

Monograph on
**Endemism in the
Highlands and Escarpments
of Angola and Namibia**



Angola Cave-Chat *Xenocopsychus ansorgei*
Photo: M Mills

Editors:

John M Mendelsohn
Brian J Huntley
Pedro Vaz Pinto

Published with support and funding from:

Ongava Research Centre (ORC)
Namibian Chamber of Environment (NCE)
Centro de Investigação em Biodiversidade
e Recursos Genéticos (CIBIO)
B2Gold Namibia
TotalEnergies

Language editor: Carole Roberts
Design and layout: Alice Jarvis

NJE Namibian Journal
of Environment

2023: Volume 8 www.nje.org.na

ISSN: 2026-8327 (online)

[» DOWNLOAD THE MONOGRAPH](#)

CONTENTS

Huntley BJ, Mendelsohn JM & Vaz Pinto P Preface to endemism on the highlands and escarpments of Angola and Namibia	i–iii
Huntley BJ, Mendelsohn JM & Vaz Pinto P The biological importance of the highlands of Angola and Namibia: Synopsis and conclusions	v–xiii

Geography of the highlands and escarpments

Jarvis AM The highlands and escarpments of Angola and Namibia: orientation maps	1–6
Mendelsohn JM & Huntley BJ Introducing the highlands and escarpments of Angola and Namibia	7–22
Miller RM Geology and landscape evolution of the highlands and escarpments of western Angola and Namibia	23–28
Huntley BJ Biomes and ecoregions of the highlands and escarpments of Angola and Namibia	29–41
Mendelsohn JM & Gomes AL The human environment in the highlands and escarpments of Angola and Namibia	43–51
Vaz Pinto P, Russo V & Veríssimo L The highlands in Angolan conservation areas	53–62

Diversity and endemism

Craven P & Kolberg H An overview of plant endemism on the highlands of Namibia	63–76
Goyder DJ, Gomes AL, Gonçalves FMP, Luís JC & Darbyshire I A botanical assessment of Mt Namba, Cuanza-Sul, Angola: an isolated mountain towards the northwestern limits of the Great Escarpment of southern Africa	77–92
Meller P, Lages F, Finckh M, Gomes A & Goyder D Diversity and endemism of geoxylic plants on the Angolan Planalto	93–109
Bruyns PV, Hanáček P & Klak C Diversity and endemism in the species-rich Ceropegieae (Apocynaceae) and Euphorbia in the highlands and escarpments of Angola and Namibia	111–134
Dexter KG, Swanepoel W, Loiseau O, Darbyshire I, Nanyeni L, Gonçalves FM, Chase F & Manzitto-Tripp EA High endemism of the genus <i>Petalidium</i> (Acanthaceae) in the highlands and escarpments of Angola and Namibia	135–147
Weeks A & Swanepoel W Commiphora of the highlands and escarpments of Angola and Namibia	149–159
Lautenschläger T, Aime MC, Clausnitzer V, Langer L, Meller P, Müller F, Nuss M, Teutloff N & Ernst R Green gem of the Northern Escarpment: biodiversity and endemism of the Serra do Pingano Forest Ecosystem	161–172
Kipping J, Clausnitzer V & Dijkstra K-DB The highlands and escarpment of Angola as an endemism hotspot for African dragonflies and damselflies (Insecta: Odonata)	173–186
Gunter F, Jürgens N & Henschel JR Observations on the diversity of termites in Angola and Namibia	187–192
Mansell MW The Neuroptera of the highlands and escarpments of Angola and Namibia	193–196
Gomez K, Hawkes PG & Fisher BL Ant endemism in the highlands and escarpments of Angola and Namibia (Hymenoptera, Formicidae)	197–203
Gardiner AJ & Williams MC The endemic butterflies of Angola and Namibia and their evolutionary implications	205–230
Prendini L & Bird TL Endemism of Arachnida (Amblypygi, Scorpiones and Solifugae) in the highlands and escarpments of Angola and Namibia: current knowledge and future directions	231–244
Becker FS, Baptista NL, Vaz Pinto P, Ernst R & Conradie W The amphibians of the highlands and escarpments of Angola and Namibia	245–257
Bauer AM, Ceríaco LMP, Marques MP & Becker FS Highland reptiles of Angola and Namibia	259–276
Conradie W, Lobón-Rovira J, Becker FS, Schmitz A & Vaz Pinto P Flat gecko (<i>Afroedura</i>) diversity, endemism and speciation in the highlands and escarpments of Angola and Namibia	277–281
Skelton PH Fishes of the highlands and escarpments of Angola and Namibia	283–292
Mills MSL & Melo M Birds of the highlands and escarpments of Angola and Namibia: ornithological significance, avifaunal patterns and questions requiring further study	293–309
Palmeirim AF, Monadjem A, Vaz Pinto P, Taylor P, Svensson MS & Beja P Mammal endemism in the highlands and escarpments of Angola and Namibia	311–322
De Matos D, Zastrow J, Val A & Mendelsohn JM Caves and their fauna in the highlands and escarpments of Angola and Namibia	323–330

The amphibians of the highlands and escarpments of Angola and Namibia

FS Becker^{1,2,3}, NL Baptista^{4,5,6,7,8}, P Vaz Pinto^{4,5,9}, R Ernst^{10,11}, W Conradie^{12,13}

URL: <https://www.nje.org.na/index.php/nje/article/view/volume8-becker>

Published online: 15th December 2023

¹ National Museum of Namibia, Windhoek, Namibia; francois.becker@moe.gov.na

² School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

³ South African National Biodiversity Institute, Claremont, Cape Town, South Africa

⁴ CIBIO-InBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, Campus Agrário de Vairão, Vairão, Portugal

⁵ BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal

⁶ Instituto Superior de Ciências da Educação da Huíla (ISCED-Huíla), Lubango, Angola

⁷ Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto, Portugal

⁸ Museum für Naturkunde – Leibniz Institute for Evolution and Biodiversity Science, Berlin, Germany

⁹ Fundação Kissama, Luanda, Angola

¹⁰ Museum of Zoology, Senckenberg Natural History Collections Dresden, Dresden, Germany

¹¹ Faculty of Biology, Technische Universität Dresden, Dresden, Germany

¹² Port Elizabeth Museum (Bayworld), Humewood, South Africa

¹³ Department of Nature Conservation Management, Natural Resource Science and Management Cluster, Faculty of Science, George Campus, Nelson Mandela University, George, South Africa

ABSTRACT

The amphibians of the highlands and escarpments of Angola and Namibia are a diverse group containing fifteen highland endemic or associated species. Both species richness and endemism are highest in the central and northern highlands of Angola, corresponding with higher rainfall. The Angolan highlands contain seven highland endemics, while the arid Namibian highlands contain only one. Few baseline data are available for much of the highlands, leading to an inadequate understanding of species occurrence patterns, population trends and conservation status. Recent surveys and phylogenetic revisions have led to the discovery of several previously undescribed species, and new species descriptions are still in progress. Both the species richness and endemism reported here are probably underestimates.

Keywords: amphibians, Angola, distribution patterns, diversity, endemism, escarpments, highlands, Namibia

INTRODUCTION

Amphibians are the most ancient tetrapod group and are comprised of three extant orders: the legless Gymnophiona (caecilians), the tailless Anura (frogs) and the tailed Urodela (salamanders and newts). Over 8,400 extant species are described (Frost 2022) and many remain unknown. Over the last decade, an average of 150 new species were described per year globally and, contrary to most other tetrapod groups, the rate of new descriptions appears to be increasing (Streicher *et al.* 2020, Womack *et al.* 2022). Amphibians are also the most threatened tetrapod group, with 36% of assessed species being threatened, compared to 23% of mammals, 19% of reptiles and 13% of birds (IUCN 2021). Approximately 2.5% of modern species are already extinct or presumed extinct (IUCN 2021).

Amphibians persist on every continent except Antarctica (although they historically occurred there; see Mörs *et al.* 2020) and the high Arctic. More than 815 amphibian species are reported from continental Africa (Channing & Rödel 2019), a number that is expected to grow in the coming years due to new species discoveries. Frogs comprise the largest

number of African amphibians (~788 species), while caecilians (~23 species) are restricted to wet equatorial and tropical Africa, and salamanders (~4 species) to northern Africa (Channing & Rödel 2019). Frogs live in a wide range of habitats in Africa including, notably, the sand dunes of the southern Namib Desert. Most species' distributions are limited by their requirement for specific aquatic habitats for breeding.

African amphibian species richness is positively correlated with rainfall, similar to the global pattern (Pyron & Wiens 2013, Ochoa-Ochoa *et al.* 2019). Equatorial Africa has the highest amphibian richness (e.g., Tanzania ~215 species, Cameroon ~225), while drier southwestern Africa (Namibia and Angola) has only recorded 144 species (Channing & Rödel 2019).

Highlands and the associated habitat and climate heterogeneity can increase localised amphibian species richness (Poynton 2000, Behangana *et al.* 2009), and may cause small-range endemism or habitat specialisation (Poynton *et al.* 2007). A large number of small-range habitat specialists are associated with African highlands. Notable highland habitats include highland forests, often with montane

streams or seepages (Rose 1962, Boycott & de Villiers 1986, Largen 1991, Menegon & Salvidio 2005, Malonza *et al.* 2010, Loader *et al.* 2011, Sandberger-Loua *et al.* 2016, Channing *et al.* 2017, Conradie *et al.* 2018, Becker *et al.* 2022), and high-altitude grassland or semi-open habitats (e.g., Armstrong 2001, Becker & Hopkins 2017, Ceriaco *et al.* 2018).

Within southwestern Africa (Namibia and Angola), the highest species richness (~47 species) is found in wetter areas of northern and eastern Angola (Marques *et al.* 2018, Channing & Rödel 2019, Ernst *et al.* 2020; Figure 1), which have more permanent aquatic habitats and forests. Richness decreases

southwestwards, with arid southwestern Namibia hosting only three to five species, and most of the Namib Sand Sea (Namibia) being void of amphibians. Approximately 132 amphibian species are recorded for Angola, of which a staggering 24 (around a sixth or 18%) are regarded as country endemics (Marques *et al.* 2018, Baptista *et al.* 2019, 2021, 2023, Ernst *et al.* 2020, Nielsen *et al.* 2020, Ceriaco *et al.* 2021), several of which are associated with highlands. However, many of these species are only known from single localities and need taxonomic revision to validate their status (Baptista *et al.* 2019). Namibia may contain up to 64 amphibian species (Griffin 2003, Herrmann & Branch 2013, Channing & Becker 2019, Becker 2022, Rödel *et al.* 2023), with the highest number (~40 species) in the mesic Zambezi Region in the northeast (Figure 1). Four species are strict country endemics and two more are regarded as near-endemics (Becker 2022, Rödel *et al.* 2023).

The highlands and escarpments of Angola and Namibia (HEAN), described by Mendelsohn and Huntley (2023), contribute significantly towards amphibian endemism in southwestern Africa, with ~45% (15 of 33) of the region's endemics being associated with these highlands. The HEAN includes the western escarpment regions which are broken into a series of inselbergs, while more substantial mountain ranges and plateaus occur farther inland (see Lautenschläger *et al.* 2023). The Southern Escarpment (Namibia and Angola) and the Karstveld (Namibia) have been highlighted as a centre of endemism for herpetofauna (Laurent 1964, Herrmann & Branch 2013, Baptista *et al.* 2018, Branch *et al.* 2019). However, these findings were primarily based on reptile data, while patterns of amphibian endemism in the HEAN are not as well understood. Hence, only preliminary patterns can be reported.

HIGHLAND ENDEMIC TAXA

Highland endemic taxa are briefly discussed below. Most of the distributions are poorly understood and very few localities have been recorded. Therefore, potential or projected distributions are displayed alongside the published records. These are projected occurrences based on the current knowledge of expected habitat requirements and proximity to known records, not on statistically modelled species distributions.

Leptopelis (Arthroleptidae)

Tree frogs are robust climbing frogs usually associated with forest or woodland, while some are grassland specialists. They lay eggs in a terrestrial nest and the tadpoles wriggle to water when they hatch (Du Preez & Carruthers 2017, Channing & Rödel 2019). They occur primarily in lowlands, with

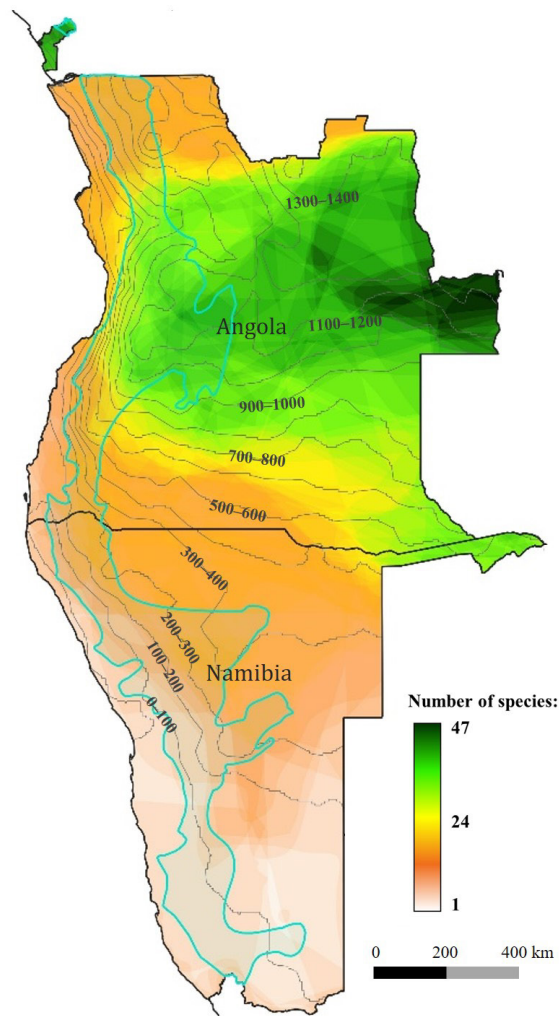


Figure 1: Amphibian species richness throughout Namibia and Angola based on IUCN distributions, showing an overall positive relationship with annual rainfall. Average annual rainfall (mm) is indicated by labelled isohyets; the outline of the highlands and escarpments of Angola and Namibia (HEAN) is indicated in cyan; species richness is indicated by coloured shading (key on map). Species richness in northwestern Angola is expected to be the highest in the region, similar to that of the Cabinda Province enclave in the far northwest. However, it is underrepresented in this map due to incompletely mapped species distributions and thus vastly underestimated here.

Table 1: Amphibian species endemic to or associated with the highlands and escarpments of Angola and Namibia (HEAN). Highland status indicates their status in HEAN; IUCN status indicates the most recent IUCN status.

Family and species	Common name	Highland status	IUCN status
Arthroleptidae			
<i>Leptopelis anchietae</i> Bocage, 1873	Anchieta's tree frog	Endemic	Least Concern
<i>Leptopelis jordani</i> Parker, 1936	Congulo forest tree frog	Endemic	Data Deficient
<i>Leptopelis marginatus</i> Bocage, 1895a	Quissanje forest tree frog	Endemic	Data Deficient
Bufonidae			
<i>Poyntonophrynus fernandae</i> Baptista <i>et al.</i> , 2023	Fernanda's pygmy toad	Endemic	Not Evaluated
<i>Poyntonophrynus hoeschi</i> (Ahl, 1934)	Hoesch's pygmy toad	Endemic	Least Concern
<i>Poyntonophrynus nambensis</i> Baptista <i>et al.</i> , 2023	Namba pygmy toad	Endemic	Not Evaluated
<i>Poyntonophrynus pachnodes</i> Ceriaco <i>et al.</i> , 2018	Serra da Neve pygmy toad	Endemic	Not Evaluated
<i>Poyntonophrynus dombensis</i> (Bocage, 1895b)	Dombe pygmy toad	Associated	Least Concern
<i>Poyntonophrynus grandisonae</i> (Poynton & Haacke, 1993)	Grandison's pygmy toad	Associated	Data Deficient
<i>Poyntonophrynus jordani</i> (Parker, 1936)	Jordan's pygmy toad	Associated	Not Evaluated
Hyperoliidae			
<i>Hyperolius chelaensis</i> Conradie <i>et al.</i> , 2012	Chela Mountain reed frog	Endemic	Data Deficient
<i>Hyperolius cinereus</i> Monard, 1937	ashy reed frog	Endemic	Least Concern
Ranidae			
<i>Amnirana parkeriana</i> (Mertens, 1938)	Congulo white-lipped frog	Endemic	Data Deficient
Ptychadenidae			
<i>Hildebrandtia ornatissima</i> (Bocage, 1879)	Angola ornate frog	Associated	Data Deficient
Microhylidae			
<i>Phrynomantis annectens</i> Werner, 1910	marbled rubber frog	Associated	Least Concern

at least 12 species in Angola (Baptista *et al.* 2019, Ernst *et al.* 2020) and only one in Namibia. Three Angolan species are national endemics and are also considered here as highland endemics (Table 1; Figure 2). The taxonomic status of many of the Angolan species is challenging and still under investigation (Baptista *et al.* 2017, Jaynes *et al.* 2021, Vaz Pinto *et al.* unpubl. data). Several cryptic species may therefore exist along the escarpment, while some previously recognised taxa may not be valid.

Leptopelis anchietae (Anchieta's tree frog; Figure 6a) is a highland endemic. A few historical records fall outside highland regions (Marques *et al.* 2018) but may contain misidentifications. Recent collecting efforts suggest that the species is strongly associated with high-elevation (more than 1,900 metres above sea level [masl]) grasslands and savannas in the central and southern Angolan highlands (Baptista *et al.* 2017, 2018, Vaz Pinto *et al.* unpubl. data). The species was assessed as Least Concern (IUCN SSC Amphibian Specialist Group 2013a).

Leptopelis jordani (Congulo Forest tree frog; Figure 6b) is described from moist coffee plantations at Congulo, at mid-elevations along Angola's Central Escarpment (Mendelsohn & Huntley 2023). The species was recently rediscovered (Baptista *et al.* 2017), but the relationships with other *Leptopelis* populations present along the escarpment are still unresolved (Vaz Pinto *et al.* unpubl. data). This species has been assessed as Data Deficient (IUCN & SA-FRoG 2020b).

Leptopelis marginatus (Quissanje Forest tree frog) may be a highland endemic, but its taxonomic status remains challenging and it is often not recognised as a valid species (Channing 2001, Channing & Rödel 2019). It was described in the 19th century from Quissanje in mid-elevation along the Angolan Central Escarpment, but the holotype was lost in the fire that destroyed the zoological collections of Museu Bocage in 1978 (Frost 2022). Topotypical material was recently collected (Vaz Pinto *et al.* unpubl. data) and may assist to clarify its taxonomic status. This species was assessed as Data Deficient (IUCN & SA-FRoG 2017b).

Hyperolius (Hyperoliidae)

Reed frogs are small, usually colourful species typically associated with large waterbodies, where males produce loud calls from elevated positions on vegetation. Lowland habitats contain most species, while a few are associated with highlands elsewhere in Africa (Channing & Rödel 2019). Four species occur in northeastern Namibia. In Angola, reed frogs are much more diverse and widely distributed, with 29 species listed, nine of which are endemic (Baptista *et al.* 2019). However, several of these species are only known from the original descriptions and some of the type specimens have been lost. Rediscovery of these 'lost' species can help infer if they represent valid taxa. Taxonomic treatment in this genus is complex. For instance, various colour forms may occur within a species, or may be used to differentiate species (Portik *et al.* 2019, Channing 2022). The genus *Alexteroon* is now considered a subgenus of

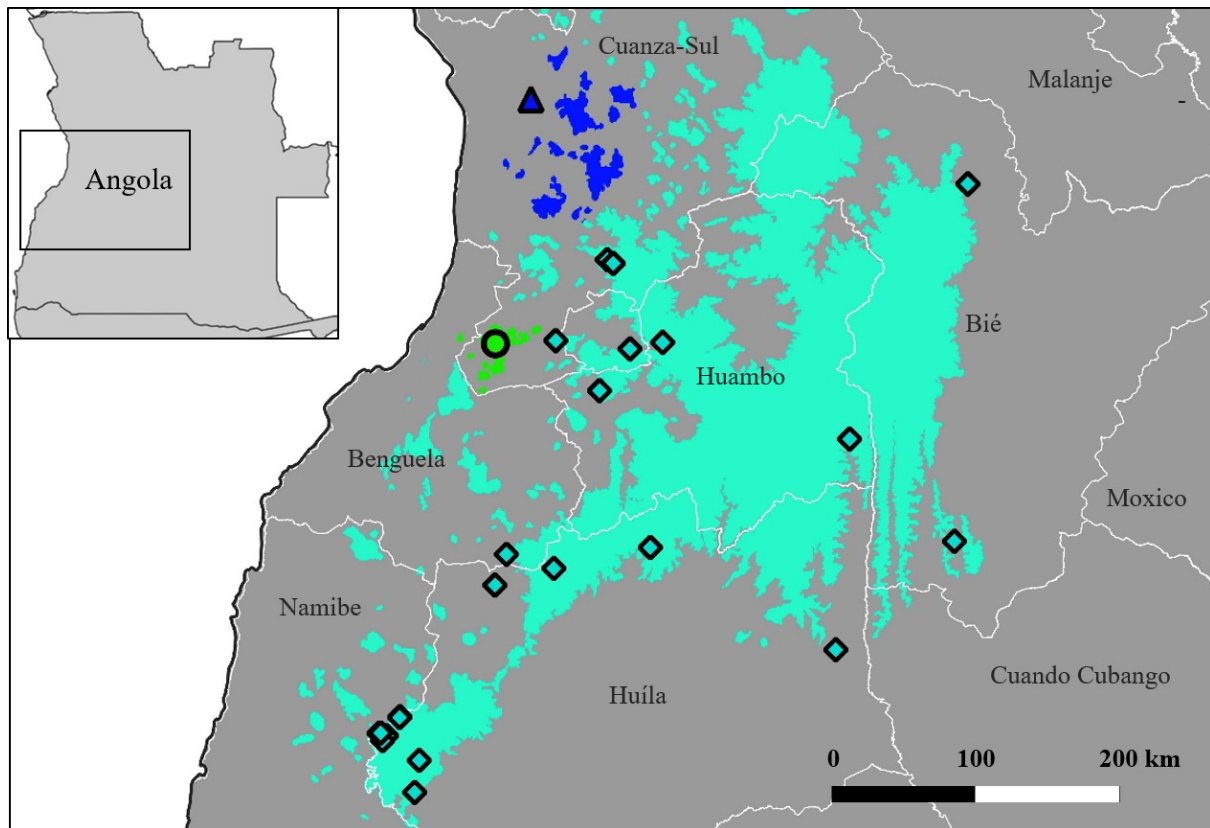


Figure 2: Occurrence records (symbols) and possible highlands occupied (cyan area) by three highland endemic *Leptopelis* species in Angola: *L. anchietae*: cyan and diamonds; *L. jordani*: dark blue and triangle; *L. marginatus*: green and circle.

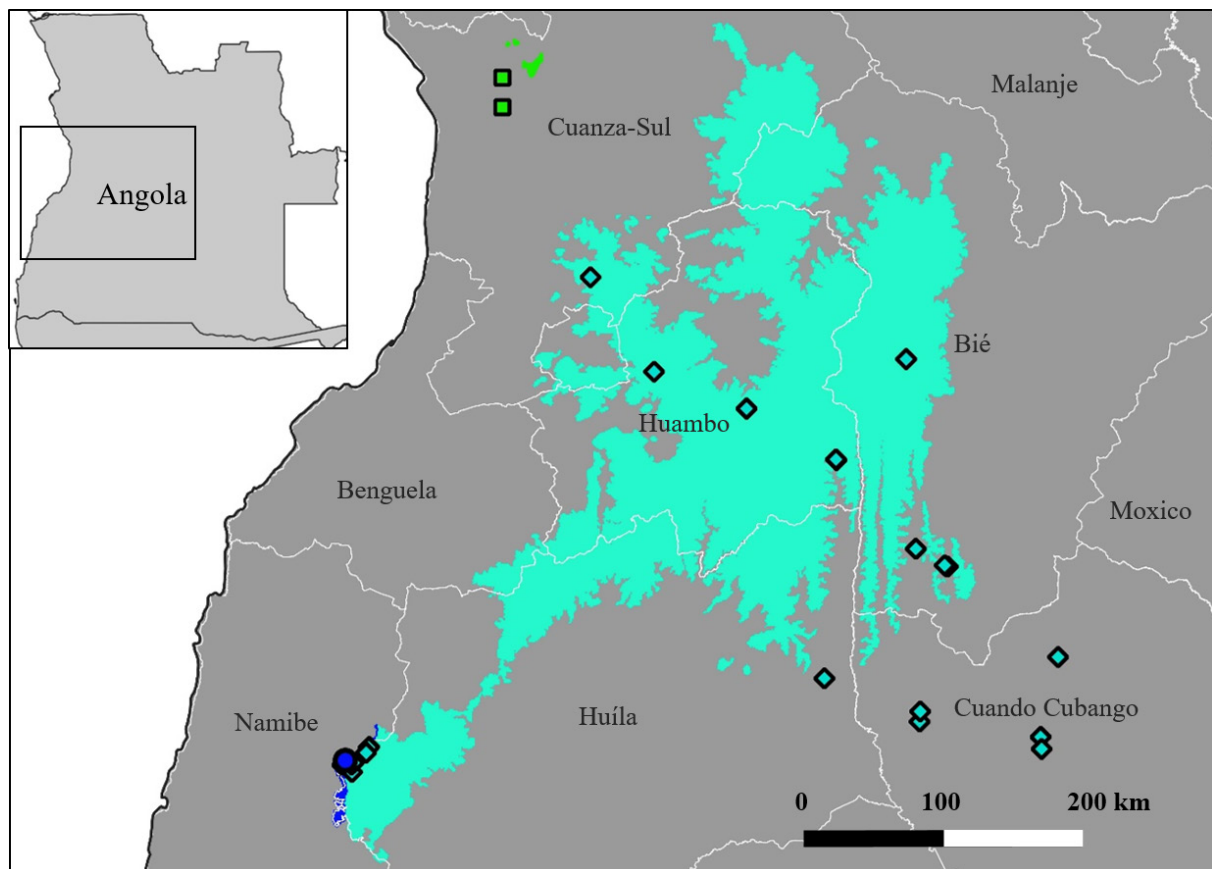


Figure 3: Occurrence records (symbols) and possible highlands occupied (cyan area) by highland endemic amphibian species in Angola: *Hyperolius cinereus*: cyan and diamonds; *H. chelaensis*: dark blue and circle; *Amnirana parkerina*: green and squares.

Hyperolius (Ernst *et al.* 2021) but future revisions may result in new generic arrangements. Only two currently recognised *Hyperolius* species, both Angolan endemics, are considered to be highland endemics (Figure 3).

Hyperolius chelaensis (Chela Mountain reed frog; Figure 6c) is only known from one mountain torrent in a relict Afromontane forest gorge of Serra da Chela on the Humpata Plateau, above 2,000 masl. This habitat is unusual for the genus, and this species is expected to have a highly restricted and fragmented distribution. Males call from water level and tadpoles occur in large rocky pools (Conradie *et al.* 2012). Although assessed as Data Deficient (IUCN SSC Amphibian Specialist Group 2017), its restricted distribution and habitat requirements suggest that it is at high risk of extinction. Two recent surveys in the vicinity of the type locality failed to locate the species. Further surveys and population monitoring are critical conservation priorities.

Hyperolius cinereus (ashy reed frog; Figure 6d) is closely related to *H. chelaensis*, but it is much more widely distributed across higher elevations of the Angolan Planalto (Conradie *et al.* 2013). It seems to be tolerant to some habitat disturbance, and it is assessed as Least Concern (IUCN SSC Amphibian Specialist Group & SA-FRoG 2017a).

Amnirana (Ranidae)

White-lipped frogs are represented by five species in Angola, and one in Namibia (Jongsma *et al.* 2018, Baptista *et al.* 2019, Channing & Rödel 2019). They generally breed in large waterbodies or forest streams, are mainly terrestrial and produce powerful skin toxins. They are usually associated with lowland habitats, although one Angolan endemic (Figure 3) is also a highland endemic (Channing & Rödel 2019).

Amnirana parkeriana (Congolo white-lipped frog) is only known from the type series collected in the Cuanza-Sul Province (Mertens 1938) and is apparently restricted to swampy forest at mid-elevations (1,000–1,250 masl) in the Central Escarpment (Parker 1940). It has been assessed as Data Deficient (IUCN SSC Amphibian Specialist Group & SA-FRoG 2020a). Surveys to establish areas of occurrence and basic population monitoring are priorities for this species.

Poyntonophrynus (Bufonidae)

Southwestern Africa is the hotspot for pygmy toads (Ceriaco *et al.* 2018, Baptista *et al.* 2023), with more than half (eleven) of all recognised species occurring in the region, including three species which are endemic or near-endemic to Namibia, four Angolan endemics, and one species endemic to the region

(Channing & Rödel 2019, Baptista *et al.* 2023). They are generally associated with arid climates, and lay strings of eggs in temporary pools, normally breeding after heavy rains. Four highland endemic species are thus far recorded (Figures 4 and 6). This group has many similar-looking species and taxonomic confusions have been common (Poynton & Broadley 1988, Baptista *et al.* 2023). Morphological features appear to be less reliable than genetic and call data for identifying species in this genus (e.g., Rödel *et al.* 2023, Baptista *et al.* 2023). Further phylogenetic studies may uncover additional cryptic species in both countries and change the current species distributions.

Poyntonophrynus pachnodes (Serra da Neve pygmy toad; Figure 6e) appears to be restricted to Serra da Neve (Figure 4), an isolated inselberg in northern Namibe Province, Angola. It is associated with miombo woodland at elevations above 1,400 masl, but little is known of its natural history (Ceriaco *et al.* 2018). Although the species was thought to be closely related to *P. fenoulheti* (*vide* Ceriaco *et al.* 2018), phylogenetic results revealed a closer relation to the western, more arid-adapted *P. dombensis* and *P. damaranus* (Baptista *et al.* 2023). It has not yet been assessed by the IUCN. There are no identifiable threats documented in this remote location, but population monitoring for this species is a priority considering its limited distribution.

Poyntonophrynus fernandae (Fernanda pygmy toad; Figures 6g and 6h) contains two divergent lineages: *P. fernandae sensu stricto* in the north and *P. cf. fernandae* in the south. *Poyntonophrynus fernandae* s.s. occurs in Angola's Central Escarpment at elevations of 520–1,303 masl (Figure 4). It appears to be strongly associated with large granite boulders in moist escarpment forest and secondary miombo habitats. It may be more widely distributed along the western escarpment and large rock outcrops in central Cuanza-Sul Province. Portions of its habitat are threatened by deforestation, agriculture and encroachment of invasive species (e.g., *Inga vera*). *Poyntonophrynus cf. fernandae* has only been recorded from Serra da Namba (1,730 m), in syntopy with *P. nambensis* (Figure 4). Clear sexual dichromatism, unusual for the genus, is present in *P. fernandae (sensu lato)*. Breeding males are yellow (less so in *P. cf. fernandae*, see Figures 6g and 6h), while females tend to be duller. However, some females of *P. fernandae* s.s. also display shades of bright green, red, orange and small patches of yellow (Figure 6g). It was suggested that *P. fernandae sensu lato* should be listed as Data Deficient (DD) (Baptista *et al.* 2023), but it has not yet been formally assessed.

Poyntonophrynus nambensis (Namba pygmy toad; Figure 6i) is only known from the region of Serra da Namba (also known as Mt Namba) in the Angolan

highlands, at 1,730–1,840 masl (Figure 4). Despite targeted surveys, it has not been found in the escarpment zone or elsewhere in the highlands, suggesting that it may be endemic to Mt Namba. The species appears to be locally common and its rupicolous habitat is probably not threatened. It has not been formally assessed, but a listing of Data Deficient (DD) has been suggested (Baptista *et al.* 2023).

Poyntonophrynus hoeschi (Hoesch's pygmy toad; Figure 6f) occurs in Namibia's Central-Western Plains and adjacent inselbergs (Figure 5). Foraging adults are normally found in the mountains or inselbergs themselves, while breeding sites tend to be in adjacent, lower-lying streams or rivers. It was assessed as Least Concern (IUCN SSC Amphibian Specialist Group 2013b), although its occupied range is more restricted than previously assumed (see Rödel *et al.* 2023). A phylogenetic comparison across the species' range is a priority for conservation and research.

Poyntonophrynus damaranus (Damaraland pygmy toad) is currently thought to be a highland endemic that occurs on the Waterberg and the northern Namibian escarpment (see, e.g., Ceriaco *et al.* 2018). However, preliminary evidence, including phylogenetic sequences and call data (Becker *et al.* unpubl. data), suggests that taxonomic confusion with other morphologically similar species has led to a misinterpretation of its habitat and range. It is most likely a widespread species associated with the Kalahari lowlands.

HIGHLAND-ASSOCIATED SPECIES

Several other species are associated with highlands, although a large portion of their habitat extends into the lowlands as well. Notable species include the Angola ornate frog, *Hildebrandtia ornatissima*, an Angolan endemic. Most of the historical records of this poorly known frog were collected in the Angolan

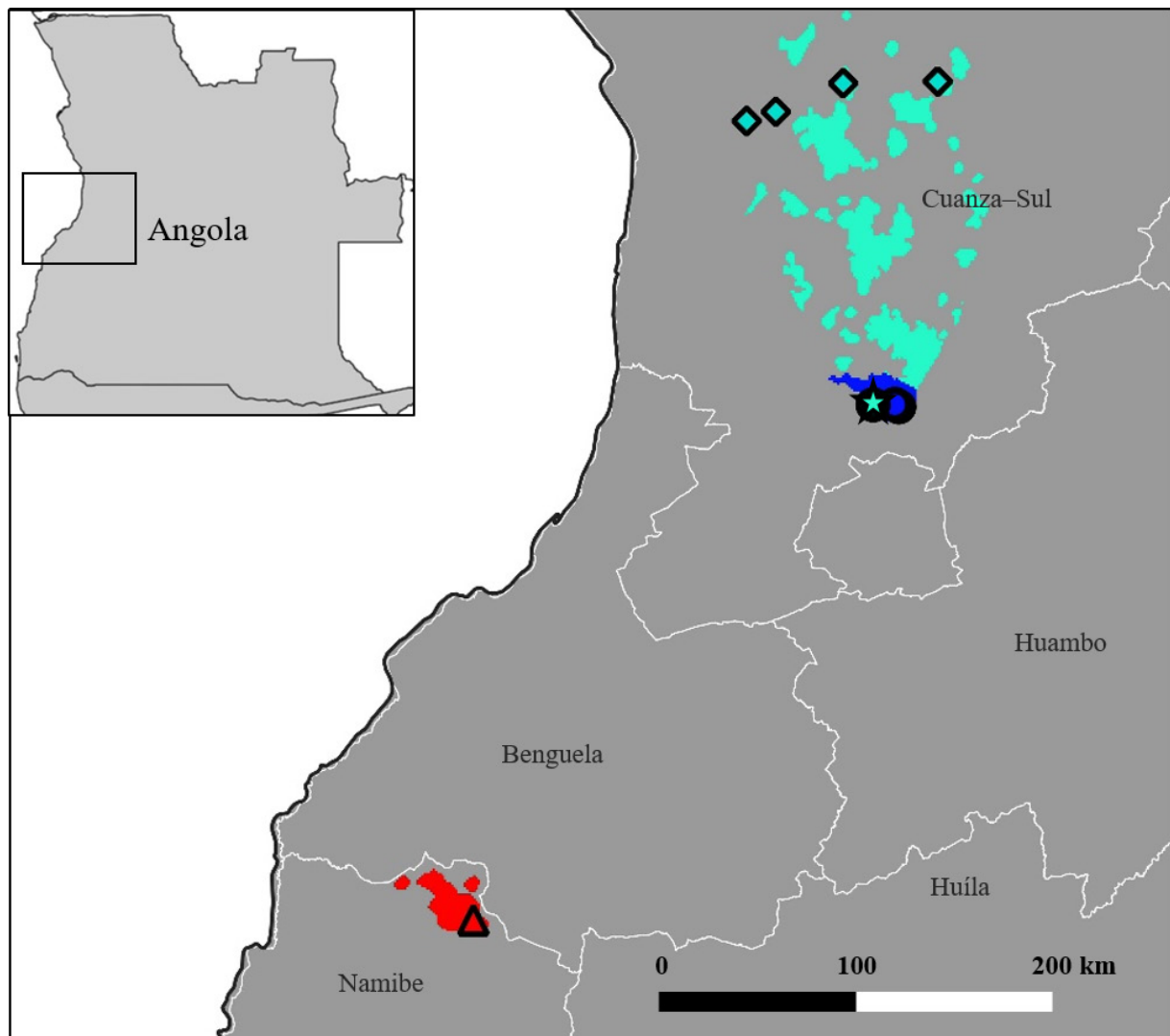


Figure 4: Occurrence records (symbols) and possible highlands occupied (shaded area) by highland endemic *Poyntonophrynus* species in Angola. *Poyntonophrynus fernandae* s.s.: cyan and diamonds; cyan star = *P. cf. fernandae*; *P. nambensis*: dark blue and circle (note syntopic occurrence with *P. cf. fernandae*); *P. pachnodes*: red and triangle.

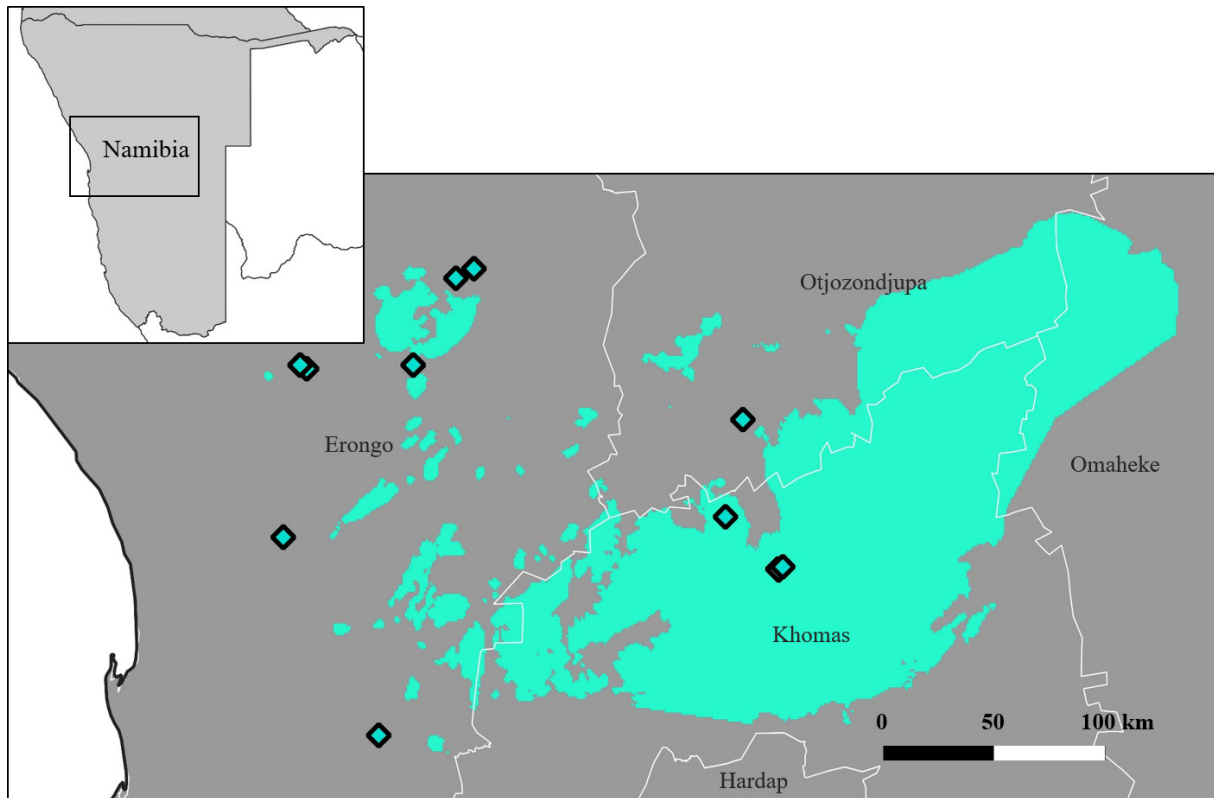


Figure 5: Occurrence records (diamonds) and possible highlands occupied (cyan-shaded area) by the highland endemic amphibian *Poyntonophrynus hoeschi* in Namibia.

Planalto, but it was also recently recorded from miombo savannas at lower elevation (Vaz Pinto unpubl. data).

Phrynomantis annectens (marbled rubber frog) is commonly found on arid mountain tops throughout Namibia and southwestern Angola. It appears to be associated with arid rocky habitats rather than with the highlands themselves, occurring more frequently in the lowlands (GBIF 2021). Different populations show considerable variation in colour pattern, which is taxonomically relevant for the genus (Ceriaco *et al.* 2021). Thus, a phylogenetic revision of this species may yet identify highland-associated cryptic taxa.

Poyntonophrynus dombensis (Dombe pygmy toad) is similarly associated with arid rocky habitat, and occurs both on and around the arid highlands of southwestern Angola and northwestern Namibia (Ceriaco *et al.* 2018, GBIF 2021).

Poyntonophrynus grandisonae (Grandison's pygmy toad) occurs almost entirely within the HEAN in southwestern Angola, but has primarily been collected from low (40 m) to mid (700–800 m) elevations, and is therefore not considered a true highland endemic species.

Poyntonophrynus jordani (Jordan's pygmy toad) is apparently associated with high- and mid-elevation sedimentary rock formations in arid southern Namibia (Rödel *et al.* 2023). Little is known about this species, although the call has been recorded and breeding occurs in temporary rocky pools (Rödel *et al.* 2023).

DISCUSSION

Amphibian highland endemism within the HEAN is most pronounced in Angola's Central Escarpment and Marginal Mountain Chain. Most of the highland endemics occur in Angola where amphibian diversity is also high, while Namibia contains only one highland endemic and three highland-associated species. (See Figures 2–4.) The Angolan Planalto hosts two widespread highland endemics (Figures 2 and 3) and additional highland-associated species. The Southern Escarpment in Angola and northwestern Namibia hosts at least two highland-associated species, but only one highland endemic in southwestern Angola (Figures 3 and 5). The Khomas Hochland in Namibia hosts one highland endemic (Figure 5), and the Nama Karoo Basin hosts one highland-associated species. Most highland endemics are limited to a particular mountain range or inselberg, while some are more widespread, but none occurs throughout the HEAN. This is probably because there is a considerable north–south rainfall gradient that requires very different adaptations.

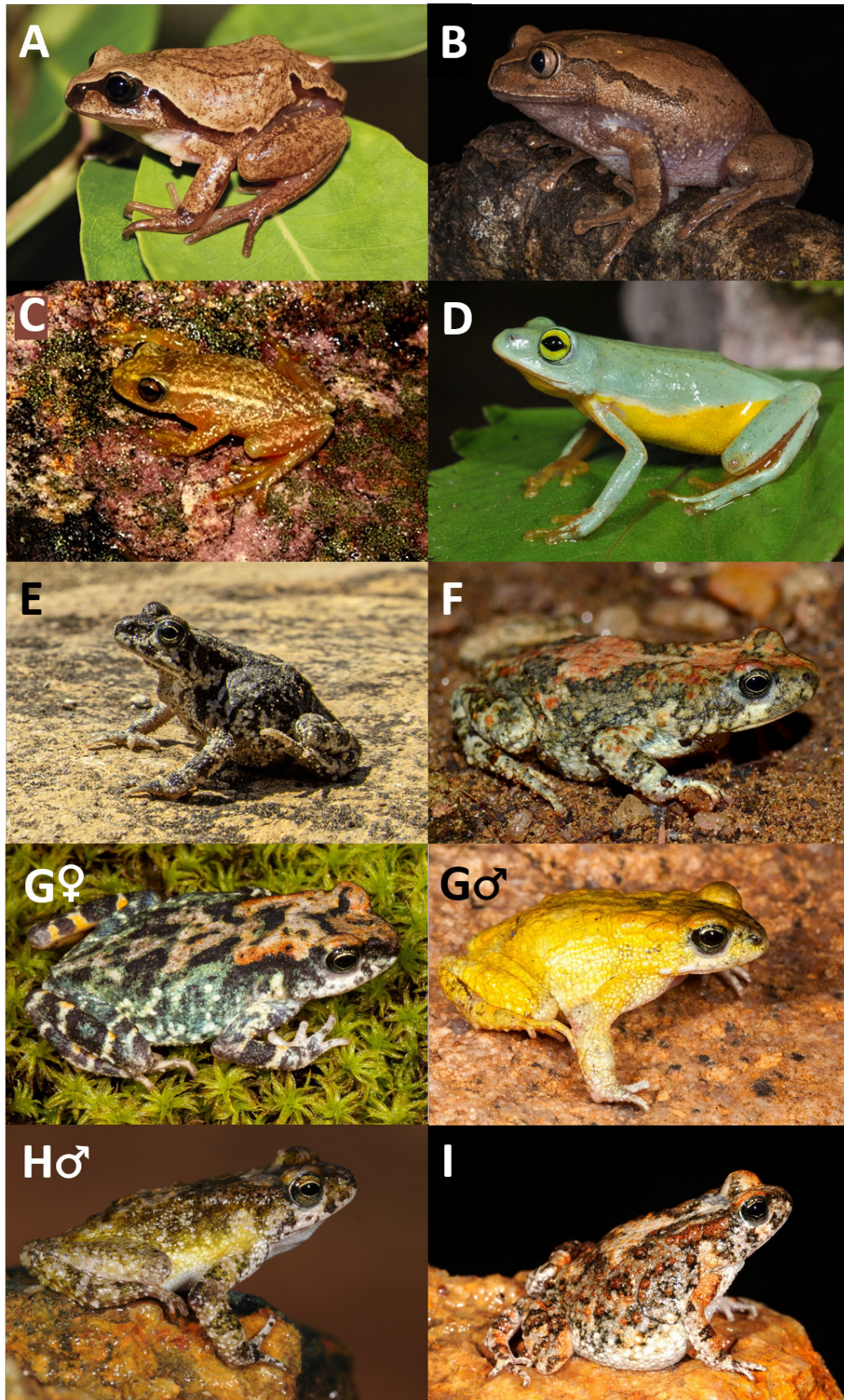


Figure 6: Highland endemic amphibians from Angola and Namibia. A) *Leptopelis anchietae*. Photo: NL Baptista. B) *L. jordani*. Photo: P Vaz Pinto. C) *Hyperolius chelaensis*. Photo: W Conradie. D) *H. cinereus*. Photo: B Branch. E) *Poyntonophrynus pachnodes*. Photo: J Lobón-Rovira. F) *P. hoeschi*. Photo: F Becker. G) *P. fernandae* s.s. (female and male). Photos: P Vaz Pinto. H) *P. cf. fernandae* (male). Photo: B Branch. I) *P. nambensis*. Photo: B Branch.

Amphibian endemism in the HEAN is lower than might be expected, compared to other taxa such as birds in Angola (Mills 2010, Mills *et al.* 2011, Mills *et al.* 2013, Dean *et al.* 2019) and reptiles, plants and scorpions in Namibia (e.g., Bauer *et al.* 2006, Prendini 2005, Craven & Vorster 2006, Bauer 2010). This is likely to be due to the understudied status of amphibians, resulting in a severe dearth of knowledge spanning from basic levels, such as species inventories or surveys (Clark *et al.* 2011, Baptista *et al.* 2018), to more complex levels such as clarifying taxonomy, distribution patterns and phylogenetic relations (Herrmann & Branch 2013). Not only is the level of highland endemism of amphibians likely to be underestimated, but conservation and scientific assessments based on current data are inaccurate. Of the 15 notable highland species mentioned in this paper, most lack a thorough phylogenetic investigation, the processes driving their speciation are unclear, and their biology, conservation status and threats are poorly understood. Further surveys and studies may reveal some highland endemics to be more widespread, while others are likely to uncover additional cryptic highland taxa (e.g., Ernst *et al.* 2014). Two new highland endemic species were described in the last year (Baptista *et al.* 2023), and additional species discoveries are likely to be made (Baptista *et al.* unpubl. data, Harvey unpubl. data). Preliminary phylogenetic studies on amphibians of northwestern Angolan forest fragments also revealed the evolutionary potential of the area, with phylogenetic lineages in several groups being distinct and showing signs of recent speciation, or speciation in progress (see Lautenschläger *et al.* 2023).

Amphibian endemism patterns in the region may be similar to those in better-studied groups, which could indicate priority areas for baseline research to mitigate the knowledge gaps. For instance, western Angola is a hotspot for bird endemism (Dean *et al.* 2019, BirdLife International 2022), and even though several amphibian endemics are already known from here, it remains a priority for further surveys. The Northern Escarpment is particularly poorly surveyed, and also displays a lower overall amphibian richness than can be expected based on rainfall (Figure 1). Specific highlands to be prioritised include the mountains of Serra do Môco, Soque, Serra do Mepo, Ebanga and Mt Namba, and the northern and central escarpment ridges. In Namibia, notable hotspots for plant richness and endemism include the Kaokoveld or Southern Escarpment and Karstveld, the Khomas Hochland, Brandberg, Otavi Mountains and Naukluft Mountains (Maggs *et al.* 1998, van Wyk & Smith 2001, Craven & Vorster 2006), whereas the entire western escarpment has been predicted to be a centre of endemism for most vertebrates and plants (Simmons *et al.* 1998). The more northern highlands have higher rainfall and therefore greater potential for

unknown amphibian endemism. However, the Khomas Hochland has been comparatively well surveyed and the Otavi Mountains do not offer a major elevational gradient. One small-range endemic is known from the South African portion of the Huns–Orange Mountains, and the wider area here is also poorly surveyed.

Beyond more intensive surveys, there are several research priorities for the HEAN (for a more detailed discussion, see Clark *et al.* 2011). The first major priority is phylogenetic and biogeographic studies, including a broad geographic scope from across species' known areas of occurrence. Such data will also serve as the basis for identifying areas of major conservation priority. For species with small distributions, population monitoring studies are a priority. Amphibian populations at high elevations appear to be especially vulnerable to chytridiomycosis, a fungal disease, and to “enigmatic declines” (Stuart *et al.* 2004). Currently, no baseline population data exist for these species to assess such threats, similar to the pattern elsewhere in Africa (Rödel *et al.* 2021). We recommend repeated surveys of known high-elevation populations to understand basic demographic trends over time, and surveys of multiple sites to understand changes in occupied range. Finally, the drivers of speciation within these highlands are still unclear. The known distribution patterns indicate that shifting climatic gradients and vicariance probably play a major role.

Few official conservation measures are being implemented to protect amphibian populations in the HEAN. In Angola, the evergreen mist forests in Cabinda are now contained within the Mayombe National Park, which was proclaimed in 2011, but most of the important highland areas still fall outside protected areas. Sections of the Afromontane and escarpment forests have frequently been proposed to be officially protected since before independence (Huntley 1974, 2010, 2017, Huntley & Matos 1994, Mills *et al.* 2013), but only recently has the Angolan Government taken concrete steps towards the protection of some key highland forest areas (Ministério do Ambiente 2018). In addition, studies commissioned by the Angolan Government have been conducted at Serra do Môco, Cumbira and Serra do Pingano (see Lautenschläger *et al.* 2023), and formal proposals to demarcate these three areas as reserves are currently pending final approval. Critical highlands which remain unprotected include the Humpata Plateau, Serra da Neve and Mt Namba. In Namibia, much of the highlands fall outside the protected area network on privately owned land (Atlas of Namibia Team 2022). Private lands contain largely intact wilderness, but offer less certainty of long-term protection (Barnard *et al.* 1998). While Namibian legislation does protect species from exploitation and habitat destruction, the lack of

baseline data on amphibian populations hinders the effective implementation thereof.

Despite the clear potential for high levels of amphibian endemism and diversity in the HEAN, these areas are severely understudied, similar to other tropical African highlands (see Liedtke *et al.* 2022). Based on the observed patterns, the Angolan Central Escarpment and Marginal Mountain Chain are the main hotspots for endemism and diversity in this region.

ACKNOWLEDGEMENTS

Fieldwork in Namibia was conducted under the National Commission on Research, Science and Technology permit AN20191118. FB thanks Alan Channing for reviewing and improving this manuscript, and for sequencing several samples that have elucidated distribution patterns in Namibia. Fieldwork in Angola was made possible through the help of the University of Kimpa Vita in Uíge and partially funded through a travel grant from the German Academic Exchange Service (DAAD) and the Strategic Partnership Programme of the Technische Universität Dresden (T Lautenschläger and C Neinhuis), as well as a grant from the Paul-Ungerer-Stiftung. Additional surveys were supported by the Ministério do Ambiente – Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC) within the Expansão e Fortalecimento do Sistema de Áreas Protegidas em Angola project agenda through a grant provided by the Global Environment Facility under the auspices of the United Nations Environment Programme. RE particularly thanks J Lau, MF Branquima and M Hölting for support in the field. Permission to conduct biodiversity research in Angola was granted by the Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC), Ministério do Ambiente, República de Angola and the Gabinete Provincial da Agricultura, Pecuária e Pescas Do Uíge under permission numbers 122/INBAC.MINAMB/2013, N° 17/014, N° 02/018; N° 05/2019. NLB was supported by FCT contract SFRH/BD/140810/2018, and BIOPOLIS 2022-19.

REFERENCES

- Ahl E (1934) Über eine kleine Froschsammlung aus Deutsch Südwestafrika. *Zoologischer Anzeiger* 107: 333–336.
- Armstrong AJ (2001) Conservation status of herpetofauna endemic to Kwazulu-Natal. *African Journal of Herpetology* 50(2): 79–96. <https://doi.org/10.1080/21564574.2001.9635453>.
- Atlas of Namibia Team (2022) *Atlas of Namibia: its land, water and life*. 242–283. Namibia Nature Foundation, Windhoek, Namibia.
- Baptista N, António T, Branch WR (2018) Amphibians and reptiles of the Tundavala region of the Angolan Escarpment. *Biodiversity & Ecology* 6: 397–403. <https://doi.org/10.7809/b-e.00351>.
- Baptista N, Conradie W, Vaz Pinto P, Branch W (2019) The amphibians of Angola: early studies and the current state of knowledge. In: Ferrand N, Huntley BJ, Lages F, Russo V (eds) *Biodiversity of Angola: Science & Conservation: A Modern Synthesis*, 1st ed. 2019. 243–289. Springer International Publishing, Springer, Cham.
- Baptista NL, Vaz Pinto P, Keates C, Edwards S, Rödel M-O, Conradie W (2021) A new species of red toad, *Schismaderma* Smith, 1849 (Anura: Bufonidae), from central Angola. *Zootaxa* 5081(3): 301–332. <https://doi.org/10.11646/zootaxa.5081.3.1>.
- Baptista N, Vaz Pinto P, Ernst E, Ferrand N, Branch WR (2017) Cryptic diversity in treefrogs (*Leptopelis*) of the Angolan escarpment – fitting the pieces together. Poster presented at 13th Conference of the Herpetological Association of Africa, Bonamanzi, South Africa. *African Herp News* 66: 64–65.
- Baptista NL, Vaz Pinto P, Keates C, Lobón-Rovira J, Edwards S, Rödel M-O (2023) Two new *Poyntonophrynus* species (Anura: Bufonidae) highlight the importance of Angolan centers of endemism. *Vertebrate Zoology* 73: 991–1031. <https://doi.org/10.3897/vz.73.e103935>.
- Barnard P, Brown CJ, Jarvis AM, Robertson A, Rooyen LV (1998) Extending the Namibian protected area network to safeguard hotspots of endemism and diversity. *Biodiversity and Conservation* 7(4): 531–547. <https://doi.org/10.1023/A:1008831829574>.
- Bauer AM (2010) A new species of *Pachydactylus* (Squamata: Gekkonidae) from the Otavi Highlands of northern Namibia. *Bonn zoological Bulletin* 57: 257–266.
- Bauer A, Lamb T, Branch W (2006) A revision of the *Pachydactylus serval* and *P. weberi* groups (Reptilia: Gekkota: Gekkonidae) of Southern Africa, with the description of eight new species. *Proceedings of the California Academy of Sciences* 57(23): 595–709.
- Becker FS (2022) Wildlife: Amphibians. In: Atlas of Namibia Team (ed) *Atlas of Namibia: its land, water and life*. 196–241. Namibia Nature Foundation, Windhoek, Namibia.
- Becker FS, Hopkins RW (2017) The rediscovery of a lost frog: *Arthroleptis troglodytes* Poynton, 1963. *African Zoology* 52(3): 183–187. <https://doi.org/10.1080/15627020.2017.1370982>.
- Becker FS, Slingsby JA, Measey J, Tolley KA, Altwegg R (2022) Finding rare species and estimating the probability that all occupied sites have been found. *Ecological Applications* 32(2). <https://doi.org/10.1002/eap.2502>.
- Behangana M, Kasoma PMB, Luiselli L (2009) Ecological correlates of species richness and population abundance patterns in the amphibian communities from the Albertine Rift, East Africa. *Biodiversity and Conservation* 18(11): 2855–2873. <https://doi.org/10.1007/s10531-009-9611-9>.
- BirdLife International (2022) Endemic bird areas factsheet: Western Angola. <http://datazone.birdlife.org/eba/search>. [Accessed 29 April 2022].
- Bocage JVB du (1873) Mélanges erpétologiques. II. Sur quelques reptiles et batraciens nouveaux. Rares ou peu connus d'Afrique occidentale. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* 4: 209–227.
- Bocage JVB du (1879) Reptiles et batraciens nouveaux d'Angola. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* 7: 97–99.
- Bocage JVB du (1895a) *Herpétologie de Angola et du Congo*. Lisbonne: Ministère de la Marine et des Colonies.
- Bocage JVB du (1895b) Sur une espèce de crapaud à ajouter à la faune herpétologique d'Angola. *Jornal de Ciências, Matemáticas, Physicas e Naturaes* 4: 51–53.
- Boycott RC, de Villiers AL (1986) The status of *Heleophryne rosei* Hewitt (Anura: Leptodactylidae) on Table Mountain and recommendations for its conservation. *South African Journal of Wildlife Research* 16(4): 129–34. https://hdl.handle.net/10520/AJA03794369_3580.
- Branch WR, Baptista N, Keates C, Edwards S (2019) Rediscovery, taxonomic status, and phylogenetic

- relationships of two rare and endemic snakes (Serpentes: Psammophiinae) from the southwestern Angolan plateau. *Zootaxa* 4590(3). <https://doi.org/10.11646/zootaxa.4590.3.2>.
- Ceríaco LMP, Marques MP, Bandeira S, Agarwal I, Stanley EL, Bauer AM, Heinicke MP, Blackburn DC (2018) A new earless species of *Poyntonophrynus* (Anura, Bufonidae) from the Serra da Neve Inselberg, Namibe Province, Angola. *ZooKeys* 780: 109–136. <https://doi.org/10.3897/zookeys.780.25859>.
- Ceríaco L, Santos B, Marques M, Bauer A, Tiutenko A (2021) Citizen science meets specimens in old formalin filled jars: a new species of banded rubber frog, genus *Phrynomantis* (Anura, Phrynomeridae) from Angola. *Alytes* 38: 18–48.
- Channing A (2001) *Amphibians of Central and Southern Africa*. Cornell University Press. <http://www.jstor.org/stable/10.7591/j.ctvv414ks>.
- Channing A (2022) Colour patterns to sequences: a perspective on the systematics of the *Hyperolius viridiflavus* group (Anura: Hyperoliidae) using mitochondrial DNA. *Zootaxa* 5134(3): 301–354. <https://doi.org/10.11646/zootaxa.5134.3.1>.
- Channing A, Becker F (2019) Correction to the type locality of *Tomopterna ahli* (Deckert, 1938) (Anura: Pyxicephalidae), with the designation of a neotype. *Zootaxa* 4688(4): 549–560. <https://doi.org/10.11646/zootaxa.4688.4.6>.
- Channing A, Measey GJ, de Villiers AL, Turner AA, Tolley KA (2017) Taxonomy of the *Capensibufo rosei* group (Anura: Bufonidae) from South Africa. *Zootaxa* 4232(2): 282. <https://doi.org/10.11646/zootaxa.4232.2.11>.
- Channing AE, Rödel M-O (2019) *Field guide to the frogs & other amphibians of Africa*. Struik Nature, Cape Town, South Africa.
- Clark VR, Barker NP, Mucina L (2011) The Great Escarpment of southern Africa: a new frontier for biodiversity exploration. *Biodiversity and Conservation* 20(12): 2543–2561. <https://doi.org/10.1007/s10531-011-0103-3>.
- Conradie W, Bittencourt-Silva GB, Farooq HM, Loader SP, Menegon M, Tolley KA (2018) New species of mongrel frogs (Pyxicephalidae: *Nothophryne*) for northern Mozambique inselbergs. *African Journal of Herpetology* 67(1): 61–85. <https://doi.org/10.1080/21564574.2017.1376714>.
- Conradie W, Branch WR, Measey GJ, Tolley KA (2012) A new species of *Hyperolius* Rapp, 1842 (Anura: Hyperoliidae) from the Serra da Chela mountains, southwestern Angola. *Zootaxa* 3269(1): 1–17. <https://doi.org/10.11646/zootaxa.3269.1.1>.
- Conradie W, Branch WR, Tolley KA (2013) Fifty shades of grey: Giving colour to the poorly known Angolan ashy reed frog (Hyperoliidae: *Hyperolius cinereus*), with the description of a new species. *Zootaxa* 3635(3): 201–223. <https://doi.org/10.11646/zootaxa.3635.3.1>.
- Craven P, Vorster P (2006) Patterns of plant diversity and endemism in Namibia. *Bothalia* 36(2): 175–189. <https://doi.org/10.4102/abc.v36i2.360>.
- Dean WRJ, Melo M, Mills MSL (2019) The avifauna of Angola: richness, endemism and rarity. In: Huntley BJ, Russo V, Lages F, Ferrand N (eds) *Biodiversity of Angola*. 335–356. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-030-03083-4_14.
- Du Preez LH, Carruthers V (2017) *Frogs of southern Africa: a complete guide*, Second edition. Struik Nature, Cape Town, South Africa.
- Ernst R, Kehlmaier C, Baptista NL, Pinto PV, Branquima MF, Dewynter M, Fouquet A, Ohler A, Schmitz A (2021) Filling the gaps: The mitogenomes of Afrotropical egg-guarding frogs based on historical type material and a re-assessment of the nomenclatural status of *Alexteroon* Perret, 1988 (Hyperoliidae). *Zoologischer Anzeiger* 293: 215–224. <https://doi.org/10.1016/j.jcz.2021.06.002>.
- Ernst R, Lautenschläger T, Branquima MF, Hölting M (2020) At the edge of extinction: a first herpetological assessment of the proposed Serra do Pingano Rainforest National Park in Uíge Province, northern Angola. *Zoosystematics and Evolution* 96(1): 237–262. <https://doi.org/10.3897/zse.96.51997>.
- Ernst R, Nianguesso ABT, Lautenschläger T, Barej MF, Schmitz A, Hölting M (2014) Relicts of a forested past: Southernmost distribution of the hairy frog genus *Trichobatrachus* Boulenger, 1900 (Anura: Arthroleptidae) in the Serra do Pingano region of Angola with comments on its taxonomic status. *Zootaxa* 3779(2): 297. <https://doi.org/10.11646/zootaxa.3779.2.10>.
- Frost DR (2022) Amphibian species of the world: an online reference. <https://amphibiansoftheworld.amnh.org/>.
- GBIF (2021) Occurrence download (Amphibians: Namibia). <https://doi.org/10.15468/DL.K7WIFYX>.
- Griffin M (2003) *Annotated checklist and provisional conservation status of Namibian reptiles*. Unpublished report: Ministry of Environment and Tourism, Windhoek, Namibia. pp. 169. https://www.lacerta.de/AF/Bibliografie/BIB_4908.pdf
- Herrmann H-W, Branch WR (2013) Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist. *Journal of Arid Environments* 93: 94–115.
- Huntley BJ (1974) Outlines of wildlife conservation in Angola. *South African Journal of Wildlife Research* 4(3): 157–166.
- Huntley BJ (2010) *Proposals for an Angolan Protected Area Expansion Strategy (APAES)*. Unpublished report: Unknown company or institution, unknown place. pp. 28.
- Huntley BJ (2017) *Wildlife at war in Angola: the rise and fall of an African Eden*, First edition. Protea Book House, Pretoria.
- Huntley BJ, Matos EM (1994) Botanical diversity and its conservation in Angola. *Strelitzia* 1: 53–74.
- IUCN (2021) The IUCN red list of threatened species. <https://www.iucnredlist.org>. [Accessed 25 March 2022].
- IUCN SSC Amphibian Specialist Group (2013a) *Leptopelis anchietae*. The IUCN red list of threatened species 2013: e.T56239A18385703. <https://doi.org/10.2305/IUCN.UK.2013-2.RLTS.T56239A18385703.en>. [Accessed 27 May 2022].
- IUCN SSC Amphibian Specialist Group (2013b) *Poyntonophrynus hoeschi*. The IUCN red list of threatened species 2013: e.T54663A18374358. <https://doi.org/10.2305/IUCN.UK.2013-2.RLTS.T54663A18374358.en>. [Accessed 27 May 2022].
- IUCN SSC Amphibian Specialist Group (2017) *Hyperolius chelaensis*. The IUCN red list of threatened species 2017: e.T76317568A76317892. <https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T76317568A76317892.en>. [Accessed 27 May 2022].
- IUCN SSC Amphibian Specialist Group & South African Frog Re-assessment Group (SA-FRoG) (2020a) *Amnirana parkeriana*. The IUCN red list of threatened species 2020: e.T58201A175966566. <https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T58201A175966566.en>. [Accessed 27 May 2022].
- IUCN SSC Amphibian Specialist Group & South African Frog Re-assessment Group (SA-FRoG) (2020b)

- Leptopelis jordani*. The IUCN red list of threatened species 2020: e.T56259A176569883. <https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T56259A176569883.en>. [Accessed 27 May 2022].
- IUCN SSC Amphibian Specialist Group, South African Frog Re-assessment Group (SA-FRoG) (2017a) *Hyperolius cinereus*. The IUCN red list of threatened species 2017: e.T76317621A18373821. <https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T76317621A18373821.en>. [Accessed 27 May 2022].
- IUCN SSC Amphibian Specialist Group, South African Frog Re-assessment Group (SA-FRoG) (2017b) *Leptopelis marginatus*. The IUCN red list of threatened species 2017: e.T56264A77164261. <https://doi.org/10.2305/IUCN.UK.2017-2.RLTS.T56264A77164261.en>. [Accessed 27 May 2022].
- Jaynes KE, Myers EA, Gvoždík V, Blackburn DC, Portik DM, Greenbaum E *et al.* (2021) Giant tree frog diversification in West and Central Africa: Isolation by physical barriers, climate, and reproductive traits. *Molecular Ecology* 31(15): 3979–3998. <https://doi.org/10.1111/mec.16169>.
- Jongsma GFM, Barej MF, Barratt CD, Burger M, Conradie W, Ernst R *et al.* (2018) Diversity and biogeography of frogs in the genus *Amnirana* (Anura: Ranidae) across sub-Saharan Africa. *Molecular Phylogenetics and Evolution* 120: 274–285. <https://doi.org/10.1016/j.ympev.2017.12.006>.
- Largen MJ (1991) A new genus and species of petropedetine frog (Amphibia Anura Ranidae) from high altitude in the mountains of Ethiopia. *Tropical Zoology* 4(1): 139–152. <https://doi.org/10.1080/03946975.1991.10539483>.
- Laurent RF (1964) *Reptiles et amphibiens de l'Angola (Troisième contribution)*. Companhia de Diamantes de Angola, 1964., Lisboa. <https://search.library.wisc.edu/catalog/999803343502121>.
- Lautenschläger T, Aime MC, Clausnitzer V, Langer L, Meller P, Müller F *et al.* (2023) Green gem of the Northern Escarpment: biodiversity and endemism of the Serra do Pingano Forest Ecosystem. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment* 8: 161–172.
- Liedtke HC, Lyakurwa JV, Lawson LP, Menegon M, Garrido-Priego M, Mariaux J *et al.* (2022) Thirty years of amphibian surveys in the Ukagurus Mountains of Tanzania reveal new species, yet others are in decline. *African Journal of Herpetology* 71(2): 119–138. <https://doi.org/10.1080/21564574.2022.2043945>.
- Loader SP, Poynton JC, Lawson LP, Blackburn DC, Menegon M (2011) Herpetofauna of montane areas of Tanzania. 3. Amphibian diversity in the northwestern Eastern Arc Mountains, with the description of a new species of *Arthroleptis* (Anura: Arthroleptidae). *Fieldiana Life and Earth Sciences* 4: 90–102. <https://doi.org/10.3158/2158-5520-4.1.90>.
- Maggs GL, Craven P, Kolberg HH (1998) Plant species richness, endemism, and genetic resources in Namibia. *Biodiversity and Conservation* 7(4): 435–446. <https://doi.org/10.1023/A:1008819426848>.
- Malonza PK, Lötters S, Measey GJ (2010) The montane forest associated amphibian species of the Taita Hills, Kenya. *Journal of East African Natural History* 99(1): 47–63. <https://doi.org/10.2982/028.099.0103>.
- Marques M, Ceriaco L, Blackburn D, Bauer A (2018) Diversity and distribution of the amphibians and terrestrial reptiles of Angola. Atlas of historical and bibliographic records (1840–2017). *Proceedings of the California Academy of Sciences* 65: 1–501.
- Mendelsohn JM, Huntley BJ (2023) Introducing the highlands and escarpments of Angola and Namibia. In: Mendelsohn JM, Huntley BJ, Vaz Pinto P (eds) Monograph on endemism in the highlands and escarpments of Angola and Namibia. *Namibian Journal of Environment* 8: 7–22.
- Menegon M, Salvidio S (2005) Amphibian and reptile diversity in the southern Udzungwa Scarp Forest Reserve, south-eastern Tanzania. *African Biodiversity*: 205–212. Springer US, Boston, MA. https://doi.org/10.1007/0-387-24320-8_18.
- Mertens R (1938) Herpetologische Ergebnisse einer Reise nach Kamerun. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main* 442: 1–52.
- Mills MSL (2010) Angola's central scarp forests: Patterns of bird diversity and conservation threats. *Biodiversity and Conservation* 19(7): 1883–1903. <https://doi.org/10.1007/s10531-010-9810-4>.
- Mills MSL, Melo M, Vaz A (2013) The Namba mountains: new hope for Afromontane forest birds in Angola. *Bird Conservation International* 23(2): 159–167. <https://doi.org/10.1017/S095927091200024X>.
- Mills MSL, Olmos F, Melo M, Dean WRJ (2011) Mount Moco: Its importance to the conservation of Swierstra's Francolin *Pternistis swierstrai* and the Afromontane avifauna of Angola. *Bird Conservation International* 21(2): 119–133. <https://doi.org/10.1017/S0959270910000493>.
- Ministério do Ambiente (2018) *Plano Estratégico para o Sistema de Áreas de Conservação de Angola (PESAC)*. Luanda, Angola.
- Monard A (1937) Contribution à la batrachologie d'Angola. *Bulletin de la Société Neuchâteloise des Sciences Naturelles* 62: 5–59. <https://doi.org/10.5169/SEALS-88730>.
- Mörs T, Reguero M, Vasilyan D (2020) First fossil frog from Antarctica: implications for Eocene high latitude climate conditions and Gondwanan cosmopolitanism of Australobatrachia. *Scientific Reports* 10(1): 5051. <https://doi.org/10.1038/s41598-020-61973-5>.
- Nielsen SV, Conradie W, Ceriaco LMP, Bauer AM, Heinicke MP, Stanley EL, Blackburn DC (2020) A new species of rain frog (Brevicipitidae, *Breviceps*) endemic to Angola. *ZooKeys* 979: 133–160. <https://doi.org/10.3897/zookeys.979.56863>.
- Ochoa-Ochoa LM, Mejía-Domínguez NR, Velasco JA, Marske KA, Rahbek C (2019) Amphibian functional diversity is related to high annual precipitation and low precipitation seasonality in the New World. *Global Ecology and Biogeography* 28(9): 1219–1229. <https://doi.org/10.1111/geb.12926>.
- Parker H (1936) Dr. Karl Jordan's expedition to South-West Africa and Angola: herpetological collection. *Novitates Zoologicae* 40: 115–146.
- Parker HW (1940) Undescribed anatomical structures and new species of reptiles and amphibians. *Annals and Magazine of Natural History* 5(27): 257–274. <https://doi.org/10.1080/00222934008527045>.
- Portik DM, Bell RC, Blackburn DC, Bauer AM, Barratt CD, Branch WR *et al.* (2019) Sexual dichromatism drives diversification within a major radiation of African amphibians. *Systematic Biology* 68(6): 859–875. <https://doi.org/10.1093/sysbio/syz023>.

- Poynton JC (2000) Evidence for an Afrotropical amphibian fauna. *African Journal of Herpetology* 49(1): 33–41. <https://doi.org/10.1080/21564574.2000.9650014>.
- Poynton JC, Broadley DG (1988) Amphibia Zambesiaca 4. Bufonidae. *Annals of the Natal Museum* 29(2): 447–490. https://doi.org/10.10520/AJA03040798_367.
- Poynton JC, Haacke WD (1993) On a collection of amphibians from Angola, including a new species of *Bufo* Laurenti. *Annals of the Transvaal Museum* 36(2): 9–16.
- Poynton JC, Loader SP, Sherratt E, Clarke BT (2007) Amphibian diversity in East African biodiversity hotspots: altitudinal and latitudinal patterns. *Biodiversity and Conservation* 16(4): 1103–1118. <https://doi.org/10.1007/s10531-006-9074-1>.
- Prendini L (2005) Scorpion diversity and distribution in southern Africa: pattern and process. *African Biodiversity*: 25–68. Springer US, Boston, MA. https://doi.org/10.1007/0-387-24320-8_2.
- Pyron RA, Wiens JJ (2013) Large-scale phylogenetic analyses reveal the causes of high tropical amphibian diversity. *Proceedings of the Royal Society B: Biological Sciences* 280(1770): 20131622. <https://doi.org/10.1098/rspb.2013.1622>.
- Rödel M-O, Adum GB, Aruna E, Asseman NE, Barej MF, Bell RC et al. (2021) Diversity, threats and conservation of western and central African amphibians (Senegal, The Gambia, Guinea Bissau, Mali, Guinea, Sierra Leone, Liberia, Ivory Coast, Burkina Faso, Ghana, Togo, Benin, Nigeria, Niger, Cameroon, Gabon, São Tomé & Príncipe, Equatorial Guinea, Central African Republic, Chad, Republic of the Congo, Democratic Republic of the Congo, northern Angola). In: Heatwole H & Rödel M-O (eds) Status and threats of Afrotropical amphibians – sub-Saharan Africa, Madagascar, Western Indian Ocean Islands. *Amphibian Biology* 11(7): 11–101.
- Rödel MF, Becker FS, Buiswalelo B, Conradie W, Channing A (2023) Re-evaluation of the status of *Bufo vertebralis grindleyi* and *Bufo jordani* (Anura: Bufonidae). *Salamandra* 59: 143–157.
- Rose W (1962) *The reptiles and amphibians of southern Africa*. Maskew Miller, Cape Town.
- Sandberger-Loua L, Doumbia J, Rödel M-O (2016) Conserving the unique to save the diverse — Identifying key environmental determinants for the persistence of the viviparous Nimba toad in a West African World Heritage Site. *Biological Conservation* 198: 15–21. <https://doi.org/10.1016/j.biocon.2016.03.033>.
- Simmons RE, Griffin M, Marais E, Kolberg H (1998) Endemism in Namibia: patterns, processes and predictions. *Biodiversity and Conservation* 7(4): 513–530. <https://doi.org/10.1023/A:1008879712736>.
- Streicher JW, Sadler R, Loader SP (2020) Amphibian taxonomy: early 21st century case studies. *Journal of Natural History* 54(1–4): 1–13. <https://doi.org/10.1080/00222933.2020.1777339>.
- Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues ASL, Fischman DL, Waller RW (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306(5702): 1783–1786. <https://doi.org/10.1126/science.1103538>.
- Van Wyk B, Smith G (2001) *Regions of floristic endemism in Southern Africa: a review with emphasis on succulents*. Umdaus Press, Hatfield, South Africa.
- Werner F (1910) Reptilia et amphibia. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 16: 279–370.
- Womack MC, Steigerwald E, Blackburn DC, Cannatella DC, Catenazzi A, Che J et al. (2022) State of the Amphibia 2020: a review of five years of amphibian research and existing resources. *Ichthyology & Herpetology* 110(4). <https://doi.org/10.1643/h2022005>.