Chapter 13
The Reptiles of Angola: History, Diversity, Endemism and Hotspots

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Abstract This review summarises the current status of our knowledge of Angolan reptile diversity, and places it into a historical context of understanding and growth. It is compared and contrasted with known diversity in adjacent regions to allow insight into taxonomic status and biogeographic patterns. Over 67% of Angolan reptiles were described by the end of the nineteenth century. Studies stagnated during the twentieth century but have increased in the last decade. At least 278 reptiles are currently known, but numerous new discoveries have been made during recent surveys, and many novelties await description. Although lizard and snake diversity is currently almost equal, most new discoveries occur in lizards, particularly geckos and lacertids. Poorly known Angolan reptiles and others from adjacent regions that

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may occur in the country are highlighted. Most endemic Angolan reptiles are lizards and are associated with the escarpment and southwest arid region. Identification of reptile diversity hotspots are resolving but require targeted surveys for their delimitation and to enable protection. These include the Kaokoveld Centre of Endemism, Angolan Escarpment and the Congo forests of the north. The fauna of Angola remains poorly known and under-appreciated, but it is already evident that it forms an important centre of African reptile diversity and endemism.

Keywords Herpetofauna · History · Priority studies · Reptilia · Review

Introduction

> Systematic biology is the backbone of biology in that it describes the taxa and their relationships which then serve as the objects of research. (Uetz and Stylianou 2018)

> The extensive territory of Angola is for herpetologists one of the least known parts of Africa. This is particularly unfortunate because there are indications that it may be one of the most interesting areas of the continent. (Gans 1976)

The need to classify things is a basic human need. Initially it was simply utilitarian, driven by the necessity for rural people to know what was edible, venomous, poisonous, or useful. As the world's diverse civilizations developed all were faced with the need to refine this knowledge, and as they migrated, came together, experienced new habitats and new life forms, the need for classification became essential. Only when new technological innovations in such things as sailing and weaponry allowed the reach of various nations to become global, did universal categorisation and classification really need to be become standardised. Driven by the Enlightenment and during the rise of critical thinking and the scientific revolution there began the first steps in developing a universally recognised system for classifying Life. The current classification system was initiated by Carl Linnaeus (1707–1778), a Swedish botanist, physician, and zoologist who formalised the modern system of naming organisms, now known as binomial nomenclature. During the 250+ years since the Linnaean revolution, the rules used to name this diversity have been refined and modified, and increasingly sophisticated methods have been developed to gain insight into the relationships of its components.

Since the equally important Darwinian Revolution and awareness of the evolutionary relatedness of Life, modern systematics places emphasis on revealing patterns of relationship among groups, often figuratively represented as trees or cladograms. The branches of these 'trees' are monophyletic when they include only the descendants of a common ancestor. All modern classifications comprise hypotheses represented as phylogenies of nested groups (clades) exhibiting monophyly. Biochemical adjuncts to traditional taxonomy have proliferated since the middle of the last century, but detailed multi-taxon genomic analysis, linked with increasingly sophisticated computer processing of sequence data, is a phenomenon of the twenty-first century. These recent technological advances have allowed objective assessments of hypotheses of phylogenetic relationships. It is important to emphasise that the assignment of any individual

specimen, first to a species and then to any higher taxonomic group, tests hypotheses of relationships. The placement of a specimen at any level in the nomenclatural hierarchy, from species to phylum, must conform to the definitions of those groups. It should be stressed, moreover, that taxonomy is a dynamic discipline and that every assignment of a specimen to a species or higher taxonomic group is a hypothesis of relationship. It is always subject to revision in the light of new knowledge.

It has become increasingly obvious that species may result from different mechanisms and histories, and there is increasing use of evolutionary and phylogenetic species concepts to reflect hypotheses about the boundaries of past and present gene transfer within evolutionary lineages of Life's diversity. Many phylogenies based on molecular/genetic data conflict with historical ideas of relationships previously based solely or largely on morphological analysis. It is evident that morphology is often conservative (maintained by selective pressures) that may mask underlying cryptic genetic diversity. This awareness has led to the burgeoning description of new species, genera, and higher categories.

History: Early Research on Angolan Reptiles

Early studies on the Angolan herpetofauna have been summarised by Baptista et al. (2019) in this volume, also see the recently published Angola Reptile and Amphibian Atlas (Marques et al. 2018). Other recent summaries can be found in introductions to regional herpetofaunas, e.g. Ceríaco et al. (2014a, 2016a) and Conradie et al. (2016). To avoid duplication much will not be repeated here, where instead emphasis is placed on the main publications discussing Angolan reptiles during and after the colonial period, and particularly the periodic attempts to overview its diversity (Bocage 1895; Monard 1937).

José Vincente Barbosa du Bocage is rightly known as the 'Father of Angolan Herpetology'. He was, however, more than just a scientist and for much of his life held multiple positions in government, administration and science, often simultaneously. De Almeida (2011) reviews diverse aspects of his multifaceted life; Madruga (2013) discusses the development of his scientific career; and Gamito-Marques (2017) explains Bocage's role in the foundation of National Museum of Lisbon and his importance, via his contacts with collectors in various Portuguese colonies as well as other zoologists at major European museums, in developing the collections and status of the museum. A list of his scientific publications is available at TRIPLOV (2018). In his first attempt to review the known Angolan herpetofauna he listed 26 reptile species from the Congo and 57 reptiles and amphibians from Angola in the Museu de Lisboa collection (Bocage 1866). Part of this material came from José de Anchieta collected during a zoological expedition in 1864 to Rio Quilo, Cabinda, and the coast of Loango, and other material was collected by Bayão Pinheiro when a military commander in the Duque de Bragança (Calandula) district. After nearly 30 years of subsequent study, during which Bocage published at least a paper a year on the herpetofauna of Portugal's African colonies (see full list in TRIPLOV 2018), he again summarised the Angolan herpetofauna in his mono-

graphic *Herpetology d'Angola et du Congo* (Bocage 1895). In this review he more than trebled his previous summary, recording 143 reptile and 39 amphibian species from Angola. Of these Bocage himself described 40 reptile species that are still considered valid, and of which no less that 26 (65%) had been collected by José de Anchieta, seven of which are still named in his honour. Following Bocage's retirement, herpetological studies at Lisbon were continued, but with less intensity, by Bethencourt Ferreira (1897, 1900, 1903, 1904, 1906), who added a number of additional species to the country list but described only one new snake, *Typhlops bocagei* (Ferreira 1904), that was later placed in the synonymy of *Afrotyphlops lineolatus* (Jan, 1864).

George A Boulenger of the British Natural History Museum remains the most prolific herpetologist of all time, and described a remarkable 659 reptiles still recognised today – no less than 5% of the world's 13,000+ known reptiles (Uetz and Stylianou 2018). In 1905 Boulenger published a note on the amphibians and reptiles collected by WJ Ansorge during a prolonged visit (1903–1905) to Angola (Boulenger 1905). The material included three new species of frogs and a snake, of which two, *Rana ansorgii* (= *Ptychadena ansorgii*) and *Psammophis ansorgii,* were named in the collector's honour. Two years later Boulenger described another three lizards and a frog collected by Ansorge, including the gecko *Phyllodactylus ansorgii,* the skinks *Mabuia ansorgii* (*Trachylepis sulcata ansorgii*) and *Mabuia laevis* (*Trachylepis laevis*), and the frog *Rana bunoderma* (= *Ptychadena bunoderma*) (Boulenger 1907a), soon followed (Boulenger 1907b) by another new frog from 'Mossâmedes' (actually Catequero, Cunene), *Rana cryptotis* (= *Tomopterna cryptotis*). Boulenger (1915) also prepared a *List of the snakes of Belgian and Portuguese Congo, Northern Rhodesia and Angola* in which he documented 139 snakes for the region, of which only 57 were considered to occur in Angola. This was lower than Bocage's (1895) assessment, but by this time Boulenger had completed his monographic, three volume 'Catalogue' of the World's snakes (Boulenger 1893, 1894, 1896), in which he had synonymised many of Bocage's taxa or shown some to be synonyms. This included Angola's most iconic snake, *Vipera heraldica,* which Boulenger (1896) surprisingly and incorrectly synonymised with *Bitis peringueyi,* and Bogert (1940) continued the confusion. There it languished until revalidated by Mertens (1958).

The dramatic discovery of the Giant Sable in Angola early in the twentieth century led to numerous expeditions to collect them as hunting trophies or taxidermy specimens for European and American museum dioramas. Some expeditions collected additional fauna, although the herpetological collections of the Vernay Angola Expedition (VAE 1925) seem to have been plagued by poor documentation. Although various specimens were incorporated in diverse taxonomic reviews, no publication dedicated to the full herpetological results was produced. Bogert (1940) incorporated 202 VAE snakes into his review of African snakes, but 10 species and 42 (21%) specimens lacked detailed locality information and were simply listed as from 'Angola'. Three new snakes were described from Angolan material: Vernay's File Snake (*Mehelya vernayi, = Limaformosa vernayi* Broadley et al. 2018) from Hanha, and Cowles' Shield Cobra (*Aspidelaps lubricus cowlesi*) and the Western

Banded Spitting Cobra (*Naja nigricollis nigricincta*) from Munhino. The first two have subsequently been discovered at numerous localities in northern Namibia (Haacke 1981; Broadley and Baldwin 2006), but remain known in Angola only from the type or a few other specimens, respectively. Loveridge (1944) described two new geckos (*Afroedura bogerti* and *Pachydactylus scutatus angolensis*) on VAE material, and Stanley et al. (2016) discussed VAE *Cordylus* material labelled simply as 'Angola' and that they assigned morphologically to a new species, *Cordylus namakuiyus*, discovered in the Namibe region. The description of at least one other new species from old VAE material is also in preparation (*Ichnotropis* sp. Branch in prep.).

The main targets of the Pulitzer Angola Expedition (1930–1931) were birds and mammals, but Rudyerd Boulton, who had earlier accompanied the VAE, also collected reptiles and amphibians. Karl Schmidt (1933, 1936) documented the reptiles and amphibians, respectively, collected during the expedition from diverse sites in the centre and south of the country. The reptiles included two new species, but *Lygodactylus laurae* was quickly synonymised when Schmidt realised he had overlooked Bocage's (1896) earlier description of *L. angolensis.* His description of *Rhoptropus boultoni* not only honoured Rudyerd's contribution to the collection of Angolan reptiles, but was also the first record of this interesting diurnal rupicolous gecko genus for the country. Two other new subspecies were also described, of which *Pachydactylus bibronii pulizerae* was latter transferred to *Chondrodactylus* (Bauer and Lamb 2005), and has also been recently validated as a full species, *C. pulizerae*, that is mainly restricted to Angola but also extends into northern Namibia (Heinz 2011; Ceríaco et al. 2014a). The Angolan Savanna Monitor (*Varanus albigularis angolensis*) was described by Schmidt (1933) from 'Gaúca, Bihe' (= Zaúca River, Malanje; Crawford-Cabral and Mesquitela 1989). Although additional material had been collected the validity of the morphological diagnosis (small nuchal scales and larger body scales) has not been reassessed, and neither has its genetic affinities.

In 1933–1934 Karl Jordan, an entomologist, collected through northern Namibia and Angola and made well documented collections and published a detailed itinerary of his trip (Jordan 1936). Among these was an important herpetological collection, particularly from scarp forest habitats at Congulo and Quirimbo. These were studied by Parker (1936), who recorded diverse Congo Basin snakes previously unknown from Angola; e.g. *Philothamnus heterodermus, Thelotornis kirtlandii, Toxicodryas blandingii, T. pulverulenta, Pseudohaje goldii, Chamaelycus parkeri* and *Hormonotus modestus,* as well as the new wolf snake *Lycophidion ornatum.*

Swiss zoologist Albert Monard explored Angola during two extensive trips (July 1928–February 1929 and April 1932–October 1933) that resulted in extensive reviews of Angolan birds (Monard 1934), mammals (Monard 1935), reptiles (Monard 1937), and amphibians (Monard 1938). Ceríaco et al. (2016a, b) note that Monard was so inspired by Angolan biodiversity that he unsuccessfully championed for the development of a local Natural History Museum that he offered to direct and manage. His detailed reptile 'Contribution' (Monard 1937) was the first overview of Angolan reptiles subsequent to Bocage's (1895) monograph, and within

it Monard presented taxonomic updates and also initiated the first attempts to generate a biogeographic overview of the herpetofauna (see section below). He noted that only 19 lizards, 10 snakes and a single terrapin had been added to the reptile fauna of Angola, and he even envisaged (incorrectly!) that most of the knowledge on the subject was complete, and he therefore concentrated on understanding biogeographic patterns. However, eight of the 19 additional lizards and three of the 10 snakes he included had already been synonymised (Boulenger 1915) or subsequently were. Certainly Monard seemed little interested in taxonomy and described relatively few novelties, only one of which may remain valid. The rejected taxa include: the worm lizards *Amphisbaenia ambuellensis* (= *Zygaspis quadrifrons*), *Monopeltis granti kuanyamarum* (= *Dalophia pistillum*), *M. devisi* (= *Monopeltis anchietae*), and *M. okavangensis* (= *M. anchietae*); the serpent plated lizard *Tetradactylus lundensis* (= *T. ellenbergeri*); and the skink *Mabuia striata angolensis*. The latter, however, remains problematic and under investigation (Conradie et al. 2016). Marques et al. (2018) provided a replacement name, *Trachylepis monardi* nom. nov., to stabilise taxonomy.

Throughout the early part of the twentieth century various other publications discussed small collections made by explorers (e.g. Angel 1921, 1923; Mertens 1938). All added new locality records within and for the country, and also described a number of new species (some no longer valid, e.g. *Psammophis rohani*, Angel 1921). Some reptile discoveries were especially serendipitous, e.g. the discovery of the new lizard species *Ichnotropis microlepidota* (Marx 1956) based on three specimens all found in the crop of a Dark Chanting Goshawk (*Melierax metabates*) collected during a bird survey of Mount Moco, that still awaits discovery in the wild!

In 1952–1954 the Hamburg Museum made an expedition to various locations in western Angola to collect mammals and herpetofauna, the most important being numerous additional snake records from forested habitats at Piri-Dembos (= Piri, Cuanza-Norte) (Hellmich 1957a, b). These confirmed, and sometimes added to Parker's (1936) records of snakes from the scarp forest isolates of Congulo and Quirimbo. These included (e.g.): *Philothamnus heterodermus, Thrasops flavigularis, Toxicodryas blandingii, T. pulverulenta, Gonionotophis poensis, Pseudohaje goldii, Atheris squamigera* and *Bitis nasicornis*. All are Congo Basin species and form an important biogeographic component of Angolan reptile diversity. Hellmich undertook a follow up expedition in 1954–1955, but his expedition suffered delays in obtaining permits and he missed the wet season activity and therefore shifted his survey to more open habitats in the southern provinces. There he undertook some of the first ecological studies on Angolan reptiles that were briefly discussed in a six-part series of popular articles on his Angolan travels (Hellmich 1954–1955). On his return he studied the reptile collections of the combined Hamburg expeditions (Hellmich and Schmelcher 1956; Hellmich 1957a, b), but the amphibians were only studied much later (Ceríaco et al. 2014b). As with Monard, Hellmich discovered relatively few taxonomic novelties, i.e. the lizards *Gerrhosaurus nigrolineatus ahlefeldti* (currently not considered valid) and *Agama agama mucosoensis* (now a full species; Wagner et al. 2012).

Between 1950 and 1960 the Belgian herpetologist Raymond F Laurent lived in Rwanda and Katanga (then Belgian colonies) and undertook detailed studies on varied herpetological groups in the Congo Basin, describing numerous new species and subspecies. During this period he studied the herpetological collections of the Museu do Dundo in northeast Angola, made by António de Barros Machado, the museum's director. Summaries of the museum's snake collections appeared first (Laurent 1950, 1954), followed by another report on Dundo material including Machado's extensive herpetological collection from the arid southwest region of the country (Laurent 1964). This was completed after Laurent had moved to the United States (1961) and the report described a number of new Angolan species, including Bogert's Speckled Western Burrowing Skink (*Typhlacontias bogerti*), two Namib Day geckos (*Rhoptropus taeniostictus* and *R. boultoni montanus*), and finally Hellmich's Wolf Snake (*Lycophidion hellmichi*), based (in part) on material collected during the Hamburg expeditions. It also included additional information of many previously poorly known species, as well as making ecological observations. It set a new standard for herpetological research in the area, but sadly was the final major Angolan herpetological work of the colonial period. Laurent did not study the historical collections in the Museu de Lisboa, and therefore did not re-assign Bocage's original material to his new taxa or identify significant new distribution records. This was unfortunate as he was one of the last herpetologists working on the Angolan herpetofauna before the disastrous fire that destroyed (1978) the collections that Bocage had studied, as well as much of his correspondence with collectors and fellow researchers. Manaças reported on collections of lizards (Manaças 1963), snakes (Manaças 1973), and venomous snakes (Manaças 1981) from Angola.

Bringing Knowledge of Angolan Reptiles into the Modern Era

Awareness of the interesting reptiles of the Angolan Namib region started incidentally following expeditions in the 1950s by the enthusiastic entomologist Charles Koch of the Transvaal Museum (TMP, now the Ditsong Natural History Museum, Pretoria, South Africa). Koch did much to inventory the amazing diversity of the tenebrionid beetle fauna of the Namib Desert, and much of his collecting involved walking at night in the desert with a pressure lamp. In addition to his numerous beetle discoveries Koch also collected many nocturnal and terrestrial reptiles, particularly geckos. These he gave to his colleague at the TMP, the Curator of Lower Vertebrates Vivian FitzSimons. Koch visited the northern Namib in Angola on four occasions (1951–1957), accompanied on the last trip by the Swedish zoologists Lundholm and Rudebeck. The herpetological collections during these trips were significant, and FitzSimons (1953, 1959) described a new genus of plated lizard *Angolosaurus* (now subsumed within *Gerrhosaurus*) as well two new species, *Pachydactylus caraculicus* and *Prosymna visseri*. Unreported, however, were many of Koch's numerous other reptile discoveries, including new records of the iconic Namib Web-footed Gecko (*Palmatogecko rangei,* now included in *Pachydactylus*)

in 1951 and 1954, then unknown from the Angolan Namib region. Laurent (1964) described the new Angolan Namib Day Gecko *Rhoptropus taeniostictus* from Angola, although nine specimens had already been collected by Koch during his trips, but remained undescribed. Also unrecorded were nine specimens of *Pachydactylus scutatus angolensis* from Lungo, Lucira and São Nicolau, the first collected since the description of the species by Loveridge (1944), and also 13 specimens of *Chondrodactylus fitzsimonsi*, at the time known from only one Angolan specimen (Pico Azevedo, Schmidt 1933).

In 1964 Wulf Haacke, born in Namibia, became the then Transvaal Museum's herpetologist with a special interest in the arid western areas of southern Africa. In March–April 1971 he undertook his first trip to Angola, concentrating on the northern extension of the Namib Desert into southwestern Angola. A follow up trip in April–June 1974 targeted specific genera to confirm the northern range limits and taxonomic status of *Cordylus, Cordylosaurus*, *Gerrhosaurus, Pachydactylus, Afroedura* and *Rhoptropus*. Both trips were exceptionally successful resulting in over 2000 specimens, the largest herpetological collections ever assembled by one researcher in Angola. Although the amphibian collections made during these trips were reviewed by Poynton and Haacke (1993), the vast majority of the numerous new and rare reptiles contained in these collections were never formally published. Haacke's second trip in 1974 was designed in particular to collect new material for his proposed thesis and revision of *Rhoptropus*. Prior to this trip, and excluding Koch's undescribed material, less than 30 specimens of *Rhoptropus* were known from Angola (Bocage 1895; Parker 1936; Mertens 1938; Laurent 1964). At the end of Haacke's surveys the Transvaal Museum held 650 specimens of the genus, included nearly 250 specimens of *R. barnardi* from over 25 localities, nearly 50 specimens of *R. biporosus*, and seven of *R. afer.* At the time *R. barnardi* in Angola was known from very few specimens (Bocage 1895; Schmidt 1933; Parker 1936; Laurent 1964) and *R. biporosus* was unknown in Angola and restricted to northern Namibia. The status of *R. afer* in Angola was particularly confused. Bocage's (1895) knowledge of Namib Day geckos (*Rhoptropus*) seems to have been limited, and he considered specimens from diverse localities from coastal Moçâmedes and the interior to Capangombe to all be applicable to *R. afer* Peters 1869. However, he noted that his material had 6–8 preanal pores whilst *R. afer*, as Peters (1869) had correctly recorded, had none. Schmidt also recorded *R. barnardi* for the first time from Angola, noting numerous other specimens from the Moçâmedes region in the British and Zoologisches museums that agreed with *R. barnardi.* These may have been the source of Bocage's confusion. The few recent records of Angolan *R. afer* have all been restricted to the vicinity of the Cunene River mouth, and it is evident that Bocage's material from further north was not based on true *R. afer.*

Due to the limited access to Angola during the protracted civil war the TM expeditions to Angola were curtailed, and for the next 34 years studies on Angolan reptiles were based on museum material collected earlier. Details of some of the geckos collected by the TM expeditions were incorporated into Haacke's studies on the burrowing geckos of southern Africa, which included the first records for Angola (Haacke 1976a) for the *Palmatogecko rangei* and *Kaokogecko vanzyli* (both now included in

Pachydactylus), and by implication *Colopus* (= *Pachydactylus*) *wahlbergii*, known to Haacke (1976b) from three specimens (TM 38526—28) from the Angola-SWA border, 18 degrees E). The bizarre and iconic Plume-tailed Gecko *Afrogecko plumicaudus*, collected during Haacke's 1971 trip, was of problematic taxonomic affinities and not described until much later (Haacke 2008). Its true affinities, however, were finally resolved later when fresh material was available for genetic analysis and it was placed in the monotypic genus *Kolekanus* (Heinicke et al. 2014). The 64 burrowing skinks of the genus *Typhlacontias* collected during these expeditions also formed an integral part of Haacke's (1997) revision of the genus, and which led to the recognition of a long overlooked Namib species, *T. johnstonii*, previously confused (Bocage 1895; Monard 1937) with *T. punctatissimus*, and described from Porto Alexandre (=Tômbwa) at the northern limit of its range. A new Angolan species, *T. rudebecki,* was also described, based on a single specimen collected from São Nicolau during Koch's 1956 expedition. Laurent's (1964) species *T. bogerti* was treated as a northern subspecies of the Speckled Burrowing Skink, *T. punctatissimus bogerti* (Haacke 1997). A number of other new Angola records were discovered by Haacke during his trips. The rupicolous gecko *Pachydactylus oreophilus,* described from northern Namibia (McLachlan and Spence 1967), was known only from the types until Haacke discovered similar material from numerous localities in southwest Angola. No additional Angolan material was collected until the Huntley expedition in the region in 2009 (see below), when it was realised that Angolan material was not conspecific with Namibian *P. oreophilus.* The status of the Angolan material is currently being investigated (Branch et al. in prep.). Haacke also collected the first records of true *P. scutatus* from Angola, as well as additional *P. angolensis* (Branch et al. 2017). Finally, Broadley (1975) referred some small skinks collected by Haacke to *Trachylepis lacertiformis*, creating a zoogeographic enigma as the nominotypic population of this small skink is restricted to the lower Zambezi River valley. Fuller details of the Koch and Haacke collections and other recent material will be incorporated into a full review of the herpetofauna of the Angolan Namib region (Branch in prep.).

Legless burrowing worm lizards (Amphisbaenidae) are rarely found due to their ability to burrow deep underground. Carl Gans (1976) described three new species from Angola, including *Monopeltis luandae* based on fresh (1971) and historical (1892) material from the Luanda region, and *M. perplexus* on material from the Vernay-Angola expedition collected from 'Hanha or Capelongo' in 1925. Similarly, Gans (1976) re-assessed old and new material when describing *Dalophia angolensis* from Calombe near Vila Luso (= Luena), and reassigned specimens identified as *M. ellenbergeri*, and then as *M. granti transvaalensis* (Monard 1937), to *D. angolensis*. None of Gans' three new species had been rediscovered in the intervening 40+ years until recently, when *M. luandae* was rediscovered from near the type locality (Branch et al. 2018). In a companion paper that radically changed understanding of the taxonomy of worm lizards in the southern half of Africa, Broadley et al. (1976) revised the genera *Monopeltis* and *Dalophia*. The revision of Broadley et al. (1976) affected most of the early names applied to Angolan worm lizards. The first large worm lizard described from Angola was *Lepidostsernon* (*Phractogonus*) *anchietae* Bocage 1873, from 'Humbe, dans l'intérior de Mossamedes', later transferred to the

genus *Monopeltis* (Boulenger 1885). Broadley et al. (1976) relegated Monard's (1937) species *M. okavangensis* and *M. devisi* to *M. anchietae,* which is now known to have a wider range in northern Namibia and adjacent Botswana. *Monopeltis vanderysti vilhenai*, described by Laurent (1954) from Dundo, Angola, was not recognised by Broadley et al. (1976) and returned to *M. vanderysti,* which is widely distributed in the Congo region. The Dundo specimen remains the only Angolan record of the species. *Monopeltis capensis* in Angola was first recorded by Bocage (1873), and later by Monard (1937). Although provisionally placed in the *M. capensis capensis* Group B (Broadley et al. 1976), with a wide range through the Kalahari region (Northern Cape, South Africa, through Botswana to southern Angola), it was later treated as a separate species, *M. infuscata* Broadley 1997a. Monard's (1937) species *Monopeltis granti kuanyamarum,* described from a single specimen from Mupanda, was transferred to *Dalophia pistillum* (Broadley et al. 1976). The only Angolan specimen of *Dalophia ellenbergeri* was collected whilst trench digging during hostilities at Cuito Cuanavale (Branch and McCartney 1992; Broadley 1997b). Gray (1865) described *Dalophia welwitschii* from Pungo Andongo, and this has not been rediscovered. It is the type species for the genus *Dalophia,* and Gans (2005) was obviously in error when treating it as *M. welwitschii* and yet still continuing to recognise *Dalophia.* A phylogeny of African amphisbaenids (Measey and Tolley 2013), albeit based on poor taxon sampling, recovered *Monopeltis* and *Dalophia* as monophyletic clades, supporting the use of *Dalophia welwitschii*.

Two species of round-headed worm lizards of the genus *Zygaspis* are now known to occur in southeast Angola, but the genus was unknown to Bocage from Angola, and the first record from the country was Monard's (1931) description of *Amphisbaena ambuellensis* from 'Chimporo' (= Tchimpolo). This was subsequently synonymised with *A. quadrifrons* by Loveridge (1941) with some misgivings, and subsequently transferred to *Zygaspis* by Alexander and Gans (1966). It remained known only from Monard's material for many years, but has recently been collected in southern Angola (Conradie et al. 2016, Baptista et al. in prep.), and the availability of Monard's *ambuellensis* for this material is being reassessed. More recently, Laurent (1964) recorded *A. q. capensis* from Alto Chicapa in northeast Angola, which was shown to be the new species *Zygaspis nigra* by Broadley and Gans (1969). This small black worm lizard is near endemic to eastern Angola, with records from adjacent Zambia (Kalobo, Broadley and Gans 1969; Ngonya Falls, Pietersen et al. 2017) and Namibia (Katima Mulilo, Broadley and Gans 1969). Recent material is known from the Okavango catchment (Conradie et al. 2016).

Following the cessation of hostilities, modern biodiversity surveys were initiated by Brian Huntley with the multinational SANBI/ISCED/UAN Angolan Biodiversity Assessment and Capacity Building Project (Huntley 2009). Surveys were undertaken by botanists and zoologists in various habitats between Lubango and the Cunene River, and 15 Angolan students were involved in fieldwork and training sessions. The immediate reptile highlights of the survey involved the discovery of two new species of the lacertid *Pedioplanis* (Conradie et al. 2012a), two specimens of the rare Shovel-snout Snake *Prosymna visseri* were collected at Espinheira, Iona National Park, only the 5th and 6th Angolan specimens since its description

(FitzSimons 1959); the 1st record of the Namib Wolf Snake (*Lycophidion namibianum*) from Angola, again at Espinheira; the southernmost records of the newly-described Plume-tailed Gecko (*Afrogecko plumicaudatus* Haacke 2008) that allowed its generic assignment to later be readjusted; and topotypic material of the rare chameleon (*Chamaeleo anchietae*) were collected around Estação Zootécnica. This chameleon has an unusual, disjunct distribution with scattered populations (treated as separate subspecies by Laurent 1951) from the Upemba region, Democratic Republic of the Congo (DRC) and Udzungwa Mountains, Tanzania. The status of these disjunct *C. anchietae* populations is currently under investigation (Branch et al. in prep.). A new species of reed frog, *Hyperolius chelaensis*, completed the new discoveries (Conradie et al. 2012b). Following the success of the 2009 survey, another expedition was organised in 2011 to Lagoa Carumbo, the second-largest Angolan freshwater lake situated in Lunda Norte Province (Huntley and Francisco 2015). The herpetological results were summarised by Branch and Conradie (2015). Significant herpetological discoveries included the discovery of at least two new species of frog, one described (*Hyperolius raymondi* Conradie et al. 2013), and the description of the other (*Amnirana* sp.) is in preparation (Jongsma et al. 2018), and also the first record for Angola (Branch and Conradie 2013) of the Banded Water Cobra (*Naja annulata*). Other reports include new insights into the distributions of venomous snakes, such as Jameson's Green Mamba, *Dendroaspis jamesoni* (Vaz Pinto and Branch 2015) and the Gaboon Adder, *Bitis gabonica* (Oliveira et al. 2016), as well as a recent summary of Angolan venomous snakes (Oliveira 2017).

The unique World Heritage site of the Okavango Delta is situated in Botswana, but depends on the Okavango drainage, which arises and is almost entirely contained within southeastern Angola. During the last six years a series of international collaborative surveys have been undertaken to explore this poorly known region of southeast Angola, and to understand the hydrology and biodiversity of the Okavango drainage. The first surveys were organised by the Okavango River Basin Water Commission (OKACOM), in accord with the Angolan National Action Plan for the Sustainable Management of the Cubango/Okavango River Basin (OKACOM 2011), and occurred in the lower catchments of the Cubango and Cuito rivers (Brooks 2012, 2013). More recent surveys (2015–2018) formed part of the ongoing National Geographic funded Okavango Wilderness Project (NGOWP 2018), which have intensely surveyed the source lakes of the major Okavango tributaries in an unexplored region where the headwaters of the Cuanza, Zambezi and Okavango basins meet. The herpetological results of the OKACOM surveys (2012–2013) and first phase of the NGOWP surveys were presented by Conradie et al. (2016), who also reviewed the region's herpetofauna. In total 67 reptiles species are now known from the region, comprising 38 snakes, 32 lizards, five chelonians, and a single crocodile (NGOWP 2018). Three reptiles new for Angola, including *Causus rasmusseni* (although the specific status of this taxon still requires genetic confirmation), *Acontias kgalagadi kgalagadi* and *Panaspis maculicollis* were discovered (Conradie and Bourquin 2013; Medina et al. 2016). The results of more recent surveys (2016–2018) were presented (Conradie et al. 2017) and fuller details are being prepared for publication, and online species lists are planned for public access.

Contemporaneous with the above surveys a number of other Angolan biodiversity initiatives began. In partnership, the Kimpa Vita University in Uíge and Dresden University, Germany, undertook herpetological surveys of Serra do Pingano, Uíge Province, discovering diverse tropical Congo Basin species (Ernst 2015), including two frogs previously unrecorded for Angola (Ernst et al. 2014, 2015). In addition the California Academy of Sciences in conjunction with the National Institute of Biodiversity and Conservation Areas and the Ministry of the Environment of Angola (MINAMB/INBAC) initiated an ongoing Atlas of Angolan amphibian and reptiles (Marques et al. 2014, 2018). Various areas have been surveyed and preliminary results published in the scientific and popular literature (Ceríaco et al. 2014a, b, 2016a, b, 2018b). As part of the Southern African Science Service Centre for Climate Change and Adaptive Land Management program (SASSCAL) the Instituto Superior de Ciências da Educação da Huíla (ISCED), Lubango, has been undertaking herpetofaunal monitoring at several areas in Huíla Province and elsewhere in Angola (Baptista et al. 2018, 2019), with emphasis on the escarpment. A herpetofaunal archive is also being developed at ISCED.

Angolan citizen science is in its infancy, but the FaceBook site *Angola Ambiente* is a public group where members post observations (https://www.facebook.com/groups/1045499302182009/). It is designed "to raise awareness of the fantastic fauna and flora of this magnificent country", and requests observations with detailed locality data. It includes irregular lists of sightings with locality details in support of mapping initiatives.

Checklist of Angolan Reptiles

How Many Species?

The first attempt to summarise the herpetofauna of Angola was undertaken by JV Barbosa du Bocage (1866), who listed 50 reptile species from Angola in the Museu de Lisboa collection, including 23 snakes, 21 lizards, four chelonians, and one crocodilian. After nearly 30 years of study he again summarised the Angolan herpetofauna in his monographic *Herpetology d'Angola et du Congo* (Bocage 1895) in which he listed 143 reptile and 39 amphibian species from the country. Of these Bocage had described 37 of the taxa (although not all are now recognised). During two trips to Angola (1928–1929 and 1932–1933) the Swiss collector Albert Monard made important collections of amphibians and reptiles. In his monograph (Monard 1937) he presented an updated checklist of Angolan reptiles, listing 169 reptile species in 10 families and 28 genera. There has been no subsequent updated and checklist of the country's reptiles, although Blanc and Fretey (2002) noted a total of 257 Angolan reptile species and published a breakdown of its composition. However, no species list was included and therefore it is impossible to assess the accuracy or the validity of the species included. In contrast, the online Reptile Database (Uetz et al. 2018, as on 14 October 2018) currently generates a list of 255 reptiles for Angola,

but unfortunately although close to the existing count, it is inaccurate in numerous respects. Some species have been included that are unrecorded from the country but may occur in the country (e.g. a snakes from the Congo Basin *Calabaria reinhardti,* Namibian *Lygodactylus lawrencei,* etc.). Moreover, many other species are duplicated and listed under both their historical and current taxonomic assignments (e.g. *Agama hispida* = *A. aculeata, Chamaesaura macrolepis* = *Ch. miopropus, Cordylus cordylus* = *C. namakuiyus, C. vittifer* = *C. machadoi,* etc.) These inaccuracies have been discussed in the recent Atlas and being rectified (see Marques et al. 2018 Appendix Table A2).

Currently (as of mid-2018), there are 278 reptile species recorded from Angola, comprising 15 chelonian, three crocodilian, 132 lizard and 128 snake species. Table 13.1 details the historical growth of knowledge of reptile diversity in Angola based on summaries in Bocage (1866, 1895), Monard (1937), and this study. Table 13.2 summarises the number of genera, species, and endemic taxa in the major reptile groups in Angola. Updated checklists of the major reptile groups, including details of common and scientific names, historical scientific names used by Bocage (1895) for the current taxa, as well as their endemic and conservation status are summarised in: Appendix 1 – chelonians; Appendix 2 – lizards; and Appendix 3 – snakes. Contained within these checklists are 43 Angolan species named by Bocage, i.e. 15.5% of the current reptile diversity. This is less than the 25.9% (37 of 143) in Bocage's (1895) summary, but no other researcher has described more from Angola.

Table 13.1 Historical development of reptile diversity in Angola based on summaries in Bocage (1866, 1895), Monard (1931), and this study

	Bocage		Monard	This study
Group	1866	1895	1937	2018
Snakes	23	71	81	128
Lizards	21	59	78	132
Chelonians	4	8	9	15
Crocodilians	2	1	1	3
Total [a]	**50**	**139**	**169**	**278**

[a]This includes 'species' known at the time of Bocage and Monard, some of which may have later been relegated to synonymy (see discussion on Monard's list)

Table 13.2 Summary of the taxonomic diversity and endemicity of the reptiles of Angola

Group	Genera	Species	Endemic
Chelonians	11	15	0
Crocodilians	3	3	0
Lizards	40	132	27
Snakes	49	128	6
Total	**103**	**278**	**33**

Recent Discoveries

In the last decade, and resulting from the burgeoning scientific interest in Angola, biodiversity surveys have led to the description of numerous new species and the validation of the specific status of others. Perhaps the most exciting was the long delayed description of the beautiful and bizarre Plume-tailed Gecko (*Afrogecko pulumicaudus* Haacke 2008) from the Angolan Namib region. Other novelties included the description of the lacertids *Pedioplanis haackei* and *P. huntleyi* (Conradie et al. 2012a and the cordylid *Cordylus namakuiyus* (Stanley et al. 2016). Some subspecies were validated as full species, including the geckos *R. boultoni benguellensis* and *R. boultoni montanus* (Ceríaco et al. 2016a) and the snake *Psammophylax rhombeatus ocellatus* (Branch et al. 2019), as well as the revival of the skink *Trachylepis damarana* from the synonymy of *T. varia* (Weinell and Bauer 2018). Some species, e.g. *Philothamnus nitidus loveridgei*, however, have been shown to lack genetic support for recognition (Engelbrecht et al. 2018) and are now not recognised.

In addition, preliminary studies have revealed numerous problematic specimens and populations that demonstrate the existence of cryptic, previously synonymised species or unnamed taxa awaiting description in numerous genera. Geckos – *Hemidactylus, Rhoptropus* (Ceríaco et al. 2016a; Bauer and Kuhn 2017), *Afroedura* (Branch et al. 2017), and various *Pachydactylus* groups (Branch et al. 2017; Ceríaco et al. 2016a; Heinz 2011); within the lacertids *Nucras, Pedioplanis* and *Heliobolus* (Branch and Tolley 2017); and a skink in the *Trachylepis varia* complex (Weinell and Bauer 2018). The descriptions of at least a dozen new species in these genera are in preparation. Ceríaco et al. (2016b, 2018b) signalled the presence of a new skink (*T.* cf. *megalura*) from Cangandala National Park. Snake-eyed skinks (*Panaspis wahlbergii-maculilabris* complex) have been shown to include numerous cryptic species in southern and east Africa (Medina et al. 2016). Records of *P. wahlbergii* in Angola are therefore also likely to represent taxonomic novelties. It is also likely that genetic studies will further validate a number of other lizard taxa currently treated as subspecies, e.g. *Ichnotropis bivittata palida* and *Trachylepis bayoni huilensis,* as full species. Moreover, the rare gecko *Afrogecko ansorgi,* described by Boulenger (1907a), as *Phyllodactylus ansorgi* and not collected again for nearly 100 years, was recently rediscovered and a re-assessment of its generic status is in preparation. In addition, ongoing surveys of the Angolan Okavango Project continue to confirm new species records for Angola, including most recently *Pachydactylus wahlbergii* (G Neef pers. comm. July 2018), previously assumed to enter southern Angola based on material collected on the Angolan-Nambian border in the 1970s (Haacke 1976b). Cryptic diversity in snakes is also being unravelled, and African forest cobras have been shown to include five species (Wüster et al. 2018), of which two enter Angola, whilst Angolan house snakes (*Boaedon*) is expected to comprise at least eight species, with four potential new country records, i.e. *B. fuliginosus, B. radfordi, B. virgatus* and *B. mentalis* (the latter signalled as a valid species by Kelly et al. 2011, and will be formally revived for western arid populations from South Africa to southwest Angola), revival from synonymy of two

Bocage names for Angolan endemics, i.e. *B. angolensis* and *B. variegatus,* and two additional taxonomic novelties (Hallermann et al. personal communication).

Overview of Reptile Diversity

Chelonians

This ancient lineage of reptiles has relatively little global diversity and includes the greatest proportion of threatened reptiles, particularly in Asia. They are relatively poorly known in Angola, and their diversity is discussed below. The first sea turtle to swim in the early South Atlantic, after the separation of Africa and South America 90 Million years ago, was the extinct chelonian *Angolachelys mbaxi,* discovered in Angola in 2009 near the village Iembe, Bengo Province (Mateus et al. 2009). Five of the seven species of sea turtles in the world have been recorded from Angolan waters (Carr and Carr 1991), although only four occur regularly. They include (in decreasing order of abundance): Olive Ridley Sea Turtle (*Lepidochelys olivacea*), Leatherback Sea Turtle (*Dermochelys coriacea*), Green Sea Turtle (*Chelonia mydas*), Loggerhead Sea Turtle (*Caretta caretta*), and Hawksbill Sea Turtle (*Eretmochelys imbricata*). Although early surveys (2000–2006) indicated the absence of Hawksbill in Angolan waters (Weir et al. 2007), juveniles were recently recorded in the Soyo and Cabinda region (Morais 2008, 2016). These may still be vagrants in Angolan waters (TTWG 2017) as Hawksbills forage on coral reefs which are absent in Angola. Nesting in Angolan waters has only been confirmed for Green, Olive Ridley and Leatherback sea turtles, and occurs during September–March, peaking in November–December in the north and a month later in the south (Morais 2017). It is widespread for the Olive Ridley, but restricted mainly to the south for the Green Sea Turtle. The latter remains common in the Cunene River estuary where adults and juveniles feed and also escape the cold waters of the Benguela Current (Elwen and Braby 2015). The giant Leatherback nests primarily in the warmer north, with little activity south of Benguela. The Angolan population (approximately 1000 in 2005–2016, Morais 2016) forms the southern part of the major Gabon nesting grounds, where 6000–7000 females breed annually (Billes et al. 2006). Sea turtles face numerous threats, including by-catch and drowning in trawler fishing nets, the collection of nesting females and their eggs for food, and disturbance of the nest sites by beach activities, etc. (Morais et al. 2005; Morais 2008; Weir et al. 2007). The Projecto Kitabanga of Universidade Agostinho Neto (https://www.facebook.com/Kitabanga/) is involved in research and public education of Angolan sea turtles.

Only three land tortoises are recorded for Angola. The Leopard Tortoise (*Stigmochelys pardalis*) is restricted to the southwest, with all records occurring below the escarpment south of Benguela and along the Cunene valley. Bell's Hinge-back Tortoises (*Kinixys belliana*) is considered widespread in Angola (TTWG 2017), and *Kinixys* material from central and eastern Angola were confirmed as this

species in a molecular phylogeny of the genus (Kindler et al. 2012). Although material from Capanda Dam has been referred to *Kinixys spekii* (Ceríaco et al. 2014a), this species is not currently considered to occur in the country (TTWG 2017), but is known from the Zambezian region of Namibia and the Ikelenge pedicle of northwest Zambia. The Forest Hinge-back Tortoise (*Kinixys erosa*) occupies moist forests of the Congo basin and West Africa, but only enters Angola in the extreme northeast (Dundo, Laurent 1964) and the Cabinda enclave (Bocage 1895).

The Nile Soft-shelled Terrapin (*Trionyx triunguis*) is restricted to the coastal region, entering the estuaries and lower stretches of the major rivers. It tolerates sea water and grows to over a metre in length. Populations in the eastern Mediterranean and lower Nile River are threatened, and its status in Angola is poorly known, but is known from the coastal region and with populations in the Cunene River mouth and extending some distance upstream in the Cuanza River. Aubry's Soft-shelled Terrapin (*Cycloderma aubryi*) was recorded once from Cabinda (Peters 1869), but there are no recent records. Trade in chelonians, particularly soft-shelled terrapins for food in Asia, has pushed many species to the brink of extinction (TTWG 2011), and involvement in Africa is confirmed by the discovery of a turtle butchery on Lake Malawi (Face of Malawi 2013) and the recent confiscation of a large *T. triunguis* in a shopping mall in Luanda (Arruda 2018). All other Angolan terrapins have hard shells and are restricted to fresh water ecosystems. They withdraw the head into the shell sideways and are represented by the Pelomedusidae in Africa, including the genera *Pelomedusa* and *Pelusios*. Although Bocage (1866) listed the forest species *Pelusios gabonensis* from Cabinda and Duque de Bragança in his first review of Angolan reptiles, the species was subsequently omitted (Bocage 1895). However, it was subsequently recorded from Dundo (Laurent 1964), and mapped to enter extreme northwest Angola south of the Congo River (TTWG 2017), but no documentation supporting this is presented. It was not recorded at Soyo (W Klein pers. comm.), although Western Hinged Terrapin (*Pelusios castaneus*) was common. The most widespread Angolan terrapins are *Pelusios nanus, P. bechuanicus* and *P. rhodesianus* in the extensive wetlands of eastern Angola (Conradie et al. 2016; TTWG 2017).

Crocodilians

Of the three crocodilians that occur in Angola, only the Nile crocodile (*Crocodylus niloticus*) is widespread, being absent only from the southwest although occurring in the lower Cunene River. The remaining two species are both denizens of the Congo Basin and have only a peripheral presence in Angola. The Sharp-snouted Crocodile (*Mecistops cataphractus*) in Angola had been discussed by Machado (1952), who noted an unusual early record from Lunda and others from Dundo, later confirmed by Laurent (1964). Recent studies (Shirley et al. 2014) have found significant molecular and morphological support for two divergent taxa in *Mecistops* – one distributed entirely in West Africa and the other in Central Africa. As the type

locality is Senegal, West African populations would keep the name and Congo Basin and Angolan populations have been considered to represent an undescribed species (Shirley et al. 2014), and was subsequently described as a new species, *Mecistops leptorhynchus* (Shirley et al. 2018). The Dwarf Crocodile (*Osteolaemus tetraspis*) is known from nineteenth century of records from the Cabinda enclave (Bocage 1866; Peters 1877), but no confirmed records exist for the natural occurrence of the species south of the Congo River (Eaton 2010). Ceríaco et al. (2018a) discuss a problematic specimen collected in the lagoon at Luanda that they consider to be indicative of an unknown population in the Cuanza River drainage and also the first record of *O. osborni* for Angola. However, the specimen's identity was not confirmed by genetic monophyly, and its presence in Angola may also result from an escapee brought to Luanda for the bushmeat trade. As with *Mecistops* recent genetic studies indicate the existence of at least three species within the *Osteolaemus tetraspis* complex (Eaton et al. 2009), but the taxonomic identity of Cabinda and the putative Cuanza *Osteolaemus* populations require further study.

Squamates

Scaled reptiles (Squamata) form the major component of reptile diversity (Pincheira-Donoso et al. 2013), with over 10,000 species currently recognised, of which over 60% are lizards. Reflecting this, lizards are also the dominant component of the Angolan reptile diversity and are the group in which most recent discoveries have been made (see above).

The 132 species of Angolan lizards are currently contained in nine families, with skinks (Scincidae) containing the greatest diversity. This contrasts with Namibia (Herrmann and Branch 2013) and South Africa (Branch 2014) where geckos form the greatest component of lizard diversity and endemicity (Table 13.3). It is likely that the current dominance of skinks in Angola is an artefact of our present knowledge. Most skinks are diurnal and active and therefore more easily discovered. Cryptic diversity has already been identified in certain Angolan gecko genera (e.g. *Afroedura, Pachydactylus* and *Rhoptropus*, see above), and the discovery of these and others is predicted to also promote geckos to dominance in diversity and endemicity in the Angolan reptile diversity. The evolutionary centre for girdled lizards (Cordylidae) occurs in southern African (Stanley et al. 2016), but the family is relatively poorly represented in Angola. Although it is unlikely to reach the species or generic diversity of even Namibia, there are indications that the diversity of rupicolous *Cordylus* in the escarpment and central uplands is under-represented (e.g. Stanley et al. 2016), and that rediscoveries and further new species await discovery and description.

The families Agamidae, Chamaeleonidae, Gerrhosauridae and Varanidae all have limited diversity in Angola, as do the last two families throughout Africa. Blue-headed tree agamas have been revised (Wagner et al. 2018), with populations from northern Namibia, Angola and northwest Zambia now referred to the revived *Acanthocercus cyanocephalus.* However, it is evident that current species boundaries

Table 13.3 Comparison of diversity and endemicity of Angolan and South African Squamates (excluding Chelonia), by genera (Gen.), species (Spp.), subspecies (Sub.), and endemism (End.)

	Angola			South Africa		
Family	Gen.	Spp.	End.	Gen.	Sp.	End.
Lizards						
Gekkonidae	8	34	8	12	89	55
Agamidae	2	7	2	2	7	0
Chamaeleonidae	2	5	0	2	19	15
Gerrhosauridae	4	8	0	5	13	6
Cordylidae	2	5	2	10	53	38
Scincidae	12	45	6	7	62	32
Lacertidae	6	15	6	8	29	9
Amphisbaenidae	3	11	3	4	12	2
Varanidae	1	2	0	1	2	0
subtotal	**40**	**132**	**27**	**51**	**286**	**157**
			(20.5%)			**(54.9%)**
Snakes						
Leptotyphlopidae	2	5	2	3	10	3
Typhlopidae	2	8	1	3	7	0
Pythonidae	1	3	0	1	2	0
Colubridae	14	31	0	9	16	0
Natricidae	2	4	0	1	2	0
Lamprophiidae[a]	15	39	2	17	42	3
Atractaspididae	6	11	0	6	16	2
Elapidae	5	14	0	6	18	1
Viperidae	3	13	1	2	14	4
subtotal	**50**	**128**	**6**	**48**	**127**	**13**
			(4.7%)			**(10.2%)**
TOTAL	**95**	**260**	**33**	**109**	**413**	**170**
			(12.7%)			**(41.2%)**
Angola/South Africa	**83%**	**63%**				

[a]Excludes additional *Boaedon* species (Hallerman et al. in prep.)

in *Agama* and *Acanthocercus* do not full reflect Angolan agamid diversity. The remaining families, Lacertidae and Amphisbaenidae, are relatively well represented in Angola, with worm lizard diversity in Angola (three genera, 11 species) second only to that in South Africa (12) for diversity in Africa. Most are associated with the sands of the Kalahari Basin, or in secondary deposition in the coastal zone of South Africa and southern Mozambique. The role of river capture and hydrological changes associated with nascent rifting on fossorial reptiles awaits fuller study. Lacertid diversity in Angola (13 species) is reduced relative to South Africa (29) and Namibia (24), but is known to be under-represented and recently described *Pedioplanis* species (Conradie et al. 2012a), and recently discovered cryptic diversity in other lacertid genera (Branch and Tolley 2017; Conradie et al. 2016) will increase species numbers in the family. A number of additional tropical lacertids may also enter the northern regions of Angola (see below).

There are several aspects of Angolan reptile diversity that stimulate interest. The first is the absence of an endemic radiation of chameleons within Angolan forest refugia. African countries with the highest chameleon diversity (Tilbury 2018), i.e. South Africa and Tanzania, have largely endemic radiations of chameleons (*Kinyongia* and *Rhampholeon* in Tanzania, *Bradypodion* in South Africa). All three genera are absent from Angola, where only *Chamaeleo* and *Trioceros* occurs. Greater knowledge of the history of forest habitats in Angola may give insight as to the absence of a forest chameleon radiation. Sandy habitats in arid southwest Angolan include a radiation of skinks of the genera *Sepsina* and *Typhlacontias* that have reduced limbs, serpentine locomotion and fossorial behaviour. The ranges of some species within these genera extend south into adjacent Namibia and Botswana. In arid habitats at the southern end of the Namib Desert, in the southern Dune Sea and adjacent Succulent Karoo biome these Angolan fossorial skink radiations are almost completely replaced by another suite of sepentiform skinks of the genera *Scelotes, Typhlosaurus* and *Acontias.* Only one species, *Typhlacontias brevipes,* of the Angolan radiation occurs in the northern parts of the southern Dune Sea. Increased knowledge of the history of aridification and dune movements of the Namib Desert may again give insight into these distributions.

That snake diversity in Angola is probably the most well known component of the reptile fauna is unsurprising. However, their distribution, particularly of forest-adapted species in the northern and scarp forest isolates, remains poorly-known. The taxonomic status of these isolated forest populations calls for genetic studies on their phylogenetic relationships to confirm their conspecificity with northern populations. The diversity and composition of snake families in Angola reflects that of Africa, with relatively low diversity in primitive groups such as scolecophidians (Typhlopidae and Leptotyphlopidae) and haenophidians (Pythonidae). Again, in Angola as in southern Africa the venomous families Elapidae and Viperidae have slightly greater species diversity, but with more tropical representatives (e.g. the elapids *Pseudohaje goldi, Naja annulata* and *N. melanoleuca*, and viperids *Causus lichtensteini, C. maculatus, Atheris squamigera* and *Bitis nasicornis*). The dominant African snake family is the Lamprophiidae, of which the Atractaspididae is closely related and sometimes treated as a subfamily. The group appears to have originated in Africa and subsequently radiated into Arabia and Asia, and the subfamilies Lamprophiinae, Prosyminae and Psammophinae form important radiations in Sub-Saharan Africa. Lamprophids thus form the dominant component of the Angolan snake fauna (39 species), but includes only two endemic psammophines. 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 olivaceus, Bothrophthalmus lineatus*, etc. Perhaps the greatest difference between South Africa and Angola is reflected in the greater diversity of colubrids (Colubridae) in Angola (28 vs 14 species). These include numerous tropical Congo Basin snakes that enter the northern and scarp forests, and of particular interest are the rare Congo Basin species *Toxicodryas blandingii, T. pulverulenta, Rhamnophis aethiopissa, Philothamnus nitidus, Dasypelis palmarum,* etc. The family is considered of Asian origin and to have entered and subsequently radiated in Africa.

Species Recorded from Angola but Poorly Known

Some species are known from Angola from either a single or very few specimens and their presence and taxonomic status requires confirmation. This summary does not include wide ranging species that peripherally enter Angola, either from the Congo Basin (e.g. *Pelusios gabonensis, Feylinia grandisquamis, Hypoptophis wilsoni,* etc.), or from the southern Kalahari or Namib deserts (e.g. *Rhoptropus afer, Pachydactylus rangei, P. vanzyli, Chamaeleo namaquensis, Amblyodipsas ventrimaculata*, etc.).

Grass Lizard – *Chamaesaura anguina oligopholis* Laurent (1964). Described from Calonda, Lunda, but with no recent material. It may deserve specific status.

Angola Girdled Lizard – *Cordylus angolensis* (Bocage, 1895). Known only from the type description of a single male from Caconda, but a population that conforms to the species has recently been discovered (Vaz Pinto Unpublished Data).

Scaled Sandveld Lizard -*Nucras scalaris* Laurent 1964. Still known only from type series of four specimens from Alto Chicapa and Alto Chilo.

Dewitte's Five-toed Skink – *Leptosiaphos dewittei* (Loveridge, 1934). Recorded by Parker (1936, as *Lygosoma dewittei*) from Congulo. However, the only known Angolan specimen lacks the diagnostic compressed tail. The species occurs in the eastern Congo Basin, a considerable disjunction from Congulo.

African Shovel-nosed Snake – *Scaphiophis albopunctatus* Peters, 1870. Only once recorded from Angola (Laurent 1950, Muita River) in Guinea-Congo savannah habitat.

The only other know record is a juvenile specimen collected from Capaia, Lunde Norte (Branch and Conradie 2015).

Collared Snake-eater – *Polemon collaris* (Peters 1881). Recorded by Peters (1881, Cuango), Ferreira (1904, Golungo Alto) and Hellmich 1957a, b, Bella Vista, as *Miodon gabonensis*). Isolated populations of small fossorial snakes such as *Polemon* often include cryptic diversity (Portillo et al. 2018), and fresh material is required for taxonomic assessment.

Lined Water Snake – *Lycodonomorphus* (?) *subtaeniatus* Laurent 1954. Described from Keseki (DRC), with four paratypes from Dundo the only Angolan records. Greenbaum et al. (2015) transferred *L. s. upembae* to *Boaedon.* This is probably where *L. subtaeniatus* belongs but fresh material is required for genetic analysis.

Speckled Wolf Snake – *Lycophidion meleagre* Boulenger 1893. Described from Angola and known from Cabinda to Luanda, but Broadley (1996) also includes records from coastal Tanzania in the species' range, creating a biogeographic anomaly that requires genetic assessment.

Parker's Banded Snake – *Chamaelycus parkeri* (Angel, 1934). Parker's (1936) Congulo specimen (as *Oophilositum parkeri*) remains the only known Angolan material. Elsewhere the species is restricted to Kivu (DRC) and Congo Brazzaville, and confirmation of the specific status of the Congulo population is required.

Angolan Coral Snake – *Aspidelaps lubricus cowlesi* Bogert 1940. Described from Munhino (101 km east of Moçamedes, via railroad), and known from Angola from the type and one additional specimen (Branch 2018). Considered widespread in northern Namibia, but genetic monophyly between Angolan and Nambian populations is required for confirmation.

Angolan Garter Snake – *Elapsoidea semiannulata moebiusi* Werner, 1897. Listed by Broadley (2006) from northern Angola, but with no specific localities given. All Bocage localities (1866, 1895, 1897) were restricted to Bissau specimens. A southern subspecies is now treated as a valid species (*E. boulengeri*). The status of *E. s. moebiusi* requires a modern taxonomic assessment and also confirmation for Angola.

Angolan Dwarf Adder – *Bitis heraldica* (Bocage, 1889). Angola's most iconic snake for which no new material was collected for over 50 years has recently been rediscovered. It has a disjunct distribution in montane grasslands of the Angolan inland plateau, and the fresh material will allow its subgeneric relationships within *Bitis* to be assessed as well as its conservation status.

Species Likely to Occur in Angola but Currently Unconfirmed

A number of species are recorded in close proximity to the Angolan border and live in habitats contiguous with those in Angola, and are therefore likely to occur in the country. They include:

Lizards

Heenen's Dwarf Day Gecko – *Lygodactylus heeneni* De Witte, 1933. This small diurnal gecko was recorded from the Ikelenge Pedicle in northwest Zambia (Broadley 1991; Haagner et al. 2000) within 25 km of the Angolan border.

Long-tailed Worm Lizard – *Dalophia longicauda* (Werner, 1915). This fossorial species was described from northern Namibia and is known to extend through the Caprivi region to western Zimbabwe (Broadley et al. 1976; Gans 2005) and also to southwest Zambia (Pietersen et al. 2017). Populations occur to the east and west of the Okavango River and are expected to occur in southeast Angola.

Maurice's Worm Lizard – *Monopeltis mauricei* Parker, 1935. This fossorial species was described from central Botswana and is known to extend through the Kalahari to Katima Mulilo in the Caprivi region (Broadley et al. 1976; Gans 2005). Elevated to a full species by Broadley (2001).

West African Striped Lizard – *Poromera fordii* (Hallowell, 1857). An arboreal species recorded during a survey in the Bas-Congo region (Nagy et al. 2013) within 30 km of the Angolan border but currently unknown from Angola.

Fine-scaled forest lizard – *Adolfus africanus* (Boulenger, 1906). A terrestrial species recorded from the Ikelenge Pedicle in northwest Zambia (Broadley 1991), within 25 km of the Angolan border.

Snakes

Western Thread Snake – *Namibiana occidentalis* (FitzSimons, 1962) occurs in extreme Kaokoveld (Broadley and Broadley 1999) but has not yet been recorded from southern Angola. The single record of the Damara Thread Snake (*N. labialis* Sternfeld, 1908) from southern Angola demonstrates that these small snakes can cross the Cunene River.

Leptotyphlops sp. An unidentified thread snake was recorded during a survey of the Bas-Congo region (Nagy et al. 2013). Based on its forest habitat it is unlikely to be referable to any known Angolan species.

Slender Quill-snouted Snake – *Xenocalamus b. bicolor* (Günther 1868). Although Broadley (1971) records no Angolan material, the species occurs in the Caprivi area and adjacent western Zambia, and it is usually associated with Kalahari sands. It is therefore likely to occur in southeast Angola

Bark Snake – *Hemirhaggheris nototaenia* (Günther, 1864). This dwarf arboreal snake is recorded from the western Caprivi and Okavango region, and extends eastwards through Zambia to East Africa. Earlier records from southwest Angola (Bocage, 1895) were later referred to *H. viperina* (Broadley and Hughes 2000). It is a secretive snake and may still be found in the miombo woodlands of southeast Angola.

Cunene Racer – *Mopanveldophis zebrinus* (Broadley and Schätti 2000). This enigmatic colubrid snake remains known from only a handful of specimens. The type locality is the Cunene River at Ruacana, western Owamboland, Namibia (17° 25'S, 14° 10′E), and it appears restricted to the Mopaneveld of northern Namibia and can be expected to occur in similar habitat in southern Angola.

Endemism in Angolan Reptiles

Species that are fully endemic or near endemic to a country (i.e. those that have over 90% of known records included in that country), should be highlighted for national conservation monitoring as their protection depends completely on the national authorities. Only six species of snake are endemic to Angola, but no chelonians or crocodilians. Endemic snakes include two species of primitive thread snake, *Namibiana latifrons* and *N. rostrata,* that are the northern members of a small genus (five species) endemic to the western arid region of southern Africa (Adalsteinsson et al. 2009). Three rare snakes are also endemic to the high plateau region, including the psammophines *Psammophis ansorgi* and *Psammophylax ocellatus* (Branch et al. 2019), as well as the rare and iconic *Bitis heraldica*, which may be now of high conservation concern. During the Hamburg Expedition 10 specimens were collected from Bela Vista (Hellmich 1957a, b), but only one other specimen (Mount Moco) has been recorded in last 60 years (FM Gonçalves, photo 2010). Extensive clearing of natural habitat for agriculture, and increased fire risk in these montane grasslands may threaten the species.

Lizards contain the greatest number of endemic and near-endemic Angolan reptiles, particularly among cordylids (two endemic, 50%), lacertids (one near endemic, six endemic, 53.8%), rupicolous geckos (eight endemic, 23.5%), amphisbaenians (one near endemic, three endemic species; 36.4%), and diverse skinks (one near endemic, six endemic, 16.3%). *Agama planiceps schacki* is certainly a full species that is well-defined morphologically, but requires genetic assessment. It would also be endemic to Angola. None of these endemic lizards are currently considered of conservation concern. Only 12.7% of all Angolan reptiles are endemic as opposed to 41.2% of those in South Africa. This number increases to nearly 20.5% when only lizards are considered, but is still much less than the 54.9% of endemic lizards in South Africa (Table 13.3). However, the number of endemic species in the country has increased with the description of new Angolan taxa (e.g. *Kolekanus plumicaudus, Pedioplanis haackei, P. huntleyi* and *Cordylus namakuiyus*), and will increase further as new species in the genera *Nucras, Heliobolus, Pedioplanis, Afroedura*, *Rhoptropus, Pachydactylus, Trachylepis* and *Boaedon* discovered during recent surveys are described.

Reptile Hotspots

The existing global protected area network and conservation priorities are heavily biased towards amphibian, avian and mammal faunas (Roll et al. 2017). Reptiles, which represent a third of terrestrial vertebrate diversity, have been largely ignored, in part, because their diversity and distribution was not globally assessed until 2017. Both the global (Roll et al. 2017) and African (Lewin et al. 2016) assessments demonstrated that whilst the distribution patterns of species richness of all reptiles combined, as well as those of snakes, revealed similar patterns to those of the other three tetrapod classes, the patterns displayed by hotspots of total and endemic lizards and chelonian richness do not overlap significantly with those of other terrestrial tetrapods. A detailed analysis of reptile hotspots within Angola awaits fuller details of species diversity and distributions, both of which are still in their formative period. However, it is already evident that certain regions and their associated habitats and reptile faunas, particularly for endemic or near endemic species, present unique associations, some of which may be confirmed as regionally important reptile hotspots.

Kaokoveld Centre of Endemism

Lizard diversity in southern Africa, particularly in the western arid regions, is the highest in Africa, and the existence of similar habitat structure and diversity in southwest Angola indicates that this African lizard hotspot may also extend into Angola in association with arid and hyper-arid habitats. In association with desert

habitats a number of characteristic Namib reptiles cross the Cunene River and just enter extreme southwest Angola, including: *Gerrhosaurus skoogi, Pachydactylus rangei, P. vanzyli, Chamaeleo namaquensis, Meroles anchietae, M. reticulata, Trachylepis puncutula,* and *Bitis caudalis.* Recent discoveries also suggest the existence of an endemic Angolan Namib reptile fauna, including the existing Angolan Namib endemics *Pedioplanis benguellensis, Typhlacontias rudebecki,* and *T. punctatissimus bogerti,* as well as a number newly described species in the region, e.g. *Kolekanus plumicaudus* (Haacke 2008), *Pedioplanis huntleyi, P. haackei* (Conradie et al. 2012a), and *Cordylus namakuiyus* (Stanley et al. 2016). Moreover, recent surveys in the region have revealed numerous examples of cryptic diversity in some lizard genera, where new species of *Afroedura, Pachydactylus, Nucras, Pedioplanis* endemic to the Angolan Namib region have been identified and await description.

At its northern and southern limits, the Namib Desert transforms into semi-arid, often succulent vegetation that may be loosely termed the 'Pro-Namib' region. In the south this forms the Succulent Karoo, a botanical hotspot of regional endemism and floral beauty (CEPF 2003). The Succulent Karoo has diverse and specialised reptile endemics (Branch 1994; Bauer and Branch 2003), and the region has been highlighted as a regional reptile hotspot, including numerous species of conservation concern (Branch 2014). As with the Succulent Karoo, the recognition of a unique reptile fauna in southwest Angola supports a corresponding northern 'Pro-Namib', in some ways analogous to the Succulent Karoo, and that has been identified as a distinctive phytogeographical region – the Kaokoveld Centre of Endemism, which extends as a narrow strip north of Namibe to Lucira and is characterised by a number of localised succulents (see Craven 2009 for fuller discussion).

Angolan Escarpment

Inland from the coastal arid herpetofauna is the Bié section (sensu Clark et al. 2011) of the Angolan Escarpment and adjacent high plateau. The southern African Great Escarpment (GE) forms a semi-continuous U-shaped mountain chain that runs for 5000 km from western Angola through Namibia and South Africa to the Zimbabwe-Mozambique border. Clark et al. (2011) noted that the GE hosts more than half of southern Africa's centres of plant endemism and is a repository of palaeo- and neo-endemics. It also has a rich endemic fauna and its fragmented sections serve as refugia and as episodic corridors for biological continuity. However, many sections of the Great Escarpment have been poorly studied, particularly in Angola where the Bié Escarpment summit and adjacent highlands is one of the most isolated sections of the Afromontane archipelago in Africa. With ca. 20 endemic bird species it forms the core of the Western Angola Endemic Bird Area. Other faunal groups have not been as extensively studied, but endemic reptiles associated with the Serra da Chela grasslands and wetlands include two endemic snakes (*Psammophylax ocellatus* and *Psammophis ansorgi*), the chameleon *Chamaeleo anchietae*, the serpentine skink *Eumecia anchietae,* the skink *Trachylepis bayoni huilensis,* the gecko *Rhoptropus*

montanus, and the lacertid *Ichnotropis bivittata pallida*. A new reed frog, *Hyperolius chelaensis* was also recently discovered (Conradie et al. 2012b). In the adjacent highlands, including Mount Moco, at least two new species of the *Afroedura bogerti* complex have also been signalled (Branch et al. 2017).

Northern Congo Forests

The Congo Basin has numerous forest specialists, particularly snakes. Many of these are found in forests in Cabinda and along the northern border of Angola. These forests have only been incidentally surveyed, particularly the numerous important snake records listed in a series of papers based on the Museu do Dundo collections (Laurent 1950, 1954, 1964; Tys van den Audenaerde 1967). Among these collections are the only known Angolan records *Gonionotophis brussauxi Letheobia praeocularis*, *Xenocalamus bicolour machadoi*, *Hypoptophis wilsoni katangae, Grayia tholloni, Philothamnus nitidus, Bothrophthalmus lineatus, Boaedon olivaceus, Lycodonomorphus subtaeniatus, Prosymna ambigua brevis* and *Causus lichtensteini.* In addition, other Congo Basin reptiles only recorded from Dundo include the terrapin *Pelusios gabonensis,* the worm lizard *Monopeltis vanderysti,* and the skinks *Lepidothyris hinkeli joei* (as *Mochlus fernandi*, Laurent 1964) and *Feylinia grandisquamis* (as *F. elegans*, Laurent 1964). Parker (1936) presented the first survey of the central scarp forests of the Angolan Escarpment and recorded numerous Congo Basin snakes. For many species these remain their southern records, and they probably occur as disjunct, relictual populations. Some were subsequently recorded further north in forest habitats from Dundo or during the Hamburg Angola Expedition at Piri Dembos (see above). They include: *Toxicodryas blandingii, T. pulverulenta, Atractaspis reticulata heterochilus, Bitis nasicornis,* and *Pseudohaje goldii*. Others remain known only from Parkers' records: i.e. the skinks *Panaspis breviceps, Leptosiaophis dewittei,* and *Trachylepis affinis*; and the snakes *Lycophidion ornatum, Chamaelycus parkeri* (as *Oophilositum parkeri*) and *Hormonotus modestus.* The Congo Basin snake *Rhamnophis aethiopissa* is recorded in Angola only from Piri Dembos (Hellmich 1957a, b). The taxonomic status of all these isolates requires genetic confirmation as some may have undergone vicariant speciation. A phylogenetic assessment may give insight towards dating the separation of these forest isolates and understanding their biogeographic importance.

The forests of Cabinda form part of the Congo Basin and a number of reptiles occur there which have not been recorded in Angola south of the Congo River. Currently Cabinda remains the southern limit of the African Dwarf Crocodile (*Osteolaemus tetraspis*) and the Soft-shelled Terrapin (*Cycloderma*). The presence of two other reptiles recorded from Cabinda by Peters (1876, 1877), e.g. Owen's Horned Chameleon (*Triceros oweni*) and the skink *Euprepes perrotetii* (= *Trachylepis perrotetii*) are problematic. The latter is widespread in West Africa but not known even from Gabon. Peters (1877) recorded *Euprepes perrotetii* from

Chinchoxo, Cabinda, and in a supplement to the same article noted a specimen from Pungo Andongo, upon which he considered it to form part of the fauna of Angola. However, no subsequent records of this distinctive species have been recorded from Angola. Although it is possible that these specimens were confused with large fire skinks (*Lepidothrys* sp.), Wagner et al. (2009) reviewed the genus and noted no misidentifications among the material they examined. It is more likely that Peters' specimens were simply accompanied by incorrect locality data. Forest chameleons are difficult to locate unless specifically targeted during faunal surveys, and Owen's Horned Chameleon is known from Gabon. No recent collections of both these species confirm their presence in Cabinda. Research underlying the proposed Mayombe Transfrontier Reserve (MTR) to protect forests in Cabinda and adjacent countries has concentrated on the large mammals, particular the Great Apes, and no detailed herpetological surveys have been undertaken. Recent surveys of the forest herpetofauna of the Serra do Pingano Ecosystem, Uíge Province (Ernst 2015) concentrated on amphibians but did record an number of interesting reptiles, particularly the arboreal lacertid *Holaspis guentheri* and water snake *Grayia ornata*, the former being the second record for the country (Laurent 1964) and the latter one of the few records for the country (Branch 2018). The northern tropical forests of Angola are threatened by massive timber extraction, and desperately need to be scientifically surveyed before their associated herpetofauna is lost.

Future Directions for Reptile Research in Angola

The Continued Need for Further Field Surveys and Taxonomic Studies

The conservation status and threats for African reptiles were reviewed by Tolley et al. (2016), who noted the large discrepancy between taxonomic sampling and documentation between many countries. They presented a scatter-plot of measured reptile species richness relative to log-transformed country area from African countries. This illustrated the great contrast between known reptile diversity in well surveyed countries such as South Africa, Kenya and Tanzania, with that of the majority of Africa. Angola is the seventh largest African country and has both habitat and topographic diversity. Together these features should generate rich biological diversity, but this is not reflected in our current knowledge of Angolan reptile diversity. Branch (2016) presented species accumulation curves documenting the growth in taxonomic knowledge of Angolan and southern African reptiles, noting that there has been no decline in the rate of new species discovery in the subcontinent during the last 150 years. This is in marked contrast to the relative stagnation of taxonomic discovery in Angola since the early part of the twentieth century (see Fig. 13.1 and Table 13.1 for comparison). As noted earlier, despite Angola and South Africa being of comparable size and habitat diversity there is a difference of over 150 species of

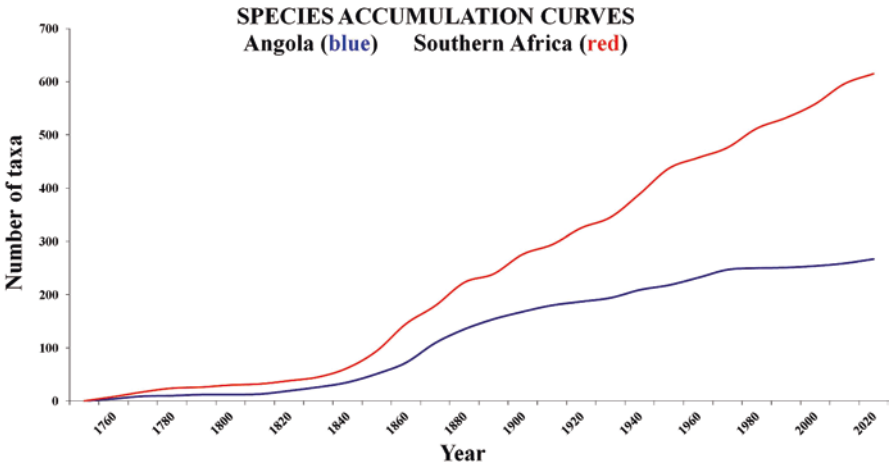

Fig. 13.1 Species accumulation curves for reptile discoveries in Angola (blue) and southern Africa (red) showing the relative stagnation of Angolan reptile species descriptions during the twentieth century. By the end of the nineteenth century 67.4% of Angolan reptiles had already been described, in contrast to less than half (47.8%) of those in southern Africa

lizards between the two countries (Angola 132, South Africa 286). This contrast is even higher in terms of endemicity, where only 27 (20.5%) of 132 Angolan lizards are endemic in contrast to 157 (54.9%) of 286 South African lizards. It would appear that perhaps as many as 75+ new lizard species await discovery in Angola, and that many of these will be endemic. Branch (2014) noted that endemicity in South African lizards was particularly evident in rupicolous forms (many geckos, cordylids and skinks) associated with rocky outcrops. Rock exposures may form an archipelago of 'sky islands' on which isolation inhibits gene flow and thus leads to speciation. It is the lizard families containing large numbers of rupicolous species, i.e. Gekkonidae, Cordylidae and Scincidae, already show the greatest levels of endemicity among Angolan reptiles, and in which recent surveys have already identified numerous cryptic taxa (Stanley et al. 2016; Branch et al. 2017).

Field Surveys of Potential Biodiversity 'Hotspots'

Many African protected areas underperform in their stated conservation goals (Lindsey et al. 2014; Bowker et al. 2017). It is now generally accepted that modern national and internationally co-ordinated networks of protected area should be designed to cover important biodiversity hotspots and also protect habitats essential for the maintenance of ecosystem services such as water flow and quality, nutrient transfer, etc. (NPAES 2010). Such a revised Angolan network was proposed many

years ago (Huntley 1974), and initial biodiversity surveys to gain insight into biodiversity in potential sites were undertaken (Huntley 2009; Huntley and Francisco 2015). Recent studies have shown that protected reserves designed to protect mammals, birds and amphibians are effective in protecting snakes, but fare badly in protecting African lizard diversity (Lewin et al. 2016; Roll et al. 2017). Future systematic biodiversity surveys should be directed to unique habitats and landforms in undersampled regions. Some of the interesting species recorded on recent field surveys are illustrated in Fig. 13.2.

Biogeography of Angolan Reptiles

Huntley (2019) in the introduction to this volume has presented a biogeographic outline, summarising various aspects of climate, geology and vegetation, etc., that characterise Angola. He noted the complexity of the Angolan landscape, where seven of the nine African biomes are represented in Angola as well as the second largest representation of ecoregion diversity in Africa. Monard (1937) and Hellmich (1957a, b) made preliminary attempts to assess biogeographic patterns among Angolan reptiles. However, they did little more than look for coarse habitat associations within the Ethiopian region. These attempts were constrained by lack of knowledge of the true reptile diversity in the region and, more importantly, by the ignorance of reptile distributions as large tracts of the country were still unexplored. Moreover, recent studies indicate that reptile distributions, particularly those of lizards, are more influenced by substrate specificity and isolation than by vegetation type (Bauer and Lamb 2005; Roll et al. 2017). Recent biogeographic studies lay greater emphasis on evolutionary relationships within the group studied, and explore correlations between genetic divergence (as a proxy for time) and known dates of major events in landscape evolution. This approach searches for historical barriers to, or corridors for migration and gene flow. These may be generated, for example, by climatic changes associated with Ice Age cycles and the resultant contraction and expansion of forest and savanna, changes in historic coastlines and/or island connectivity, as well as the development of an ‘arid’ corridor at an Ice Age maxima, etc. The biological consequences of nascent rifting on river capture and other hydrological consequences on palaeolakes and wetlands have also been explored (Cotterill and De Wit 2011). However, the application of such approaches requires more detailed knowledge of reptile distribution within Angola, as well as the availability of genetic material and adequate taxon sampling within a chosen group. These will allow historic climatic and landform events to be meaningful correlated with speciation and radiation within groups for testing phylogeographic hypotheses. Such studies depend on meaningful progress in the topics discussed earlier in this section. Advances in all these areas are required to fully understand and conserve the diversity and evolution of Angolan reptiles.

Fig. 13.2 Angolan reptiles. Top to bottom, left to right. Bogert's Flat Gecko (*Afroedura* cf. *bogerti*), Omahua Lodge, Namibe; Angolan Namib Day Gecko (*Rhoptropus taeniostictus*), Chapéu Armado, Namibe; Ansorge's Leaf-toed Gecko (*Afrogecko ansorgii*), Meve, Benguela; Anchieta's Chameleon (*Chamaeleo anchietae*), Humpata, Huíla; Kaokoveld Girdled Lizard (*Cordylus namakuiyus*), Rio Makonga, Namibe; Bayon's Legless Skink (*Sepsina bayoni*), Quiçama National Park, Luanda; Water Cobra (*Naja annulata*), Lagoa Carumbo, Lunde Norte; Angolan Skaapstekker (*Psammophylax ocellatus*), Humpata, Huíla

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Appendices

Appendix 1

Checklist of Angolan Chelonians and Crocodilians. C: Cabinda; Status: CITES (I, II = Appendix 1 or 2), IUCN Conservation Status[1]. Species listed under ORDER|**Family**

Common Name	Scientific Name	C	Bocage (1895)	Status
CHELONIA | **Chelonidae**				
Loggerhead Sea Turtle	*Caretta caretta* (Linnaeus, 1758)		*Thalassochelys caretta*	I, VU
Green Sea Turtle	*Chelonia mydas* (Linnaeus, 1758)	Y	*Chelonia mydas*	I, EN
Olive Ridley Sea Turtle	*Lepidochelys olivacea* (Eschscholtz, 1829)	Y		I, VU
Hawksbill Sea Turtle	*Eretmochelys imbricata* (Linnaeus, 1766)			I, CR
CHELONIA | **Dermochelyidae**				
Leatherback Sea Turtle	*Dermochelys coriacea* (Vandelli, 1761)	Y		I, VU
CHELONIA | **Testudinidae**				
Bell's Hinge-back Tortoise	*Kinixys belliana* (Gray, 1831)		*Cinixys belliana*	II
Forest Hinge-back Tortoise	*Kinixys erosa* (Schweigger, 1812)	Y	*Cinixys erosa*	II, EN[a]
Leopard Tortoise	*Stigmochelys pardalis* (Bell, 1828)		*Testudo pardalis*	II
CHELONIA | **Pelomedusidae**				
Southern Marsh Terrapin	*Pelomedusa subrufa* (Bonnaterre, 1789)		*Pelomedusa galeata*	
Okavango Hinged Terrapin	*Pelusios bechuanicus* (FitzSimons, 1932)			
Gabon Hinged Terrapin	*Pelusios gabonensis* (Duméril, 1856)			

(continued)

Common Name	Scientific Name	C	Bocage (1895)	Status
Dwarf Hinged Terrapin	*Pelusios nanus* (Laurent, 1956)			
Variable Hinged Terrapin	*Pelusios rhodesianus* (Hewitt, 1927)		*Sternothaerus sinuatus*	
Western Hinged Terrapin	*Pelusios castaneus* (Schweigger, 1812)	Y	*Sternothaerus Derbianus*	
CHELONIA | **Trionycidae**				
Nile Soft-shelled Terrapin	*Trionyx triunguis* (Forskål, 1775)	Y	*Trionyx triunguis*	II, VU[a]
Aubrey's Flap-shelled Terrapin	*Cycloderma aubryi* (Dumeri,, 1856)	Y	*Cycloderma Aubryi*	II, VU[a]
CROCODYLIA | **Crocodylidae**				
Nile Crocodile	*Crocodylus niloticus* (Laurenti, 1768)		*Crocodilus vulgaris*	II
Central African slender-snouted Crocodile	*Mecistops leptorhynchus* (Shirley et al. 2018)		*Crocodylus cataphractus*	I, DD
African Dwarf Crocodile	*Osteolaemus tetraspis* (Cope, 1861)	Y	*Ostelolaemus tetraspis*	I, EN

[a]Turtle Working Group 2017, Draft Red List
[b]IUCN Conservation Status categories. *CR* Critically Endangered, *EN* Endangered, *VU* Vulnerable, *DD* Data Deficient

Appendix 2

Checklist of Angolan Lizards. C: Cabinda; Obs: Observations (E:endemic; NE: near-endemic). Species listed under ORDER|**Family**|Subfamily

Common name	Scientific name	C	Bocage (1895)	Obs
SAURIA | **Agamidae**				
Angolan Tree Agama	*Acanthocercus cyanocephalus* (Falk, 1925)		*Stellio angolensis* Bocage 1866 is a nomen nudum *Stellio atricollis*	
Ground Agama	*Agama aculeata* (Merrem, 1820)		*Agama armata*	
Anchieta's Agama	*Agama anchietae* (Bocage, 1896)			
Congo Agama	*Agama congica* (Peters, 1877)	Y	*A. colonorum*	
Mucoso Agama	*Agama mucosoensis* (Hellmich, 1957)			E
Namib Rock Agama	*Agama planiceps planiceps* (Peters, 1862)		*Agama planiceps*	
Schack's Rock Agama	*Agama p. schacki* (Mertens, 1938)			E

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Sauria | **Amphisbaenidae**				
Angola Blunt-tailed Worm Lizard	*Dalophia angolensis* (Gans, 1976)			NE
Ellenberger's Blunt-tailed Worm Lizard	*Dalophia ellenbergeri* (Angel, 1920)			
Zambezi Blunt-tailed Worm Lizard	*Dalophia pistillum* (Boettger, 1895)			
Welwitch's Blunt-tailed Worm Lizard	*Dalophia welwitschii* (Gray, 1865)		*Monopeltis Welwitschii*	E
Anchieta's Spade-snouted Worm Lizard	*Monopeltis anchietae* (Bocage, 1873)		*Monopeltis anchietae*	
Infuscate Spade-snouted Worm Lizard	*Monopeltis infuscata* (Broadley, 1997)		*Monopeltis capensis*	
Luanda Spade-snouted Worm Lizard	*Monopeltis luandae* (Gans, 1976)			E
Confusing Spade-snouted Worm Lizard	*Monopeltis perplexus* (Gans, 1976)			E
Vanderyst's Spade-snouted Worm Lizard	*Monopeltis vanderysti* (De Witte, 1922)			
Balck Round-headed Worm Lizard	*Zygaspis nigra* (Broadley and Gans, 1969)			
Kalahari Round-headed Worm Lizard	*Zygaspis quadrifrons* (Peters, 1862)			
Sauria | **Chamaeleonidae**				
Angolan Chameleon	*Chamaeleo anchietae* (Bocage, 1872)		*Chamaeleo anchietae*	
Flap-necked Chameleon	*Chamaeleo dilepis* (Leach, 1819)	Y	*Chamaeleon dilepis & C. quilensis*	
Etienne's Chameleon	*Chamaeleo gracilis etiennei* (Schmidt, 1919)	Y	*Chamaeleon gracilis*	
Namaqua Chameleon	*Chamaeleo namaquensis* (Smith, 1831)		*Chamaeleon namaquensis*	
Owen's Three-horned Chameleon	*Trioceros oweni* (Gray, 1831)			
Sauria | **Cordylidae**				
Northern Grass Lizard	*Chamaesaura miopropus* (Boulenger, 1895)		*Chamaesaura macrolepis*	
Angola Grass Lizard	*Chamaesaura anguina oligopholis* (Laurent, 1964)			E
Angola Girdled Lizard	*Cordylus angolensis* (Bocage, 1895)		*Zonurus cordylus*	E
Machado's Girdled Lizard	*Cordylus machadoi* (Laurent, 1964)			
Kaokoveld Girdled Lizard	*Cordylus namakuiyus* (Stanley et al, 2016)			E

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
SAURIA | **Gekkonidae**				
Bogert's Flat Gecko	*Afroedura bogerti* (Loveridge, 1944)			
Ansorge's Leaf-toed Gecko	*Afrogecko ansorgii* (Boulenger, 1907)			E
Button-scaled Gecko	*Chondrodactylus fitzsimonsi* (Loveridge, 1947)			
Pulitzer's Gecko	*Chondrodactylus pulitzerae* (Schmidt, 1933)		*Pachydactylus Bibronii* (part)	
Fisher's Gecko	*Chondrodactylus laevigatus* (Fischer, 1888)		*Pachydactylus Bibronii* (part)	
Pulitzer's Gecko	*Chondrodactylus pulitzerae* (Smith, 1933)			
Bayão's House Gecko	*Hemidactylus bayonii* (Bocage, 1893)		*Hemidactylus bayonii*	E
Benguela House Gecko	*Hemidactylus benguellensis* (Bocage, 1893)		*Hemidactylus benguellensis*	E
Western House Gecko	*Hemidactylus brooki angulatus* (Hallowell 1852)			
Long-headed House Gecko	*Hemidactylus longicephalus* (Bocage, 1873)		*Hemidactylus bocagii*	
Tropical House Gecko	*Hemidactylus mabouia* (Moreau De Jonnès, 1818)	Y	*Hemidactylus mabouia & H. benguellensis*	
Forest House Gecko	*Hemidactylus murecius* (Peters, 1870)		*Hemidactylus murecius*	
Plume-tailed Geco	*Kolekanos plumicaudus* (Haacke, 2008)			E
Angola Dwarf Day Gecko	*Lygodactylus angolensis* (Bocage, 1896)			
Bradfield's Dwarf Day Gecko	*Lygodactylus bradfieldi* (Hewitt, 1932)			
Cape Dwarf Day Gecko	*Lygodactylus capensis* (Smith, 1849)		*Lygodacylus capensis*	
Hewitt's Punctate Gecko	*Pachydactylus amoenoides* (Hewitt, 1935)		*Pachydactylus ocellatus*	
Angola Thick-toed Gecko	*Pachydactylus angolensis* (Loveridge, 1944)			E
Caricul Thick-toed Gecko	*Pachydactylus caraculicus* (FitzSimons, 1959)			
Kaokoveld Thick-toed Gecko	*Pachydactylus* cf. *oreophilus* (McLachlan and Spence, 1976)			

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Punctate Thick-toed Gecko	*Pachydactylus punctatus* (Peters, 1854)			
Web-footed Gecko	*Pachydactylus rangei* (Andersson, 1908)			
Scherz's Thick-toed Gecko	*Pachydactylus scherzi* (Mertens, 1954)			
Rough-scaled Thick-toed Gecko	*Pachydactylus* cf. *rugosus* (Smith, 1849)			NR
Large-scaled Thick-toed Gecko	*Pachydactylus scutatus* (Hewitt, 1927)			
Kalahari Ground Gecko	*Pachydactylus wahlbergii* (Peters, 1869)			
Van Zyl's Web-footed Gecko	*Pachydactylus vanzyli* (Steyn and Haacke, 1966)			
Common Namib Day Gecko	*Rhoptropus afer* (Peters, 1869)			
Barnard's Namib Day Gecko	*Rhoptropus barnardi* (Hewitt, 1926)		*Rhoptropus afer* ?	
Benguella Namib Day Gecko	*Rhoptropus benguellensis* (Mertens 1938)			E
Two-pored Namib Day Gecko	*Rhoptropus biporosus* (FitzSimons, 1957)			
Boulton's Namib Day Gecko	*Rhoptropus boultoni* (Schmidt, 1933)			
Montane Namib Day Gecko	*Rhoptropus montanus* (Laurent, 1964)			E
Angolan Namib Day Gecko	*Rhoptropus taeniostictus* (Laurent, 1964)			E
SAURIA | **Gerrhosauridae**				
Dwarf Plated Lizard	*Cordylosaurus subtessellatus* (Smith, 1844)		*Cordylosaurus trivittatus*	
Kalahari Plated Lizard	*Gerrhosaurus auritus* (Boettger, 1887)			
Laurent's Plated Lizard	*Gerrhosaurus bulsi* (Laurent, 1954)			
Keeled Plated Lizard	*Gerrhosaurus multilineatus* (Bocage, 1866)			
Black-lined Plated Lizard	*Gerrhosaurus nigrolineatus* (Hallowell, 1857)	Y	*Gerrhosaurus nigrolineatus*	
Desert Plated Lizard	*Gerrhosaurus skoogi* (Andersson, 1916)			
Western Giant Plated Lizard	*Matobosaurus maltzahni* (De Grys, 1938)		*Gerrhosaurus validus*	
Ellenberger's Snake Lizard	*Tetradactylus ellenbergeri* (Angel, 1922)		*Caitia africana* Gray	

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Sauria | **Lacertidae**				
Bushveld Lizard	*Heliobolus lugubris* (Smith, 1838)		*Eremias lugubris*	
Northern Blue-tailed Tree Lizard	*Holaspis guentheri* (Gray, 1863)			
Western Rough-scaled Lizard	*Ichnotropis b. bivittata* (Bocage, 1866)		*Ichnotropis capensis*	
Pale Rough-scaled Lizard	*Ichnotropis b. pallida* (Laurent, 1964)			E
Cape Rough-scaled Lizard	*Ichnotropis c. capensis* (Smith, 1838)			
Overlaete's Rough-scaled Lizard	*Ichnotropis c. overlaeti* (Witte and Laurent 1942)			
Small-scaled Rough-scaled Lizard	*Ichnotropis microlepidota* (Marx, 1956)			E
Shovel-snouted Lizard	*Meroles anchietae* (Bocage, 1867)		*Pachyrhynchus Anchietae*	
Reticulate Desert Lizard	*Meroles reticulatus* (Bocage, 1867)		*Scaptira reticulata*	
Rough-scaled Desert Lizard	*Meroles squamulosus* (Peters, 1854)			
Laurent's Sandveld Lizard	*Nucras scalaris* (Laurent, 1964)			E
Western Sandveld Lizard	*Nucras* aff. *tesselata* (Smith, 1838)			NE
Benguella Sand Lizard	*Pedioplanis benguellensis* (Bocage, 1867)		*Eremias namaquensis*	E
Haacke's Sand Lizard	*Pedioplanis haackei* Conradie et al. 2012			E
Huntley's Sand Lizard	*Pedioplanis huntleyi* (Conradie et al. 2012)			E
Sauria | **Scincidae** | Acontinae				
Japp's Burrowing Skink	*Acontias jappi* (Broadley, 1968)			
Kalahari Burrowing Skink	*Acontias kgalagadi kgalagadi* (Lamb et al., 2010)			
Western Burrowing Skink	*Acontias occidentalis* (FitzSimons, 1941)			
Sauria | **Scincidae** | Eugongylinae				
Shorted-headed Snake-eyed Skink	*Panaspis breviceps* (Peters, 1873)			
Cabinda Snake-eyed Skink	*Panaspis cabindae* (Bocage, 1866)	Y	*Ablepharus cabindae*	
Speckle-lipped Snake-eyed Skink	*Panaspis maculicollis* (Jacobsen and Broadley, 2000)			

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Angolan Snake-eyed Skink	*Panaspis* aff. *wahlbergii* complex		*Ablepharus wahlbergii*	
De Witte's Leaf-litter Skink	*Leptosiaphos dewittei* (Loveridge, 1934)			
Sauria | **Scincidae** | Lygosominae				
Hinkel's Red-sided Skink	*Lepidothyris hinkeli* (Wagner et al., 2009)			
Sundevall's Writhing Skink	*Mochlus sundevalli* (Smith, 1849)		*Lygosoma Sundevallii*	
Sauria | **Scincidae** | Mabuyinae				
Anchieta's Snake Skink	*Eumecia anchietae anchietae* (Bocage, 1870)		*Lygosoma Anchietae*	
Lunda Western Snake Skink	*Eumecia a. major* (Laurent, 1964)			E
Iven's Water Skink	*Lubuya ivensii* (Bocage, 1879)		*Lygosoma Ivensii*	
Wedge Snouted Skink	*Trachylepis acutilabris* (Peters, 1862)	Y	*Mabuia acutilabris*	
Senegal Skink	*Trachylepis affinis* (Gray, 1838)	Y	*Mabuia Raddonii* (not in Angola)	
Monard's Skink	*Trachylepis monardi* (Marques et al. 2018)			E
Bayão's Skink	*Trachylepis b. bayoni* (Bocage, 1872)		*Mabuia Bayonii*	
Huila Skink	*Trachylepis b. huilensis* (Laurent, 1964)			E
Ovambo Stree Skink	*Trachylepis binotata* (Bocage, 1867)		*Mabuia bionotata*	
Bocage's Skink	*Trachylepis bocagii* (Boulenger, 1887)		*Mabuia Petersi*	
Chimba Skink	*Trachylepis chimbana* (Boulenger, 1887)		*Mabuia chimbana*	
Damara Skink	*Trachylepis damarana* (Peters, 1870)		*Mabuia varia* (part)	
Hoesch's Skink	*Trachylepis hoeschi* (Mertens, 1954)			
Bronze Rock Skink	*Trachylepis* cf. *lacertiformis* (Peters, 1854)			
Angolan Blue-tailed Skink	*Trachylepis laevis* (Boulenger, 1907)			
Speckled-lipped Skink	*Trachylepis maculilabris* (Gray, 1845)	Y	*Mabuia maculilabris*	
Grass Skink	*Trachylepis* cf. *megalura* (Peters, 1878)			
Western Three Striped Skink	*Trachylepis occidentalis* (Peters, 1867)		*Mabuia occidentalis*	

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Speckled Skink	*Trachylepis punctulata* (Bocage, 1872)		*Mabuia punctulata*	
Kalahari Tree Skink	*Trachylepis spilogaster* (Peters, 1882)			
Striped Skink	*Trachylepis striata* (Peters, 1844)		*Mabuia striata*	
Ansorge's Rock Skink	*Trachylepis sulcata ansorgii* (Boulenger, 1907)		*Mabuia sulcata*	
Angolan Variable Skink	*Trachylepis* cf. *albopunctata* (Bocage, 1867)		*Mabuia varia* (part)	
Wahlberg's Skink	*Trachylepis wahlbergi* (Peters, 1869)			
SAURIA | **Scincidae** | Scincinae				
Curror's giant burrowing Skink	*Feylinia currori* (Gray, 1845)	Y	*Feylinia Currori*	
Large-scaled burrowing Skink	*Feylinia grandisquamis* (Müller, 1910)			
Western Limbless Skink	*Melanoseps occidentalis* (Peters, 1877)			
Angolan burrowing Skink	*Sepsina angolensis* (Bocage, 1866)		*Sepsina angolensis*	
Bayão's Burrowing Skink	*Sepsina bayoni* (Bocage, 1866)	Y	*Sepsina Bayonii*	NE
Cope's Burrowing Skink	*Sepsina copei* (Bocage, 1873)		*Sepsina Copei*	E
Johnson's Western Burrowing Skink	*Typhlacontias johnsonii* (Andersson, 1916)			
Speckled Western Burrowing Skink	*Typhlacontias p. punctatissimus* (Bocage, 1873)		*Typhlacontias punctatissimus*	
Bogert's Western Burrowing Skink	*Typhlacontias p. bogerti* (Laurent, 1964)			E
Rohan's Western Burrowing Skink	*Typhlacontias rohani* (Angel, 1923)			
Rudebeck's Western Burrowing Skink	*Typhlacontias rudebecki* (Haacke, 1997)			E
SAURIA | **Varanidae**				
Savanna Monitor	*Varanus albigularis angolensis* (Schmidt, 1933)		*Varanus albigularis*	
Water Monitor	*Varanus niloticus* (Linneaus, 1766)	Y	*Varanus niloticus*	

Appendix 3

Checklist of Angolan Snakes. C: Cabinda; Obs: Observations (E:endemic; NE: near-endemic; NR: new record for Angola; RC: requires confirmation). Species listed under Order | **Family** | Subfamily

Common name	Scientific name	C	Bocage (1895)	Obs
Scolecophidia | **Leptotyphlopidae**				
Shaba Thread Snake	*Leptotyphlops kafubi* (Boulenger, 1919)			
Peter's Thread Snake	*Leptotyphlops scutifrons* (Peters, 1854)		*Stenosoma scutifrons*	
Damara Thread Snake	*Namibiana labialis* (Sternfeld, 1908)			
Benguela Thread Snake	*Namibiana latifrons* (Sternfeld, 1908)			E
Angolan Beaked Thread Snake	*Namibiana rostrata* (Bocage, 1886)		*Stenosoma rostratum*	E
Scolecophidia | **Typhlopidae**				
Angolan Blind Snake	*Afrotyphlops angolensis* (Bocage, 1866)		*Typhlops punctatus*	
Angolan Giant Blind Snake	*Afrotyphlops anomalus* (Bocage, 1873)		*Typhlops anomalus & T. anchietae*	
Blotched Blian Snake	*Afrotyphlops congestus* (Duméril and Bibron, 1844)	Y		
Lined Blind Snake	*Afrotyphlops lineolatus* (Jan, 1864)	Y	*Typhlops punctatus* var. *lineolatus & Typhlops boulengeri*	
Schmidt's Blind Snake	*Afrotyphlops schmidti* (Laurent, 1956)			
Schlegel's Blind Snake	*Afrotyphlops schlegelii* (Bianconi, 1847)		*Typhlops petersii, Typhlops humbo & Typhlops hottentotus*	
Giant Blind Snake	*Afrotyphlops mucruso* (Peters, 1854)		*Typhlops mucruso*	
Leopoldville Beaked Blind Snake	*Letheobia praeocularis* (Stejneger, 1894)			
Henophidia | **Pythonidae**				
Namib Dwarf Python	*Python anchietae* (Bocage, 1887)		*Python anchietae*	
Southern African Python	*Python natalensis* (Smith, 1840)		*Python natalensis*	
Northern African Python	*Python sebae* (Gmelin, 1789)	Y		

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Henophidia | **Colubridae** | Colubrinae				
White-lipped Snake	*Crotaphopeltis hotamboeia* (Laurenti, 1768)	Y	*Crotaphopeltis rufescens*	
Barotse Water Snake	*Crotaphopeltis barotseensis* (Broadley, 1968)			NR
Confusing Egg-eater	*Dasylepis confusa* (Trape and Mané, 2006)			NR
Palm Egg-Eater	*Dasypeltis palmarum* (Leach, 1818)	Y	*Dasypeltis scabra* var. *palmarum*	
Rhombic Edd-Eater	*Dasypeltis scabra* (Linnaeus, 1758)		*Dasypeltis scabra*	
Shreve's Tree Snake	*Dipsadoboa shrevei* (Loveridge, 1932)			
Punctate Boomslang	*Dispholidus typus punctatus* (Laurent, 1955)		*Bucephalus capensis* (part)	
Green Boomslang	*Dispholidys t. viridis* (Smith, 1838)		*Bucephalus capensis* (part)	
Emerald Snake	*Hapsidophrys smaragdinus* (Schlegel, 1837)	Y	*Hapsidophrys smaragdina*	
Angolan Green Snake	*Philothamnus angolensis* (Bocage, 1882)	Y	*Philothamnus irregularis*	
Thirteen-scaled Green Snake	*Philothamnus carinatus* (Andersson, 1901)			
Striped Green Snake	*Philothamnus dorsalis* (Bocage, 1866)		*Philothamnus dorsalis*	
Emerald Green Snake	*Philothamnus heterodermus* (Hallowell, 1857)		*Philothamnus heterodermus*	
Slender Green Snake	*Philothamnus heterolepidotus* (Günther, 1863)		*Philothamnus heterolepidotus*	
Southeastern Green Snake	*Philothamnus hoplogaster* (Günther, 1863)			
Loveridge's Green Snake	*Philothamnus nitidus loveridgei* (Laurent, 1960)			
Ornate Green Snake	*Philothamnus ornatus* (Bocage, 1872)		*Philothamnus ornatus*	
Spotted Bush Snake	*Philothamnus semivariegatus* (Smith, 1840)		*Philothamnus semivariegatus*	
Large-eyed Green Treesnake	*Rhamnophis aethiopissa* (Günther, 1862)			
Hook-nosed Snake	*Scaphiophis albopunctatus* (Peters, 1870)		*Scaphiophis albopunctatus*	
Damara Tiger Snake	*Telescopus finkeldeyi* (Haacke, 2013)			
Western Tiger Snake	*Telescopus polystictus* (Mertens, 1954)		*Crotaphlopeltis semiannulatus*	
Oates' Vine Snake	*Thelotornis capensis oatesi* (Günther, 1881)		*Thelotornis kirtlandii*	

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Forest Vine Snake	*Thelotornis kirtlandii* (Hallowell, 1844)		*Thelotornis kirtlandii*	
Yellow-throated Treesnake	*Thrasops flavigularis* (Hallowell, 1852)	Y	*Thrasops flavigularis*	
Jackson's Treesnake	*Thrasops jacksoni* (Günther, 1895)			
Blanding's Treesnake	*Toxicodryas blandingii* (Hallowell, 1844)	Y	*Dipsas Blandingii*	
Powdered Treesnake	*Toxicodryas pulverulenta* (Fischer, 1856)	Y	*Dipsas pulverulenta*	
Henophidia | **Colubridae** | Grayinae				
Ornate Water Snake	*Grayia ornata* (Bocage, 1866)	Y	*Grayia ornata*	
Smith's Water Snake	*Grayia smithii* (Leach, 1818)		*Grayia triangularis*	
Thollon's Water Snake	*Grayia tholloni* (Mocquard, 1897)			
Henophidia | **Natricidae**				
Bangweulu Swamp Snake	*Limnophis bangweolicus* (Mertens, 1936)			
Striped Swamp Snake	*Limnophis bicolor* (Günther, 1865)		*Helocops bicolour*	
Broadley's Marsh Snake	*Natriciteres bipostocularis* (Broadley, 1962)			
Olive Marsh Snake	*Natriciteres olivacea* (Peters, 1854)	Y	*Mizodon olivaceus*	
Henophidia | **Lamprophiidae** | Atractaspidinae				
Common Purple-glossed Snake	*Amblyodipsas polylepis* (Bocage, 1873)		*Calamelaps polylepis*	
Kalahari Purple-glossed Snake	*Amblyodipsas ventrimaculata* (Roux, 1907)			NR
Cape Centipede Eater	*Aparallactus capensis* (Smith, 1849)		*Uriechis capensis*	
Birbon's Burrowing Asp	*Atractaspis bibronii* (Smith, 1849)		*Atractaspis Bibronii*	
Congo Burrowing Asp	*Atractaspis congica* (Peters, 1877)	Y	*Atractaspis congica*	
Reticulate Burrowing Asp	*Atractaspis reticulata heterochilus* (Boulenger, 1901)			RC
Wilson's burrowing snake	*Hypoptophis wilsoni* (Boulenger, 1908)			
Collared Snake-Eater	*Polemon collaris* (Peters, 1881)		*Microsoma collare*	
Bi-coloured Quill-snouted Snake	*Xenocalamus bicolor machadoi* (Laurent, 1954)			
Elongate Quill-snouted Snake	*Xenocalamus mechowii mechowii* (Peters, 1881)			
Inorante Elongate Quill-snouted Snake	*Xenocalamus m. inorantus* (de Witte and Laurent, 1947)			

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Henophidia | **Lamprophiidae** | Lamprophiinae				
Angolan House Snake	*Boaedon angolensis* (Bocage, 1895)		*Boodon lineatus* var. *angolensis,* Bocage, 1895	
Brown House Snake[a]	*Boaedon fuliginosus* (Boie, 1827)			
Olive House Snake	*Boaedon olivaceus* (Dumeril, 1856)	Y	*Boodon olivaceus*	
Red-Black Striped House Snake	*Bothrophthalmus lineatus* (Peters, 1863)		*Bothrophthalmus lineatus*	
Parker's Banded Snake	*Chamaelycus parkeri* (Angel, 1934)			
Mocquard's Dwarf File Snake	*Gonionotophis brusseauxi* (Mocquard, 1889)			
Yellow Forest Snake	*Hormonotus modestus* (Duméril, Bibron and Duméril, 1854)			
Western Forest File Snake	*Mehelya poensis* (Smith, 1849)			
Cape File Snake	*Limaformosa capensis* (Smith, 1847)		*Heterolepis Guirali ?*	
Savorgan's File Snake	*Limaformosa savorgani* (Moquard, 1887)	?		NR
Vernay's File Snake	*Limaformosa vernayi* (Bogert, 1940)			
White-bellied Water Snake	*Lycodonomorphus* (?) *subtaeniatus* (Laurent, 1954)			
Hellmich's Wolf Snake	*Lycophidion hellmichi* (Laurent, 1964)			
Flat Wolf Snake	*Lycophidion laterale* (Hallowell, 1857)		*Lycophidium laterale*	
Speckled Wolf Snake	*Lycophidion meleagre* (Boulenger, 1893)		*Lycophidium meleagris*	
Spotted Wolf Snake	*Lycophidion multimaculatum* (Boettger, 1888)	Y	*Lycophium capense*	
Namib Wolf Snake	*Lycophidion namibianum* (Broadley, 1991)			NR
Ornate Wolf Snake	*Lycophidion ornatum* (Parker, 1936)	?		
Viperine Rock Snake	*Hemirhagerrhis viperina* (Bocage, 1873)		Psammophylax nototaenia	
Henophidia | **Lamprophiidae** | Psammophinae				
Angolan Sand Snake	*Psammophis angolensis* (Bocage, 1872)		*Amphiophis angolensis*	
Ansorge's Sand Snake	*Psammophis ansorgii* (Boulenger, 1905)			E
Jalla's Sand Snake	*Psammophis jallae* (Peracca, 1896)			

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Leopard Sand Snake	*Psammophis leopardinus* (Bocage, 1887)			
Namib Sand Snake	*Psammophis namibensis* (Broadley, 1975)			
Karoo Sand Snake	*Psammophis notostictus* (Peters, 1867)			
Mozambique Grass Snake	*Psammophis mossambicus* (Peters, 1882)	Y	*Psammophis sibilans* (Linnaeus, 1758)	
Strip-bellied Sand Snake	*Psammophis subtaeniatus* (Peters, 1882)			
Western Sand Snake	*Psammophis trigrammus* (Günther, 1865)			
Fork-marked Sand Snake	*Psammophis trinasalis* (Werner, 1902)			
Zambezi Sand Snake	*Psammophis zambiensis* (Hughes and Wade, 2000)			
Striped Beaked Skaapstekker	*Psammophylax acutus* (Günther, 1888)		*Rhageheris acutus*	
Huila Skaapstekker	*Psammophylax ocellatus* (Bocage, 1873)		*Psammophylax rhombeatus*	E
Striped Skaapstekker	*Psammophylax tritaeniatus* (Günther, 1868)		*Rhagerhis tritaeniata*	
Henophidia | **Lamprophiidae** | Prosymnidae				
Zambezi Shovel-snout Snake	*Prosymna ambigua* (Bocage, 1873)		*Prosymna ambigua*	
Angola Shovel-snout Snake	*Prosymna angolensis* (Boulenger, 1915)		*Prosymna frontalis*	
South-west Shovel-snout Snake	*Prosymna frontalis* (Peters, 1867)			
Visser's Shivel-snout Snake	*Prosymna visseri* (FitzSimons, 1959)			
Henophidia | **Lamprophiidae** | Pseudaspidae				
Mole Snake	*Pseudaspis cana* (Linnaeus, 1758)		*Pseudaspis cana*	
Western-keeled Snake	*Pythonodipsas carinata* (Günther, 1868)			
Henophidia | **Lamprophiidae** | Elapidae				
Cowles' Shield Cobra	*Aspidelaps lubricus cowlesi* (Bogert, 1940)			
Jameson's Mamba	*Dendroaspis jamesoni* (Traill, 1843)	?	*Dendroaspis neglectus*	
Black Mamba	*Dendroaspis polylepis* (Günther, 1864)	?	*Dendroaspis angusticeps*	
Günther's Garter Snake	*Elapsoidea guentherii* (Bocage, 1866)		*Elapsoidea Guentherii*	

(continued)

Common name	Scientific name	C	Bocage (1895)	Obs
Angolan Garter Snake	*Elapsoidea s. semiannulata* (Bocage, 1882)			
Western Garter Snake	*Elapsoidea s. moebiusi* (Werner, 1897)			
Anchiete's Cobra	*Naja* (*Ureaus*) *anchietae* (Bocage, 1879)		*Naja anchietae & Naja haje*	
Banded Water Cobra	*Naja* (*Boulengerina*) *annulata* (Peters, 1876)			
Central African Forest Cobra	*Naja* (*Boulengerina*) *melanoleauca* (Hallowell, 1857)			
Savanna Forest Cobra	*Naja* (*Boulengerina*) *subfulva* (Laurent, 1956)	?		
Mozambique Cobra	*Naja* (*Afronaja*) *mossambica* (Peters, 1854)			
Western Banded Spitting Cobra	*Naja* (*Afronaja*) *nigricincta* (Bogert, 1940)			
Black Spitting Cobra	*Naja* (*Afronaja*) *nigricollis* (Reinhardt, 1843)		*Naja nigricollis*	
Gold's Tree Cobra	*Pseudohaje goldii* (Boulenger, 1895)			
Henophidia | **Viperidae**				
Variable Bush Viper	*Atheris squamigera* (Hallowell, 1854)		*Atheris squamigera*	
Puff Adder	*Bitis arietans* (Merrem, 1820)		*Vipera arietans*	
Horned Adder	*Bitis caudalis* (Smith, 1839)		*Vipera caudalis*	
Gaboon Adder	*Bitis gabonica* Duméril, (Bibron and Duméril, 1854)	?	*Vipera rhinoceros*	
Angolan Adder	*Bitis heraldica* (Bocage, 1889)		*Vipera heraldica*	E
Rhinoceros Viper	*Bitis nasicornis* (Shaw, 1802)	?		
Peringuey's Adder	*Bitis peringueyi* (Boulenger, 1888)	?		
Two-lined Night Adder	*Causus bilineatus* (Boulenger, 1905)			
Lichtenstein's Night Adder	*Causus lichtensteini* (Jan, 1859)			
West African Night Adder	*Causus maculatus* (Hallowell, 1842)			
Rasmussen's Night Adder	*Causus rasmusseni* (Broadley, 2014)			
Angola Green Night Adder	*Causus resimus* (Peters, 1862)		*Causus resimus*	
Rhombic Night Adder	*Causus rhombeatus* (Lichtenstein, 1823)	Y	*Causus rhombeatus*	

[a]Don't include the additional *Boaedon* species (Hallerman et al. in prep.)

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