Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

Angola Cave-Chat *Xenocopsychus ansorgei*
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ABSTRACT

Approximately 238 species of reptiles are found in the highlands and escarpments of Angola and Namibia (HEAN). Of the 430 species present in the two countries in total, 46 are strictly endemic (or nearly so) to the HEAN and another 16 have extensive portions of their ranges in these areas. Geckos constitute the majority of HEAN endemics with 32 species; in addition, there are nine cordylids, six skinks, four lacertids and one chameleon, as well as nine snakes (in five families) and a single tortoise comprising the remainder. Many of these species are substrate specialists and therefore rock types and textures may be a more important determinant of their distributions than elevation per se. Reptile diversity is greatest in the larger highland areas of the Khomas Hochland and Angolan Planalto, but many areas support at least some regional highland endemics including the Marginal Mountain Chain and Central Escarpment, and the Serra do Môco and the Serra da Neve in Angola, and the Karasberge, Waterberg and the Otavi, Erongo, Numib, Tiras, Baynes and Otjihipa mountains as well as numerous inselberg clusters (e.g., Huns–Orange and Huab outliers) in Namibia. The vast majority of the highland taxa have been assessed as Least Concern by the International Union for Conservation of Nature (IUCN), with several taxa considered Data Deficient or Near Threatened and only three Vulnerable. Most highland and escarpment areas in Angola and Namibia remain woefully understudied from a herpetological perspective and the description of 20% of the endemics in the last ten years suggests that true reptile diversity remains underestimated.

Keywords: Angola, diversity, endemism, highlands, Namibia, reptiles

INTRODUCTION

The extant Reptilia is a paraphyletic group of tetrapod vertebrates encompassing the Squamata (lizards, snakes, amphisbaenians and the tuatara) and the living Archelosauria exclusive of Aves (e.g., chelonians and crocodilians). Squamates comprise more than 11,500 species distributed globally, whereas chelonians and crocodilians together are represented by 390 species (Uetz 2023). Although substantially more diverse at lower elevations, several species have been documented to occur above 5,000 masl (Cerdeña *et al*. 2001). Biologically, members of the group are highly diverse, ranging in body size from under 30 mm to over 5 m in total length. Arboreal, rupicolous, terrestrial and fossorial forms are common among squamates, whereas chelonians and crocodilians are chiefly aquatic or semiaquatic. Activity is diurnal in most species, although nocturnality is common among geckos and many snakes. Lizards are chiefly arthropod feeders, although larger species (e.g., varanids) may take vertebrate prey, and a small number are partly or entirely herbivorous. Snakes include blind snakes and thread snakes that feed chiefly on social insects, but most snakes feed on vertebrate prey which is sometimes of greater diameter and mass than themselves. All crocodilians are carnivorous, whereas chelonians include herbivorous forms (e.g., tortoises) as well as carnivorous or omnivorous species. All archelosaurs are oviparous, but both oviparity and viviparity occur among squamates.

Within Africa, reptiles are ubiquitous except for some of the highest elevations (over 4,500 masl), although diversity is very low in some of the most climatically extreme and topographically homogeneous portions of the Sahara Desert. A minimum of 1,800 species of reptiles has been reported for mainland Africa and its Atlantic island groups (Uetz 2023). The lowest diversity is in North Africa (Sahara and Mediterranean regions), in portions of the Horn of Africa and in some inland regions of East and southern Africa (Bauer 1993, Roll *et al*. 2017). Diversity is greatest in Equatorial Africa (e.g., Albertine Rift, Cameroon Highlands, Eastern Arc Mountains) and in portions of southeastern Africa (Böhm *et al*. 2013, Lewin *et al*. 2016, Tolley

et al. 2016, Roll *et al*. 2017). There are substantial differences in distribution patterns of the major groups of reptiles, however, with snakes sharing the pattern of the group as a whole, whereas lizards (including amphisbaenians) also have high species richness in arid regions, most notably the Horn of Africa and the arid portions of southwestern Africa from central Angola to the Cape provinces of South Africa, and in areas of high habitat heterogeneity (Lewin *et al.* 2016, Roll *et al.* 2017). Chelonians and crocodilians, because of their small numbers, contribute little to overall reptile diversity, and most (exclusive of tortoises, Testudinidae) are limited to areas of fresh water.

The currently recognised species of reptiles occurring in Namibia and Angola combined include 430 species, with an additional 16 recognised subspecies and a minimum of 20 additional undescribed species. Of the described taxa, 279 occur in Namibia and 306 in Angola, with 123 of these being present in both countries. Although many of these (238) occur in the highlands and escarpments of Angola and Namibia (HEAN), only 46 are strictly endemic (~90% or more of recorded localities) and another 16 are considered to be near-endemic (~70–90% of localities) to HEAN. Many of these species are actually more appropriately categorised as substrate specialists preferring or requiring rocky areas, often those providing retreats or oviposition sites of particular dimensions, orientations or exposures. These may be more common in highland areas but may also be present in rocky lowlands. In some cases inselbergs provide appropriate substrates even at or near their bases (Griffin 2000, Marques *et al*. 2019, 2020) and, paradoxically, higher elevations may not harbour these highland endemics. In much the same way, escarpment faces and the walls of canyons are just as likely to support HEAN endemics at their feet as they are at their summits. In some cases the occupation of highland habitat is regional. For example, *Cordylus namakuiyus* occurs in the Baynes and Otjihipa mountains in Namibia but is a lowland species in the bulk of its range in Angola. Several lizard and snake species that are widespread at all elevations in eastern Africa also have disjunct populations in the central and northern HEAN.

METHODS

Species distributions for taxa determined by the authors to be strict or near-strict endemics were obtained from the International Union for Conservation of Nature (IUCN) Red List website, from a database used in Meiri *et al.* (2017), and included some unpublished records and records from the original species descriptions (Marques *et al*. 2020, Branch *et al*. 2021, Lobón-Rovira *et al.* 2021), chiefly in the case of recent descriptions. All distributions were converted into shapefile format, then into high-resolution raster files, and overlapped using package raster (Hijmans 2021) in the program R (R Core Team 2021). The combined distributions were then clipped to the highland areas, as a combination of the plateaus and inselbergs. The layers were then assembled into a map (Figure 1) using QGIS (2021).

HIGHLAND TAXA

Gekkonidae

***Afroedura*:** Eight described species of this primarily rock-inhabiting genus of geckos occur largely or entirely in the HEAN. Molecular phylogenies have been generated that include all of these except *Afroedura tirasensis*, which was raised to full species from *A. africana* (Jacobsen *et al*. 2014, Branch *et al*. 2021, Conradie *et al*. 2022b). The *A. bogerti* complex, with six Angolan taxa, includes five HEAN endemics or species with isolated highland populations (see Table 1). *Afroedura otjihipa* is endemic to the Otjihipa Mountains in Namibia and is sister to the lowland Angolan species *A. donveae* (see Conradie *et al*. 2022b, 2023). *Afroedura africana* (Figure 2a) and *A. tirasensis* are mostly limited to exfoliating granites (Haacke 1965, Griffin 2003). The latter is known only from the Tirasberge, but the former occurs in the Erongo Mountains, Brandberg, Spitzkoppe, Swakop–Khan inselberg complex and in the west of the Khomas Hochland. Even within the Erongo Mountains, there is high genetic divergence, suggesting that this species may include hidden diversity (Jacobsen *et al*. 2014). Both *A. africana* and *A. tirasensis* have been assessed as Least Concern (Bauer & Becker 2020a,b).

***Goggia*, *Lygodactylus*, *Rhoptropella*:** These three genera are represented in the region by a single HEAN endemic each. *Goggia gemmula* is known from several localities in the Huns–Orange highland complex (Bauer *et al*. 1996), while *Rhoptropella ocellata* is known from a single specimen collected in the same region. The recently described *Lygodactylus baptistai* (Figure 2b) has thus far only been found at lower elevations of Serra da Neve (Marques *et al*. 2020). All three taxa have been included in recent molecular phylogenetic analyses (Heinicke *et al*. 2017a, Marques *et al.* 2020, Gippner *et al*. 2021). *Goggia gemmula* is strictly rupicolous, whereas the other two taxa may be found on vegetation in association with rocky habitat. *Rhoptropella ocellata* and *G. gemmula* have been assessed as Least Concern (Bates 2022a,b), while *L. baptistai* has been considered as Data Deficient by its describers (Marques *et al*. 2020). Although it is not traded internationally, *R. ocellata* has been included in Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix II because of its similarity to its close and heavily-traded relatives in the genus *Phelsuma*. Collection of

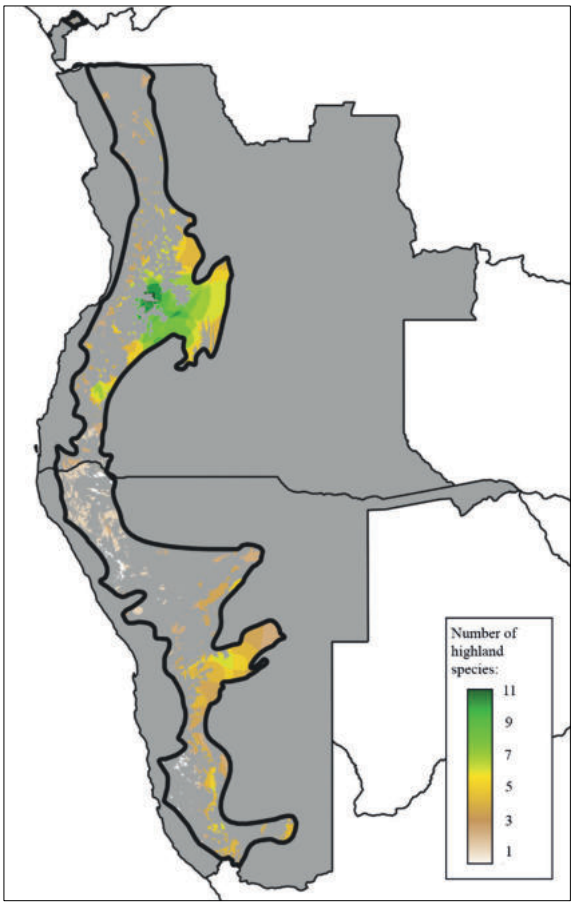

Figure 1: *Map of Angola and Namibia showing highland areas and inselbergs colour coded by the number of highland endemics and near-endemics (Table 1) co-occurring in these regions. See text for sources of data.*

basic life history data as well as thorough surveys to establish the distribution of all of these species are high priorities.

Hemidactylus: Southwest African taxa of this species-rich, nearly cosmopolitan genus have been the recent focus of taxonomic revision and molecular phylogenetic study (Ceriaco *et al.* 2020a,b, Lobón-Rovira *et al.* 2021). *Hemidactylus benguellensis* (Figure 2c) has a distribution which spans several Angolan main biogeographic units (sensu Lobón-Rovira *et al*. 2021) and a broad elevational range. It occupies a diversity of rocky substrates as well as tree trunks. The two geographically restricted highland endemics, *H. cinganji* and *H. faustus,* exhibit little genetic diversity and are known thus far from granitic boulders of the Central Escarpment in Angola and the Angolan Planalto and from the conglomerate inselberg complex of Pungo Andongo. None of these species has been formally assessed by the IUCN and we consider them all to be Data Deficient, although the broad distribution of *H. benguellensis* suggests that it may be of Least Concern.

***Narudasia*:** The monotypic *Narudasia* is the only genus of reptile entirely restricted to Namibia. *Narudasia festiva* (Figure 2d) is rupicolous and mostly terrestrial. It is not restricted to highland areas but the bulk of its distribution occurs in or around the Karasberge, Khomas Hochland, Huns–Orange complex, Naukluft Mountains, and Swakop–Khan inselberg complex (Daza *et al*. 2011). The species has been assessed as Least Concern (Bauer & Becker 2020c).

***Pachydactylus, Rhoptropus*:** *Pachydactylus*, as exemplified by *P. gaiasensis* (Figure 2e) and *P. reconditus* (Figure 2f), is the most species-rich southern African genus of geckos and it has been the subject of several molecular phylogenetic studies (Bauer & Lamb 2005, Bauer *et al.* 2006, Heinicke *et al*. 2017b). The most recent of these also included all described species of *Rhoptropus*, a related group of diurnal geckos, such as *R. montanus* (Figure 2g), mostly restricted to the arid zone of southwestern Africa. The status of most Namibian *Pachydactylus* species is generally well established, but this is not true of Angolan forms (Branch *et al.* 2017), and several species complexes that are shared between both countries remain unresolved. Fourteen species are highland endemics or near endemics, 12 of which occur only in Namibia and one uniquely in Angola, with a single additional taxon, *P. oreophilus*, shared between the two countries. This taxon is, in fact, a species complex (Baptista *et al*. 2020a) and only *P. oreophilus sensu stricto*, limited to Namibia, is a highland form. Within *Rhoptropus* there are three highland species. This genus also includes undescribed taxa (Kuhn 2016), one of which may be highland restricted. All but one HEAN endemic in both genera have been assessed as Least Concern (Bates & Bauer 2018a,b, Baptista *et al*. 2020a,b, Bates *et al*. 2020, Bauer 2020, Bauer & Becker 2020d–l, Ceríaco *et al*. 2020c), with the recently described *Pachydactylus maiatoi* tentatively considered Vulnerable by its describers (Marques *et al*. 2023). Two species, *P. weberi* and *P. namaquensis,* are probably peripheral to the region, being known from single localities in the Huns–Orange complex. The majority of the HEAN endemics are restricted to rocky substrates, often, but not always of a particular type (e.g., granites, sandstones, etc.). In northern Namibia and in Angola most are restricted to single highland areas, but in the south several species occur across numerous mountainous areas.

Lacertidae

***Pedioplanis, Ichnotropis, Nucras*:** This highly speciose group, represented in southern Africa by five genera, is primarily associated with lowlands although some species occur peripherally in the highlands. Only four species in three genera are represented among the HEAN endemics: *Pedioplanis rubens* (Figure 2h), *Ichnotropis bivittata* (Figure 3a), *I. microlepidota* and *Nucras scalaris*. The position of

Table 1: *Checklist of reptiles that occur in the highlands and escarpments of Angola and Namibia (HEAN).*

Taxa	Strict HEAN endemic[1]	Area of occurrence	Elevational range (masl)	Endemism status[2]	Threats	IUCN/ CITES conservation status[3]
SQUAMATA | LACERTILIA						
GEKKONIDAE						
Afroedura						
A. africana (Boulenger, 1888)	Y	NAMIBIA: Erongo Mountains, Brandberg, Spitzkoppe, Swakop–Khan inselbergs, Khomas Hochland	500–1,500	N	Mining activity	LC
A. bogerti Loveridge, 1944	Y	ANGOLA: Mt Namba	1,750–1,850	A	–	LC
A. otjihipa Conradie *et al*., 2022	Y	NAMIBIA: Otjihipa Mountains	1,800–1,900	N	–	(DD)[a]
A. praedicta Branch *et al.,* 2021	Y	ANGOLA: Serra da Neve	1,900–2,000	A	Habitat fragmentation or destruction	(NT)[b]
A. pundomontana Conradie *et al*., 2022	Y	ANGOLA: Central Escarpment	670–946	A	Habitat exploitation for building material	(DD)[a]
A. tirasensis Haacke, 1965	Y	NAMIBIA: Tirasberge	1,500	N	–	LC
A. vazpintorum Branch, *et al.,* 2021	N	ANGOLA: Marginal Mountain Chain, Humpata (isolated population)	2,000 (±)	A	–	(NT)[b]
A. wulfhaackei Branch *et al*., 2021	Y	ANGOLA: Angolan Planalto (Cuanza-Sul, Huambo and Benguela provinces)	920–2,055	A	Habitat fragmentation or destruction	(NT)[b]
Goggia						
G. gemmula (Bauer *et al*., 1996)	Y	NAMIBIA: Huns–Orange complex	300–1,200 (800–1,200 in Namibia)	N, SA	–	LC
Hemidactylus						
H. benguellensis Bocage, 1893	N	ANGOLA: Southern Escarpment, Marginal Mountain Chain, Central Escarpment, base of Serra da Neve; NAMIBIA: Baynes–Otjihipa mountains, Etendeka Mountains	200–1,800	A, N	Habitat fragmentation or destruction	(DD)[c]
H. cinganji Lobón-Rovira *et al*., 2021	Y	ANGOLA: Angolan Planalto and escarpment	828–1,916	A	–	(DD)[d]
H. faustus Lobón-Rovira *et al.,* 2021	Y	ANGOLA: Pungo Andongo	1,217	A	–	(DD)[d]
Lygodactylus						
L. baptistai Marques *et al*., 2020	Y	ANGOLA: Serra da Neve	800	A	–	(DD)[e]
Narudasia						
N. festiva Methuen & Hewitt, 1914	Y	NAMIBIA: Groot and Klein Karasberge, Khomas Hochland, Swakop–Khan inselbergs, Huns–Orange complex, most highland areas south of Tropic of Capricorn	200–1,300	N	–	LC
Pachydactylus						
P. acuminatus FitzSimons, 1941	Y	NAMIBIA: Nubib Mountain, Tirasberge, inselbergs around Aus, Karasberge	800–1,600	N	–	LC

Table 1: *Continued*

Taxa	Strict HEAN endemic[1]	Area of occurrence	Elevational range (masl)	Endemism status[2]	Threats	IUCN/ CITES conservation status[3]
P. boehmei Bauer, 2010	Y	NAMIBIA: Otavi Mountains	1,400	N	–	LC
P. etultra Branch *et al.,* 2011	Y	NAMIBIA: Nubib Mountain	800–1,000	N	–	LC
P. gaiasensis Steyn & Mitchell, 1967	Y	NAMIBIA: Huab outliers, Brandberg	400–900	N	–	LC
P. haackei Branch *et al*., 1996	N	NAMIBIA: Huns–Orange complex, Groot and Klein Karasberge, Brukkaros, Tirasberge, Onder-Rooirand	100–1,600 (~1,200 in Namibia)	N, SA	–	LC
P. kobosensis FitzSimons, 1938	Y	NAMIBIA: Khomas Hochland	1,500–1,600	N	–	LC
P. namaquensis (Sclater, 1898)	Y	NAMIBIA: Namuskluft Mountain (Huns–Orange complex)	500–1,500	SA/N*	–	LC
P. maiatoi Marques *et al*., 2023	Y	ANGOLA: Serra da Neve; Southern Escarpment	363–1,614	A		(VU)[f]
P. oreophilus Mclachlan & Spence, 1967	N	NAMIBIA: Etendeka and southern Otjihipa mountains	200–1,000	N	–	LC
P. otaviensis Bauer *et al*., 2006	Y	NAMIBIA: Otavi Mountains	1,400–1,500	N	–	LC
P. reconditus Bauer *et al.*, 2006	Y	NAMIBIA: Khomas Hochland	1,200–1,700	N	–	LC
P. robertsi Fitzsimons, 1938	Y	NAMIBIA: Karasberge	1,400–1,600	N	Livestock activity	LC
P. waterbergensis Bauer *et al.,* 2006	Y	NAMIBIA: Waterberg Plateau	1,300–1,400	N	–	LC
P. weberi Roux, 1907	Y	NAMIBIA: Skerpioenkop (Huns–Orange complex)	0–1,500 (~600 in Namibia)	SA/N*	–	LC
Rhoptropella						
R. ocellata (Boulenger, 1885)	Y	NAMIBIA: Huns–Orange complex	0–1,500 (~1,200 in Namibia)	SA/N*	Habitat fragmentation or destruction	LC CITES II
Rhoptropus						
R. benguellensis Mertens 1938	Y	ANGOLA: Angolan Planalto	700–1,500	A	–	LC
R. diporus Haacke, 1965	N	NAMIBIA: Huab outliers	400–1,500	N	–	LC
R. montanus Laurent, 1964	Y	ANGOLA: Marginal Mountain Chain	1,293–2,237	A	Livestock activity; fire; habitat fragmentation or destruction	LC
LACERTIDAE						
Ichnotropis						
I. bivittata pallida Laurent, 1964	Y	ANGOLA: Marginal Mountain Chain	1,200 (+)	A, CA	–	LC (species)
I. microlepidota Marx, 1956	Y	ANGOLA: Serra do Môco	1,600	A	Habitat fragmentation or destruction; fire	DD
Nucras						
N. scalaris Laurent, 1964	Y	ANGOLA: Angolan Planalto	1,300–1,570	A		(LC)[g]

Table 1: *Continued*

Taxa	Strict HEAN endemic[1]	Area of occurrence	Elevational range (masl)	Endemism status[2]	Threats	IUCN/ CITES conservation status[3]
Pedioplanis						
P. rubens (Mertens, 1954)	Y	NAMIBIA: Waterberg Plateau	1,400–1,600	N	–	LC
CORDYLIDAE						
Chamaesaura						
C. miopropus Boulenger, 1895	Y	ANGOLA: Angolan Planalto	1,500–2,500	A, CA	Fire	LC
Cordylus						
C. angolensis (Bocage, 1895)	Y	ANGOLA: Angolan Planalto escarpment, Central Escarpment	1,600	A	–	DD CITES II
C. machadoi Laurent, 1964	Y	ANGOLA: Marginal Mountain Chain	1,500–2,300	A	Livestock activity; fire	NT CITES II
C. phonolithos Marques *et al*., 2019	Y	ANGOLA: Serra da Neve	750–2,000	A	–	LC CITES II
Karusasaurus						
K. jordani (Parker, 1936)	N	NAMIBIA: Khomas Hochland, all mountain groups south to Karasberge exclusive of desert inselbergs	1,000–1,800	N	–	LC CITES II
Namazonurus						
N. campbelli (Fitzsimons, 1938)	Y	NAMIBIA: Naukluft Mountains, Tsaris Mountains, Nubib Mountain, Onder-Rooirand, Tirasberge	1,200–1,700	N	–	LC CITES II
N. namaquensis (Methuen & Hewitt, 1914)	N	NAMIBIA: Groot and Klein Karasberge	1,500–1,700	N	–	LC CITES II
N. pustulatus (Peters, 1862)	Y	NAMIBIA: Khomas Hochland, particularly Auas Mountains, Swakop–Khan inselbergs, Gamsberg, Rantberge	1,500–2,479	N	Habitat fragmentation or destruction	LC CITES II
Platysaurus						
P. attenboroughi Whiting *et al*., 2015	N	NAMBIA: Huns–Orange ridges along Orange and Fish rivers	69–1,268	N, SA	–	LC
SCINCIDAE						
Eumecia						
E. anchietae anchietae Bocage, 1870	Y	ANGOLA: Central and Southern escarpments, Marginal Mountain Chain and Angolan Planalto	1,000–2,200	A, CA	Livestock farming; fire	LC
Leptosiaphos						
L. dewittei (Loveridge, 1934)	Y	ANGOLA: Central Escarpment around Congulo	300–800	A, DRC	Habitat fragmentation or destruction	DD
Panaspis						
P. breviceps (Peters, 1873)	Y	ANGOLA: Central Escarpment around Congulo	300–800	A, CA	Habitat fragmentation or destruction	LC

Table 1: *Continued*

Taxa	Strict HEAN endemic[1]	Area of occurrence	Elevational range (masl)	Endemism status[2]	Threats	IUCN/ CITES conservation status[3]
P. namibiana Ceríaco *et al*., 2018	N	NAMIBIA: Otavi Mountains, Khomas Hochland, higher elevation areas in the Kaokoveld	650–1,200 (+)	N	–	LC
P. wahlbergii (Smith, 1849)	N	ANGOLA: Central and Southern escarpments	0–2,200 (800–2,200 in Angola)	A, SA, CA	–	LC
Trachylepis						
T. ansorgii (Boulenger, 1907)	Y	ANGOLA: Angolan Planalto, Central Escarpment and Marginal Mountain Chain	800–2,200	A	–	NE
CHAMAELEONIDAE						
Chamaeleo						
C. anchietae Bocage, 1872	Y	ANGOLA: Marginal Mountain Chain	750–1,800	A, CA	Direct persecution; livestock farming; fire	LC, CITES II
SQUAMATA | SERPENTES						
LEPTOTYPHLOPIDAE						
Leptotyphlops						
L. incognitus (Broadley & Watson, 1976)	Y	NAMIBIA: Khomas Hochland (isolated disjunct population)	0–1,800 (1,300–1,800 in Namibia)	N, SA, CA	–	LC
Namibiana						
N. gracilior (Boulenger, 1910)	N	NAMIBIA: Inselbergs around Aus and escarpment	1,400–1,600	N, SA	–	LC
VIPERIDAE						
Bitis						
B. heraldica (Bocage, 1889)	Y	ANGOLA: Serra do Môco and Angolan Planalto	1,800–2,000	A	Habitat fragmentation or destruction; direct persecution	VU
B. xeropaga Haacke, 1975	N	NAMIBIA: Huns–Orange complex	100–800	N, SA	–	LC
LAMPROPHIIDAE						
Gracililima						
G. nyassae (Günther, 1888)	N	NAMIBIA: Khomas Hochland, Otavi Mountains	0–1,600 (900–1,450 in Namibia)	N, SA, CA	–	LC
Lamprophis						
L. guttatus (Smith, 1843)	Y	NAMIBIA: Tirasberge, Rooikoppe	0–2,300 (1,000–1,800 in Namibia)	N, SA	Pet trade (low level)	LC

Table 1: *Continued*

Taxa	Strict HEAN endemic[1]	Area of occurrence	Elevational range (masl)	Endemism status[2]	Threats	IUCN/ CITES conservation status[3]
ATRACTASPIDIDAE						
Polemon						
P. collaris (Peters, 1881)	N	ANGOLA: Angolan Planalto	0–1,200 (800–1,200 in Angola)	A, CA	–	LC
PSAMMOPHIIDAE						
Psammophis						
P. ansorgii Boulenger, 1905	Y	ANGOLA: Angolan Planalto	1,800–2,286	A	Fire	LC
Psammophylax						
P. tritaeniatus (Günther, 1868)	N	ANGOLA: Angolan Planalto, Marginal Mountain Chain and Central Escarpment	200–1,800	A, N, CA, SA	Habitat fragmentation or destruction	LC
TESTUDINES						
TESTUDINIDAE						
Chersobius						
C. solus (Branch, 2007)	N	NAMIBIA: Escarpment inselbergs, inselbergs around Aus, Rooirand, Kowiesberge	50–1,700	N	–	VU CITES II

[1] Y – endemic only to the HEAN area
N – near-endemic (mostly occurs in HEAN area, but some populations at lower elevations or extralimital)

[2] A – Angola
N – Namibia
CA – Central and/or East Africa (widespread)
DRC – Democratic Republic of the Congo
SA – southern Africa
* = peripheral – known from a single locality within the region and more widespread extralimitally.

[3] Conservation status according to the current IUCN Conservation Status (available on https://www.iucnredlist.org/):
DD – Data Deficient
LC – Least Concern
NT – Near Threatened
VU – Vulnerable
See text for citations to particular species evaluations. Where the status is presented in parentheses this indicates that no formal IUCN evaluation has been completed but the threat status has been proposed by the describing authors:
[a] Conradie *et al.* (2022b)
[b] Branch *et al*. (2021)
[c] Ceríaco *et al.* (2020a)
[d] Lobón-Rovira *et al.* (2021)
[e] Marques *et al.* (2020)
[f] Marques *et al*. (2023)
[g] Baptista *et al*. (2020f)

Figure 2: *Representative highland reptiles from Angola and Namibia: a)* Afroedura africana *(Gekkonidae), Erongo Mountains, Erongo Region, Namibia. Photo: AM Bauer©; b)* Lygodactylus baptistai *(Gekkonidae), Serra da Neve, Namibe Province, Angola. Photo: LMP Ceríaco©; c)* Hemidactylus benguellensis *(Gekkonidae), Serra da Neve, Namibe Province, Angola. Photo: LMP Ceríaco©; d)* Narudasia festiva *(Gekkonidae), Farm Narudas (Great Karasberge), Karas Region, Namibia. Photo: J Marais©; e)* Pachydactylus gaiasensis *(Gekkonidae), vicinity Gaias (Huab outliers), Kunene Region, Namibia. Photo: J Marais©; f)* Pachydactylus reconditus *(Gekkonidae), Rehoboth (Central Highlands), Hardap Region, Namibia. Photo: J Marais©; g)* Rhoptropus montanus *(Gekkonidae), Tundavala (Marginal Mountain Chain), Huíla Province, Angola. Photo: LMP Ceríaco©; h)* Pedioplanis rubens *(Lacertidae), Waterberg Plateau National Park, Otjozondjupa Region, Namibia. Photo: J Penner©.*

P. rubens within its genus has recently been investigated using molecular systematics (Childers *et al*. 2021) as has that of *N. scalaris* within *Nucras* (Baptista *et al*. 2020f), but phylogenetic information on *Ichnotropis* remains rudimentary (Edwards *et al*. 2013, Bandeira 2019). *Ichnotropis bivittata* (at the species level), *N. scalaris* and *P. rubens* have been assessed as Least Concern (Howell *et al*. 2021a, Baptista *et al*. 2020c Bauer & Becker 2020m), whereas *I. microlepidota*, known only from its types, is considered Data Deficient (Ceríaco *et al.* 2020d).

Cordylidae

***Chamaesaura, Platysaurus*:** Most cordylids are heavily armoured, viviparous lizards with robust limbs. *Chamaesaura*, however, is reduced-limbed and attenuate and *Platysaurus* is oviparous and largely free of osteoderms (Stanley 2013). *Chamaesaura miopropus* is known from the Angolan Planalto (Marques *et al*. 2018), being isolated from the nearest known populations in Katanga, Democratic Republic of the Congo (DRC), and farther eastwards into East Africa. Determining whether this isolation is real or an artefact of poor sampling in the eastern regions of Angola requires further fieldwork. *Platysaurus attenboroughi* is a rock-dweller that occupies cliffs and boulder faces of highland areas in the Huns–Orange complex along the Orange and Fish river systems. Other species in the genus are found chiefly in the southeastern highlands of Africa. Both species have been assessed as Least Concern (Tolley & Alexander 2021, Weeber *et al*. 2022).

***Cordylus*:** The Angola populations of the genus *Cordylus* represent a northern radiation of the genus (Stanley *et al*. 2016). Three species in Angola are mostly restricted to highlands: *C. machadoi* in the Lubango–Humpata plateau area, *C. phonolithos* (Figure 3b) in Serra da Neve and *C. angolensis* in the Caconda region (Marques *et al.* 2018, 2019). The Namib endemic, *C. namakuiyus,* is mostly distributed in lowland areas but has been recorded in higher elevation areas in Namibia. All species are on CITES Appendix II and while *C. phonolithos* is Least Concern (Ceríaco *et al.* 2020e), *C. machadoi* is Near Threatened (Baptista *et al*. 2020d) and *C. angolensis* is Data Deficient (Ceríaco *et al.* 2020f).

***Karusasaurus, Namazonurus*:** These genera are chiefly Namibian in distribution. All are rock-dwelling specialists that retreat into crevices and although largely distributed in highland areas, ongoing research (DeBoer unpublished) suggests that most species may be more widespread than currently recognised. *Karusasaurus jordani* is widespread in the southern two-thirds of Namibia, whereas the three species of *Namazonurus* (*N. campbelli, N. namaquensis* (Figure 3c), and *N. pustulatus*) largely replace one another in adjacent highland regions from central to southern Namibia. All have been included in a molecular phylogeny (Stanley *et al.* 2011) and their biology, while incompletely known, is currently under study (Heaton & DeBoer 2018, Heaton *et al*. 2018, DeBoer unpublished). All species are CITES Appendix II listed and all have been assessed as Least Concern (Bauer & Becker 2020n–p, Becker *et al*. 2020).

Scincidae

***Panaspis, Leptosiaphos*:** These are related genera of relatively small, terrestrial skinks that are widespread in sub-Saharan Africa (Medina *et al*. 2016). *Panaspis* is mostly associated with lowlands across its distributional range. A single record of *Panaspis breviceps* from Congulo, on the escarpment in Cuanza-Sul Province (Parker 1936), either represents a relict population of this "Congolese" taxon or may be an undescribed species. *Panaspis namibiana*, a recently described species from Namibia, occurs in the Otavi Mountains, the Khomas Hochland and in highland areas of the Kaokoveld (Ceríaco *et al*. 2018). The species may also occur in the intervening regions at higher elevations. *Panaspis wahlbergii* (Figure 3d) occurs in the highlands of the Lubango region in southwestern Angola, although it is not restricted by elevation in other parts of its range. Despite its disjunction from topotypical populations in South Africa, genetic data have confirmed that it is conspecific (Ceríaco *et al*. 2020g). *Leptosiaphos* is known in southwestern Africa, like *P*. cf. *breviceps*, only from a record of *L. dewittei* in Congulo (Parker 1936), widely disjunct from the DRC population in Upemba National Park (Marques *et al.* 2018). Further surveys and taxonomic work are required. This species has been assessed as Data Deficient (Cox 2021), but all of the *Panaspis* have been assessed as Least Concern (Bauer & Becker 2020q, Luiselli *et al*. 2021a, Sindaco *et al*. 2021).

***Trachylepis, Eumecia*:** The genus *Trachylepis* is one of the most species-rich genera of reptiles in southwestern Africa (Marques *et al*. 2018) and occupies a diversity of terrestrial, rupicolous and arboreal habitats. A recent molecular phylogeny exists for the genus as a whole (Weinell *et al*. 2019) and a revision of Angolan forms is in progress (Ceríaco *et al*. in prep.) and will likely increase the known diversity in the group. While most species occur in lowlands or across a range of elevations, *Trachylepis ansorgii* (Figure 3e), a rock-dwelling form long considered a subspecies of *T. sulcata* and limited to the Central Escarpment and Marginal Mountain Chain and adjacent escarpment, has recently been elevated to full species by Butler (2020). Although not yet evaluated, its conservation status is likely Least Concern. *Eumecia* is a large, attenuate, reduced-limbed, grassland skink allied to *Trachylepis* and characterised by semi-aquatic habits and extreme matrotrophy (Metallinou *et al.* 2016,

Figure 3: *Representative highland reptiles from Angola and Namibia. a)* Ichnotropis bivittata *(Lacertidae), Tundavala (Marginal Mountain Chain), Huíla Province, Angola. Photo: LMP Ceríaco©; b)* Cordylus phonolithos *(Cordylidae), Serra da Neve, Namibe Province, Angola. Photo: LMP Ceríaco©; c)* Namazonurus namaquensis *(Cordylidae), Farm Narudas (Great Karasberge), Karas Region, Namibia. Photo: RA Sadlier©; d)* Panaspis wahlbergii *(Scincidae), Bicuar National Park (Southern Escarpment), Huíla Province, Angola. Photo: LMP Ceríaco©; e)* Trachylepis ansorgii *(Scincidae), Caconda (Marginal Mountain Chain), Huíla Province, Angola. Photo: LMP Ceríaco©; f)* Eumecia anchietae anchietae *(Scincidae), Tundavala (Angolan Planalto), Huíla Province, Angola. Photo: LMP Ceríaco©; g)* Bitis heraldica *(Viperidae), Serra do Môco, Huambo Province, Angola. Photo: D Brayne©; h)* Chersobius solus *(Testudinidae), vicinity Auas (Huns–Orange complex), Karas Region, Namibia. Photo: J DeBoer©.*

Weinell *et al*. 2019). Only the nominotypic subspecies, *Eumecia anchietae anchietae* (Figure 3f), occurs in the Angolan Planalto, Marginal Mountain Chain and parts of the Central and Southern escarpments (Marques *et al*. 2018, Ceríaco *et al*. 2020h). It has been assessed as Least Concern (Spawls *et al*. 2020) but requires taxonomic revision.

Chamaeleonidae

***Chamaeleo*:** Of the four species of chamaeleons occurring naturally in Namibia and Angola, only *Chamaeleo anchietae* is a highland species. It is, in fact, a species complex with *C. anchietae* sensu stricto being endemic to patches of highland plateaus in southwestern Angola, whereas the populations in southern DRC and Tanzania constitute another species (Main 2019, Main *et al*. 2019). Like all chamaeleons, *C. anchietae* has a short, laterally compressed body, grasping zygodactylous feet and independently mobile eyes. In Angola it is associated with the Marginal Mountain Chain. Overall, the species is of Least Concern (Tolley *et al*. 2015) but a reappraisal of the Angolan (nominotypical) population is required.

Serpentes

A total of nine species of snakes belonging to the families Leptotyphlopidae, Viperidae, Lamprophiidae and Psammophiidae can be considered highland endemics in Angola and Namibia, although some of these occur in widespread lowland areas elsewhere in Africa. This is a surprisingly low number, as both countries have a considerable diversity of snakes – 142 species or subspecies in Angola and 93 in Namibia (Hermann & Branch 2013, Ceríaco & Marques 2021, Becker 2022, Conradie *et al*. 2022a).

Leptotyphlopidae: The thread snakes are very small, non-venomous arthropod feeders, and include the smallest snakes in the world. Most burrow into soil or leaf litter and only come to the surface under certain conditions. The taxonomy and systematics of this group, as well as aspects of biology, remain incompletely known. *Leptotyphlops incognitus* occurs chiefly in South Africa and Zimbabwe, but a disjunct population occurs in the Khomas Hochland. It appears to be a paraphyletic species complex in South Africa, although genetic material from the type locality in Zimbabwe, and from Namibia, has not yet been obtained (see Adalsteinsson *et al*. 2009, as *L. conjunctus*). *Namibiana gracilior* occurs in disjunct highland or rocky habitats in southern Namibia, and the Western Cape of South Africa. Its phylogenetic position is unknown, but it is included in the genus *Namibiana* by geographical association. Within *Namibiana* only *N. occidentalis* (Adalsteinsson *et al.* 2009) has been genetically evaluated. Both *L. incognitus* and *N. gracilior* have been assessed as Least Concern (Alexander & Tolley 2021, Alexander 2022).

Viperidae: This venomous group inhabits a range of habitats, but several small species specialise in highlands. The poorly known and iconic Angolan adder, *Bitis heraldica* (Figure 3g), occurs exclusively in the Angolan highlands, from Serra do Môco to northern Huíla Province and Bié (Marques *et al*. 2018, Gonçalves *et al*. 2019). Until very recently, its phylogenetic position was uncertain, but Ceríaco *et al*. (2020i) showed that the species is closely related to species of the subgenus *Macrocerastes*, whose species are mostly distributed in western and Central Africa. *Bitis xeropaga* occurs in the Huns–Orange complex in southern Namibia and in rocky areas along the Orange River system eastward. This species has been phylogenetically assessed (Lenk *et al.* 1999), and most recently placed as sister to *B. cornuta* (Wittenberg *et al*. 2015), but the Namibian populations have not yet been genetically analysed. *Bitis heraldica* has been assessed as Vulnerable (Ceríaco 2021), whereas *B. xeropaga* is Least Concern (Maritz *et al*. 2021).

Elapoidea (Lamprophiidae, Atractaspididae, Psammophiidae): Members of these three families are members of the larger clade Elapoidea and familial assignment has been unstable. The current familial classification follows Zaher *et al*. (2019). Lamprophiidae is a non-venomous family widespread in lowland habitats in most of Africa. *Gracililima nyassae* follows this pattern in southeastern and East Africa, but a disjunct population occurs in the Khomas Hochland. This species had previously been placed in different genera of file snakes, but Broadley *et al*. (2018), using a molecular phylogenetic approach, placed it in the monotypic *Gracililima*. The genetic distinctiveness of the Namibian population has not yet been investigated. *Lamprophis guttatus* is a chiefly South African species preferring rocky habitats, but isolated populations occur in the southern Namibian highlands. Phylogenetic evidence suggests that there may be several cryptic species (Kelly *et al*. 2011) but the Namibian populations have not yet been evaluated in this regard. Atractaspidids are chiefly mildly to moderately venomous rear-fanged species. They are represented by *Polemon collaris* which is widespread across the Central and Northern Escarpment areas of Angola (Marques *et al*. 2018) and occurs at lower elevations elsewhere in its range. *Polemon collaris* is a snake-feeding inhabitant of savannas and forests and it has been included in molecular phylogenetic analyses (Portillo *et al*. 2018, 2019). Psammophiids are slender, diurnal, chiefly visual predators occurring in Africa, Europe and parts of Asia. Two species occur in the HEAN. *Psammophylax tritaeniatus* is a widespread species across southern Africa, and while it can occur in non-highland areas, its distribution in Angola is mostly associated with highland areas (Marques *et al*. 2018). In Namibia, it occurs in the Khomas Hochland and Otavi Mountains, but also across the northern

Kalahari sand system. The other psammophiid species, *Psammophis ansorgii,* is endemic to the southern Angolan Planalto in Huambo and Huíla provinces (Marques *et al*. 2018, Branch *et al*. 2019). The taxonomic validity of this species was dubious until Branch *et al*. (2019) collected fresh material and confirmed its status as a full species. All five species of highland elapoid snakes have been assessed as Least Concern (Baptista *et al*. 2020e, Bates *et al*. 2021, Howell *et al*. 2021b, Luiselli *et al*. 2021b, Maritz 2022).

Testudinidae

Chersobius: Land tortoises are not diverse, with only 47 species recognised globally (Uetz 2023), eight of which occur in Namibia and Angola, with only one of these being tightly associated with highlands. The small tortoise *Chersobius solus* (Figure 3h) occurs in and around the base of inselbergs near Aus in southern Namibia. It has recently been genetically evaluated (Hofmeyr & Branch 2018) after years of taxonomic confusion (Branch 2007). The species is considered Vulnerable C2a (Branch 2018) but requires an updated study of threats and of its localised distribution. Like testudinids in general it is herbivorous, but its somewhat flexible carapace and plastron and its climbing ability are unique among the *Homopus* + *Chersobius* lineage.

DISCUSSION

There is a distinct phylogenetic pattern among the highland taxa. No crocodilians occur in the HEAN and only a single chelonian species, *Chersobius solus*, which is largely restricted to inselbergs in the area of Aus in southern Namibia. Nine snakes are largely endemic to highlands; four of these occupy disjunct populations in Namibian highlands but have their main distributions in South Africa and/or Zimbabwe (*Leptotyphlops incognitus*, *Namibiana gracilior*, *Lamprophis guttatus*, *Gracililima nyassae*). By far the majority of highland reptiles are lizards and of these, two families, Cordylidae and Gekkonidae, account for the majority of species (9 and 32, respectively), with the remainder comprising four lacertids, six scincids and one chameleon. Both geckos and cordylids tend to be substrate specialists, usually rock specialists, and thus their association with highland areas is not surprising.

There is considerable species turnover across these highlands, particularly along the north–south gradient, with many highland endemics having small distributions. Few species occur broadly, and none occur throughout these highlands. The larger highland areas tend to have higher numbers of highland endemics, particularly highlands that have higher rainfall than the surrounding lowlands (Figure 1).

Not surprisingly, given their large areas, the Khomas Hochland and Angolan Planalto harbour the greatest diversity of highland taxa. However, in Angola, the Lubango and Congulo escarpments, Serra do Môco and Serra da Neve are also represented. In Namibia, the Karasberge, Waterberg, the Otavi, Erongo, Numib, Tiras, Baynes and Otjihipa mountains as well as numerous inselberg clusters (Huns–Orange, Etendeka, Otjikondavirongo and Huab outliers) support strict highland endemics or near-endemics (Table 1), some restricted to single areas. The Brandberg, Namibia's highest and most well-known inselberg, also has populations of more widespread highland endemics, but interestingly no species are strictly endemic to the Brandberg (van den Elzen 1983, Griffin 2000). Inselbergs and small mountain ranges, with few exceptions, do not stand out in our map of endemic density (Figure 1) because of microendemism but, for example, if the Huns–Orange complex of highlands were treated as a single unit, it would be seen to have a relatively high density of endemics.

For most reptile species occurring in the southwestern highlands, phylogenetic data are available and species-level relationships are generally clear. However, more data are needed for species with disjunct populations in the HEAN (e.g., *Eumecia anchietae*, *Panaspis breviceps*, *Leptodactylus incognitus*, *Lamprophis guttatus*), and population level genetic data would be desirable for species that extend across multiple disjunct highland areas. This is seen most clearly in species that occupy some of the montane regions and inselbergs of southern Namibia (e.g., *Narudasia festiva*, *Pachydactylus acuminatus*). Biological data are lacking for most species beyond anecdotal dietary and reproductive records and when available these are usually restricted to short-term or one-time observations in single localities.

Most reptile species across the region have been assessed by the IUCN (Table 1) and nearly all are considered Least Concern, although a few are Data Deficient, Near Threatened or Vulnerable. As such, conservation concerns are not a primary determinant of priorities for highland study. Taxonomically, geckos of the genera *Afroedura* (see Conradie *et al*. 2023) and *Pachydactylus*, as well as cordylids in general, are each represented by multiple taxa that are highland endemics and these may be good candidates for focal studies on both genetics and natural history. These and many of the other highland taxa (Table 1) share a preference for rocky substrates, often in arid to semi-arid environments.

In Angola, the long period of scientific inactivity stemming from the war for independence and then the civil war (Marques *et al*. 2018) has meant that most highland research has only been possible in

the last 20 years. In comparison to Namibia, infrastructural limitations have also retarded herpetological research in certain areas. By far the most well-studied areas are in Namibe, Benguela and Huíla provinces but, even in these areas, numerous inselbergs remain unstudied. Sampling across the Angolan Planalto has been sporadic and northern highlands (Ernst e*t al.* 2020) have been largely ignored, including those in Cabinda.

With respect to priority areas for reptiles, some stand out because of known endemism of multiple groups. In Angola, the Marginal Mountain Chain and adjacent areas of the Central Escarpment and Angolan Planalto are particularly rich, and Serra da Neve and Serra do Môco both appear to have strict endemics. Nevertheless, perhaps with the exception of the Huíla Plateau and escarpment, our herpetological knowledge of southwest African highlands is rudimentary. Ongoing and future research in the area will likely provide novelties in terms of undescribed taxa, and also expand the list of species known to inhabit them. Highland areas in northern Angola are far less explored than those in the south. The known 'relict' populations of Central Africa taxa in Congulo (Cuanza-Sul, Angola), for example, may prove to be closely related to their Congolese congeners but belonging to different and undescribed taxa.

In Namibia, the Waterberg and Otavi Mountains, the central highlands (Khomas Hochland, Auas Mountains, etc.), Karasberge and Huns–Orange highland complex and inselbergs also stand out. Many highland areas do not stand out in our cursory analysis here because of a lack of sampling. In Namibia, targeted sampling in the Otjikondavirongo, Etendeka, Otjihipa, Hartmann, Baynes and other far northwestern complexes would provide much needed basic distributional data for many taxa and in some cases might reveal cryptic or truly novel species. Likewise, the Paresis, Otavi and Erongo mountains and many of the Swakop–Khan and Middle Ugab highlands have been understudied, whereas Spitzkoppe, the Naukluft Mountains, and much of the Khomas Hochland have been adequately surveyed, although should not be considered fully explored herpetologically. The Brandberg has been surveyed around the lower elevations, but more comprehensive surveys on the top of the mountain are needed. From the Tsaris Mountains south to the Huns–Orange complex there has been very little focused sampling of reptiles, apart from the region near Aus (Mertens 1955) and the Aurus Mountain (Branch 1994). The Huns–Orange complex is a particularly high priority as it harbours several taxa otherwise only known from South Africa, and in recent years a number of new country records have come from the region. The inselbergs of the southern sand sea are also a high priority as these have yielded new taxa despite very limited exploration by herpetologists (Haacke 1975).

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