobra complex, including an endemic species on São Tome. Description of these cryptic taxa was delayed by Broadley's illness, and the São Tome population subsequently described as *Naja (Boulengerina) peroescobari* (Ceriaco et al. 2017). The delay also led to some nomenclatural confusion for other forest cobra populations, with various authors prematurely adopting some of the taxonomic findings. Broadley and Blaylock (2013) referred southern populations to Laurent's (1955) savannah-inhabiting subspecies *N. m. subfulva*, and noted that unpublished molecular data indicated it deserved specific status. They also used subgenera within *Naja* as proposed by Wallach et al. (2009), but some authors subsequently elevated these subgenera to full genera, e.g., Wallach et al. (2014) and Ceriaco et al. (2016b), even though the intention of using subgenera was to avoid medical issues possibly arising from nomenclatural changes in the names of medically important snakes. Chirio and Ineich (2006) and Ceriaco et al. (2017) also revived *N. subfulva*, the latter based on genetic divergence of Mozambique material. Wüster et al. (2018) mapped populations of *N. subfulva* from large parts of Angola. However, the assignment was presumably based on historical aspects, as no analysis was presented for Angolan *N. subfulva* morphology or genetic divergence compared with other populations. The status and distribution of *N. subfulva* in Angola therefore requires further study.

Mozambique Cobra

Naja (Afronaja) mossambica (Peters 1854)

Naja mossambica Peters, 1854. Diagnosen neuer Batrachier, welche zusammen mit der früher (24. Juli und 17. August) gegebenen Übersicht der Schlangen und Eidechsen mitgeteilt werden. *Ber. Bekanntmach. Geeignet. Verhandl. Königl.-Preuss. Akad. Wiss.*, Berlin 1854: 625.

Broadley (1974) first signaled the presence of *N. mossambica* in Angola when he identified a specimen from

Maconjo (MBL 1964, now lost) that Bocage (1895) had referred to *N. nigricollis* var. *fasciata*. Broadley (1968) treated *mossambica* as a full species after finding sympatry between *N. nigricollis* and *N. mossambica* in Zambia. The species is poorly known in Angola and the few records are restricted to the southern provinces (Conradie et al. 2016).

Western Barred Spitting Cobra

Naja (Afronaja) nigricincta nigricincta (Bogert 1940)

Naja nigricollis nigricincta Bogert, 1940. Herpetological results of the Vernay Angola Expedition. I. Snakes, including an arrangement of the African Colubridae. *Bull. Amer. Mus. Nat. Hist.* 77: 89.

Broadley (1974), after examination of Bocage's original material, assigned Bocage's (1895) *N. nigricollis* var. *fasciata* to Bogert's *N. nigricollis nigricincta*, and designated MBL 1968 (now lost) from Benguela as the lectotype. He was also unable to find Bocage's var. *fasciata* from Dondo, and this record may be in error. Molecular studies later supported the elevation of *N. nigricincta* to a full species, with a southern subspecies *N. n. woodi* (Wuster et al. 2007). However, no Angolan material was included in this analysis and the status of Namibian material needs confirmation, as the type locality for *N. nigricincta* is "Munhino (101 km east of Mossamedes via railroad," and nominotypical Angolan *N. nigricincta* have a different color pattern to those in Namibia.



Fig. 32. *Naja nigricincta*, 40 km N Caracul, Namibe.

Black Spitting Cobra

Naja (Afronaja) nigricollis (Reinhardt 1843)

Naja nigricollis Reinhardt, 1843. Beskrivelse af nogle nye Slangearter. *Danske Vidensk. Selsk. Afhandl.* 10: 369.

Broadley (1968) had reinstated *N. mossambica* as a full species after confirming sympatry with *N. nigricollis* in eastern Zambia. He treated *pallida*, *katiensis*, *nigricincta* and *woodi* as subspecies of *N. mossambica*, whilst various other names, e.g., *crawshayi*, *occidentalis*, and *atri-*

ceps were considered synonyms of *N. nigricollis*. Later, Broadley (1974) assigned Bocage's (1895) *N. nigricollis* var. *occidentalis* to *N. nigricollis nigricollis*, and designated MBL 1963 (now lost) from Dondo as the lectotype. He also noted that *Naja nigricollis* var. *melanoleuca* Bocage, 1895, described from Angola, was preoccupied by *N. melanoleuca* (Hallowell). Finding additional sympatry between *N. mossambica* and *N. nigricollis nigricincta* in Angola, he treated *nigricincta* and the all-black *woodi* from western South Africa and southern Namibia as subspecies of *N. nigricollis*. Following a molecular analysis of African spitting cobras, Wuster et al. (2007) validated *N. nigricincta* as a valid species, with *N. nigricincta woodi* as a southern race. The Black Spitting Cobra, *N. nigricollis*, therefore reverted to binomials. It is widespread in Angola, but generally absent from closed-canopy forest.

Gold's Tree Cobra

Pseudohaje goldii (Boulenger 1895)

Naja goldii Boulenger, 1895. On some new or little-known reptiles obtained by W. H. Crosse Esq. on the Niger. *Ann. Mag. Nat. Hist.* (6) 16: 34.

Parker (1935, as *Naja goldii*) recorded the first examples of this arboreal cobra from south of the Congo River and for Angola. The specimens were collected from remnant scarp forest near Quirimbo. The only other historical Angolan material is from Peri (Hellmich 1957) and Dundo (Laurent 1950, 1954).

Family: Viperidae

Compared with other snake families, African Viperidae have had relatively little taxonomic change, with various new species described (e.g., *Bitis harensa*, Gower et al. 2016; *Causus rasmusseni* Broadley, 2014) or species boundaries readjusted (e.g., revival of *Bitis rhinoceros*, Lenk et al. 1999) but few generic re-arrangements. With the exception of confusion over night adder identifications (see below), few taxonomic changes have affected Angolan vipers. As with the genus *Naja*, vipers of the genus *Bitis* had a number of subgenera proposed, and these are adopted in the following species accounts.

Variable Bush Viper

Atheris squamigera (Hallowell 1854)

Echis squamigera Hallowell, 1854. Descriptions of new reptiles from Guinea. *Proc. Acad. Nat. Sci. Philadelphia* 1854: 193.

Bocage (1895) knew of no Angolan material except Peters' (1881) record from Cuango. Later material was recorded from Gulongo Alto (Ferreira 1904), Piri (Hellmich 1957), and Dundo and Luachimo River (Laurent 1954, 1964). *Atheris squamigera* is widespread in

the Congo Basin, and a highly variable species. Laurent (1964) only tentatively attributed four specimens from the Dundo region to *A. squamigera*, as he believed that there were two sympatric species in the lower Congo, and that *A. anisolepis* may be valid. Recognition of Mocquard's *anisolepis* had been problematic, placed first in the synonymy of *A. squamigera* by Boulenger (1896), revived as a subspecies by Bogert (1940), treated again as a full species by Broadley (1998b), until finally again synonymized by Lawson and Ustach (2000).

Puff Adder

Bitis (Bitis) arietans (Merrem 1820)

Vipera (Echidna) arietans Merrem. 1820. Versuch eines Systems der Amphibien I (Tentamen Systematis Amphibiorum). J. C. Kriegeri, Marburg: 152.

Although Bocage (1895) noted that the species was common in Angola, there are few records from the southwest region. Günther's (1865) record from Moçâmedes (= Namibe) may have reflected the collector's home base.

Horned Adder

Bitis (Calechidna) caudalis (Smith 1839)

Vipera (Cerastes) caudalis Smith, 1839. Illustrations of the Zoology of South Africa, Reptilia. Smith, Elder, and Co., London: 7.

Although common through the western arid regions of southern Africa (Branch 1998) there are few Angolan records of the species. Bocage (1867) first signalled its presence (as *Cerastes caudalis*) with a specimen from Namibe collected by Anchieta. Subsequent records were added by Bocage (1895, Capangombe, Rio Curoca), and Laurent (1964, "35 km south of Namibe").



Fig. 33. *Bitis caudalis*, Baba, Namibe.

Gaboon Adder

Bitis (Macrocerastes) gabonica (Duméril, Bibron and Duméril 1854)

Echidna gabonica Duméril, Bibron and Duméril 1854. *Erpétol-*

ogie générale ou histoire naturelle complète des reptiles. Tome septième. Deuxième partie, comprenant l'histoire des serpents venimeux. Paris, Librairie Encyclopédique de Roret: 1428.

At the time of his monograph Bocage (1895) knew this iconic species only from Lândana, Cabinda, and considered that the species was unlikely to occur south of the Kwanza River. However, a year later he reported two specimens from Hanha collected by Anchieta (Bocage 1896). Subsequently others have been recorded: Ferreira (1903), Laurent (1950, 1954, 1964), Tys van den Audenaerde (1967), Oliveira et al. (2016), and Conradie et al. (2017). It is widespread in Angola in suitable forest edge habitat.

Angolan Adder

Bitis (?) *heraldica* (Bocage 1889)

Vipera heraldica Bocage, 1889. Mélanges erpétologiques. II. Sur une vipère apparemment nouvelle d'Angola. *Journ. Sci., Lisboa* (2) 2: 127.

Bocage (1889) described this endemic Angolan snake from “sur les bords de la rivière Calae, l'un des affluents du Cunene, entre le 13 et le 14 parallèle à l'est de Caconda, Angola” (= Caluè River, a tributary of the Cunene River, east of Caconda, Huíla District, Angola). Soon after its description the species was incorrectly synonymized with the *Bitis peringueyi*, a dwarf adder from Namib Desert dune habitat (Boulenger 1896), leading to over 50 years of confusion. Early records of ‘*B. peringueyi*’ in southern Angola were all based on Boulenger’s synonymization of *B. heraldica*: i.e., a female from “Between Benguela and Bié” (Boulenger 1905), one from Caluquembe (Monard 1937), and another from “Mombolo, Angola” from the Vernay, Lang, Boulton, expedition of 1925 (Bogert 1940). The specific status of *Bitis heraldica* was revalidated by Mertens (1958) following the collection of a series of *Bitis heraldica* from Piri (Hellmich 1957) and the species confirmed as endemic to the Angolan highlands. Due to the absence of any fresh genetic material the subgenera status remains uncertain.

Rhinoceros Viper

Bitis (*Macrocerastes*) *nasicornis* (Shaw 1802)

Coluber nasicornis Shaw, 1802. General Zoology or Systematic Natural History, vol. 3, Pt 1. Thomas Davison, London: 94.

Unknown to Bocage (1895) from Angola or Congo, it was first recorded from Angola from scarp forest at Quirimbo (Parker 1936). That it could be regionally common is shown by Hellmich’s (1957) astonishing record of 53 specimens from Piri. Recent material was recorded from Uige (Ernst et al. 2016).

Two-lined Night Adder

Causus bilineatus (Boulenger 1905)

Causus bilineatus Boulenger, 1905. A list of the batrachians and reptiles collected by Dr. W. J. Ansorge in Angola with descriptions of new species. *Ann. Mag. Nat. Hist.* (7) 16: 114.

Night adders in Angola have been a source of great confusion, with Bocage (1895) and most subsequent authors recognizing only two species in Angola, *C. rhombeatus* and *C. resimus*. Bocage (1895), however, did note well-marked adders with lateral stripes from Calandula, Quissange, Caconda, and Huíla, but made no taxonomic descision. Boulenger (1905) on receiving additional material from Anchieta noted these same features and proposed the name *bilineatus*. This name was overlooked by subsequent authors until Laurent (1955) described *Causus lineatus* for material from DRC. Later, when looking at material from Dundo that he realized was referable to Boulenger’s *bilineatus* and also conspecific with his DRC material, Laurent (1964) used trinomials and treated his DRC material as the subpecies *C. bilineatus lineatus* and Angolan material from Calundo, Moxico, as nominotypic *C. b. bilineatus*. Broadley (1968), based on unpublished analysis in his Ph.D. thesis (Broadley 1966a), synonymized *C. b. lineatus* with *C. bilineatus*, and this was supported by Rasmussen (2005), who reviewed *C. bilineatus*, re-assessed and mapped Angolan night adders, and corrected many early misidentifications by Hellmich (1957) and Laurent (1964). He noted that *C. bilineatus* occurred in sympatry with *C. rhombeatus* in the Benguela-Bié area, Caconda, and Chitau, and with *C. rhombeatus* and *C. maculatus* at Piri.

Angola Green Night Adder

Causus resimus (Peters 1862)

Heterophis resimus Peters, 1862. Über die von dem so früh in Afrika verstorbenen Freiherrn von Barnim und Dr. Hartmann auf ihrer Reise durch Aegypten, Nubien und dem Sennâr gesammelten Amphibien. *Monatsber. Akad. Wiss.*, Berlin 1862: 277.

Bocage (1895) tentatively proposed the name *C. resimus*, var. *angolensis* for night adders from several localities in Angola, including Rio Dande, Rio Bengo, Cazengo, Sumbe, Quissange, Rio Chimha, Bibala, and Maconjo. Additional records of *C. resimus* have also been reported from Cazengo, Caculo, Cabcicula (Ferreira 1904), Quirimbo, Fazenda Congulo (Parker 1936), and Hanha (Bogert 1940). Few of these have been accepted by Rasmussen (2005). The Green Night Adder is currently distributed in four isolated populations around the Congo Basin, with the most isolated being that recorded from Angolan scarp forest refugia. The taxonomic status of the Angolan population, and the applicability of Bocage’s (1895) *C. resimus*, var. *angolensis* or *C. nasalis* Stej-

neger, 1893, remain unresolved. A preliminary molecular phylogeny of *Causus* (Tolley et al. in prep.) indicates cryptic diversity within *C. resimus*, and supports the distinctiveness of Angolan material. Rasmussen (2005) mapped 13 localities for *C. resimus* in Angola, including one from Cabinda.

Rasmussen's Night Adder

Causus cf. *rasmusseni* (Broadley 2014)

Causus rasmusseni Broadley, 2014. A new species of *Causus* Lichtenstein from the Congo/Zambezi watershed in north-western Zambia (Reptilia: Squamata: Viperidae). *Arnoldia Zimbabwe* 10 (29): 342.

Broadley (2014) described *C. rasmusseni* based on four specimens from northern Zambia. It is weakly differentiated from sympatric *C. rhombeatus* by having slightly fewer ventrals in males (130–132, versus 134–150 in Zambian *C. rhombeatus*) and reduced blotches or uniform dorsal coloration. Although the un-patterned dorsal pattern and low ventral counts of a specimen from Rio Longa (Conradie et al. 2016) conform to Broadley's concept of *C. rasmusseni*, we caution acceptance of its presence in Angola, and indeed its specific status. A preliminary molecular phylogeny of night adders (Tolley et al., in prep.) supports such caution.



Fig. 34. *Causus* cf. *rasmusseni*, Rio Longa, Cuando Cubango.

Rhombic Night Adder

Causus rhombeatus (Lichtenstein 1823)

Sepedon rhombeata Lichtenstein, 1823. Verzeichniss der Doubletten des zoologischen Museums der Königl. Universität zu Berlin nebst Beschreibung vieler bisher unbekannter Arten von Säugethieren, Vögeln, Amphibien und Fischen. Königl. Preuss. Akad. Wiss./T. Trautwein, Berlin: 106.

Bocage consistently used this name (Bocage 1879, 1880, 1895) and considered it widespread in the interior of Angola. Additional material was noted from Golungo Alto (Ferreira 1904), Mt Moco, Quirimbo (Parker 1936), Calundo, Dundo, and Cossa (Laurent 1964). Bocage

(1895) considered material from Calandula, Quissange, Caconda, and Huila formed “une variété bien caractérisée du *C. rhombeatus*” which was later described as *C. bilineatus* by Boulenger (1905). Rasmussen (2005) mapped the species in Angola, and corrected misidentified material (Hellmich 1957, Laurent 1964), following confusion with *C. maculatus* in northern populations.

West African Night Adder

Causus maculatus (Hallowell 1842)

Distichurus maculatus Hallowell, 1842. Description of a new genus of Serpents from Western Africa. *J. Acad. nat. Sci. Philadelphia* 8: 337.

This species was confused with *C. rhombeatus* by Bocage, and the first material from Angola was noted by Laurent (1964) from Dundo. Rasmussen (2005) noted the importance of the lateral oblique scale row number in distinguishing between the two species, corrected earlier misidentifications, and showed that *C. maculatus* occurs in sympatry with both *C. rhombeatus* and *C. bilineatus* at Piri. It is restricted to the northern parts of Angola.

Lichtenstein's Night Adder

Causus lichtensteini (Jan 1859)

Aspidelaps lichtensteini Jan, 1859. Additions et rectifications aux Plan et Prodrome de l'Iconographie descriptive des Ophiidiens. *Rev. Mag. Zool.* 11: 511.

Laurent (1964) recorded the first and only specimens of *C. lichtensteini* in Angola from Dundo and the Lukashi River, 50 km east Dundo. In the Dundo region it occurs in sympatry with both *C. rhombeatus* and *C. maculatus* (Rasmussen 2005).

Species not confirmed for Angola that may occur

Hallowell's House Snake

Boaedon virgatus (Hallowell 1854)

Coelopeltis virgata Hallowell, 1854. Remarks on the geographical distribution of reptiles, with descriptions of several species supposed to be new, and corrections of former papers. *Proc. Acad. Nat. Sci. Philadelphia* 1854: 98–105.

Known from both Congo (Brazzaville) and Gabon (Pauwels and Vande weghe 2008), and therefore likely to occur in forested habitats in Cabinda.

Plain Striped House Snake

Bothrophthalmus brunneus (Günther 1863)

Bothrophthalmus lineatus brunneus Günther, 1863. Third account of new species of snakes in the collection of the British

Museum. *Ann. Mag. Nat. Hist.* (3) 12: 348.

Not known to Bocage (1895) from Angola. Although *Bothrophthalmus lineatus* was recorded from Dundo (Laurent 1950, 1954, 1964; Tys van den Audenaerde 1967), the plain western subspecies *B. l. brunnaeus*, from Cameroon to Gabon, is now treated as a full species (Pauwels and Vande weghe 2008). It is possible that *B. brunnaeus* may extend south to the Cabinda forests, and those in Angola just south of the border.

Mopane Racer

Mopanveldophis zebrinus (Broadley and Schätti 2000)

Broadley, D.G. and Schätti, B. 2000. A new species of *Coluber* from northern Namibia (Reptilia: Serpentes). *Madoqua* 19(2): 171.

This unusual and rare snake was described (Broadley and Schätti 2000) from a single specimen collected near Ruacana on the Cunene River, western Owamboland, Namibia (17°25'S, 14°10'E). It is known from only three other specimens from the Kaokoveld (Bauer et al. 2001), and from the Kunene River mouth (Cunningham et al. 2018), and was provisionally considered to form part of a Trans-Kunene mopaneveld fauna, and that it may therefore occur in southern Angola. Even at the time of its description, however, its inclusion in the genus *Coluber* was provisional as the genus was undergoing reassessment and division, particularly the African representatives (e.g., Schätti and Charvet 2003). Schätti and Utiger (2001) erected a monotypic genus for the unusual Socotran racer, *Hemerophis socotrae*, but deferred a decision on *C. zebrinus* as its phylogenetic relationships were unknown. However, it was subsequently prematurely placed in *Hemerophis* (Wallach et al. 2014), creating a 3,000 km+ zoogeographic enigma, before being finally placed in the monotypic *Mopanveldophis* (Figueroa et al. 2016). This generic name is as non-euphonious as it is a misnomer, as Mopane veld has a much wider distribution than that of the snake, and there is as yet no confirmation that this attractive small racer is restricted to mopaneveld.

Bark Snake

Hemirhaggheris nototaenia (Günther 1864)

Coronella nototaenia Günther, 1864. Contribution to the knowledge of snakes of tropical Africa. *Ann. Mag. Nat. Hist.* (6) 1: 309.

Hemirhaggheris in Africa was reviewed by Broadley and Hughes (2000), who showed that all historical Angolan records of *H. nototaenia* (e.g., Bocage 1895, Monard 1937) were confused with *H. viperina*. The species may enter extreme eastern Angola as it is recorded from Caprivi (Broadley and Hughes 2000), the adjacent Ike-

lenge pedicel in extreme northwest Zambia (Broadley 1991a), and Ngonye Falls, southwest Zambia (Pietersen et al. 2017).

Lined Grass Snake

Psammophis lineatus (Duméril, Bibron and Duméril 1854)

Dryophylax lineatus Duméril, Bibron and Duméril 1854. *Erpétologie générale ou histoire naturelle complète des reptiles*. Tome septième. Deuxième partie, comprenant l'histoire des serpents venimeux. Paris, Librairie Encyclopédique de Roret: 1124.

Its presence in Angola is based on a single record (as *Dromophis lineatus*, Bogert 1940) from "Angola," (AMNH 50611, Vernay, Lang, Boulton 1925). The specimen lacks detailed locality data, and members of the Vernay-Lang Angola expedition did not visit eastern or northern Angola, although they visited other areas in Africa after the expedition (Hill and Carter 1940). The species is known from savannah habitats in adjacent countries (Hughes 2004), but Bogert's record should be treated with caution until the discovery of additional material. *Dromophis* was synonymized with *Psammophis* (Kelly et al. 2008).

Boulenger's Garter Snake

Elapsoidea boulengeri (Boettger 1895)

Elapsoidea boulengeri Boettger, 1895. Zwei neue Reptilien vom Zambesi. *Zool. Anz.* 18: 62.

Broadley (1998) mapped parapatry between *Elapsoidea boulengeri* and *E. s. semiannulata* from the eastern Caprivi and it is possible that *E. boulengeri* enters extreme southeast Angola.

Peringuey's Adder

Bitis peringueyi (Boulenger 1888)

Vipera peringueyi Boulenger, 1888. On new or little known South African reptiles. *Ann. Mag. Nat. Hist.* (6) 2: 141.

Haacke (1975) when reviewing the small adders of the western arid of southern Africa recorded no *B. peringueyi* from Angola, and no confirmed records have subsequently been recorded. Despite this, the species continued to be incorrectly listed for the country (e.g., Branch 1998; Dobiey and Vogel 2007; Uetz and Hozek 2017). Possibly suitable habitat occurs in the small extension of the Namib Desert into extreme southwest Angola, but there remain no records.

Discussion

The diversity and composition of snake families in Angola basically reflects that of Sub-Saharan Africa and

particularly the adjacent subcontinent. There is relatively low diversity in primitive groups such as scolecophidi-ans (Typhlopidae and Leptotyphlopidae) and particularly haenophidians (Pythonidae). The main venomous families Elapidae and Viperidae are well-represented in both Angola and the subcontinent, but with more tropical representatives in Angola (e.g., the elapids *Pseudohaje goldi* and *Naja annulata*, and viperids *Causus lichtensteini*, *C. maculatus*, *Atheris squamigera*, and *Bitis nasicornis*). In both regions cobras (*Naja*, *Hemachatus*) dominate the elapid fauna. Among viperids, however, both regions have local but different radiations of small viperids. Small adders of the *Bitis atropos-cornuta* (7–10 species) and *Bitis caudalis-schneideri* (4–6 species) complexes in southern Africa may be regionally common, highly endemic and taxonomically difficult (Branch 1997, 1999; Kelly et al. 2011b). Only a single component of this radiation, *Bitis caudalis*, enters Angola (the phylogenetic affinities of *B. heraldica* remain unresolved), whereas night adders (*Causus*) are marginally present in the subcontinent but in Angola are their most diverse anywhere in Africa (Rasmussen 2005).

The dominant African snake family is the Lamprophiidae which appears to have originated in Africa, and within which some lineages subsequently radiated into Arabia and Asia. It appears to have been a rapid radiation, and untangling the relationships and even content of the many subfamilies is proving difficult (e.g., Kelly et al. 2008; Pyron et al. 2011; Figuerio et al. 2016) and a consequently unstable higher-level classification. The Atractaspidinae (here included within lamprophids, but sometimes treated as a separate family; Figuerio et al. 2016), Lamprophiinae, Prosymyinae and Psammophinae form important lamprophid radiations in Sub-Saharan Africa, and together also form the dominant component of the Angolan snake fauna (37 species). As with elapids and viperids a number of Congo Basin species enter the northern forests, including some currently known from very few Angolan specimens, e.g., *Lycodonomorphus* (?) *subtaeniatus*, *Chamaelycus parkeri*, *Boaedon* cf. *olivaceus*, *Bothrophthalmus lineatus*, etc. Perhaps the greatest difference between South Africa and Angola is reflected in the greater diversity of colubrids (Colubridae) in Angola (29 species). These include numerous tropical Congo Basin snakes that enter the northern and scarp forests, and of particular interest are the Congo Basin species *Toxicodryas blandingii*, *T. pulverulenta*, *Rhampophis aethiopiassa*, *Philothamnus nitidus*, *Dasyzelis palmarum*, etc. The family is considered of Asian origin and to have entered and subsequently radiated in Africa.

Although a number of new Angolan lizards have been described (Haacke 2008; Conradie et al. 2012; Stanley et al. 2016) or identified (e.g., Branch et al. 2017) since the end of civil hostilities and the start of modern biodiversity surveys, no new snakes have yet been described. It is therefore unsurprising that snake diversity in Angola appears to be the most well-known component of

the country's reptile fauna. However, the distributions of snakes in Angola remain poorly-known, particularly those of forest-adapted species in tropical forest associated with the Congo Basin along the northern border, and with the evergreen forest isolates associated with the escarpment along the western edge of the country. Angola harbours the second highest level of vertebrate endemism associated with the disjunct components of the African Great Escarpment (Clark et al. 2011). Studies on the phylogenetic relationships of the snakes associated with these isolated forest populations are needed to confirm their conspecificity with northern populations, and to understand the consequences and timing of the disjunctions between these forests. Similarly, the montane grassland habitats associated with the Humpata plateau of the escarpment, particularly in the Tundavala region, includes numerous regional reptile endemics (Baptista et al. 2018a), including two psammophine snakes (Branch et al. 2018).

As noted in the Introduction, this checklist is a first step towards stimulating increased interest in the herpetofauna of Angola. Bocage's early studies, culminating in his monographic summary of Angola's herpetological riches, placed the country among the few African countries with a well-studied herpetofauna during the early colonial period. Sadly, this was followed by a century of relative neglect, but with an early scientific revival in the 1970s that was nipped in the bud by civil conflict. However, overviews of both reptile (Branch et al. 2018b) and amphibian diversity (Baptista et al. 2018b) are included in an updated synopsis of the countries' biodiversity (Huntley et al. 2018), and finally with peace and welcoming borders, studies on Angolan biodiversity are entering the new Millennium.

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Literature Cited

Adalsteinsson SA, Branch WR, Trape S, Vitt LJ, Hedges SB. 2009. Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopi-

- dae (Squamata, Scolecophidia). *Zootaxa* 2244: 1–50.
- Angel F. 1921. Description d'un ophidien nouveau de l'Angola appartenant au genre *Psammophis*. *Bulletin de la Société Zoologique de France* 46(8–10): 116–118.
- Angel F. 1923. Reptiles. Extrait de la Mission Rohan Chabot, Angola et Rhodésia 1912–1914. *Imprimerie Nationale*, Paris 4(1): 157–169.
- Auerbach RD. 1987. *The Amphibians and Reptiles of Botswana*. Okwepa Consulate, Botswana, Africa. V + 295 p., text figs., 19 plates.
- Baptista N, António T, Branch WR. 2018a. Amphibians and Reptiles of the Tundavala Region of the Angolan Escarpment. Pp. 397–403 In: *Climate Change and Adaptive Land Management in Southern Africa – Assessments, Changes, Challenges, and Solutions*. Editors, Revermann R, Krewenka KM, Schmiedel U, Olwoch JM, Helmschrot J, Jürgens N. *Biodiversity & Ecology*, 6, Klaus Hess Publishers, Göttingen and Windhoek. doi:10.7809/b-e.00351
- Baptista N, Conradie W, Vaz Pinto P, Branch WR. 2018b. Amphibians of Angola: Early studies, status of current knowledge, and the way forward. In: *Angolan Biodiversity: A Modern Synthesis*. Editors, Huntley BJ, Ferrand N, Russo V, Lages F. Springer, (in press).
- Bates MF. 2013. First records of the egg-eating snake *Dasypeltis confusa* (Trape and Mane 2006) in Nigeria and Chad, with range extensions for Ghana. *Navorsing van die Naionale Museum* (Bloemfontein) 29(2): 17–27.
- Bates MF, Broadley DG. 2018. A revision of the egg-eating snakes of the genus *Dasypeltis* Wagler (Squamata: Colubridae: Colubrinae) in north-eastern Africa and south-western Arabia, with descriptions of three new species. *Indago* 34(1): 1–95.
- Bates MF, Broadley DG, Barlow A, Wuster W, Tolley K. 2012. Taxonomy and distribution of the African egg-eating snakes of the genus *Dasypeltis* (abstract of presentation at 7th World Congress Herpetology, Vancouver). *African Herp News* 58: 27–28.
- Bauer AM, Lamb T, Branch WR, Babb RD. 2000. New Records of Two Rare Snakes from Northern Namibia, with Comments on the Trans-Kunene Distribution of Mopaneveld Squamates (Squamata: Serpentes: Colubridae). *Herpetozoa* 14(1–2): 75–79.
- Baynham T. 2010. Geographic distribution: Reptilia: Squamata: Elapidae: *Dendroaspis polylepis polylepis*. *African Herp News* 51: 25–27.
- Bocage JVB. 1866a. Lista dos reptis das possessões portuguesas d' Africa occidental que existem no Museu de Lisboa. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) 1: 37–56.
- Bocage JVB. 1866b. Reptiles nouveaux ou peu connus recueillis dans les possessions portugaises de l'Afrique occidentale, qui se trouvent au Muséum de Lisbonne. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) 1: 57–79.
- Bocage JVB. 1872. Diagnoses de quelques espèces nouvelles de Reptiles d'Afrique occidentale. *Jornal de Ciências Mathematicas, Physicas e Naturaes* (Lisboa) 4: 72–82.
- Bocage JVB. 1879. Reptiles et batraciens nouveaux d'Angola. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) 7: 97–99.
- Bocage JVB. 1882a. 1. Noticia ácerca de alguns reptil d'Angoche que existem no Museu Nacional de Lisboa. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) 8: 286–290.
- Bocage JVB. 1882b. Notice sur les espèces du genre “*Philothamnus*” qui se trouvent au Muséum de Lisbonne. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) 9: 1–20.
- Bocage JVB. 1887a. Sur un Python nouveau d'Afrique. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) 12: 87–88.
- Bocage JVB. 1887b. Mélanges herpétologiques. V. Reptiles et Batraciens de Quissange (Benguella) envoyés par M. J. d'Anchieta. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) XI(44): 208–211.
- Bocage JVB. 1888. Mélanges erpétologiques. VI. Espèces du genre *Dendraspis*. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) XII(47): 138–147.
- Bocage JVB. 1889. Mélanges erpétologiques. II. Sur une vipère apparemment nouvelle d'Angola. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) Series 2, 2: 127–128.
- Bocage JVB. 1895. *Herpétologie d'Angola et du Congo*. Imprimerie Nationale, Lisbonne. 203 p.
- Bocage JVB. 1897. Mammiferos, Aves e Reptis da Hanha, no Sertão de Benguella. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* (Lisboa) Series 2, 4: 207–211.
- Bocage JVB. 1903. Contribution à la faune des quatre îles du Golfe de Guinée. *Jornal de Ciências, Matemáticas, Physicas e Naturaes*, Series 2, 7: 25–59.
- Bogert CM. 1940. Herpetological results of the Vernay-Angola Expedition, with notes on African reptiles in other collections. I. Snakes, including an arrangement of African Colubridae. *Bulletin of the American Museum of Natural History* 77:1–107.
- Boulenger GA. 1893. *Catalogue of the Snakes in the British Museum* (Natural History). Volume I, containing the families Typhlopidae, Glauconiidae, Boidae, Ilysiidae, Uropeltidae, Xenopeltidae and Colubridae aglyphae, part. British Museum (Natural History), London, England. Xiv + 448 p., 26 figs., 28 plates.
- Boulenger GA. 1894. *Catalogue of the Snakes in the British Museum* (Natural History). Volume II, containing the conclusion of the Colubridae aglyphae. British Museum (Natural History), London, England. Xii + 382 p., 25 figs., 20 plates.
- Boulenger GA. 1895. Descriptions of two new snakes from Usambara, German East Africa. *Annals and*

- Magazine of Natural History*, Series 6, 16: 171–173.
- Boulenger GA. 1896. *Catalogue of the Snakes in the British Museum* (Natural History). Volume III, containing the Colubridae (Opisthoglyphae and Proteroglyphae), Amblycephalidae, and Viperidae. British Museum (Natural History), London, England. Xiv + 727 p., 37 figs., 25 plates.
- Boulenger GA. 1905. A list of the batrachians and reptiles collected by Dr. W. J. Ansorge in Angola, with descriptions of new species. *Annals and Magazine of Natural History*, Series 7, 16: 105–115.
- Boulenger GA. 1915. A list of the snakes of the Belgian and Portuguese Congo, northern Rhodesia, and Angola. *Proceedings of the Zoological Society* (London) 1915: 193–223.
- Bourgeois M. 1968. Contribution à la morphologie comparée du crâne des Ophidiens de l’Afrique Centrale. *Des Publications de l’Université Officielle du Congo a Lubumbashi* 13: 1–239.
- Branch WR, Shine R, Harlow P, Webb JK. 1997. Sexual dimorphism, diet, and aspects of reproduction of the Western Keeled Snake, *Pythonodipsas carinata* (Serpentes: Colubridae). *African Journal of Herpetology* 46(2): 89–97.
- Branch WR. 1998. *Field Guide to Snakes and other Reptiles of Southern Africa*. Struiks, Cape Town, South Africa. 399 p.
- Branch WR. 1999. Dwarf adders of the *Bitis cornutainornata* complex (Serpentes: Viperidae) in Southern Africa. In: *Systematics, Phylogeny and Biology of the Viperidae*. Editors, Joger U, Nilson G. *Kaupia* 8: 39–63.
- Branch WR. 2018. Auf Reptiliensuche in der angolanischen Okavango-Wildnis (Herping the Angolan Okavango Wilderness). *Sauria* (Berlin) 40(1): 25–57.
- Branch WR, Bauer AM. 2014. Systematics and Phylogeny. Pp. 10–21. In: *Atlas and Red Data Book of the Reptiles of South Africa, Lesotho and Swaziland*. Editors, Bates MF, Branch WR, Bauer AM, Burger M, Marais J, Alexander GJ, de Villiers MS. *Suricata* 1, South African National Biodiversity Institute, Pretoria, South Africa. 483 p.
- Branch WR, Conradie W. 2013. Geographical Distribution: *Naja (Boulengerina) annulata annulata* Burcholtz and Peters, 1876 Banded Water Cobra. *African Herp News* 59: 51–54.
- Branch WR, Conradie WC. 2015. Herpetofauna da região da Lagoa Carumbo (Herpetofauna of the Carumba Lagoon Area). Pp. 194–209 In: *Relatório sobre a Expedição Avaliação rápida da Biodiversidade de região da Lagoa Carumbo, Lunda Norte - Angola* (Expedition Report. Rapid Biodiversity assessment of the Carumba Lagoon area, Lunda Norte, Angola). Editor, Huntley B. Republica de Angola Ministerio do Ambiente, Luanda, Angola. 219 p.
- Branch WR, McCartney CJ. 1992. A report on a small collection of reptiles from southern Angola. *Journal of the Herpetological Association of Africa* 41: 1–3.
- Branch WR, Haacke W, Vaz Pinto P, Conradie W, Baptista N, Verburgt L. 2017. Loveridge’s Angolan geckos, *Afroedura karroica bogerti* and *Pachydactylus scutatus angolensis* (Sauria, Gekkonidae): New distribution records, comments on type localities and taxonomic status. *Zoosystematics Evolution* 93(1): 157–166.
- Branch WR, Bayliss J, Bittencourt-Silva GB, Conradie W, Engelbrecht HM, Loader S, Menegon M, Nannonamuquitxo, C, Tolley KA. 2018a. A new species of tree snake (*Dipsadoboa*, Serpentes: Colubridae) from ‘sky island’ forests in northern Mozambique, with notes on other members of the *Dipsadoboa werneri* group. Zootaxa, submitted.
- Branch WR, Baptista N, Vaz Pinto P, Conradie W. 2018b. The Reptiles of Angola – History, updated checklists, endemism, hot spots, and future directions for research. In: *Angolan Biodiversity: A Modern Synthesis*. Editors, Huntley BJ, Ferrand N, Russo V, Lages F. Springer, (in press).
- Brandstätter F. 1995. Eine Revision der Gattung *Psammophis* mit Berücksichtigung der Schwesterngattungen innerhalb der tribus Psammophiini (Colubridae: Lycodontinae). Teil 1: Die Gattungen und Arten der Tribus Psammophiini. Teil 2: Rasterelektronenmikroskopische Untersuchungen zur Schuppe-nultrastruktur bei den Arten der Tribus Psammophiini mit besonderer Berücksichtigung der Arten der Gattung *Psammophis*. Unpublished D.Sc thesis. Universität des Saarlandes, Saarbrücken, Germany. 480 p.
- Brandstätter F. 1996. *Die Sandrennattern*. Westarp.-Wiss., Magdeburg; Spektrum Akad. Verlag, Heidelberg, Germany. 142 p.
- Broadley DG. 1961. A provisional check list of the snakes of Rhodesia and Nyasaland, incorporating proposed English names for species. *Journal of the Herpetological Association of Rhodesia* 15(1): 3–7.
- Broadley DG. 1962. On some reptile collections from the north-western and north-eastern districts of Southern Rhodesia 1958–61, with descriptions of four new lizards. *Occasional Papers of the National Museum of Southern Rhodesia* 3B(26): 787–843.
- Broadley DG. 1966a. The Herpetology of South-east Africa. Ph.D. thesis, Department of Zoology, University of Natal, South Africa. 685 p.
- Broadley DG. 1966b. A review of the genus *Natriciteres* Loveridge (Serpentes: Colubridae). *Arnoldia* (Rhodesia) 2(35): 1–11.
- Broadley DG. 1966c. A review of the African Stripebelly Sand-snakes of the genus *Psammophis*. *Arnoldia* (Rhodesia) 2(36): 1–9.
- Broadley DG. 1968. A review of the African cobras of the genus *Naja* (Serpentes: Elapinae). *Arnoldia* (Rhodesia) 3: 1–14.
- Broadley DG. 1971a. A revision of the African snake genera *Amblyodipsas* and *Xenocalamus*. *Occasional Papers of the National Museum of Rhodesia* B4(33):

- 629–697.
- Broadley DG. 1971b. A revision of the African snake genus *Elapsoidea* BOCAGE (Elapidae). *African Herp News* 29: 31–32.
- Broadley DG. 1971c. A review of *Rhamphiophis acutus* (Günther) with the description of a new subspecies from Zambia (Serpentes: Colubridae). *Arnoldia* (Rhodesia) 5(8): 1–8.
- Broadley DG. 1974. A review of the Cobras of the *Naja nigricollis* complex in southwestern Africa (Serpentes: Elapidae). *Chimbebasia* 2(14): 1–8.
- Broadley DG. 1977. A revision of the African Snakes of the Genus *Psammophylax* Fitzinger (Colubridae). *Occasional Papers of the National Museum of Rhodesia* 1976 B6(1): 1–44.
- Broadley DG. 1979a. Problems presented by geographical variation in the African Vine snakes, genus *Thelotornis*. *South African Journal Zoology* 14: 125–131.
- Broadley DG. 1979b. Predation on Reptile Eggs by African Snakes of the Genus *Prosymna*. *Herpetologica* 35(4): 338–341.
- Broadley DG. 1980. A Revision of the African snake genus *Prosymna* Gray (Colubridae). *Occasional Papers of the National Museum of Rhodesia* 6(7): 481–556.
- Broadley DG. 1983. *FitzSimons' Snakes of Southern Africa*. Revised Edition. Delta Books, Johannesburg, South Africa. 376 p.
- Broadley DG. 1984. A review of geographical variation in the African Python, *Python sebae* (Gmelin). *British Journal of Herpetology* 6: 359–367.
- Broadley DG. 1991a. The Herpetofauna of Northern Mwinilunga District, Northwest Zambia. *Arnoldia* (Zimbabwe) 9(37): 519–538.
- Broadley DG. 1991b. A review of the Namibian snakes of the genus *Lycophidion* (Serpentes: Colubridae), with the description of a new endemic species. *Annals of the Transvaal Museum* 35(14): 209–215.
- Broadley DG. 1995. The Snouted Cobra, *Naja annulifera*, a valid species in southern Africa. *Journal of the Herpetological Association of Africa* 44(2): 26–33.
- Broadley DG. 1996. A revision of the genus *Lycophidion* Fitzinger (Serpentes: Colubridae) in Africa south of the equator. *Syntarsus* 3: 1–33.
- Broadley DG. 1998a. The reptilian fauna of the Democratic Republic of the Congo (Congo-Kinshasa). In: *Contributions to the Herpetology of the Belgian Congo*. Editors, Schmidt KP, Noble GK. SSAR Facsimile reprints in Herpetology, 780 p.
- Broadley DG. 1998b. A review of the African *Elapsoidea semiannulata* complex (Elapidae). *African Journal of Herpetology* 47: 13–23.
- Broadley DG. 1999. The southern African python, *Python natalensis* A. Smith 1840, is a valid species. *African Herp News* (29): 31–32.
- Broadley DG. 2000. A review of *Hemirhagerrhis viperina* (Bocage) (Serpentes: Colubridae), a rupicolous Psammophine snake. *Madoqua* 19(2): 161–169 [1997].
- Broadley DG. 2001. A review of the genus *Thelotornis* A. Smith in eastern Africa, with the description of a new species from the Usambara Mountains (Serpentes: Colubridae: Dispholidini). *African Journal of Herpetology* 50: 53–70.
- Broadley DG. 2014. A new species of *Causus* Lichtenstein from the Congo/Zambezi watershed in northwestern Zambia (Reptilia: Squamata: Viperidae). *Arnoldia* (Zimbabwe) 10(29): 341–350.
- Broadley DG, Baldwin AS. 2006. Taxonomy, natural history, and zoogeography of the Southern African Shield Cobras, Genus *Aspidelaps* (Serpentes: Elapidae). *Herpetological Natural History* 9(2): 163–176.
- Broadley DG, Blaylock R. 2013. *The Snakes of Zimbabwe and Botswana*. Chimaira, Frankfurt, Germany. 387 p.
- Broadley DG, Broadley S. 1999. A review of the African worm snakes from south of latitude 12°S (Serpentes: Leptotyphlopidae). *Syntarsus* 5: 1–36.
- Broadley DG, Hughes B. 2000. A revision of the African genus *Hemirhagerrhis* Boettger 1893 (Serpentes: Colubridae). *Syntarsus* 6: 1–17.
- Broadley DG, Schätti B. 2000. A new species of *Coluber* from northern Namibia (Reptilia: Serpentes). *Madoqua* 19(2): 171–174.
- Broadley DG, Wallach V. 2002. Review of the Dispholidini, with the description of a new genus and species from Tanzania (Serpentes, Colubridae). *Bulletin of the Natural History Museum* (London) 68: 57–74.
- Broadley DG, Doria CT, Wigge J. 2003. *Snakes of Zambia. An Atlas and Field Guide*. Edition Chimaira, Frankfurt am Main, Germany. 280 p.
- Broadley DG, Wallach V. 2007a. A revision of the genus *Leptotyphlops* in northeastern African and southwestern Arabia (Serpentes: Leptotyphlopidae). *Zootaxa* 1408: 1–78.
- Broadley DG, Wallach V. 2007b. A review of East and Central African species of *Letheobia* Cope, revived from the synonymy of *Rhinotyphlops* Fitzinger, with descriptions of five new species (Serpentes: Typhlopidae). *Zootaxa* 1515: 31–68.
- Broadley DG, Wallach V. 2009. A review of the eastern and southern African blind-snakes (Serpentes: Typhlopidae), excluding *Letheobia* Cope, with the description of two new genera and a new species. *Zootaxa* 2255: 1–100.
- Broadley DG, Watson C. 1976. A revision of the Worm Snakes of southeastern Africa (Serpentes: Leptotyphlopidae). *Occasional Papers of the National Museum of Rhodesia*, Series B. Natural Science 5(8): 465–510.
- Broadley DG, Wüster W. 2004. A review of the southern African ‘non-spitting’ cobras (Serpentes: Elapidae: *Naja*). *African Journal of Herpetology* 53: 101–122.
- Broadley DG, Tolley KA, Conradie W, Wishart S, Trape J-F, Burger M, Kusamba C, Zassi-Boulou

- A-G, Greenbaum E. 2018. A phylogeny and genus-level revision of the African File Snakes *Goni-*onotophis** Boulenger (Squamata: Lamprophiidae). *African Journal Herpetology* 67(1): 43–60. doi: 10.1080/21564574.2018.1423578.
- Cadle J. 1994. The colubrid radiation in Africa (Serpentes: Colubridae): Phylogenetic relationships and evolutionary patterns based on immunological data. *Zoological Journal of the Linnean Society* 110: 103–140.
- Carlino P, Pauwels OSG. 2013. First documented record of *Thrasops jacksonii* Günther, 1895 (Squamata: Colubridae) in Gabon. *North-Western Journal of Zoology* 9(1): art.132501, 3p.
- Ceríaco LMP, Bauer AM, Blackburn DC, Lavres ACFC. 2014a. The herpetofauna of the Capanda Dam Region, Malanje, Angola. *Herpetological Review* 45(4): 667–674.
- Ceríaco LMP, Blackburn DC, Marques MP, Calado FM. 2014b. Catalogue of the amphibian and reptile type specimens of the Museu de História Natural da Universidade do Porto in Portugal, with some comments on problematic taxa. *Alytes* 31(1): 13–36.
- Ceríaco LMP, de Sá SAC, Bandeira S, Valério H, Stanley EL, Kuhn AL, Marques MP, Vindum JV, Blackburn DC, Bauer AM. 2016a. Herpetological Survey of Iona National Park and Namibe Regional Natural Park, with a Synoptic list of the Amphibians and Reptiles of Namibe Province, Southwestern Angola. *Proceedings of the California Academy Sciences* 63(2): 15–61.
- Ceríaco LMP, Marques MP, Bandeira SA. 2016b. *Anfíbios e Répteis do Parque Nacional da Cagandala*. Publ. Instituto Nacional da Biodiversidade e Áreas de Conservação, Luanda, Angola and Museu Nacional de História Natural e da Ciência, Lisboa, Portugal. 96 p.
- Ceríaco LMP, Marques MP, Schmitz A, Bauer AM. 2017. The “Cobra-preta” of São Tomé Island, Gulf of Guinea, is a new species of *Naja* Laurenti, 1768 (Squamata: Elapidae) *Zootaxa* 4324(1): 121–141.
- Chirio L, Ineich I. 2006. Biogeography of the reptiles of the Central African Republic. *African Journal of Herpetology* 55(1): 23–59.
- Clark VR, Barker NP, Mucina L. 2011. The Great Escarpment of southern Africa: A new frontier for biodiversity exploration. *Biodiversity and Conservation* 20: 2,543–2,561.
- Conradie W, Branch WR, Measey GJ, Tolley KA. 2012a. Revised phylogeny of Sand lizards (*Pedioplanis*) and the description of two new species from south-western Angola. *African Journal of Herpetology* 60(2): 91–112.
- Conradie W, Bills R, Branch WR. 2016. The herpetofauna of the Cubango, Cuito, and lower Cuando river catchments of south-eastern Angola. *Amphibian & Reptile Conservation* 10(2) [Special Section]: 6–36.
- Conradie WC, Bills R, Baptista N, Verburt L, Harvey J, Branch WR. 2017. Oral presentation (abstract). Across river basins: Exploring the unknown south-eastern Angola. *African Herp News* 66: 14–15.
- Conradie W, Branch WR. 2017. Herpetology. Pp.116–131. In: *National Geographic Okavango Wilderness Project. Initial Findings from Exploration of the Upper Catchments of the Cuito, Cuanavale, and Cuando Rivers, May 2015 to December 2016*. Available: http://www.wildbirdtrust.com/wp-content/uploads/2018/03/NGOWP_report_1_FOR_PRINT_V14_English.pdf [Accessed: 26 August 2018].
- Crawford-Cabral J, Mesquitela LM. 1989. *Índice toponímico de colheitas zoológicas em Angola*. Instituto de Investigação Científica Tropical, Centro de Zoologia, Lisbon, Portugal. 206 p.
- Cunningham PL, Maartens L, Prickett M. 2018. A contribution to the reptiles of the Kunene River Mouth area. *Namibian Journal of Environment* 2 B: 1–8.
- Dobey M, Vogel G. 2007. *Venomous Snakes of Africa/Giftschlangen Afrikas*. Edition Chimaira, Terralog 15. 150 p.
- Eimermacher TG. 2012. Phylogenetic systematics of Dispholidine colubrids (Serpentes: Colubridae), Unpublished Ph.D. thesis, University of Texas at Arlington, Arlington, Texas, USA. i-xi, 109 p.
- Engelbrecht HM, Branch WR, Greenbaum E, Alexander GJ, Jackson K, Burger M, Conradie W, Kusamba C, Zassi-Boulou A-G, Tolley KA. 2018. Diversifying into the branches: Species boundaries in African green and bush snakes, *Philothamnus* (Serpentes: Colubridae). *Molecular Phylogenetics and Evolution*, submitted.
- Ferreira JB. 1903. Reptis de Angola da região norte do Quanza da collecção Pereira do Nascimento (1902). *Jornal de Ciências, Matemáticas, Physicas e Naturaes*, 2nd série, 7(25): 9–16.
- Ferreira JB. 1904. Reptis e amphíbios de Angola da região ao norte do Quanza (Collecção Newton – 1903). *Jornal de Ciências, Matemáticas, Physicas e Naturaes*, Lisboa 2nd série, 7(26): 111–117.
- Ferreira JB. 1906. Algumas espécies novas ou pouco conhecidas de amphíbios e reptis de Angola (Collecção Newton – 1903). *Jornal de Ciências, Matemáticas, Physicas e Naturaes*, Lisboa 2nd série, 7(26): 159–171.
- Figuroa A, McKelvy AD, Grismer LL, Bell CD, Lailvaux SP. 2016. A Species-Level Phylogeny of Extant Snakes with Description of a New Colubrid Subfamily and Genus. *PLOS One*. <http://dx.doi.org/10.1371/journal.pone.0161070>.
- FitzSimons VFM. 1946. Notes on some South African snakes, including a description of a new subspecies of *Xenocalamus*. *Annals of the Transvaal Museum* 20(4): 379–393, 20 figs.
- FitzSimons VFM. 1959. Some new reptiles from southern Africa and southern Angola. *Annals of the Transvaal Museum* 23: 405–409.
- FitzSimons VFM. 1962. *Snakes of Southern Africa*. Purnell and Sons, Cape Town, South Africa. 423 p., 106

- figs., 43 plates, 75 colored plates.
- Frost DR, Hillis DM. 1990. Species in concept and practice: Herpetological considerations. *Herpetologica* 46: 87–104.
- Gans C. 1959. A taxonomic Revision of the African Snake Genus *Dasypeltis* (Reptila: Serpentes). *Annales du Musée royal du Congo belge. Tervuren, Belgium. Series 8, 74*: 1–237.
- Gower DJ, Wade EOZ, Spawls S, Böhme W, Buechley ER, Sykes D, Colston TJ. 2016. A new large species of *Bitis* Gray, 1842 (Serpentes: Viperidae) from the Bale Mountains of Ethiopia. *Zootaxa* 4093(1): 41–63.
- Gravlund P. 2001. Radiation within the advanced snakes (Caenophidia) with special emphasis on African opistoglyph colubrids, based on mitochondrial sequence data. *Biological Journal of the Linnean Society* 72: 99–114.
- Greenbaum E, Portillo F, Jackson K, Kusamba C. 2015. A phylogeny of Central African *Boaedon* (Serpentes: Lamprophiidae), with the description of a new cryptic species from the Albertine Rift. *African Journal of Herpetology* 64(1): 18–38.
- Günther A. 1888. Contribution to the knowledge of snakes of tropical Africa. *Annals Magazine of Natural History* 1: 322–335.
- Günther A. 1895. Notice of Reptiles and Batrachians collected in the eastern half of tropical Africa. *Annals Magazine of Natural History* 15: 523–529.
- Haacke WD. 1975. Description of a new adder (Viperidae, Reptilia) from Southern Africa, with a discussion of related forms. *Cimbebasia (A)* 4: 115–128.
- Haacke WD. 1981. The file snakes of the genus *Meheleya* in Southern Africa with special reference to South West Africa/Namibia. *Madoqua* 12(4): 217–224.
- Haacke WD. 2008. A new leaf-toed gecko (Reptilia: Gekkonidae) from south-western Angola. *African Journal Herpetology* 57(2): 85–92.
- Haacke WD. 2013. Description of a new Tiger Snake (Colubridae, *Telescopus*) from south-western Africa. *Zootaxa* 3737(3): 280–288.
- Haacke WD, Finkeldey H. 1967. The Angola garter-snake *Elapsoidea sundevallii semiannulata* Bocage, a new record from southern Africa. *South West Africa Scientific Society, Special Publication* 8: 1–12.
- Haagner GV, Branch WR, Haagner AJF. 2000. Notes on a collection of reptiles from Zambia and adjacent areas of the Democratic Republic of the Congo. *Annals of the Eastern Cape Museum* 1: 1–25.
- Hedges SB, Marion AB, Lipp KM, Marin J, Vidal N. 2014. A taxonomic framework for typhlopoid snakes from the Caribbean and other regions (Reptilia, Squamata). *Caribbean Herpetology* 49: 1–61.
- Hellmich W. 1957a. Die Reptilien Ausbeute der Hamburgischen Angola Expedition. *Mitteilungen aus dem Hamburg Zoologischen Museum Institut* 55: 39–80.
- Hellmich W. 1957b. Herpetologische Ergebnisse Einer Forschungsreise in Angola. *Veröffentlichungen der Zoologischen Staatssammlung München* 5: 1–92.
- Hill ER, Carter TD. 1941. The Mammals of Angola, Africa. *Bulletin American Museum of Natural History* 78(1): 1–211.
- Hsiang AY, Field DJ, Webster TH, Behlke ADB, Davis MB, Racicot RA, Guthrie JA. 2015. The origin of snakes: Revealing the ecology, behavior, and evolutionary history of early snakes using genomics, phenomics, and the fossil record. *BMC Evolutionary Biology* (2015) 15:87 doi: 10.1186/s12862-015-0358-5
- Hughes B. 1985. Progress on a taxonomic revision of the African green tree snakes (*Philothamnus* spp.). Pp. 511–530 In: *Proceedings of the International Symposium on African Vertebrates*. Editor, Schuchmann K-L. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. 585 p.
- Hughes B. 1997. *Dasypeltis scabra* and *Lamprophis fuliginosus* - Two pan-African snakes in the Horn of Africa: A tribute to Don Broadley. *African Journal of Herpetology* 46: 68–77.
- Hughes B. 1999. Critical review of a revision of *Psammophis* (Linnaeus, 1758) (Serpentes: Reptilia), by Frank Brandstätter. *African Journal of Herpetology* 48: 63–70.
- Hughes B. 2004. Misidentification of *Dromophis lineatus* (Duméril and Bibron, 1854) as *Psammophis sibilans* (Linné 1758) and the perpetuation of error. *African Journal of Herpetology* 53(1): 63–76.
- Hughes B, Wade E. 2002. On the African leopard whip snake, *Psammophis leopardinus* Bocage, 1887 (Serpentes, Colubridae), with the description of a new species from Zambia. *Bulletin of the Natural History Museum, Zoology Series*, 68(2): 75–81, 5 figs.
- Huntley B. 2009. SANBI/ISCED/UAN Angolan Biodiversity Assessment and Capacity Building Project, Report on Pilot Project. South African National Biodiversity Institute, Unpublished Report.
- Huntley B. 2015. Expedition report. Rapid Biodiversity Assessment of Carumbo Lagoon area, Lunda Norte, Angola. República de Angola Ministério do Ambiente, Luanda, Angola. 218 p.
- Huntley BJ, Ferrand N, Russo V, Lages F, Editors. 2018. *Angolan Biodiversity: A Modern Synthesis*. Springer, (in press).
- Kelly CMR, Barker NP, Villet MH. 2003. Phylogenetics of Advanced Snakes (Caenophidia) Based on Four Mitochondrial Genes. *Systematic Biology* 52(4): 439–459.
- Kelly CMR, Barker NP, Villet MH, Broadley DG, Branch WR. 2008. The snake family Psammophiidae (Reptilia: Serpentes): Phylogenetics and species delimitation in the African sand snakes (*Psammophis* Boie, 1825) and allied genera. *Molecular Phylogenetics and Evolution* 47(3): 1,045–1,060.
- Kelly CMR, Branch WR, Broadley DG, Barker NP, Villet MH. 2011a. Molecular systematics of the African snake family Lamprophiidae Fitzinger, 1843 (Serpentes,

- tes: Elapoidea), with particular focus on the genera *Lamprophis* Fitzinger 1843 and *Mehelya* Csiki 1903. *Molecular Phylogenetics and Evolution* 58(2): 415–426.
- Kelly CMR, Branch WR, Villet MH, Barker NP. 2011a. Adders and afro-montane phylogeography: The Great Escarpment and Cape Fold Mountains as a speciation hot-bed for dwarf *Bitis* (Serpentes: Viperidae). (abstract) p 52. In: *Proceedings of the Congresses of the Southern African Society for Systematic Biology*. Editors, Villet MH, Crous KL. Southern African Society for Systematic Biology, Grahamstown, South Africa. 19-21st January 2011.
- Lanza B, Broadley DG. 2014. A review of the genus *Gonionotophis* in north-eastern Africa (Squamata: Lamprophiidae). *Acta Herpetologica* 9(1): 89–97.
- Laurent RF. 1950. Reptiles et Batraciens de la région de Dundo (Angola du Nord-Est). *Publicações culturais da Companhia de Diamantes de Angola* 10: 7–17.
- Laurent RF. 1952. Amphibiens et Reptiles. In: *Résult. Sci. Explor. Hydrobiol. Lac Tanganyika (1946-1947)*. 3(3): 1–22, 1 plate.
- Laurent RF. 1954. Reptiles et Batraciens de la région de Dundo (Angola) (Deuxième Note). *Publicações culturais da Companhia de Diamantes de Angola* 23: 35–84.
- Laurent RF. 1955. Diagnoses préliminaires des quelques Serpents venimeux. *Revue de zoologie et de botanique africaines* 51: 127–139.
- Laurent RF. 1956. *Contribution à l'herpétologie de la région des Grands Lacs de l'Afrique centrale*. I. Généralités, II. Cheloniens, III. Ophidiens. *Annales du Musée Royal du Congo Belge*, Tervuren, Belgique. 48: 1–390, 50 figs., 31 plates.
- Laurent RF. 1960. Notes complémentaires sur les chéloniens et les ophidiens du Congo Oriental. *Annales du Musée Royal du Congo Belge*, Tervuren, Belgique. 84: 1–87.
- Laurent RF. 1964. Reptiles et Amphibiens de l'Angola (Troisième contribution). *Publicações culturais da Companhia de Diamantes de Angola* 67: 11–165.
- Laurent RF. 1968. A re-examination of the snake genus *Lycophidion* Duméril and Bibron. *Bulletin Museum of Comparative Zoology* (Harvard, Cambridge, Massachusetts, USA) 136(12): 461–482.
- Lawson R, Slowinski JB, Crother BI, Burbrink FT. 2005. Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 37: 581–601.
- Loveridge A. 1932. New Opisthoglyphous Snakes of the Genera *Crotaphopeltis* and *Trimerorhinus* from Angola and Kenya Colony. *Proceedings of the Biological Society of Washington* 45: 83–86.
- Loveridge A. 1936. African Reptiles and Amphibians in the Field Museum of Natural History. *Zoology Series Field Museum Natural History, Chicago* 22(1): 1–122.
- Loveridge A. 1939. Revision of the African snakes of the genera *Mehelya* and *Gonionotophis*. *Bulletin Museum of Comparative Zoology* 86: 131–162.
- Loveridge A. 1940. Revision of the African snakes of the genera *Dromophis* and *Psammophis*. *Bulletin Museum of Comparative Zoology* 87(1): 1–69.
- Loveridge A. 1944. Further revisions of African snake genera. *Bulletin Museum Comparative Zoology* 95(2): 121–247.
- Loveridge A. 1953. Zoological results of a fifth expedition to East Africa. III. Reptiles from Nyasaland and Tete. *Bulletin Museum of Comparative Zoology* 110: 143–322.
- Loveridge A. 1957. Check list of the reptiles and amphibians of East Africa (Uganda; Kenya; Tanganyika; Zanzibar). *Bulletin Museum of Comparative Zoology* 117(2): 153–362.
- Loveridge A. 1958. Revision of five African snake genera. *Bulletin Museum of Comparative Zoology* 119: 1–198.
- Manaças S. 1973. Alguns ofídeos de Angola. *Memórias da Junta de Investigações do Ultramar* (2)43: 187–200.
- Manaças S. 1981 Ofídeos venenosos da Guiné, S. Tomé, Angola e Moçambique. *Garcia de Orta: Série de Zoologia* 10(1/2): 13–46.
- Marin J, Donnellan SC, Hedges SB, Puillandre N, Aplin KP, Doughty P, Hutchinson MN, Couloux A, Vidal N. 2014. Hidden species diversity of Australian burrowing snakes (*Ramphotyphlops*). *Biological Journal of the Linnean Society* 110: 427–441.
- Marques MP, Ceriaco LMP, Bauer AM, Blackburn DC. 2014. Geographic distribution of Amphibians and reptiles of Angola: Towards an Atlas of Angolan herpetofauna. Poster. 12th Herpetological Association of Africa Conference, Gobabeb, Namibia, 20–22 November, 2014.
- McDowell SB. 1968. Affinities of the snakes usually called *Elaps lacteus* and *E. dorsalis*. *Journal of the Linnean Society* (Zoology) 47: 561–578.
- McLachlan GR. 1987. A first record of *Prosymna visseri* in southern Africa. *Madoqua* 15(1): 89–90.
- Mertens R. 1937. Reptilien und Amphibien aus dem südlichen Inner-Afrika. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 435: 1–23.
- Mertens R. 1938. Amphibien und Reptilien aus Angola. *Senckenbergiana* 20: 425–442.
- Mertens R. 1954. Neue Schlangengrassen aus Südwest- und Südafrika. *Zoologischer Anzeiger* 152(9/10): 213–219.
- Mertens R. 1958. *Bitis heraldica*, eine oft verkannte Otter aus Angola. *Senckenbergiana biologica* 39(3/4): 145–148.
- Mertens R. 1971. Die Herpetofauna Südwest-Afrikas. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 529: 1–110.
- Monard A. 1931. Reptiles. Mission Scientifique Suisse

- dans Angola, Resultats Scientifiques. *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 55: 89–111.
- Monard A. 1937. Contribution à l'Herpétologie d'Angola. *Arquivos do Museu Bocage* 8(1937): 19–154.
- Nagy ZT, Vidal N, Vences M, Branch WR, Pauwels OSG, Wink M, Joger U. 2005. Molecular systematics of African Colubroidea (Squamata: Serpentes). Pp. 221–228 In: *African Biodiversity: Molecules, Organisms, Ecosystems*. Editors, Huber BA, Sinclair BJ, Lampe K-H. Proc. 5th Intern. Symp. Trop. Biol., Museum Koenig, Bonn, Germany. 443 p.
- Nagy ZT, Marion AB, Glaw F, Miralles A, Nopper J, Vences M, Hedges SB. 2015. Molecular systematics and undescribed diversity of Madagascan scolecophidian snakes (Squamata: Serpentes). *Zootaxa* 4040(1): 31–47.
- de Oliveira PRS. 2017. *Sepentes em Angola*. Uma visão toxinológica e clínica dos envenenamentos. Glaciari, Lisbon, Portugal. 159 p.
- de Oliveira PRS, Rocha MT, Castro AG, Betancourt IR, Wen FH, Neto AP, Bastos ML, Tambourgi DV, Sant'anna SS. 2016. New records of Gaboon viper (*Bitis gabonica*) in Angola. *Herpetological Bulletin* 136: 42–43.
- Parker HW. 1936. Dr. Karl Jordan's Expedition to South West Africa and Angola: Herpetological collection. *Novitates Zoologicae* 40: 115–146.
- Parker HW. 1949. The snakes of Somaliland and the Sokotra islands. *Zoologische Verhandlungen* 6: 1–115.
- Pauwels OSG, Christy P, Honorez A. 2005. Reptiles and national parks in Gabon, Western Central Africa. *Hamadryad* 30(1–2): 181–196.
- Pauwels OSG, Vande Weghe JP. 2008. *Reptiles du Gabon*. Washington: Smithsonian Institution. 272 p.
- Peters WCH. 1865. Nachtrag zu seiner Abhandlung über Typhlopina. *Monatsberichte der königlich Akademie der Wissenschaften zu Berlin* 1865: 259–263.
- Peters WCH. 1877. Übersicht der Amphibien aus Chinchoco (Westafrika), welche von der Africanischen Gesellschaft dem Berliner zoologischen Museum übergeben sind. *Monatsberichte der königlich Akademie der Wissenschaften zu Berlin* 1877(10): 611–620.
- Peters WCH. 1881. Über das Vorkommen schildförmiger Verbreiterungen der Dornfortsätze bei Schlangen und über neue oder weniger bekannte Arten dieser Abtheilung der Reptilien. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 1881(3): 49–52.
- Portillo F, Branch WR, Conradie W, Rödel M-O, Penner J, Barej MF, Kusambah C, Muningah WM, Aristotei MA, Bauer AM, Trape J-P, Nagy ZT, Carlinom P, Pauwels OSG, Menegon M, Burger M, Mazuch T, Jackson K, Hughes DF, Behanganas M, Greenbaum E. 2018. Phylogeny and biogeography of the African burrowing snake subfamily Aparallactinae (Squamata: Lamprophiidae). *Molecular Phylogenetics and Evolution* 127: 288–303 <https://doi.org/10.1016/j.ympev.2018.03.019>.
- Pyron RA, Burbrink FT, Colli GR, de Oca ANM, Vitt LJ, Kuczynski CA, et al. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution* 58: 329–342.
- Pyron RA, Burbrink FT, Wiens JJ. 2013. A phylogeny and revised classification of Squamata, including 4,161 species of lizards and snakes. *BMC Evolutionary Biology* 13: 93. doi: 10.1186/147121481393. pmid:23627680.
- Pyron RA, Graham RR, Burbrink FT. 2014. A Taxonomic Revision of Boas (Serpentes: Boidae). *Zootaxa* 3846(2): 249–260.
- Pyron RA, Wallach V. 2014. Systematics of the blind-snakes (Serpentes: Scolecophidia: Typhlopoidea) based on molecular and morphological evidence. *Zootaxa* 3829: 1–81.
- Rasmussen JB. 1986. On the taxonomic status of *Dipsadoboa werneri* (Boulenger), *D. shrevei* (Loveridge), and *Chrotaphopeltis hotamboeia kageleri* Uthmüller (Boiginae, Serpentes). *Amphibia-Reptilia* 7: 51–73.
- Rasmussen JB. 1997. On two little-known African water snakes (*Crotaphopeltis degeni* and *Crotaphopeltis barotseensis*). *Amphibia-Reptilia* 18: 191–206.
- Rasmussen J. 2005. On the identification and distribution of the two-striped night adder (*Causus bilineatus*) and related forms. *African Journal of Herpetology* 54(1): 1–15.
- Raw LRG. 1973. A review of the dusky-bellied water snake, *Lycodonomorphus laevisissimus* (Günther), with descriptions of two new subspecies. *Annals of the Natal Museum* 21: 713–718.
- Reynolds RG, Niemiller ML, Revell LJ. 2014. Toward a Tree-of-Life for the boas and pythons: Multilocus species-level phylogeny with unprecedented taxon sampling. *Molecular Phylogenetics and Evolution* 71: 201–213.
- Roux-Estève R. 1974. Révision systématique des Typhlopidae d'Afrique. Reptilia. Serpentes. *Memoir du Museum national d'histoire naturelle* Paris, France. Series A, 87: 1–313.
- Roux-Estève R, Guibe J. 1965. Étude comparée de *Boaedon fuliginosus* (Boié) et *Boaedon lineatus* D. et B. (Ophiidiens). *Bulletin de l'Institut Fondamental de l'Afrique Noire* 27(A-1): 397–409.
- Schätti B, Charvet C. 2003. Systematics of *Platyceps brevis* (Boulenger 1895) and related East African racers (Serpentes Colubrinae). *Tropical Zoology* 16(1): 93–111
- Schätti B, Utiger U. 2001. *Hemerophis*, a new genus for *Zamenis socotrana* Günther, and a contribution to the phylogeny of Old World racers, whip snakes and related genera. *Revue Suisse Zoologie* 108(4): 919–948.
- Schmidt KP. 1933. The reptiles of the Pulitzer-Angola Expedition. *Annals of the Carnegie Museum* 22: 1–15.

- Siegel DS, Miralles A, Aldridge RD. 2011. Controversial snake relationships supported by reproductive anatomy. *Journal of Anatomy* 218(3): 342–348.
- Spawls S, Howell K, Hinkel H, Menegon M. 2018. *A Field Guide to the Reptiles of East Africa*. 2nd edition. Bloomsbury, London, England. 624 p.
- Stanley EL, Ceriaco LMP, Bandeira S, Valerio H, Bates MF, Branch WR. 2016. A review of *Cordylus machadoi* (Squamata: Cordylidae) in southwestern Angola, with the description of a new species from the Pro-Namib desert. *Zootaxa* 4061(3): 201–226.
- Sternfeld R. 1908. Neue und ungenügend bekannte afrikanische Schlangen. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* 4: 92–95.
- Sternfeld R. 1917. Reptilia und Amphibia. In: *Wissenschaftliche Ergebnisse der Zweiten Deutschen Zentral-Afrika-Expedition, 1910-1911 unter Führung Adolph Friedrichs, Herzog zu Mecklenburg*. Herausgeber, Schubotz H. Leipzig: Klinkhardt and Biermann, vol. 1: *Zoologie* 11: 407–510.
- Thorpe RS, McCarthy CJ. 1978. A preliminary study, using multivariate analysis, of a species complex of African house snakes (*Boaedon fuliginosus*). *Journal of Zoology* 184: 489–506.
- Trape JF, Roux-Esteve R. 1995. Les serpents du Congo: Liste commentée et clé de détermination. *Journal of African Zoology* 109(1): 31–50.
- Trape J-F, Baldé C. 2014. A checklist of the snake fauna of Guinea, with taxonomic changes in the genera *Philothamnus* and *Dipsadoboa* (Colubridae) and a comparison with the snake fauna of some other West African countries. *Zootaxa* 3900(3): 301–338.
- Trape J-F, Mané Y. 2005. Une nouvelle espèce du genre *Mehelya* (Serpentes: Colubridae) de Haute-Casamance (Sénégal). *Bulletin de la Société Herpétologique de France* 115: 23–30.
- Trape J-F, Mané Y. 2006. Le genre *Dasyplectis* Wagler (Serpentes : Colubridae) en Afrique de l'Ouest: Description de trois espèces et d'une sous-espèce nouvelles. *Bulletin de la Société Herpétologique de France* 119: 27–56.
- Trape J-F, Mané Y. 2015. The snakes of Niger. *Amphibian & Reptile Conservation* 9(2) [Special Section]: 39–55.
- Trape J-F, Mediannikov O. 2016. Cinq serpents nouveaux du genre *Boaedon* Duméril, Bibron and Duméril, 1854 (Serpentes : Lamprophiidae) en Afrique centrale. *Bulletin de la Société Herpétologique de France* 159: 61–111.
- Tys van den Audenaerde DFE. 1967. Les serpents des environs de Dundo (Angola) (Note complémentaire). *Publicações culturais da Companhia de Diamantes de Angola* 76: 31–37.
- Uetz P, Stylianou A. 2018. The original descriptions of reptiles and their subspecies. *Zootaxa* 4375(2): 257–264.
- Uetz P, Freed P, Hošek J, Editors. 2018. The Reptile Database. Available: <http://www.reptile-database.org>. [Accessed 23 February 2018].
- Underwood G, Kochva E. 1993. On the affinities of the burrowing asps *Atractaspis* (Serpentes: Atractaspididae). *Zoological Journal of the Linnean Society* 107: 3–64.
- Vaz Pinto P, Branch WR. 2015. Geographical Distribution: *Dendroaspis jamesoni* (Thraill, 1843), Jameson's Mamba. *African Herp News* 62: 45–47.
- Vidal N, Hedges SB. 2002. Higher-level relationships of caenophidian snakes inferred from four nuclear and mitochondrial genes. *Comptes Rendus de l'Académie des Sciences*, Paris, France. 325: 987–995.
- Vidal N, Delmas A-S, David P, Cruaud C, Couloux A, Hedges SB. 2007. The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. *Comptes Rendus de l'Académie des Sciences* 330: 182–187.
- Vidal N, Rage J-C, Couloux A, Hedges SB. 2009. Snakes (Serpentes). Pp. 390–397 In: *The Timetree of Life*. Editors, Hedges SB, Kumar S. Oxford University Press, New York, New York, USA. 551 p.
- Vidal N, Marin J, Morini M, Donnellan S, Branch WR, Thomas R, Vences M, Wynn A, Cruaud C, Hedges SB. 2010. Blindsnake evolutionary tree reveals long history on Gondwana. *Biology Letters* 6(4): 558–561.
- Wallach V, Williams KL, Boundy J. 2014. *Snakes of the World: A Catalogue of Living and Extinct Species*. Taylor and Francis, CRC Press, Boca Raton, Florida, USA. 1,237 p.
- Wallach V, Wüster W, Broadley DG. 2009. In praise of subgenera: Taxonomic status of cobras of the genus *Naja* Laurenti (Serpentes: Elapidae). *Zootaxa* 2236: 26–36, 1 fig.
- de Witte GF. 1933. Reptiles recoltés au Congo Belge par le Dr. H. Schouteden et par G. F. de Witte. *Annales du Musée Royal du Congo Belge (Série in Octavao, Science Zoologique, Tervuren, Belgique. Series 1)* 3(2): 57–99.
- de Witte GF. 1953. Reptiles. Exploration des Parc National de l'Upemba. Mission de G.F. de Witte. *Institut des Parcs Nationaux du Congo Belge* (Bruxelles, Belgique) 6) 1–322.
- de Witte GF. 1963. The colubrid snake genera *Chamaelycus* Boulenger and *Oophilositum* Parker. *Copeia* 1963(4): 634–636.
- de Witte GF, Laurent RF. 1947. Revision d'un groupe de Colubridae africains: Genres *Calamelaps*, *Miodon*, *Aparallactus*, et formes affines. *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, Série 2, 29: 1–134.
- Wüster W, Broadley DG. 2003. A new species of spitting cobra (*Naja*) from north-eastern Africa (Serpentes, Elapidae). *Journal of Zoology* 259(4): 345–359, 8 figs.
- Wüster W, Broadley DG. 2007. Get an eyeful of this: A new species of giant spitting cobra from eastern and

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north-eastern Africa (Squamata, Serpentes, Elapidae, *Naja*). *Zootaxa* 1532: 51–68, 7 figs.

Wüster W, Crookes S, Ineich I, Mané Y, Pook CE, Trape J-F, Broadley DG. 2007. The phylogeny of cobras from mitochondrial DNA sequences, evolution of venom spitting and the phylogeography of the African spitting cobras (Serpentes, Elapidae, *Naja nigricollis* complex). *Molecular Phylogenetics and Evolution* 45(2): 437–453.

Wüster W, Chirio L, Trape J-F, Ineich I, Jackson K, Greenbaum E, Barron C, Kusamba C, Nagy ZT, Sto-

rey R, Hall C, Wüster CE, Barlow A, Broadley DG. 2018. Integration of nuclear and mitochondrial gene sequences and morphology reveals unexpected diversity in the forest cobra (*Naja melanoleuca*) species complex in Central and West Africa (Serpentes: Elapidae). *Zootaxa* 4455(1): 68–98.

Zaher, H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History* 240: 1–168.



London-born **Bill Branch** was employed as Curator of Herpetology at the Port Elizabeth Museum for over 30 years (1979–2011), and although now retired remains Curator Emeritus Herpetology. His herpetological studies have concentrated mainly on the systematics, phylogenetic relationships, and conservation of African reptiles, but he has been involved in numerous other studies on the reproduction and diet of African snakes. He has published over 300 scientific articles, as well as numerous popular articles and books. The latter include: *South African Red Data Book of Reptiles and Amphibians* (1988), *Dangerous Snakes of Africa* (1995, with Steve Spawls), *Field Guide to the Reptiles of Southern Africa* (1998), *Tortoises, Terrapins and Turtles of Africa* (2008), and *Atlas and Red Data Book of the Reptiles of South Africa, Lesotho and Swaziland* (multi-authored, 2014), as well as smaller photographic guides. In 2004 he was the 4th recipient of the “Exceptional Contribution to Herpetology” award of the Herpetological Association of Africa. He has undertaken field work in over 16 African countries, and described nearly 50 species, including geckos, lacertids, chameleons, cordylids, tortoises, adders, and frogs.