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Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist

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ABSTRACT

Namibia is mostly an arid and semi-arid country with a high number of reptile and fewer amphibian species. We review the herpetological literature dealing with Namibian species over the past fifty years, and provide up-to-date amphibian and reptile accounts using a widely accepted taxonomy and nomenclature. We critically discuss species accounts, draw attention to the historical development of species inventories for the country, and indicate species endemism for Namibia and the Namib Desert. In Namibia, the lizard families Gekkonidae, Lacertidae, and Scincidae have undergone adaptive radiations and are species-rich. This also applies to the snake family Psammophiidae.

Areas of herpetological research that have received most attention are systematics (with its disciplines faunistics (area inventories), taxonomy, and phylogeny), ecology, and physiology. The former is indicative of early stages of herpetological research such as area inventories and the subsequent analyzes of the collections. The latter two were largely enabled by (1) species highly adapted to life in the hyper-arid Namib Desert, and (2) by the accessibility of these species in the Namib Desert through the infrastructure provided by the Gobabeb Research and Training Center. The majority of the eco-physiological research has focused on three highly psammophilus, diurnal lizard species; *Meroles anchietae*, *M. cuneirostris*, and *Gerrhosaurus skoogi*, whilst diverse geckos form the basis of eco-morphological studies.

The concentration of research localities around cities and the Gobabeb Research and Training Center is characteristic for opportunistic research. Geographic centers of herpetological research have been the central Namib Desert (i.e. Gobabeb), and areas around Swakopmund and Windhoek. Extensive parts of Namibia remain barely touched. Herpetological publication frequency has been approximately the same since its beginning in the early 1800's until the 1970's. The period between 1986 and 2003 experienced a remarkable increase of publication activity that has slightly subsided around 2004 and picked up again in recent years.

Recent conservation related studies investigate the impact of overgrazing with land degradation and water related issues such as canals and hydroelectric dam projects on herpetological communities. In the near future the impact of mining, especially Uranium mining in the Namib Desert, and the effects of climate change with the predicted drying and warming will demand increased attention.

Advances in biotechnology with ever-increasing amounts of data and decreasing cost have and will progressively enable advances in traditional disciplines like taxonomy, phylogeny, and systematics. Additionally, these technologies will increasingly empower the newer disciplines of molecular ecology and conservation biology in Namibia.

Annotated, updated species checklists highlight Namibian and Namib diversity and endemicity, and also direct researchers to the numerous taxonomic problems that still confound full understanding of the region's herpetofauna.

1. Introduction

The Namib Desert is one of the oldest and driest deserts in the world (Hartley et al., 2005; Ward et al., 1983) and has remarkable reptile and amphibian diversity, with a high percentage of endemism (Griffin, 2000, 2003). It extends as a narrow arid belt of

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variable width along the length of the Namibian coastline, and into southern Angola as far as Namibe (previously Mossamedes). The Succulent Karoo forms an adjacent transitional semi-arid habitat in the northern Cape coastal region, South Africa. The age of the Namib Desert is dated to the Cretaceous at least 80 million years ago with at least semi-arid conditions ever since. The cold Benguela current formed much later during the late Miocene and has accentuated the desertic conditions. Climate along the approximately 2000 km south–north-extension of the narrow Namib Desert varies with the southern Namib experiencing winter rains, the central desert being extremely arid with unpredictable rain patterns, and the northern Namib with summer rains (Ward et al., 1983).

The lizard diversity in the Namib and adjacent semi-arid regions is especially high, with radiations of Gekkonidae, Lacertidae, and Scincidae. Snakes, particularly sand snakes (Psammophiidae), are also species-rich. Reptiles play an integral role in subtropical and tropical arid areas, where hyper-arid environments cannot support large numbers of mammals with high-energy requirements and consequent dependency on large amounts of water and nutrients.

Compared to reptiles, amphibians are more water dependent and therefore are much less abundant in deserts. Amphibians satisfy their oxygen requirements largely through their moist skin and have a bi-phasic life cycle (tadpoles and frogs). These biological constraints pose major challenges in arid environments. However, amphibians can and do survive in the arid regions of Namibia and some exhibit radical adaptations in water metabolism and reproductive biology (i.e. *Breviceps macrops*; du Preez and Carruthers, 2009; Channing and Wahlberg, 2011).

The Namib represents a hotspot of reptile evolution, particularly geckos (Bauer, 1999). Herpetological research in the Namib Desert and Namibia during the last 50 years has been dominated by faunistic surveys and alpha taxonomic efforts (i.e. amphibian and reptile species inventories and the description of new species). More recently there has been an increase in molecular phylogenetic and natural history observations on lizards and snakes. This has been complemented by studies in physiology, ecology, and behavior of several true sand dune lizard species, often facilitated by the Gobabeb Research and Training Center in the Central Namib. Gobabeb is situated at the intersection of three main habitat types: extended sand dunes ("sand sea"), large gravel plains, and the mostly dry Kuiseb River.

A few short notes published decades ago addressed the state of herpetology and herpetological research in Namibia (Berger-Dell'mour, 1987; Griffin, 1990; Haacke, 1972, 1977). The more comprehensive publications by Griffin (2000, 2002, 2003) provided summaries of the history of herpetology in Namibia, whilst a related publication outlined "The rules of Namibian herpetology" (Griffin and Morsbach, 1993). This contribution described the legal aspects of herpetological research in Namibia and was written by members of the Namibian wildlife authorities. It clarified what was permissible and what type of research was encouraged and where. A modern update by conservation authorities is needed, possibly online, and would be of great value to the herpetological research community.

Here we provide a review of herpetological research in the Namib Desert with a focus on the last 50 years. This review covers the most important research contributions for the Namib Desert and extends beyond this region into other neighboring arid and semi-arid regions of Namibia, including the non-arid Caprivi region (Griffin, 1995). It addresses new challenges, such as the remaining taxonomic problems, conservation issues related to water resources and mineral mining, and examines climate change as related to amphibians and reptiles. We conclude with a perspective for future herpetological research, with special emphasis on the innovative new field of conservation genetics.

2. Herpetological species in the Namib Desert and Namibia

2.1. Amphibians

Higher taxonomic relationships within amphibians are in a state of flux. We adopt the classification of Frost (2011), acknowledging that there exist conflicting views and that future refinements are probable. Currently 60 species of anurans from 12 different families are known to occur in Namibia (Table 1). Amphibian distribution shows two very different patterns that are determined by (1) the localized occurrence of wetlands, or (2) systematic groups of anurans which are well adapted to arid and semi-arid environments. Not unexpectedly, the highest species richness occurs in the Caprivi wetlands (Poynton and Broadley, 1985, 1986, 1987, 1988). Four frogs are currently endemic to Namibia (Table 1), although the recently described *Ptychadena mapacha* (Channing, 1993) probably has a wider distribution in wetlands adjacent to the Caprivi, and two arid-adapted Damaraland species, *Poyntonophrynus damaranus* and *Tomopterna damarensis,* may also occupy similar habitat in southern Angola. Due to its general aridity few amphibians inhabit the sand dunes of the Namib Desert, with the unusual burrowing frog *Breviceps macrops* inhabiting the fog-belt of the southern Namib and extending into the Namaqualand coastal sands of South Africa. The related species, *B. namaquensis* and *B. branchi* (Channing, 2012), are also specialist Namaqua sand dune inhabitants, but neither has yet been recorded as far north as Namibia. These potential Namibian inhabitants and another five species are found within close proximity of the country's borders in habitats that extend into Namibia. In the south these include *Vandijkophrynus robinsoni* and *Strongylopus springbokensis*, which have both been recorded in the Richtersveld (Bauer and Branch, 2001), and *Amietophrynus rangeri*, and *Tomopterna delalandii* from the Lower Orange River valley (du Preez and Carruthers, 2009). In the eastern Caprivi the possible presence of *Hyperolius pusillus* remains problematic (Table 1). Conversely, the presence of *Vandijkophrynus gariepensis* in Namibia is based on a single record from Oranjemund (Channing and Griffin, 1993) that may represent a translocation.

2.2. Reptiles

As with amphibians, the higher classification of reptiles is fluid, with a number of competing arrangements proposed (see full discussion in Branch, 2010). We accept the phylogeny of Vidal and Hedges (2009) as the most well supported current hypothesis of relationships among squamates, and for African snakes we adopt the classification of Kelly et al. (2011), with minor refinements proposed by Pyron et al. (2011). The familial arrangement of lizards is relatively stable, albeit that the Gekkonidae *sensu lato*, as understood by Branch (1998) and Griffin (2003) has been split into four families (Gamble et al. 2008a,b), of which, co-incidentally the Gekkonidae (in a reduced sense) is still the only family of gekkotans found in Namibia. Currently 268 reptile species in 27 families (Table 2) are known to occur in Namibia. Lizards, with 166 species in nine families top the list, followed by snakes with 86 species in twelve families. Turtles are represented by 15 species in five families and crocodilians by only *Crocodylus niloticus*.

Gekkonidae represented by 68 species, is by far the most species-rich reptile and lizard family in Namibia. This large number is explained by the high substrate specificity of gekkonid taxa and the dynamic mosaic of substrate types resulting from complex subdivision due to past climate changes and underlying geology (Bauer, 1999). Additionally, the large number of known gecko species is the consequence of recent focused research efforts including strategic sampling across geographic areas, the systematic revision of genera, and the use of molecular phylogenetic

Table 1
Amphibian species of Namibia as referenced in Channing (1991), Channing (2001), Channing and Griffin (1993), du Preez and Carruthers (2009), and Frost (2011). Records in parentheses are species expected to occur in Namibia but not yet recorded.

Species	Channing, 1991	Channing and Griffin, 1993	Channing, 2001	du Preez and Carruthers, 2009	Frost, 2011	Namibia endemic
Arthroleptidae						
Leptopelis bocagii (Günther, 1865)	X	X	X	X	X	
Brevicipitidae						
Breviceps adspersus Peters, 1882	X	X	X	X	X	
Breviceps macrops Boulenger, 1907	X	X	X	X	X	
Bufonidae						
Amietophrynus garmani (Meek, 1897)				X	X	
Amietophrynus gutturalis (Power, 1927)	X	X	X	X	X	
Amietophrynus lemairii (Boulenger, 1901)	X	(X)	X	X	X	
Amietophrynus maculatus (Hallowell, 1854)	X	X	X	X	X	
Amietophrynus poweri (Hewitt, 1935)	X	X	X	X	X	
Amietophrynus rangeri (Hewitt, 1935)[a]						
Poyntonophrynus damaranus (Mertens, 1954)				X	X	X
Poyntonophrynus dombensis (Bocage, 1895)	X	X	X	X	X	
Poyntonophrynus fenoulheti (Hewitt and Methuen, 1912)	X	X	X	X	X	
Poyntonophrynus hoeschi (Ahl, 1934)	X	X	X	X	X	X
Poyntonophrynus kavangensis (Poynton and Broadley, 1988)	X	X	X	X	X	
Schismaderma carens (Smith, 1848)	X	X	(X)	X		
Vandijkophrynus gariepensis (Smith, 1848)[a]	X	X	X	X	X	
Vandijkophrynus robinsoni (Branch and Braack, 1995)[b]						
Hemisotidae						
Hemisus guineensis Cope, 1865			(X)	X	X	
Hemisus marmoratus (Peters, 1854)	X	X	X	X	X	
Hyperoliidae						
Hyperolius benguellensis Bocage, 1893				X	X	
Hyperolius marmoratus Rapp, 1842						
Hyperolius nasutus Günther, 1865	X	X	X	X	X	
Hyperolius parallelus Günther, 1858	X[c]	X[c]	X[c]	X	X	
Hyperolius pusillus (Cope, 1862)[d]						
Kassina senegalensis (Duméril and Bibron, 1841)	X	X	X	X	X	
Microhylidae						
Phrynomantis affinis Boulenger, 1901	X	X	X	X	X	
Phrynomantis annectens Werner, 1910	X	X	X	X	X	
Phrynomantis bifasciatus (Smith, 1847)	X	X	X	X	X	
Phrynobatrachidae						
Phrynobatrachus mababiensis FitzSimons, 1932	X	X	X	X	X	
Phrynobatrachus natalensis (Smith, 1849)	X	X	X	X	X	
Phrynobatrachus parvulus (Boulenger, 1905)			(X)	X	(X)	
Pipidae						
Xenopus laevis (Daudin, 1802)	X	X	X	X	X	
Xenopus muelleri (Peters, 1844)	X	X	X	X	X	
Xenopus petersii Bocage, 1895	X		X	X	X	
Ptychadenidae						
Hildebrandtia ornata (Peters, 1878)	X	X	X	X	X	
Ptychadena anchietae (Bocage, 1868)	X	X	X	X	X	
Ptychadena guibei Laurent, 1954		X	(X)	X	X	
Ptychadena mapacha Channing, 1993		X[e]	X	X	X	X
Ptychadena mascareniensis (Duméril and Bibron, 1841)	X	X	X	X	X	
Ptychadena mossambica (Peters, 1854)	X	X	X	X		
Ptychadena oxyrhynchus (Smith, 1849)	X	X	X	X	X	
Ptychadena porosissima (Steindachner, 1867)	X	(X)			X	
Ptychadena subpunctata (Bocage, 1866)	X	X	X	X	X	
Ptychadena taenioscelis Laurent, 1954	X	X	X	X	X	
Ptychadena upembae (Schmidt and Inger, 1959)[f]	?					
Pyxicephalidae						
Amietia angolensis (Bocage, 1866)	X[g]	(X)[g]	(X)[h]	X	X	
Amietia fuscigula (Duméril and Bibron, 1841)	X[g]	X[g]	X[h]		X	
Cacosternum boettgeri (Boulenger, 1882)	X	X	X	X	X	
Cacosternum namaquense Werner, 1910	X	X	X	X	X	
Tomopterna cryptotis (Boulenger, 1907)	X	X	X	X	X	
Tomopterna damarensis Dawood and Channing, 2002				X	X	X
Tomopterna delalandii (Tschudi, 1838)		(X)			(X)	
Tomopterna krugerensis Passmore and Carruthers, 1975	X	X	X	X	X	
Tomopterna marmorata (Peters, 1854)[i]	?	?				
Tomopterna tandyi Channing and Bogart, 1996			X	X	X	
Tomopterna tuberculosa (Boulenger, 1882)	X	X	X	X	X	

Table 1 (*continued*)

Species	Channing, 1991	Channing and Griffin, 1993	Channing, 2001	du Preez and Carruthers, 2009	Frost, 2011	Namibia endemic
Pyxicephalus adspersus Tschudi, 1838[j]		X	X	X	X	
Pyxicephalus edulis Peters, 1854[j]				X	(X)	
Ranidae						
Hylarana darlingi (Boulenger, 1902)	X	X	(X)[k]	X	X	
Rhacophoridae						
Chiromantis xerampelina Peters, 1854	X	X	X	X	X	

[a] The record (Channing and Griffin, 1993) of *Bufo* (=*Vandijkophrynus*) *garipensis* from "a little inland along the (Orange) river" (QDS 2816DA) was shown (Branch and Braack, 1995) to be based on misidentified specimens of *Amietophrynus rangeri*, which was believed to have been translocated (possibly naturally in floods) from upstream. No further records of *A. rangeri* from the lower Orange River have been reported (Bauer and Branch, 2001). *Vandijkophrynus gariepensis* is known from various localities in the Richtersveld (Bauer and Branch, 2001), with a single record from Oranjemund (Channing and Griffin, 1993), which remains the only record for Namibia.

[b] Although not recorded from Namibia it was described from the adjacent Richtersveld (Branch and Braack, 1995), where it has a very localized and patchy distribution (Bauer and Branch, 2001). It may be present at springs in the mountains of the Sperrgebiet or around Rosh Pinah.

[c] As *Hyperolius angolensis*.

[d] Channing (2001) records *Hyperolius pusillus* from two records in the Okavango Delta, suggesting that it may extend into the Caprivi Strip of Namibia. However, these records are considerably separated from the main distribution along the east African coast from Somalia to the Eastern Cape, South Africa. Neither Poynton and Broadley (1987), nor du Preez and Carruthers (2009), include Okavango records of *H. pusillus* and their status remains problematic.

[e] As *Ptychadena* sp.

[f] Channing's (1991) record of *P. upembae* from the Caprivi appears to be due to confusion with other species. The nearest confirmed records are from the Barotse Floodplain (Poynton and Broadley, 1985; du Preez and Carruthers, 2009).

[g] As *Rana*.

[h] As *Afrana*. Channing (2011) has noted that both *A. angolensis* and *A. fuscigula* contain cryptic diversity, although the isolated population of river frogs in the Namib-Naukluft is currently still referable to the latter.

[i] The early records of *Tomopterna marmorata* from the Caprivi (Channing, 1991; Channing and Griffin, 1993) have not been recently confirmed and may be due to confusion with other *Tomopterna* species.

[j] There remains confusion over the exact ranges of both *Pyxicephalus*. Although Channing (2001) considered *P. edulis* to be more restricted to the eastern half of the continent, other authors (e.g. Parry, 1982; Poynton and Broadley, 1985; du Preez and Carruthers, 2009) all consider the species to enter the eastern Caprivi.

[k] As *Amnirana*.

methods to uncover cryptic species (Bauer and Branch, 1991, 1995; Bauer and Good, 1996; Bauer and Lamb, 2005; Bauer et al., 1993, 2002, 2006a,b; Lamb and Bauer, 2001). Due to these extensive studies new species continue to be discovered, with two new species described in 2011 (Heinicke et al., 2011; Branch et al., 2011). Others still await description (Bauer pers. comm.). There have also been increasing numbers of phylogenetic studies, with changing generic assignments, e.g. the expansion of *Chondrodactylus* to include a number of other large-bodied rupicolous geckos previously included in *Pachydactylus* (i.e. *C. bibroni*, *C. turneri* and *C. fitzsimonsi*), and the transfer of *Palmatogecko rangei* and *Kaokogecko vanzylii* to *Pachydactylus* (Bauer and Lamb, 2005). The phylogenetic relationships of barking geckos (*Ptenopus*) remain intractable (Bauer pers. comm.), whilst the genetic assignment of *Rhoptropella ocellata* remains controversial (Austin et al., 2004; Bauer, 1990; Good and Bauer, 1995; Rocha et al., 2010; Roell, 1999; Russell, 1977; Russell and Bauer, 1990).

Only two of the 33 formally described skink species (Table 2) have been discovered within the past 50 years. The status of Namibian *Afroblepharus*, previously placed in *Panaspis wahlbergi*, (Branch, 1998) but treated as *Panaspis* sp. by Griffin (2003), is unresolved but probably represents a taxonomic novelty (Medina and Greenbaum, pers. comm.). With the exception of Haacke's revision of *Typhlacontias* (Haacke, 1997), including the description of a new subspecies, a recent reassessment of generic assignments in the Acontinae (Lamb et al., 2010), and a partial revision of *Trachylepis sulcata* (Portik et al., 2010, 2011), skinks have been relatively neglected despite their abundance and diversity. It is likely that Namibian skinks, like geckos, include yet undiscovered and cryptic species.

True lizards of the family Lacertidae occur with 26 species in Namibia. Two of the 26 species have been described within the last 50 years (*Ichnotrophis grandiceps*, *Pedioplanis husabensis*) and other, as yet undescribed, species have been signaled. Griffin (2003) considered that the southern population of *Meroles anchietae* deserved specific recognition, based on allozyme studies (Gordon and Griffin, 1989), which were subsequently supported by gene sequencing (Lamb and Bauer, 2003). Despite these preliminary observations, the matter remains unresolved. Bauer (in litt.) considers that an additional undescribed *Meroles*, related to *M. reticulatus*, occurs in the Kaokoveld, and cryptic taxa may also occur within *Pedioplanis inornata*, *Pedioplanis namaquensis* (Makhoka et al., 2007) and *P. undata* (Mayer and Berger-Dell'mour, 1987). Resolution of cryptic diversity in the latter is complicated by the discovery of another radiation of lizards of the *P. undata* complex in adjacent Angola (Conradie et al., 2012).

Griffin (2002, 2003) discussed a number of species that had been erroneously reported to occur in Namibia, and others that occurred in the close proximity to its borders and which may occur in the country. An additional erroneous record is that of Uetz (2011), who lists *Pachydactylus formosus* as part of the Namibian herpetofauna, presumably due to confusion with *P. rugosus*. Previously treated as a southern subspecies of *P. rugosus* (Branch, 1998; McLachlan, 1979), *P. formosus* was subsequently raised to specific status (Bauer and Branch, 2001). The status of *Scelotes schebeni* Sternfeld 1910 remains controversial. The species is known from a single lost holotype reputedly from Windhoek. Brygoo and Roux-Esteve (1982) transferred it to *Melanoseps*, and Mertens (1955) and Bauer et al. (2003) considered the type locality to be in error. Its inclusion in the Namibian herpetofauna is deferred pending modern material.

Of the Namibian snake groups only Sand snakes (Psammophiidae) have undergone a radiation comparable to the three lizard families above. Sand snakes, with 18 species in Namibia, represent the most remarkable snake group for Namibia and the only one with elevated species numbers. This group of largely diurnal rear-fanged snakes has a long and complicated taxonomic history (Broadley, 2002). Kelly et al. (2008) provided the first comprehensive molecular phylogeny for the Psammophiidae. A comparable study of the snake family Lamprohiidae, and particularly the genera *Lamprophis* and *Mehelya* (Kelly et al., 2011), revealed considerable paraphyly that led to significant generic rearrangement.

Table 2
Reptile species of Namibia as referenced in Branch (1998), Griffin (2003), and Uetz (2011). Nomenclature follows Uetz (2011) and most recent taxonomic changes. Records in parentheses are species expected to occur in Namibia but not yet recorded.

Species	Branch, 1998	Griffin, 2003	Uetz, 2011	Namibia endemic	Namib Desert endemic
Crocodylidae					
Crocodylus niloticus Laurenti, 1768	X	X	X		
Pelomedusidae					
Pelomedusa subrufa (Bonnaterre, 1789)[a]	X	X			
Pelusios bechuanicus Fitzsimons, 1932	X	X	X		
Pelusios rhodesianus Hewitt, 1927[b]	X	X			
Pelusios subniger (Lacépède, 1789)[c]	X				
Testudinidae					
Chersina angulata (Schweigger, 1812)	X	X	X		
Homopus solus Branch, 2007	X	X	X	X	
Kinixys spekii Gray, 1863	X	X			
Psammobates oculifer (Kuhl, 1820)	X	X	X		
Psammobates tentorius (Bell, 1828)	X	X	X		
Stigmochelys pardalis (Bell, 1828)	X[d]	X[d]	X		
Cheloniidae					
Caretta caretta (Linnaeus, 1758)[e]			X		
Chelonia mydas (Linnaeus, 1758)	X	X			
Lepidochelys olivacea (Eschscholtz, 1829)	X	X			
Dermochelyidae					
Dermochelys coriacea Vandelli, 1761	X	X			
Trionychidae					
Trionyx triunguis (Forskål, 1775)	X	X	X		
Gekkonidae					
Afroedura africana (Boulenger, 1888)[f]	X	X	X		
Afroedura cf. *bogerti* Loveridge, 1944	X	X			
Afrogecko porphyreus (Daudin, 1802)[g]		X			
Chondrodactylus angulifer Peters, 1870	X	X	X		
Chondrodactylus bibronii (Smith, 1846)	X[h]	X[h]	X		
Chondrodactylus fitzsimonsi (Loveridge, 1947)[i]	X[h]	X[h]	X		
Chondrodactylus turneri (Gray, 1864)[j]	X[h]	X[h]	X		
Colopus kochii (Fitzsimons, 1959)[k]	X[h]	X[h]	X	X	
Colopus wahlbergii Peters, 1869[k]	X	X	X		
Goggia gemmula (Bauer, Branch & Good,1996)	X	X	X		
Goggia lineata (Gray, 1838)	X	X	X		
Hemidactylus longicephalus Bocage, 1873	X	X			
Hemidactylus mabouia (Moreau de Jonnés, 1818)	X	X			
Lygodactylus angolensis Bocage, 1896			X[l]		
Lygodactylus bradfieldi Hewitt, 1932	X	X	X		
Lygodactylus capensis (Smith, 1849)	X	X	X		
Lygodactylus chobiensis Fitzsimons, 1932	X	X	X		
Lygodactylus lawrencei Hewitt, 1926	X	X	X	X	
Narudasia festiva Methuen and Hewitt, 1914	X	X	X	X	
Pachydactylus acuminatus Fitzsimons, 1941			X		
Pachydactylus atorquatus Bauer, Barts & Hulbert, 2006			X		
Pachydactylus barnardi Fitzsimons, 1941			X		
Pachydactylus bicolor Hewitt, 1926	X	X	X	X	
Pachydactylus boehmei Bauer, 2010				X	
Pachydactylus capensis (Smith, 1845)	X	X			
Pachydactylus caraculicus Fitzsimons, 1959	X	X	X		
Pachydactylus carinatus Bauer, Lamb & Branch, 2006			X		
Pachydacylus etultra Branch, Bauer, Jackman & Heinicke, 2011				X	X
Pachydactylus fasciatus Boulenger, 1888	X	X	X	X	
Pachydactylus gaiasensis Steyn and Mitchell, 1967	X	X	X	X	X
Pachydactylus griffini Bauer, Lamb & Branch, 2006			X	X	
Pachydactylus haackei Branch, Bauer & Good, 1996	X	X	X	X	
Pachydactylus kobosensis Fitzsimons, 1938		X	X	X	
Pachydactylus laevigatus Fischer, 1888			X		
Pachydactylus latirostris Hewitt, 1923	X[m]	X[m]	X[m]		
Pachydactylus maraisi Heinicke, Adderly, Bauer & Jackman, 2011				X	X
Pachydactylus mclachlani Bauer, Lamb & Branch, 2006			X	X	
Pachydactylus monicae Bauer, Lamb & Branch, 2006			X		
Pachydactylus montanus Methuen and Hewitt, 1914			X		
Pachydactylus namaquensis (Sclater, 1898)[n]	X	X	X		
Pachydactylus oreophilus McLachlan and Spence, 1967	X		X	X	
Pachydactylus otaviensis Bauer, Lamb & Branch, 2006			X	X	
Pachydactylus parascutatus Bauer, Lamb & Branch, 2002		X	X	X	X
Pachydactylus punctatus Peters, 1854	X	X	X		
Pachydactylus purcelli Boulenger, 1910			X		
Pachydactylus rangei (Andersson, 1908)	X[o]	X[o]	X		X
Pachydactylus reconditus Bauer, Lamb & Branch, 2006			X	X	

Table 2 (*continued*)

Species	Branch, 1998	Griffin, 2003	Uetz, 2011	Namibia endemic	Namib Desert endemic
Pachydactylus robertsi Fitzsimons, 1938		X	X	X	
Pachydactylus rugosus Smith, 1849	X	X	X		
Pachydactylus sansteynae Steyn and Mitchell, 1967	X	X	X	X	X
Pachydactylus scherzi Mertens, 1954	X	X	X	X	X
Pachydactylus scutatus Hewitt, 1927	X	X	X	X	
Pachydactylus serval Werner, 1910	X	X	X		
Pachydactylus vanzyli (Steyn and Haacke, 1966)	X[o]	X[o]	X		X
Pachydactylus visseri Bauer et al., 2006			X		
Pachydactylus waterbergensis Bauer and Lamb, 2003			X	X	
Pachydactylus weberi Roux, 1907	X	X	X		
Pachydactylus werneri Hewitt, 1935			X		
Ptenopus carpi Brain, 1962	X	X	X	X	X
Ptenopus garrulus (Smith, 1849)	X	X	X		
Ptenopus kochi Haacke, 1964	X	X	X	X	X
Rhoptropella ocellata (Boulenger, 1885)	X[p]	X[p]	X		
Rhoptropus afer Peters, 1869	X	X	X	X	X
Rhoptropus barnardi Hewitt, 1926	X	X	X	X	
Rhoptropus biporosus Fitzsimons, 1957	X	X	X		
Rhoptropus boultoni Schmidt, 1933	X	X	X		
Rhoptropus bradfieldi Hewitt, 1935	X	X	X	X	X
Rhoptropus diporus Haacke, 1965	X[q]	X	X[q]	X	X
Agamidae					
Acanthocercus cyanocephalus (Falk, 1925)[r]	X	X	X		
Agama aculeata Merrem, 1820	X	X	X		
Agama anchietae Bocage, 1896	X	X	X		
Agama armata Peters, 1855		X	X		
Agama atra Daudin, 1802[s]	X	X	X		
Agama etoshae McLachlan, 1981	X	X	X	X	
Agama hispida Kaup, 1827	X	X	X		
Agama knobeli Boulenger and Power, 1921[t]	X[t]	X[t]			
Agama planiceps Peters, 1862	X	X	X		
Chamaeleonidae					
Bradypodion occidentale (Hewitt, 1935)			X		
Bradypodion pumilum (Gmelin, 1789)[u]	X	X	X		
Chamaeleo dilepis Leach, 1819	X	X	X		
Chamaeleo namaquensis (Smith, 1831)	X	X	X		
Scincidae					
Acontias gariepensis (Fitzsimons, 1941)	X[v]	X[v]	X[v]		
Acontias kgalagadi Lamb, Biswas & Bauer, 2010	X[w]	X[w]	X[w]		
Acontias lineatus Peters, 1879	X	X	X		
Acontias occidentalis FitzSimons, 1941	X[x]	X	X[x]		
Afroablepharus wahlbergi (Smith, 1849)	X[y]		X		
Afroablepharus maculicollis (Jacobson and Broadley, 2000)[z]		X			
Afroablepharus sp. (Griffin 2003)[z]		X		(X)	
Mochlus sundevalli (Smith, 1849)	X[aa]	X[aa]	X		
Scelotes capensis (Smith, 1849)	X	X	X		
Sepsina alberti Hewitt, 1929	X	X	X	X	
Sepsina angolensis Bocage, 1866	X	X	X		
Trachylepis acutilabris (Peters, 1862)	X	X	X		
Trachylepis binotata (Bocage, 1867)	X	X	X		
Trachylepis capensis (Gray, 1831)	X	X	X		
Trachylepis chimbana (Boulenger, 1887)	X	X	X		
Trachylepis hoeschi (Mertens, 1954)	X	X	X		
Trachylepis laevis (Boulenger, 1907)	X	X	X		
Trachylepis occidentalis (Peters, 1867)	X	X	X		
Trachylepis punctatissima (Smith, 1849)		X			
Trachylepis punctulata (Bocage, 1872)	X[ab]	X	X		
Trachylepis sparsa (Mertens, 1954)	X[ac]	X	X		
Trachylepis spilogaster (Peters, 1882)	X	X	X		
Trachylepis striata (Peters, 1844)	X[ad]	X[ad]	X		
Trachylepis sulcata (Peters, 1867)[ae]	X	X	X		
Trachylepis varia (Peters, 1867)	X	X			
Trachylepis variegata (Peters, 1870)	X	X	X		
Typhlacontias brevipes Fitzsimons, 1938	X	X	X	X	X
Typhlacontias gracilis Roux, 1907			X		
Typhlacontias johnsonii Andersson, 1916	X	X			
Typhlacontias punctatissimus Bocage, 1873	X	X	X		
Typhlacontias rohani Angel, 1923	X	X			
Typhlosaurus braini Haacke, 1964	X	X	X	X	X
Typhlosaurus meyeri Boettger, 1894	X	X	X		
Lacertidae					
Heliobolus lugubris (Smith, 1838)	X	X	X		
Ichnotropis capensis (Smith, 1838)	X	X	X		

(*continued on next page*)

Table 2 (*continued*)

Species	Branch, 1998	Griffin, 2003	Uetz, 2011	Namibia endemic	Namib Desert endemic
Ichnotropis grandiceps Broadley, 1967	X	X	X		
Ichnotropis squamulosa Peters, 1854	X	X	X		
Meroles anchietae (Bocage, 1867)	X	X	X		X
Meroles ctenodactylus (Smith, 1838)	X	X	X		X
Meroles cuneirostris (Strauch, 1867)	X	X	X		X
Meroles knoxii (Milne-Edwards, 1829)	X	X	X		
Meroles micropholidotus Mertens, 1938	X	X	X	X	X
Meroles reticulatus (Bocage, 1867)	X	X	X		X
Meroles sp.[af]		X		X	X
Meroles suborbitalis (Peters, 1869)	X	X	X		
Nucras intertexta (Smith, 1838)	X	X	X		
Nucras taeniolata (Smith, 1838)	X	X	X		
Nucras tessellata (Smith, 1838)	X	X	X		
Pedioplanis benguelensis (Bocage, 1867)	X	X	X		
Pedioplanis breviceps (Sternfeld, 1911)	X	X	X	X	X
Pedioplanis gaerdesi Mertens, 1954	X	X	X	X	
Pedioplanis husabensis Berger-Dell'mour and Mayer, 1989	X	X	X	X	X
Pedioplanis inornata Roux, 1907[ag]	X	X			
Pedioplanis laticeps (Smith, 1849)[ah]		X	X		
Pedioplanis lineoocellata (Duméril and Bibron, 1839)[ai]	X	X	X		
Pedioplanis namaquensis (Duméril and Bibron, 1839)[aj]	X	X	X		
Pedioplanis puchella (Duméril and Bibron, 1839)[ai]	X	X			
Pedioplanis rubens Mertens, 1955	X	X	X	X	
Pedioplanis undata (Smith, 1838)[ak]	X	X	X	X	
Cordylidae					
Platysaurus capensis Smith, 1844[al]	X	X	X		
Platysaurus broadleyi Branch and Whiting, 1997[am]					
Cordylus angolensis (Bocage, 1895)[an]			(X)		
Cordylus machadoi Laurent, 1964[ao]	X	X			
Karusasaurus jordani (Parker, 1936)	X[ap]	X[ap]	X[ap]	X	
Karusasaurus polyzonus (Smith, 1838)	X[ap]	X[ap]	X[ap]		
Namazonurus campbelli (Fitzsimons, 1938)	X[ap]	X[ap]	X[ap]	X	
Namazonurus namaquensis (Methuen and Hewitt, 1914)	X[ap]	X[ap]	X[ap]	X	
Namazonurus pustulatus (Peters, 1862)	X[ap]	X[ap]		X	
Gerrhosauridae					
Cordylosaurus subtessellatus (Smith, 1844)	X	X	X		
Gerrhosaurus flavigularis Wiegmann, 1828	X	X			
Gerrhosaurus multilineatus Bocage, 1866	X[aq]	X[ar]	X		
Gerrhosaurus nigrolineatus Hallowell, 1857	X	X	X		
Gerrhosaurus skoogi Andersson, 1916	X[as]	X	X		X
Gerrhosaurus typicus (Smith, 1837)[at]		X			
Gerrhosaurus validus Smith, 1849	X	X	X		
Varanidae					
Varanus albigularis (Daudin, 1802)	X	X	X		
Varanus niloticus (Linnaeus, 1758)	X	X	X		
Amphisbaenidae					
Dalophia longicauda (Werner, 1915)	X	X	X		
Dalophia pistillum (Boettger, 1895)	X	X	X		
Monopeltis anchietae (Bocage, 1873)	X	X	X		
Monopeltis infuscata Broadley, 1997	X	X	X		
Monopeltis leonhardi Werner, 1910	X	X	X		
Monopeltis mauricei Parker, 1935	X[au]	X	X		
Zygaspis nigra Broadley and Gans, 1969	X	X	X		
Zygaspis quadrifrons (Peters, 1862)	X	X	X		
Leptotyphlopidae					
Leptotyphlops conjunctus (Jan, 1861)[av]	X		X		
Leptotyphlops scutifrons (Peters, 1854)[av]	X	X	X		
Namibiana gracilior (Boulenger, 1910)	X	X	X		
Namibiana labialis (Sternfeld, 1908)	X	X	X		
Namibiana occidentalis Fitzsimons, 1962	X	X	X		
Typhlopidae					
Megatyphlops schlegelii (Bianconi, 1847)[aw]	X	X	X		
Rhinotyphlops boylei (Fitzsimons, 1932)	X	X	X		
Rhinotyphlops lalandei (Schlegel, 1839)[ax]	X	X	X		
Rhinotyphlops schinzi (Boettger, 1887)	X	X	X		
Boidae					
Python anchietae Bocage, 1887	X	X	X		
Python natalensis Smith, 1840	X	X	X		
Colubridae					
Coluber zebrinus Broadley and Schätti, 1999[ay]	X	X	X	X	
Crotaphopeltis hotamboeia (Laurenti, 1768)	X	X			

Table 2 (*continued*)

Species	Branch, 1998	Griffin, 2003	Uetz, 2011	Namibia endemic	Namib Desert endemic
Dasypeltis scabra (Linnaeus, 1758)[az,ba]	X	X	X		
Dispholidus typus (Smith, 1828)	X	X	X		
Philothamnus angolensis Bocage, 1882	X	X	X		
Philothamnus hoplogaster (Günther, 1863)	X	X			
Philothamnus ornatus Bocage, 1872		X			
Philothamnus semivariegatus (Smith, 1840)	X	X	X		
Telescopus beetzi (Barbour, 1922)	X	X	X		
Telescopus semiannulatus Smith, 1849	X	X	X		
Telescopus sp.[bb]		X		X	X
Thelotornis capensis Smith, 1849	X	X	X		
Natricidae					
Natriciteres olivacea (Peters, 1854)	X	X			
Limnophis bangweolicus (Mertens, 1936)	X	X			
Lamprophiidae					
Boaedon capensis (Duméril and Bibron, 1854)	X[bc]	X[bc]	X[bc]		
Lamprophis guttatus (Smith, 1843)	X	X	X		
Lycophidion capense (Smith, 1831)	X	X	X		
Lycophidion hellmichi Laurent, 1964[bd]	X	X	X		
Lycophidion multimaculatum Boettger, 1888	X	X			
Lycophidion namibianum Broadley, 1991[be]	X	X	X		(X)
Gonionotophis capensis (Smith, 1847)	X[bf]	X[bf]	X[bf]		
Gonionotophis nyassae (Günther, 1888)	X[bf]	X[bf]	X[bf]		
Gonionotophis vernayi (Bogert, 1940)	X[bf]	X[bf]	X[bf]		
Prosymnidae					
Prosymna angolensis Boulenger, 1915	X	X	X		
Prosymna bivittata Werner, 1903	X	X	X		
Prosymna frontalis (Peters, 1867)	X	X	X		
Prosymna sundevalli (Smith, 1849)		X			
Prosymna visseri Fitzsimons, 1959	X	X	X		
Pseudaspididae					
Pseudaspis cana (Linnaeus, 1758)[ba]	X	X	X		
Pythonodipsas carinata Günther, 1868	X	X	X		(X)
Psammophiidae					
Dipsina multimaculata (Smith, 1847)	X	X	X		
Hemirhagerrhis nototaenia (Günther, 1864)	X	X	X		
Hemirhagerrhis viperina (Bocage, 1873)	X	X	X		
Psammophis angolensis (Bocage, 1872)	X	X	X		
Psammophis brevirostris (Peters, 1881)			X		
Psammophis jallae Peracca, 1896	X	X	X		
Psammophis leopardinus Bocage, 1887	X[bg]	X	X		
Psammophis lineatus (Duméril, Bibron and Duméril, 1854)	X[bh]	X[bh]	X		
Psammophis mossambicus Peters, 1882	X	X			
Psammophis namibensis Broadley, 1975	X[bi]	X	X	X	X
Psammophis notostictus Peters, 1867	X	X	X		
Psammophis subtaeniatus Peters, 1881	X	X	X		
Psammophis trigrammus Günther, 1865	X	X	X		
Psammophis trinasalis Werner, 1902	X[bi]	X	X		
Psammophylax rhombeatus (Linnaeus, 1758)	X	X	X		
Psammophylax tritaeniatus (Günther, 1868)	X	X	X		
Psammophylax variabilis Günther, 1893	X	X			
Rhamphiophis oxyrhynchus (Reinhardt, 1843)	X[bj]	X			
Atractaspididae					
Amblyodipsas polylepis (Bocage, 1873)	X	X	X		
Amblyodipsas ventrimaculata Roux, 1907	X	X	X		
Aparallactus capensis Smith, 1849	X	X	X		
Atractaspis bibronii Smith, 1849	X	X	X		
Atractaspis congica Peters, 1877	X	X	X		
Atractaspis duerdeni Gough, 1907	X	X	X		
Xenocalamus bicolor Günther, 1868	X	X	X		
Xenocalamus mechowii Peters, 1881	X	X	X		
Elapidae					
Aspidelaps lubricus (Laurenti, 1768)	X	X	X		
Aspidelaps scutatus (Smith, 1849)	X	X	X		
Dendroaspis polylepis Günther, 1864	X	X	X		
Elapsoidea boulengeri Boettger, 1895	X	X	X		
Elapsoidea semiannulata Bocage, 1882	X	X	X		
Elapsoidea sundevallii (Smith, 1848)	X	X	X		
Naja anchietae Bocage, 1879	X[bk]	X	X		
Naja mossambica Peters, 1854	X	X	X		
Naja nigricincta Bogert, 1940	X[bl]	X	X		

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Table 2 (*continued*)

Species	Branch, 1998	Griffin, 2003	Uetz, 2011	Namibia endemic	Namib Desert endemic
Naja nigricollis Reinhardt, 1843	X	X	X		
Naja nivea (Linnaeus, 1758)	X	X	X		
Pelamis platura (Linnaeus, 1766)[bm]	X	X			
Viperidae					
Bitis arietans (Merrem, 1820)[ba]	X	X	X		
Bitis caudalis (Smith, 1839)	X	X	X		
Bitis cornuta (Daudin, 1803)	X	X	X		
Bitis peringueyi (Boulenger, 1888)	X	X	X		X
Bitis schneideri Boettger, 1886	X	X	X		X
Bitis xeropaga Haacke, 1975	X	X	X		
Causus rhombeatus (Lichtenstein, 1823)	X	X			

[a] Vargas-Ramírez et al. (2010) noted deep genetic divergence between nine clades in the Pan-African *Pelomedusa subrufa*, and indicated that a number of cryptic species await description. No Namibian material was included, but *P. galeata damarensis* Hewitt, 1935 is morphologically distinctive and may deserve specific recognition (Branch, unpubl. obs.).

[b] Fritz et al. (2010) noted distinct genetic lineages within *Pelusios rhodesianus* suggestive of cryptic taxa.

[c] Although Branch (1998) mapped *P. subniger* as peripherally occurring in the Caprivi, this is not confirmed by voucher specimens.

[d] As *Geochelone*.

[e] Haacke et al. (1997) and Griffin (2003) had no confirmed records for the Loggerhead Sea Turtle in Namibian waters. However, Petersen (2008) noted that turtles tagged in Tongaland, South Africa, had been recorded off Namibia.

[f] The geographically isolated subspecies *A. a. tirasensis* Haacke (1965) may deserve specific recognition.

[g] Early Namibian records (reviewed in Mertens, 1955 (as *Phyllodactylus*) and Griffin, 2002) have also not been confirmed by recent records. The gecko's commensal habits have resulted in a number of introductions out of its known range, e.g. many Cape offshore islands (Branch, 1991), and even St Helena Island (FitzSimons, 1943). A specimen from Swakopmund, Namibia (Griffin, 2002) may have resulted from a similar accidental introduction.

[h] As *Pachydactylus*.

[i] Cryptic diversity is known to occur within *C. fitzsimonsi* and will be described shortly (Bauer, pers. comm.).

[j] Cryptic diversity is known to occur within *C. turneri* complex and will be described shortly (Heinz et al., 2011; Bauer, pers. comm.).

[k] *Pachydactylus kochii* FitzSimons, 1959 was transferred to *Colopus* by Bauer and Lamb (2005). However, subsequent full taxon sampling of *Pachydactylus* and its relatives indicates that *Colopus* is embedded within *Pachydactylus* in which case the contained species should be transferred to the latter (Bauer et al., 2011a,b).

[l] Although Griffin (2002, 2003) consider the species could be expected in Namibia, and it is listed as such by Uetz (2011), the presence of the species in the country is not confirmed by voucher specimens (Bauer pers. comm.; Branch unpubl. obs). It may enter the region in the Eastern Caprivi.

[m] As *mariquesis,* which is now endemic to South Africa.

[n] Known from a single Namibian specimen (Namaskluft Inselberg, Branch et al., 1996) that requires confirmation.

[o] As *Palmatogecko*.

[p] As *Phelsuma*.

[q] As *bradfieldi diporus*.

[r] As *Acanthocercus atricollis*. Tree agamas comprise a suite of species (Wagner, in litt.), with the population in northern Namibian referable to *A. cyanocephalus* (Falk, 1925).

[s] Phylogeographic studies on *Agama atra* (excluding *A. knobeli* see [t]) have revealed significant genetic diversity, with a distinct Northern-central Southern African clade (Matthee and Flemming, 2002; Swart et al., 2009) that enters southern Namibia. Its taxonomic status has still to be addressed.

[t] As *A. atra knobeli*, which was subsequently shown to be a full species (Matthee and Flemming, 2002; Swart et al., 2009).

[u] Not indigenous to Namibia.

[v] As *Typhlosaurus*.

[w] A replacement name for *Typhlosaurus lineatus*.

[x] As *percivali*.

[y] As *Panaspis*.

[z] Eastern Caprivi specimens are referable to *A. maculilabris* (Jacobsen and Broadley, 2000). The status of the northern Namibian population (noted as being a potential new species by Griffin, 2003) is under investigation (Medina and Greenbaum, pers. comm.)

[aa] As *Riopa sundevalli*.

[ab] As *variegata punctulata*.

[ac] As *striata sparsa*.

[ad] As *striata wahlbergi*.

[ae] Portik et al. (2010) demonstrated that *T. sulcata nigra* was a coastal melanistic ecomorph that did not deserve genetic recognition. The status of Angolan *T. s. ansorgi* remains unresolved.

[af] Griffin (2003) signaled the presence of an undescribed *Meroles* sp. in Namibia, supported by allozyme differences between populations of *M. anchietae* in the southern and northern sand seas. Further studies, requiring modern gene sequencing are required to resolve this issue. However, Bauer (in litt.) considers an undescribed *Meroles*, related to *M. reticulatus,* to occur in the Kaokoveld.

[ag] Makhoka et al. (2007) noted deep genetic divergence between northern and southern populations and signaled the presence of cryptic species.

[ah] The apparently isolated population near Warmbad, Karasburg District (not shown in Branch, 1998) needs further study.

[ai] Bauer and Branch (2001) noted that the subspecies *P. l. pulchella* was allopatric and exhibited substantial morphological and ecological differences, and thought it best treated as a full species. This was confirmed by the genetic studies of Makhoka et al. (2007). The status of *P. l. inocellata*, which Haacke (1965) considered distinctive, remains unresolved.

[aj] Although Makhoka et al. (2007) noted deep genetic divergence between northern and southern populations of the species they sampled no specimen from southern Namibia and noted no morphological differences between the putative taxa. The status of these populations remains unresolved.

[ak] Angolan specimens previously refered to *P. undata* represent a separate radiation, and *P. undata* is thus endemic to Namibia (Conradie et al., 2012). The ranges of the new Angolan species *P. haackei* and *P. huntleyi* (Conradie et al., 2012) may both extend in to extreme northern Namibia.

[al] The taxonomic status of the isolated Fish River population is currently being assessed (Whiting in. litt.).

[am] *P. broadleyi* is common in cliffs on the south bank of the Orange River at Onseepkans, but remains uncollected on the north bank in Nambia (Branch and Whiting, 1997).

[an] Loveridge (1944) listed *C. cordylus angolensis* from Namibia, but Mertens (1955) reviewed the situation and considered early records to be due to confusion with *C. pustulatus*. The species is not known from Namibia. Griffin's (2003) possible report of *Cordylus* from the Brandberg remains unconfirmed.

[ao] The specific status of *C. machadoi* was confirmed by Stanley et al. (2011), but material from extreme northern Namibia was not assessed.

[ap] As *Cordylus*.

[aq] As *multilineatus auritus*.

[ar] As *auritus*.

[as] As *Angolosaurus*.

[at] Griffin (2003) listed the species as provisionally entering southern Namibia based on a visual sighting at Skilpadberg on the Lower Orange River. Bauer and Branch (2001) did not record it from the adjacent Richtersveld, but considered its presence there as possible. Its presence in Namibia remains unconfirmed.

[au] As *sphenorhynchus maurecei*. Treated as a race of *M. sphenorhynchus* by Broadley et al. (1976), but re-elevated to specific status by Broadley (2001).

[av] The status of *L. conjunctus* in Namibia is problematic. It was previously treated as a full species (Broadley and Watson, 1976) or with an eastern race *L. c. incognitus* (Branch 1998). However, Adalsteinsson et al. (2009) revealed deep genetic divergence among numerous populations assigned to both *L. scutifrons* and *L. conjunctus*. Although they studied no Nambian material the status of both species in Namibia needs further assessment.

[aw] Broadley and Wallach (2009), when proposing *Megatyphlops* for the giant southern African species, relegated the race *R. schlegeli petersi* (Branch, 1998) to synonymy.

[ax] The status of the isolated population of *R. lalandei* in central and southern Namibia should be assessed using molecular analysis.

[ay] Conservatively retained in *Coluber* pending molecular studies (Schätti and Ineich, 2004).

[az] The taxonomy of *Dasypeltis* is under review and Namibia may contain cryptic taxa (Bates et al., 2011; Bates, in litt.).

[ba] Wüster and Barlow (2011) report that a number of widespread species (e.g. *Dasypeltis scabra, Pseudaspis cana* and *Bitis arietans*) show strong phylogeographic patterns with multiple deep clades.

[bb] Although as new species to be described by Wulf Haacke has been signalled (e.g. Griffin 2003) it remains undescribed.

[bc] As *Lamprophis*.

[bd] Once considered more widespread due to confusion with *L. namibianum*; now known from a single Namibian record (Etengua; Broadley, 1991b).

[be] Recently recorded from Espinheira, southern Angola (Branch, unpub. obs.).

[bf] As *Mehelya*.

[bg] As *brevirostris*.

[bh] As *Dromophis lineatus*.

[bi] As *leightoni*.

[bj] As *rostratus*.

[bk] As *annulifera*.

[bl] As *nigricollis*.

[bm] Based on two vagrant specimens washed ashore at Henties Bay and Jakkalsputz (Griffin, 2002). The species is currently considered to be excluded from the Atlantic Ocean by the cold Benguela Current. However, the efficacy of this barrier may be compromised by continued global warming and extreme El Nino warm-water events.

3. General patterns of herpetological research

Herpetological research in Namibia has a long history, and Bauer (2003) discusses early German studies in the region. To indirectly assess herpetological research activity in Namibia yearly counts of publications on the herpetofauna since it's beginning in the 1800's are summarized in Fig. 1. Early publications (pre-1960) are derived from Channing and Griffin (1993) for amphibians and Griffin (2003) for reptiles, supplemented by recent publications abstracted from the literature. The analysis shows an almost even output until the 1960's with a slight increase during the 1970's. There is then an abrupt increase in the 1990's and early 2000's, with an equally remarkable drop-off around 2004. In Fig. 2, the publication frequency for the major herpetological research areas during the last fifty years are illustrated. As some research areas overlap considerably (i.e. ecology and physiology), only studies with a major focus in one of the seven research areas were considered. Two trends are prominent: (1) most contributions occur in faunistics and taxonomy, natural history, and to some extent systematics, with most of the research at the alpha taxonomy level but recently including beta taxonomic revisions and phylogenies (i.e. systematics); and (2) physiological and ecological studies targeting a few extremely psammophilous lizards. The species *Meroles anchietae* and *M. cuneirostris* in the dune fields of the Namib received most research attention in eco-physiological studies directed at temperature regimes, diet composition and reproduction or a combination of these (i.e. Cooper and Robinson, 1990; Nagy et al., 1991; Robinson, 1990a,b; Robinson and Cunningham, 1978). This also applies to aspects of natural history like reproduction, which largely overlaps with physiology. A few "model" lizard species (i.e. *Meroles anchietae*, *M. cuneirostris*, *Gerrhosaurus skoogi*), have been the most closely examined research subjects. Other groups receiving considerable attention are geckos (Nagy et al., 1993; Odendaal, 1979; Peterson, 1990), agamids (Heideman, 1994, 1995, 2002), and one gerrhosaurid species (*Gerrhosaurus* (previously *Angolosaurus*) *skoogi*; Clarke and Nicolson, 1994; Mitchell et al., 1987; Nagy et al., 1991;

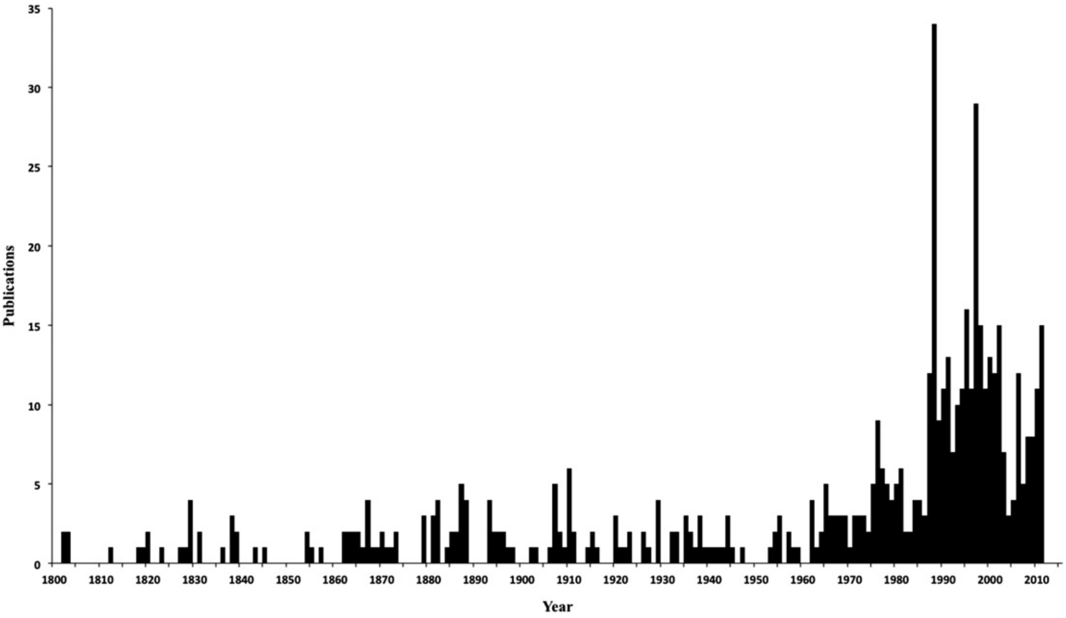

Fig. 1. Number of publications referenced by Channing and Griffin (1993, amphibians) and Griffin (2003, reptiles) by year of publication. Recent herpetological publications not referenced in either study or published after 1993/2003 are added.

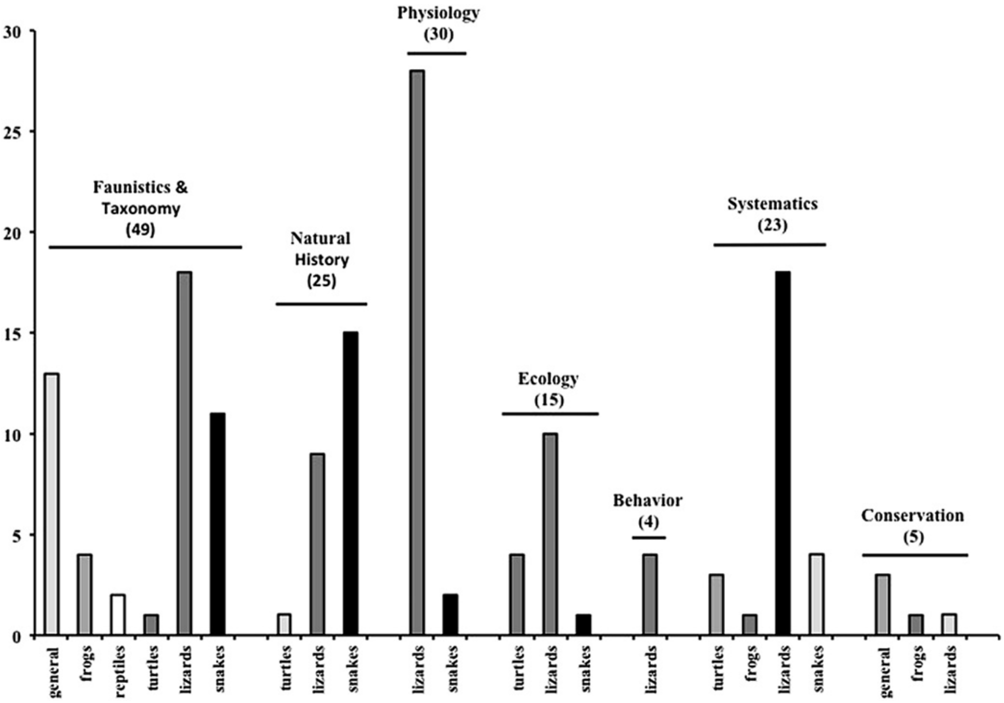

Fig. 2. Herpetological publications by research area and systematic group. Note that some studies can be placed in more than one research area. Thus the figure should be understood as depicting overall trends rather than distinct discipline specific numbers.

Pietruszka, 1988; Seely et al., 1988, 1990). Amphibians, chelonians and snakes have drawn less attention, except for a few studies on faunistics, alpha taxonomy, and molecular phylogenies.

When study locations are analyzed (Fig. 3), it is obvious that locations like Windhoek, Swakopmund, and especially Gobabeb, have attracted much attention. This is due to the infrastructure that exists at institutions of higher education, or the availability of housing and laboratories for researchers. Another popular study location (seven studies) is in the northern Namib dunes (Skeleton Coast National Park), situated at the Unjab river mouth and frequented by teams from Gobabeb to study the lizard *Gerrhosaurus skoogi*. This location is at the southern distribution limit for the species. Other study locations reflect the special interests of individual researchers and their logistics arrangements (e.g. guest farms, camps, etc.). Large areas of Namibia, such as most of the southern, eastern and northern areas, have not received much herpetological attention, and strategic sampling informed by geographic information systems (GIS) may identify areas of special interest and focus future efforts.

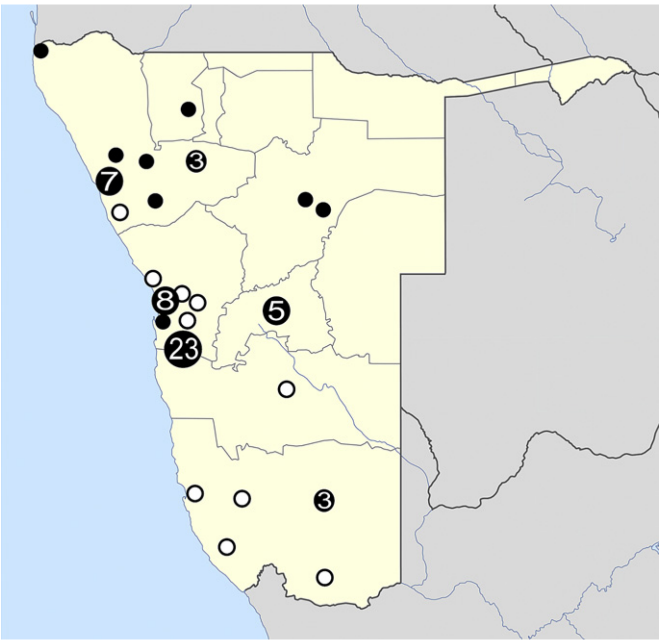

Fig. 3. Herpetological publications by geographical study location. Numbers within closed circles represent number of studies. Closed circles without numbers equal two studies, open circles equal one study. Note that only studies with a limited geographical scope are considered.

3.1. Faunistics, checklists, and studies on phylogeny and systematics

The foundation for a herpetofauna of Namibia was set by Mertens (1938, 1955, 1971) who listed 239 species (currently 338 species). More recent national lists for amphibians include Channing (1991, including an illustrated key to the species) and Channing and Griffin (1993). Reptiles were last summarized in Griffin's (2003) comprehensive annotated checklist that included comments on the species' conservation status. Excellent and up-to-date online databases include "Amphibian Species of the World" (Frost, 2011) and "The Reptile Database" (Uetz, 2011), both of which can be searched by country. For a summary and updated species checklists see Tables 1 and 2.

van den Elzen (1980) reviewed Namibian snakes in the scientific collection of the Zoologisches Forschungsmuseum Alexander Koenig, Germany. At the time the herpetological collection did not include any specimens from the Namib Desert. Bauer (1999) and Griffin (2000) note that Namibia has one of the richest lizard faunas in Africa, with high endemism mostly related to the Namib Desert. Herpetofaunal lists which include collections from geographic areas within Namibia are available for the southernmost area of Namibia (Burrage, 1978, although see cautionary comments in Branch, 1990), the Namib Desert Park (Stuart, 1980), the Sperrgebiet in the southern part of the Namib (Branch, 1994), the Gobabeb

Research and Training Center (Henschel et al., 2006), several locations in central Namibia (Bates, 1995), the Etosha National Park (Hoffmann, 1989), the Kamanjab district and adjacent Damaraland (Bauer, 1992; Bauer et al., 1993), and the northern Damaraland (Liebenberg, 1998). Bauer et al. (2001) noted the existence of a Trans-Kunene Mopaneveld center of endemism for herpetofauna, Heideman (1997) addressed the distribution of *Agama etoshae* in Ovamboland, and Tarr (1987) noted the occurrence of *Chelonia mydas* at the Kunene river mouth.

A number of regional phylogenetic studies and systematic reviews include large numbers of specimens from Namibia. Within lizards, gekkonids and lacertids have received by far the most attention. Brain (1962a) reviewed Barking geckos (*Ptenopus*) and described a new species. Haacke (1975a,b, 1976a,b,c,d) presented a series of publications dealing with the burrowing geckos of southern Africa, including systematic reviews and phylogenetic analyses (1975a; *Ptenopus*, 1976a; *Pachydactylus rangei* and *P. vanzylii*, 1976b; *Chondrodactylus angulifer*, 1976c; phylogenetic analysis, 1976d). Haacke and Odendaal (1981) discussed the distribution of *Rhoptropus* species in the central Namib Desert, focusing on the three species *R. afer*, *R. barnadi* and *R. bradfieldi* around Gobabeb, and presenting ecological as well as distribution data. In an initial phylogeny of *Rhoptropus*, Bauer and Good (1996) compared morphological and allozyme data, later adding mitochondrial DNA to the data set Lamb and Bauer (2001). They found discrete clades, including a "Namib group" and a "Pre-Namib group", and also elevated *R. bradfieldi diporus* to a full species (Bauer and Lamb, 2001). Intense study on *Pachydactylus* was initiated by McLachlan and Spence (1966, 1967) and Steyn and Mitchell (1967), with the description of new species from poorly known regions of northern Namibia. Bauer and Branch (1991) reviewed *Pachydactylus fasciatus*, and then the western populations of the *P. punctatus* complex (Bauer and Branch, 1995), resulting in the validation of *P. scherzi* as a distinct species. Two additional species were also described, based on further discoveries in northern Namibia (*P. parascutatus*, Bauer et al., 2002; *P. waterbergensis*, Bauer and Lamb, 2003), and phylogenetic relationships within the *Pachydactylus capensis* complex were reassessed (Bauer and Lamb, 2002). Branch et al. (1996) reviewed the *Pachydactylus namaquensis* complex, describing a new species (*P. haackei*) from the Karasberg. In a revision of the small, rupicolous geckos of the *Pachydactylus serval* and *weberi* groups, Bauer et al. (2006a) described a new species from the lower Orange River (*P. atorquatus*), and revived from synonymy or elevated from subspecies six taxa and adding a further eight new species to the genus (Bauer et al., 2006b). Still further discoveries in the *Pachydactylus serval–weberi* complex resulted in the description of two more Namibian species (*P. boehmei*, Bauer, 2010; *P. etultra*, Branch et al., 2011). Two phylogenetic studies of *Pachydactylus* and related genera used both mitochondrial and nuclear genes to elucidate systematic relationships (Bauer and Lamb, 2005; Lamb and Bauer, 2002). The study confirmed many of Benyr's (1995) earlier specific findings on specific boundaries in the larger species, and also necessitated significant generic readjustment, with the *P. bibronii* group being transferred to *Chondrodactylus*, *P. kochii* to *Colopus*, and *Palmatogecko rangei* and *Kaokogecko vanzylii* were subsumed within *Pachydactylus*. Lamb and Bauer (2006) demonstrated that reduction of subdigital lamellae occurred independently in different lineages of padless burrowing geckos. Leaf-toed geckos (previously *Phyllodactylus*) were reviewed in southern Africa (Bauer et al., 1996a; Branch et al., 1995a), with the erection of new genera to accommodate the southern African radiations (i.e. *Afrogecko* and *Goggia* in Namibia, Bauer et al., 1997). Roell et al. (2010) provide a multigene phylogenetic analysis of the day gecko genus *Lygodactylus*, although there is little diversification in the genus in Namibia.

Lacertid lizards have received considerable taxonomic attention (Arnold, 1991; Berger-Dell'mour and Mayer, 1989; Harris et al., 1998; Lamb and Bauer, 2003; Makhoka et al., 2007; Mayer and Berger-Dell'mour, 1988). The results have led to robust phylogenetic hypotheses and a good understanding of lacertid systematics in Southern Africa, that have been strengthened by recent studies on southern Angolan lacertids (Conradie et al., 2012). Early evolutionary studies on the southern African lacertid radiation employed phylogenetic analysis of morphology (Arnold, 1989). Later, Arnold (1991) used a large set of morphological characters and parsimony analysis to analyze relationships within *Meroles*, with which he synonymized the monotypic *Aporosaura*. Harris et al. (1998) add mitochondrial DNA characters to Arnold's analysis and revealed how branch length in lineages with adaptations to extreme environments, such as the Namib Desert, vary between morphological and genetic datasets. Lamb and Bauer (2003) revisited the genus *Meroles*, adding additional mitochondrial genes and samples from all described *Meroles* species ("complete taxon sampling"). They demonstrated that the pectinate pattern of the resulting phylogenetic tree reflected the evolutionary adaptive radiation from solid (rock), via loose (sand) substrates, to the extreme of aeolian sand dunes. Another lacertid genus, *Pedioplanis*, has been the subject of a molecular phylogenetic study using mitochondrial and nuclear genes (Makhoka et al., 2007), recently expanded by Conradie et al. (2012). The former authors suggest that the major *Pedioplanis* clades formed in the Miocene as a result of the emergence of the Benguela current and the associated change in climate.

Among agamas both the *Agama hispida* complex and *A. atra* have been the subjects of detailed studies. McLachlan (1981) revised the taxonomy of *A. hispida* and *A. aculeata* and described the new species *A. etoshae*. In a molecular study using mitochondrial genes, Matthee and Flemming (2002) found distinct clades within the southern rock agama *A. atra*, validating *A. knobeli* as a full species (it was previously treated as a subspecies of *A. atra* restricted to southern Namibia). Subsequent studies using additional nuclear genes confirmed these findings, and that of a divergent clade in the Northern Cape that enters Namibia in the Karasberg region (Swart et al., 2009), and whose taxonomic status has still to be addressed.

Contrary to Uetz (2011) and following Tilbury (2010) *Chamaeleo quilensis* is not treated as a valid species but a "variant" of *dilepis*. This agrees with Broadley and Howell (1991) who list *quilensis* as a synonym of *dilepis* in Tanzania.

In his revision of the southern African scincines of the genus *Typhlacontias*, Haacke (1997) described a new subspecies from Namibia. In a recent paper Lamb et al. (2010) synonymizd the genus *Microacontias* (Daniels et al., 2006), and transferred the two species *Typhlosaurus gariepensis* and *T. lineatus* to *Acontias*. As the name *Acontias lineatus* was pre-occupied the new name combination *Acontias kgalagadi* was proposed for *T. lineatus*. In addition, the subspecies *Acontias percivalli occidentalis* was raised to species status with *A. percivalli* restricted to East Africa and *A. occidentalis* occurring in Namibia.

The phylogenetic relationships of *Angolosaurus skoogi* were studied by Lamb et al. (2003), who revealed that despite its morphological uniqueness and numerous adaptations to life in sand dunes, it was embedded within *Gerrhosaurus*, of which *Angolosaurus* became a synonym. The case resembles that of *Meroles anchietae*, which, before genetic analyzes, had been placed in the monotypic genus *Aporosaura*. In both cases adaptation to the extreme habitat of aeolian slip faces led to substantial morphological change which confused phylogenetic placement. Both mirror the taxonomic confusion of the Web-footed gecko, previously placed in the monotypic genus *Palmatogecko*.

A recent revision of the family Cordylidae (Stanley et al., 2011) based on mitochondrial and nuclear genes had taxonomic consequences for five Namibian species. The former *Cordylus* species *jordani* and *polyzonus* now constitute the genus *Karusasaurus*, whilst *C. campbelli*, *C. namaquensis*, and *C. pustulatus* are now placed in the new genus *Namazonurus*.

Studies on Namibian snakes have not been as extensive as those on lizards. Broadley (1975, 1977, 2002) has studied the systematics and taxonomy of sand snakes (*Psammophis*), and Kelly et al. (2008) provided an excellent molecular phylogeny of the Psammophiidae that resulted in a number of significant changes to the taxonomy of the group. *Dromophis* was synonymized with *Psammophis* (i.e. *Psammophis lineatus*), *Psammophis philippsii* and *P. subtaeniatus* were shown to be distinct monophyletic lineages, and *P. phillipsii* and *P. mossambicus* were conspecific. Moreover, little support was found for Broadley's (2002) action in raising *P. trinasalis* and *P. namibiensis* to specific status (both had previously been treated as subspecies of *P. leightoni*). The taxonomic status of both remains unresolved.

Haacke (1981) reviewed file snakes (*Mehelya*) in Southern Africa, particularly new Namibian material, including the first record of *Mehelya nyassae* in the country and confirming the status of *M. vernayi*. Kelly et al. (2011) showed that *Mehelya* was paraphyletic with respect to west and central African *Gonionotophis* Boulenger, 1893. The latter has priority and therefore necessitated the generic reassignment of all former *Mehelya* to *Gonionotophis*. Other major taxonomic readjustments resulting from this study (Kelly et al., 2011) was resurrection of *Boaedon* Duméril, Bibron and Duméril, 1854 for the brown house snake complex, with *Lamprophis* restricted to a clade of small house snakes mainly occurring in South Africa but with *L. guttatus* extending into southern Namibia. Hughes (1997) revived *capensis* for southern African house snakes previously assigned to *fuliginosus*. However, Kelly et al. (2011) showed additional deep genetic divergence within brown house snakes from the subcontinent, which are the subject of ongoing study (Kelly pers. comm.).

Broadley revised the southern African members of *Atractaspis* (1991a), reviving *A. duerdeni*. The status of the apparently isolated Namibian population requires genetic assessment. He also reviewed Namibian file snakes (*Lycophidion*), describing the new species *Lycophidion namibianum* (Broadley, 1991b), and southern African shield cobras (*Aspidelaps*), rejecting the race *Aspidelaps lubricus infuscatus* (Broadley and Baldwin, 2006). The taxonomy of spitting cobras in Namibia has been confused. The Black spitting cobra (*Naja nigricollis*) is know from very few specimens from Caprivi, and has a marginal presence in the subcontinent. Two southern races of this species were recognized (Branch, 1998), with *N. nigricollis woodi* in the south and *N. n. nigricincta* in the north. Griffin (2003) treated both as full species, but Wallach et al. (2009), elevated the latter to a full species, with *N. nigricinta woodi* as a southern race. After a detailed comparison with small *Bitis* species from southern Namibia, Haacke (1975b) described *Bitis xeropaga* from Southern Namibia and the Northern Cape province, whilst Branch (1999) reviewed the southern races of *Bitis cornuta*, raising them to specific status and making *B. cornuta* monotypic.

There have been few recent studies on the systematics of Namibian chelonians. The taxonomic confusion concerning the small tortoise from the vicinity of Aus, which for a long time was known as *Homopus* 'bergeri', was resolved and a new name (*Homopus solus*) described (Branch, 2007). Similarly, Fritz et al. (2010) confirmed that morphological variation in Leopard tortoises, *Stigmochelys* (previously *Geochelone*) *pardalis*, including Namibian material, was ecotypic and rejected all subspecies. Cooper and Branch (1999) described subfossil tortoise material (Testudinidae) from the Brandberg, whilst Lapparent de Broin (2003) reviewed Miocene chelonians from southern Namibia. Although no Namibian material was included in the study of Vargas-Ramírez et al. (2010) on pelomedusid terrapins, Damara material (for which the name *Pelomedusa galeata damarensis* Hewitt, 1935 is available) are morphologically distinctive and may deserve specific recognition (Branch, unpubl. obs.). Deep genetic divergence was also noted within *Pelusios rhodesianus*, again indicating the presence of cryptic taxa (Fritz et al., 2011).

Tomopterna is the only Namibian amphibian group that has been studied phylogenetically. Dawood et al. (2002) provide a molecular phylogeny of southern African *Tomopterna*, which resulted in the description of *T. damarensis* from the vicinity of Khorixas (Dawood and Channing, 2002). They found that acoustic and molecular characters were diagnostically important as morphological characters failed to distinguish *T. damarensis* from close relatives.

3.2. New species discoveries in Namibia

Over the last 50 years a total of six amphibian and 38 reptile species with distributions in Namibia were formally described. Three of the frog species are in the genus *Tomopterna* and two of the four new species (*Ptychadena mapacha*, *Tomopterna damarensis*) are currently endemic to Namiba (see note in Table 1). The new reptile species include one tortoise, 30 lizards, two amphisbaenids, and six snakes. Thirty of the reptile species were described from Namibia and 22 of these are endemic (*Homopus solus*, *Pachydactylus boehmei, P. etultra, P. gaiasensis*, *P. griffini*, *P. haackei*, *P. maraisi*, *P. mclachlani*, *P. oreophilus*, *P. otaviensis*, *P. parascutatus*, *P. reconditus*, *P. sansteynae*, *P. waterbergensis*, *Ptenopus carpi*, *P. kochi*, *Rhoptropus diporus*, *Agama ethosae*, *Typhlosaurus braini*, *Pedioplanis husabensis*, *Coluber zebrinus*, *Psammophis namibiensis*). Of the 38 reptile species described, 22 (58%; 73% of lizards) are geckos and 15 of these were described between 1996 and 2011 (Bauer and Lamb, 2005; Bauer et al., 1996a, 2002, 2006a,b; Bauer, 2010; Branch et al., 1996, 2011; Heinicke et al., 2011). Eighteen of the newly described species are members of *Pachydactylus*, which represents 46% of all Namibian species in the genus and 26% of all Namibian gecko species.

3.3. Life history and ecology

3.3.1. Life history and ecology observations

Life history and ecology are extensive fields that can cover every aspect of an animals' life. Contributions range from comprehensive in-depth studies of one or two species that address a wide array of different biological aspects to short notes on very specific aspects of a species' biology. Certain species or groups, possibly linked to accessibility and researcher interest, seem to be more "popular" than others.

There have been a few ecological studies on chelonians in Namibia, including captive studies on the endemic Nama padloper, *Homopus solus* (Cunningham and Simang, 2007; Schleicher, 2004; Schleicher and Loerh, 2001), and on wild Bushmanland tent tortoise *Psammobates tentorius verroxii* (Cunningham and Simang, 2008). In the latter study four females were radio-tracked over a short period of time. The authors found a bimodal activity pattern with peaks in the morning and late afternoon and a female home range of 32 ha. Diet analysis by observation of feeding tortoises confirmed a diet of 17 different plants with grasses, herbs, bulbs, and succulents being the most abundant (combined 93%) and some instances of weathered bone. Four plant species accounted for about three quarters of all observed instances.

Due to their visibility and often specialized morphologies, lizards have attracted more attention from ecologists, particularly the Namib plated lizard (*Gerrhosaurus skoogi*). Pietruszka (1988) studied the social structure and sexual dimorphism of the species. His findings showed that males possessed spur scales, had black coloration on their head, neck, and ventrum, and were considerably larger than females. Combat injuries between males occurred during the breeding season, and male larger size may be a result of sexual selection or due to advantage conferred in combat. Females were smaller, investing considerable energy in reproduction. He also discussed the application of stomach-flushing to Namib Desert lizards (Pietruszka, 1987).

The charismatic Namib geckos and their natural history and ecology have been addressed multiple times (Brain, 1958). Werner (1977) studied the ecology of geckos in the vicinity of Gobabeb for a period of five days. Bauer et al. (1989) commented on the role of a termite species accessible as food to five gecko species during short termite activity bouts, and highlighted their importance as short-term high-energy foods resources for the lizards. Russell and Bauer (1990) examined the unusual fully webbed feet in *Pachydactylus rangei* and concluded that the morphology, and the associated excavation behavior, was very specialized, since it impedes the movement of single digits and is restricted to specific substrates. *Pachydactylus rangei* males show spermatogenesis in spring and summer with eggs being laid from November to May, whilst females produce multiple clutches per year with two eggs each (Goldberg, 2008). Furman (1994) noted various observations on the biology of wild and captive Web-footed geckos. Barking geckos (*Ptenopus garrulus*) eat mostly termites, by number and volume (Hibbitts et al., 2005). Males of this species mature late, possibly related to their ability to "bark" in "barking competition" which becomes more competitive with increasing body size. Females lay only one egg, which always develops in the right ovary. In rare occasions a second egg develops, also in the right ovary. This is very exceptional as two eggs are a very consistent trait for the entire family Gekkonidae. The large ground-dwelling species *Chondrodactylus angulifer* lays up to two clutches with two eggs each from November to January (Goldberg, 2006a). The reproductive cycle is very similar to *Chondrodactylus bibronii*, a species closely related to *C. angulifer* that retains toe pads and is abundant in vertical habits on rocks, trees, and buildings. The diverse and well-studied gecko radiation in Namibia has allowed a number of comparative ecomorphological studies to be assessed within a phylogenetic framework (e.g. Bauer et al., 1996b; Johnson et al., 2005; Russell and Bauer, 1990). In addition, captive studies on some geckos have shed light on aspects of reproduction and growth (Barts, 2002, 2007, 2008, 2009; Barts and Kolwalski, 2006; Boone and Barts, 2006).

The relation of diet as a possible indicator of size-related microhabitat partitioning was studied in *Trachylepis striata* (Heideman and Bates, 1999). In an interesting comparative study, including aspects of both diet and morphology, Castanzo and Bauer (1998) noted ecological convergence between sympatric lacertids and the terrestrial skink *Trachylepis acutilabris*.

Burrage (1973) provided a comprehensive study on the ecology of *Chamaeleo namaquensis*, contrasting it with that of *Bradypodion pumilum*, a dwarf chameleon from the southwestern Cape, South Africa. He examined a large number of life history traits such as water balance, activity patterns, home range, diets, and reproduction. *Bradypodion pumilum* is not indigenous to Namibia, although it has been introduced to gardens in Lüderitz, Swakopmund, and Walvis Bay (Griffin, 2003).

Meroles suborbitalis is the dominant diurnal lizard in the gravel plains east of Swakopmund (Erb, 1984). The growth rate is slow and lizards reach maturity in their third year. Clutch sizes reach from four to eight eggs. Arnold (1995) compared sand diving in lizards, including Namibian species (*Meroles*), and concluded that their adaptations to aeolian substrates represented striking examples of convergence. Males of the Bushveld lizard *Heliobolus lugubris* produce sperm almost all year around (Goldberg, 2006b), but neonates hatch from January to April in synchrony with summer rainfall in many areas. Heideman (1998) described reproduction in *Agama etoshae*, and also noted that males have larger head sizes than females whilst subadult males do not, implying growth during adulthood (Heideman, 2001). Cooper and Whiting (2007) showed that the flight initiation distance in three lizard species from different systematic groups (*Agama planiceps*, *Trachylepis acutilabis*, *Rhoptropus boultoni*) was universal but that escape tactics depend on the habitat of each species. Several studies (Phillips, 1995; Phillips and Millar, 1998; Phillips and Packard, 1994) contributed details on the ecology and reproductive biology of *Varanus albigularis* in Etosha National Park. Food shortage, not temperature, limits the activity of *V. albigularis* during the cool dry season. Estimates of monitor biomass in the study area surprisingly rivaled the biomass of large predators such as lions.

Not surprisingly, venomous snakes are a popular herpetological group, with a relatively high number of natural history notes. Peringuey's adder (*Bitis peringueyi*) can be active at any time of the day, produces litter sizes of four to ten neonates, and has a three to one ratio of black versus tan tail tips (Robinson and Hughes, 1978). Later, Reiserer and DeNardo (2000) revisited litter size and tail tip color in the species and confirmed that the tail tip color ratio in their litters followed a non-sex-linked two-allele system with tan dominant to black. Douglas (1981) observed litter sizes of 16 and 27 in two female *Bitis caudalis* from the Swakop river valley, and Hoffmann (1988a) reported on a number of natural history aspects of the species based on specimens from Gobabeb. An exceptionally large female *B. caudalis* (TL 60 cm, mass 262 g) came from the Eastern National Water Carrier, a canal east of the Waterberg plateau (Haacke, 1995). Branch et al. (2002) reported on a small *B. caudalis* (TL 14 cm, mass 2.02 g) that has eaten an adult (TL 8.5 cm, mass 3.2 g) Carp's barking gecko (*Ptenopus carpi*), representing a relative prey mass (RPM) of 1.6, which may be the largest RPM recorded for any snake. A specimen of *Aspidelaps lubricus* was caught at Gobabeb and accepted a variety of gecko species as food (Hoffmann, 1988b). Studies on non-venomous snakes are rare, and mainly restricted to charismatic species (e.g. *Pythonodipsas carinata*, Stuart, 1976).

3.3.2. *Life history and ecology studies based on scientific specimen collections*

Over the last decades the examination of preserved specimens from scientific collections for life history traits such as sexual dimorphism, reproductive status, diet, and overall body condition has become a substantial part of life history studies in reptiles. *Meroles anchietae* and *M. cuneirostris* show differences in their reproductive cycles although they inhabit almost the same habitat. This may be related to the feeding strategy differences in the two species (Goldberg and Robinson, 1979). In a study examining about 100 specimens of each species a diet of coleopterans and hymenopterans was identified for *Meroles cuneirostris* and of mainly seeds for *M. anchietae* (Murray and Schramm, 1987). The authors suggested that the latter diet can be reduced depending on the abundance of insect prey, which in turn depends on climatic conditions, e.g. precipitation. Heideman (1993) examined the social organization and behavior during the breeding season of two agamids (*Agama aculeata* and *A. planiceps*), and the reproductive strategies (Heideman, 1994), whilst Billawer and Heideman (1996) investigated the diurnal activity of males. Although congeners, the two species differ in their biology: *A. planiceps* is a rock dweller with a relatively larger investment in offspring, whereas *A. aculeata* is a ground dweller with relatively less investment in offspring.

Snakes are notoriously elusive and in many cases difficult to study under field conditions. Shine and colleagues used the many snake fatalities in the Eastern Water Carrier (Griffin et al., 1989), supplemented with preserved specimens from scientific collections, to investigate natural history aspects of shield nose snakes (*Aspidelaps scutatus*; Shine et al., 1996), the Western Keeled snake

(*Pythonodipsas carinata*; Branch et al., 1997), horned adders (*Bitis caudalis*; Shine et al., 1998), burrowing snakes (Atractaspididae; Shine et al., 2006a), psammophiid snakes (Shine et al., 2006b), and scolecophidians (Webb et al., 2001, 2000a) and amphisbaenians (Webb et al., 2000b). By doing so the authors accrued data on large numbers of snakes on which they were able to perform statistical analyzes to tease apart sexually dimorphic traits. Some surprising insights were obtained. Despite their reproductive combat behavior, male *Bitis caudalis* are smaller than females, and specimens from arid areas are larger in size but not mass, eat more homoeothermic prey, and have larger litter sizes. Psammophiid snakes were found (Shine et al., 2006b) to display no sexual size dimorphism, to have low to moderate egg numbers, and diets that varied with size with larger specimens eating more mammals. Overall, the biology of psammophiid snakes is unusual and warrants additional attention.

3.4. The eco-physiology of Meroles anchietae, M. cuneirostris and Gerrhosaurus skoogi and other reptiles

The majority of eco-physiological studies in Namibia have focused on only three lizard species in the central Namib. The Gobabeb Research Station has played a predominant role, both as a study site and a supporting research facility. Eco-physiological herpetological studies started with temperature tolerance studies on three lacertid and one gekkonid species in the central Namib (Brain, 1962b). Other studies on lizard temperature and lizard thermoregulation followed (*Meroles anchietae* Holm, 1973; *Rhoptropus* Louw and Holm, 1972; Mitchell et al., 1987; Odendaal, 1979: *Gerrhosaurus skoogi* – Seely et al., 1988; Seely et al., 1990). One study (DeNardo et al., 2002) used Horned adders (*Bitis caudalis*) from Namibia for ambient temperature activity trials in captivity. The study showed, in captivity, that snakes were relatively inactive at lower ambient temperatures including those at which gecko prey remain active. The study concluded that field studies were needed to understand the natural dynamics of predator–prey interactions at low ambient temperatures.

In arid environments water plays a pivotal role and in concert with food is often the limiting resource for survival and reproduction. Consequently, a number of studies focus on the water physiology and diet of reptiles in the Namib Desert and other arid areas. Louw (1962) studied the utilization of fog water by the sand dune dwellers *Meroles anchietae* and *Bitis peringueyi*. After a typical Namib Desert fog event the extended stomachs of *Meroles anchietae* are filled with water, which, within a few days, is contained in the caecum. Food varied from kelp flies at coastal locations, where kelp is washed up the beach, to mostly grass seeds further inland. *Bitis peringueyi* exhibits behavioral adaptations for fog water harvesting. Another Gobabeb study proved that *Meroles cuneirostris* had a carnivorous diet (like most lizards), whereas *Meroles anchietae* was omnivorous, shifting between plant and insect depending on the abundance of the respective food types (Robinson and Cunningham, 1978). As insect abundance is correlated to rainfall, the lizards dietary flexibility can be viewed as an adaptation to the hyper-variable desert habitat, where the water and prey abundance vary dramatically (Robinson, 1987). *Meroles cuneirostris*' carnivory may not be obligatory, but shaped by a different microhabitat (inter-dune valleys), which do not require an omnivorous strategy as in the dune slip-face habitat of *M. anchietae*. Murray (1984) corroborates that *M. anchietae* eats more seeds in dry years. However, mature seeds cannot be digested efficiently (Nagy and Shemanski, 2009), and as a consequence, mostly young moist ovules were ingested. Territorial males exhaust their energy reserves (large fat bodies) completely until they are unable to defend their territories (Robinson, 1984). Cooper and Robinson (1990) studied the water balance and bladder function in *Meroles anchietae* and concluded that the lizards almost always exhibit a negative water budget. Nagy et al. (1991) and Clarke and Nicolson (1994) followed with similar studies on *Gerrhosaurus skoogi*. Heideman (2002) compared the diets of the two *Agama* species, *aculeata* and *planiceps*, relative to breeding and non-breeding season, and found that the diet largely mirrors the abundance of prey items per season. Females seem to fit a "wait-and-sit-predation" strategy, possibly induced by their heavy egg load. In another study the same author (Heideman, 1995) compared the abdominal fat body and liver condition of males of the two species and correlated this to reproductive activity.

Herbivory in lizards is exceptional. A Namibia herbivorous lizard is *Gerrhosaurus skoogi*, which inhabits the Namib sand dune environment (Pietruszka et al., 1986). This lizard is largely dependent on the melon *Acanthosicyos horridus* (!Nara) for fog water, which collects on the plant. The lizard will also eat the plant, if other water sources are unavailable. Additionally, *G. skoogi* eats grasses, seeds, and very occasionally insects (only 18% of the diet, Mitchell et al., 1987). However, !Nara seems to constitute the main water source whereas seeds supply energy.

A paradoxically low metabolic rate was discovered in the diurnal gecko *Rhoptropus afer*. This species exhibits lower metabolic rates than found in nocturnal geckos. The habitat, with very few resources and almost no competitors, seems to allow for this phenomenon (Peterson, 1990). Only the diurnal night lizards (sic) of the genus *Xantusia* in North America display an equally low metabolic rate (Nagy et al., 1993).

The eco-physiologies of *Meroles anchietae*, *M. cuneirostris*, and *Gerrhosaurus skoogi* are among the most studied of any lizard species, and their well-understood thermal biology make them excellent candidates for climate change studies.

4. Herpetological conservation

With 2.6 inhabitants per square kilometer Namibia has the second lowest human population density in the world (CIA World Fact Book, online available at https://www.cia.gov/library/publications/the-world-factbook/geos/wa.html). Large areas experience low to very low human impact, even from agricultural practices such as cattle ranching. Consequently, environmental pressure through anthropogenic activities is generally low. However, there are areas of concern. As Namibia is predominately an arid to semi-arid country, wetlands are few and where they exist they are often heavily impacted by human use. Water is a limited resource and structures related to providing water to humans and their livestock impact the surroundings. This is exemplified by the faunal impacts of the Eastern Water carrier (Griffin et al., 1989). Mining for minerals is a major revenue contributor to Namibia's economy and often degrades the natural environment over extended areas. It is dependent on large amounts of energy and water and impacts these resources with their environmental footprint accordingly. Rangeland mismanagement in agricultural areas has led to bush encroachment with effects on the local herpetofauna. In addition, the impacts of climate change in Namibia are not yet understood and need attention. Alien herpetological species are restricted to localized populations of chameleons and tortoises that have had no significant faunal impacts. However, the common translocation of tortoise specimens across Namibia and South Africa has possibly led to increased genetic pollution in indigenous populations (Griffin, 2000). The Namibian populations of the lizard species *Afrogecko porphyreus* and *Bradypodion pumilum* are considered introduced. The former species is only known from one specimen in Namibia, but is known to have been translocated to numerous locations in South Africa, and even to St Helena Island (Branch, 1991). The latter is very limited in its Namibian range, where it is restricted to human settlements. It lacks the characteristics of an invasive species.

4.1. *Species conservation status*

Although no Namibian amphibian and reptile species are listed as Endangered by Namibian conservation authorities (Checklist and Provisional National Conservation Status of Amphibians, Reptiles and Mammals Known or Expected to Occur in Namibia, 1999, http://www.nnf.org.na/rarespecies/rare_library/documents/CHKLST.PDF; Griffin, 2003), this list is dated and for some species may be inaccurate. Many recent descriptions of new species make comments on conservation issues (e.g. Bauer, 2010; Bauer et al., 2011a,b; Branch et al., 2011), with most being either of Least Concern or Data Deficient. No Namibian amphibians are listed as threatened. Four tortoise species (*Stigmochelys pardalis*, *Kinixys spekii*, *Psammobates oculifer*, *P. tentorius*), both monitor species (*Varanus albigularis*, *V. niloticus*), and one python species (*Python natalensis*) are locally listed as vulnerable, and all are listed on CITES Appendix II, which controls their international trade. The Nama padloper (*Homopus solus*) is still listed as Vulnerable (IUCN Red List, 2010), although Branch (2007) noted there was no evidence of declines in either species number or extent of quality of habitat. The diversity, distribution and conservation of chelonians in southern Africa was reviewed by Branch et al. (1995b). Some charismatic species, e.g. Peringuey's dwarf adder (*Bitis peringueyi*) and the Dwarf desert python (*Python anchietae*) may be specifically targeted for the international pet trade. Both species, however, have extensive ranges, albeit they may suffer local extirpation at accessible sites. Branch and Griffin (1996) assessed the distribution and conservation of *P. anchietae*, whilst Hebbard and Cunningham (2002) discuss captive reproduction. Most reptile species of conservation concern are concentrated in the area northwest of Windhoek extending to the Kunene river region (Griffin, 2000).

4.2. *Water and wetlands*

An example for water related conservation issues is the Eastern National Water Carrier, a canal built to transport water from the Okavango River in the north, where water is abundant, to the dry interior of Namibia. The canal was partially completed and stopped in 1996 after concerns arose about the Okavango River water flow and the future of the Okavango delta in Botswana. In an extensive survey over 150 days, large numbers of amphibians and reptiles were found along the approximately 200 km of the open canal section (Griffin et al., 1989). The canal acted as a trap and resulted in heavy mortalities. Over its length the canal was in sections dry or filled with water and both, the presence and the absence of water, eventually had lethal effects with animals being trapped in the canal due to the steep sides. Most impacted herpetological groups were snakes, tortoises, and frogs, especially *Pyxicephalus adspersus* of which more than 1500 adult specimens were found in the canal. However, the impact of the canal as a sink for neighboring populations was considered non-detrimental as the mortality numbers remained unchanged over several years (Griffin, 2000). The long-term impact of the carrier on these populations, however, remains unassessed.

Another water-related area of concern is “large dam projects”, planned to secure electrical power to sustain national demand. One such hydroelectric power dam already exists at the Ruacana waterfalls of the Kunene, the third largest river in Namibia, which marks the border to Angola. Since the early 1990's another large dam is planned at the Epupa waterfalls or more recently further downstream at the Baynes Mountains. Simmons et al. (1993) discuss the unique tropical avi- and herpetofauna of the lower Kunene and its estuary, and note flow parameters and geomorphology. They caution that the proposed dam will alter conditions at these unique sites with potentially severe impacts on the ecological communities. The Kunene river mouth with its populations of sea and softshell turtles constitutes a unique habitat (Griffin and Channing, 1991). Griffin and Channing (1991) point out that a number of wetland-associated species, such as *Phrynomantis affinis* and *Poyntonophrynus hoeschi*, lack biological data. None of these species, however, are considered threatened. Curtis et al. (1998) addressed the species richness and conservation of freshwater fauna. Most of the freshwater habitats in Namibia are unprotected and threatened by overexploitation and flow regulation.

4.3. *Endemism*

Endemism in Namibia is mainly restricted to unprotected areas (Simmons et al., 1998; Tables 1 and 2; Griffin, 2000). Geographical endemism patterns in snakes and amphibians do not correlate with other major animal (including lizards) and plant groups. The authors assumed hidden endemism and predicted that molecular genetics would reveal a number of yet unrecognized species. They recommended that planning of proposed conservation areas take endemism hotspots into account. The most specious genus in the Namibian herpetofauna is the gekkonid genus *Pachydactylus*, with a large number of recently discovered species and possibly more awaiting discovery. Within Namibian *Pachydactylus* 19 species are endemic, and the genus is particularly diverse along the Northern Namibian Escarpment, which corresponds to a regional center of endemism for reptiles in general (Bauer, 2010). The high species richness and endemism within *Pachydactylus* is related to substrate specificity as a cladogeneic agent (Bauer, 1999).

4.4. *Bush encroachment*

Overgrazing and the disruption of natural fire cycles cause bush encroachment, mainly by *Acacia mellifera*, in Namibian rangeland (Joubert et al., 2008). It constitutes a major problem for agriculture and the environment. Meik et al. (2002) compared lizard assemblages in open savanna habitat with bush encroached habitat on commercial rangeland. Their findings provide a first indication that lizard communities in bush encroached habitat are impoverished, although certain species (i.e. *Trachylepis*) may thrive and become super-abundant. A study on the lacertid *Pedioplanis lineoocellata* in grazing-induced degraded areas in the southern Kalahari showed that lizards change their behavior and home range size in degraded areas (Wasiolka et al., 2009a,b).

4.5. *Mining*

Namibia is rich in minerals and mining diamonds, uranium, gold, zinc, copper and lead. Recently, Namibia has experienced a uranium-mining boom with two large active mines and ten or more uranium mines in the prospecting stages. Several of the uranium mines will be located within the Namib-Naukluft National Park at a relatively short distance from Gobabeb. The recent boost in uranium mining in Namibia is largely caused by the world market price of uranium at a 30 year high and the increasing demand for nuclear power as an alternative to other commodities such as oil, gas, and coal. Additionally, nuclear power is seen as a cleaner energy alternative to more traditional energy sources, notably as a climate change sensitive alternative. Worldwide, nuclear power contributes 17% to electric power generation (Mischo, 2008), more than oil (11%) and gas (14%). Uranium mining is large-scale open pit mining with extensive water and energy demands.

In Namibia, uranium deposits are concentrated in the central Namib region and the northwestern part of the country (Kunene region). Five main impacts of uranium mining in Namibia have been identified (Pallett, 2008): (1) dust pollution and airborne radiation, (2) groundwater contamination, (3) cumulative water and energy demands, (4) fragmentation of habitats, and (5) socio-economic effects on the environment through the increased number of people working and living in the areas. All these impacts have significant cumulative effects. Furthermore, they can have effects on habitats geographically separate from the mining areas such as the Kunene river. Hydroelectric dam projects are proposed along the Kunene in biologically sensitive areas to satisfy national and mining energy demands. As amphibians and especially reptiles are dominant vertebrates in the arid environment of the Namib Desert they will be impacted by mining activities, and therefore are good indicator and model species. Thorough surveys and monitoring efforts of impacted populations are necessary to assess, manage, mitigate, and possibly restore, mining impacts.

4.6. Climate change

Climate change is likely to exacerbate the dry conditions in Namibia, with rain falling less evenly and in a burst like fashion leading to localized flooding (Reid et al., 2008). Moise and Hudson (2008) predict a 10–20% increase of drying in parts of Namibia. How climate change will affect amphibian and reptile species is unknown. Although the connection of climate warming and amphibian and reptile decline has remained controversial, recent studies have linked climate change to a decline in biodiversity with severe impact on amphibian and reptile populations and species (D'Amen and Bombi, 2009; Galloy and Denoël, 2010; Rohr and Raffel, 2010; Sinervo et al., 2010; Sohdi et al., 2008).

5. Future directions

Strategic sampling and surveying is still warranted for selected areas in Namibia. To identify these areas geographic information systems can be of assistance. In parallel with new surveying in selected areas, known populations of herpetological species need surveys and monitoring to assess their conservation status. This is especially warranted for Data Deficient species.

A major trend in biology is the application of genetics and, more recently, genomics. In both, evolutionary and conservation biology, these technologies offer unparalleled resolution and insight, and will become increasingly applicable as cost decreases. Although there is increasing use of molecular phylogenetic studies on amphibians and reptiles in Namibia, studies at the population level and conservation genetics are largely absent. Next Generation Sequencing platforms allow for the development of large DNA marker panels, which are important for genetic comparisons at the individual (e.g. kinship studies, wildlife forensics) and at the population level (population differentiation, population fragmentation, genetic bottleneck analysis, etc.). The first amphibian and reptile genomes will be publicly available soon, and genomics together with low cost genetic technologies will empower herpetological conservation genetics in Namibia.

Here we summarize areas where DNA marker and genome-enabled studies will become important:

(1) Excellent molecular phylogenies including Namibian taxa (especially geckos, lacertid lizards, and psammophiid snakes) have been produced in the recent past (see above). Other groups in need of such detailed studies are Namibian *Poyntonophrynus*, *Tomopterna*, *Pyxicephalus*, *Trachylepis*, and several snake groups including *Lamprophis*, *Aspidelaps*, the *Naja nigricollis–nigricincta* complex, and the viper species *Bitis caudalis* and *B. peringueyi.* These taxa are likely to show deep divergence and to include cryptic species. Phylogenetic studies should be based on comprehensive sampling across geographic areas ("complete taxon sampling"), striving to provide a complete set of samples across species and populations of interest.

(2) Genetic monitoring of populations impacted by mining and large hydroelectric dam projects. High-resolution genetics allow the study of population impacts in real time, and can reveal what exactly happens to natural populations and how they recover from or adapt to habitat alteration.

(3) Habitat fragmentation and its impact on populations. Although habitat fragmentation is one of the major drivers of evolutionary processes, population fragmentation is now predominately caused by anthropogenic structures and activities and happens at an unparalled pace. In Namibia, examples of such man-made barriers are the Eastern National Water Carrier, which poses a barrier for herpetofauna and other faunal groups, and mining operations with access roads, open pits, and numerous other habitat altering consequences.

(4) Amphibians and reptiles are ectotherms and are excellent vertebrate models for climate change studies. Generally, they are more or less restricted to their immediate surroundings as they are relatively sedentary with reduced ability to migrate in the face of rapid climate change. Many species have short generation times with a relatively fast fixation of mutations in populations, allowing genetic correlations with climate variables.

(5) The results of such studies will provide data to help wildlife managers mitigate impacts, and provide basic understanding of population dynamics in altered environments. If mitigation is not feasible, population genetics can aide augmentation, translocation or re-introduction scenarios.

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