Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

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

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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)

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-preface

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A TRIBUTE

This monograph brings together knowledge on plants and animals that live specifically, often only, on the highlands and escarpments of Angola and Namibia. Much of the information is based on specimens and observations collected decades ago by intrepid, mostly self-trained naturalists whose tenacity led them across Africa in search of new ants, birds, euphorbias, grasses and much more. Their work laid the groundwork to this monograph.

Nowadays, most biologists are trained and paid professionals. But there remain a few unpaid naturalists who doggedly continue to build important foundational knowledge about the animals and plants of southwestern Africa. We dedicate this monograph to two of them who died recently: Mark Williams and Rogério Ferreira. Their presence is to be found on many of the pages ahead.

Rogério used his enthusiasm, energy, sharp eyes and camera skills to record hundreds of different animal species in Angola. His images were often the first ever taken. Many led to the recognition of new species or distribution records. He also travelled widely, seeking out places that were poorly known. Angola is worse off for his loss. Young people will do well to follow Rogério's example, paying special attention to the values of passion, modesty and hard work.

Mark Williams dedicated his life to the study of butterflies in Africa, a moderate part of which is to be found in the paper on butterflies in this monograph (Gardiner & Williams 2023). First published in 2006, *Butterflies and Skippers of the Afrotropical Region* (Williams 2022) was one of his most important contributions. He also added more than 700 species and subspecies to the monumental catalogue published as *Carcasson's African Butterflies* (Ackery *et al*. 1995). Mark's valuable contributions to the knowledge of Afrotropical butterflies will be missed.

The Great Escarpment of southern Africa, and its associated mountains, plateaus and inselbergs, includes representative areas of over half of the subcontinent's centres of plant diversity (Clark *et al.* 2011). It also hosts a rich vertebrate and invertebrate fauna, including many endemics. Despite this biological wealth, the Great Escarpment has attracted few focused studies on the evolution and diversification of its biota, the patterns and relationships of speciation and endemism, and the ecological services and conservation needs of its landscapes. The paucity of biological research across the Great Escarpment is nowhere more evident than along the highlands and escarpments of southwestern Africa, especially of Angola.

The need for a synthesis of what is known – and not known – about the highland biota of southwestern Africa recently triggered discussions between colleagues from Angola, Portugal, Namibia and South

Africa towards developing an interdisciplinary research programme to fill identified knowledge gaps. The project would focus on the highlands and escarpments of Angola and Namibia (HEAN). The original, and ambitious, objectives of this project were to:

- Document the occurrence of endemic species and the patterns of endemism on highlands in Angola and Namibia.
- Refine the taxonomy of potential endemics, understand their evolutionary histories and relationships and identify likely refugia.
- Record and understand the land uses and socio-economic conditions on and around highlands in Namibia and Angola to identify threats and opportunities for improved conservation.
- Develop conservation priorities to safeguard biota endemic to the highlands of Namibia and Angola.

While the initiation of a new, collaborative programme of research on the biota of the HEAN has yet to find funding, the first steps towards synthesising available knowledge has advanced, providing the content of the present volume. What is evident is that the information base is very uneven, both in terms of geographical coverage and of taxonomic groups studied. Levels of information range from tentative inventories of species distribution, to detailed revisions of selected genera based on molecular phylogenies. The information base differs markedly between Namibia and Angola.

Namibia has a rich history of biological research, with a major focus on the ecosystems and biota of the Namib Desert, backed by detailed studies on the vegetation, flora and fauna and the abiotic environment that determines these at national scale, synthesised in such volumes as Barnard (1998) and the latest edition of the Atlas of Namibia (Atlas of Namibia Team 2022). Angola is less endowed in terms of biological surveys. Following the termination of civil war in 2002, however, a resurgence of interest in its ecosystems and biota has been witnessed, and the results documented in synthesis volumes such as the present and in Marques *et al.* (2018), Huntley *et al.* (2019) and Huntley (2023).

An exception to the lack of focused study of the biota of the highlands and escarpments of southwestern Africa is a paper published over sixty years ago. In 1957, Patricia Hall of the Natural History Museum, London, collected material of 250 species of passerine birds along the Angolan escarpment and adjoining landscapes. Based on her field knowledge and on thousands of specimens housed in the museums of Europe and North America, she proposed a set of hypotheses to explain regional patterns of speciation, diversity and endemism: The Faunistic Importance of the Scarp of Angola (Hall 1960). Her work stimulated conservation proposals (Huntley 1974) and more recently, an acceleration of ornithological research across Angola (Dean *et al.* 2019, Mills & Melo 2023). Hall's seminal paper provides a theoretical framework on the evolution of the highland biota, concepts that the current phase of research and the availability of modern technologies will be able to test.

What is immediately clear is that there is no distinctive escarpment or highland 'centre of endemism' unique to the HEAN. The steep climatic and habitat gradients from the tropical rainforests of the low escarpment of Cabinda, through the cooler montane forests and grasslands of the Angolan highlands, the mix of moist and arid savannas along the spine of the HEAN, ending in the arid mountains of southwestern Angola and across Namibia, reflect a continuum of change in the physiognomic structure and genetic composition of the vegetation, flora and fauna across 2,700 km of latitude. Dotted across this landscape are a great many inselbergs, some of them supporting high numbers of endemics.

The present state of knowledge suggests that species richness and endemism relate to habitat, rather than to any 'centre of endemism' or biological 'hotspot'. This does not preclude the identification of such centres once phylogenies of more taxa, and more georeferenced distribution data become available. What is evident is that the dramatic topography of the HEAN provides habitats that favour narrowly endemic species and subspecies, and frequent disjunct distribution patterns between closely related taxa, separated over short distances to thousands of kilometres. The finer definition and explanation of such patterns remains a work in progress.

WITH THANKS

A synthesis such as this would not be possible without the commitment of many dozens of collaborators and specialists, 60 of whom are identified as authors of the papers. This product is a tribute to their dedication and patience through the two years absorbed in compiling the volume. The Ongava Research Centre initiated the project and together with the Namibian Chamber of Environment and the Centre for Research in Biodiversity and Genetic Resources (CIBIO), University of Porto, funded aspects of the work. Alice Jarvis was responsible for the page layout while her meticulous editing and that of Carole Roberts greatly enhanced the product. Additional support was provided by Chris Brown, Tony Cunningham, Nuno Ferrand, John Irish, Jasper Knight, António Martins, Andy Moore, Tony Robertson, Elizabeth Shangano, Ken Stratford and William Versfeld.

The papers were reviewed by Aaron Bauer, Rolf Becker, António Bivar-de-Sousa, Alan Channing, Wouter Dekoninck, Robert Dowsett, Françoise Dowsett-Lemaire, Paul Eggleton, Seth Eiseb, Lincoln Fishpool, Stefan Foord, David Goyder, Chris Hines, Brian Huntley, John Irish, Roy Miller, Andy Moore, Yves Roisin, Michael Samways, Renato (Spaggs) Spaggiari, Vivienne Uys, Ben van der Waal and Braam van Wyk.

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The biological importance of the highlands of Angola and Namibia: synopsis and conclusions

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-synopsis

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ABSTRACT

Twenty-six papers in this volume provide a broad sweep of information on the geography, biodiversity and endemism of the highlands and escarpments of Angola and Namibia (HEAN). The original objectives of the project, which included the launch of field surveys, phylogenetic analyses and conservation strategies, were reduced by the constraints of the COVID-19 pandemic to a set of desk studies and syntheses on available information on the diversity and endemism of HEAN biota. The geographical delineation and characterisation of the HEAN and terms used in the volume are defined, and the challenges of limited information and an outline of the richness and endemism of taxa are presented. Current considerations on the origin and evolution of the biota are summarised based on the individual papers in the volume. It is concluded that despite the differing levels of taxonomic, geographic and phylogenetic understanding of the HEAN biota, sufficient information is available to recognise the HEAN as a regional zone of important biodiversity and endemism deserving of accelerated research activities and greatly increased conservation measures.

Keywords: Angola, biological importance, escarpments, highlands, Namibia, synopsis

OBJECTIVES OF THIS VOLUME

Since the seminal paper by Hall (1960), on the faunistic importance of the Angolan escarpment, biologists have been fascinated by the diversity of ecosystems occupying the highlands and escarpments of Angola and Namibia, and the possibility that these poorly studied environments harbour concentrations of endemic taxa. Access constraints, especially for fieldwork, relaxed after the Angolan peace accords of 2002, allowing a series of expeditions to that country. Interest in the biodiversity of both Angola and Namibia was further stimulated during the preparation of two broad synthesis volumes (Huntley *et al.* 2019, Atlas of Namibia Team 2022). This momentum of interest was paralleled by proposals from the Ongava Research Centre for a major project on endemism within the highlands and escarpments of Angola and Namibia.

The original and rather ambitious objectives of the project on the highlands and escarpments of Angola and Namibia, which led to the publication of this monograph, are described in the preface to this volume (Huntley *et al.* 2023). The more realistic results presented in this collection of papers relate to questions including:

- How are the highlands and escarpments of Angola and Namibia (HEAN) defined and delimited, and how and when were they formed?
- What are the physiographic, climatic, biotic and human characteristics and units of the HEAN?
- How diverse are the taxonomic groups represented in the HEAN, and how many endemics have been catalogued for the HEAN?
- Where do the centres of diversity and endemism within different taxonomic groups occur?
- How are taxa in the HEAN related to taxa elsewhere in Africa?
- What ecological characteristics, strategies and traits (such as growth form, or resilience to aridity, fire or herbivory) are common among HEAN endemics?

The extent to which these questions have been addressed in each paper reflects the current state of knowledge of each taxonomic group or geographic area reviewed within the HEAN. As will be apparent, the knowledge base is uneven, both taxonomically and geographically, most especially for Angola.

HEAN, ITS ENDEMICS AND TERMINOLOGY

The HEAN falls within the broader concept of the Great Escarpment of southern Africa, (Clark *et al.* 2011, Miller 2023) which stretches as an arc from western Angola, through Namibia, South Africa, Lesotho and eSwatini to the Eastern Highlands of Zimbabwe and neighbouring Mozambique. The escarpment also forms a shoulder to the rift that formed when South America parted ways from Namibia and Angola during the breakup of Gondwana (Miller 2023). More locally, the HEAN is circumscribed to include the highlands, scarps, escarpments, inselbergs and plateaus that form a broken spine through Angola and Namibia from Cabinda in the north to the Orange River in the south (Jarvis 2023, Mendelsohn & Huntley 2023). Two major highland plateaus above 1,700 masl – the Angolan Planalto in Angola and the Khomas Hochland in Namibia – dominate the highlands. High mountains rise above these landscapes (Angola's Serra do Môco at 2,620 masl and Namibia's Moltkeblick at 2,479 masl). Isolated inselbergs, such as the Serra da Neve (2,489 masl) and Brandberg (2,573 masl), and dramatic escarpments (the Serra da Chela and central Namibia's string of escarpments between Usakos and Aus) are prominent features of the HEAN.

A **taxon** is usually a species or subspecies. An **endemic** is defined here as a species that only occurs in the defined area of concern (e.g., Angola, Namibia, the HEAN as a whole or any defined area within the HEAN such as the Angolan Planalto, Khomas Hochland, Brandberg, Serra da Neve, etc.). **Near-endemics** are species with a limited distribution outside the core area which defines the endemic. **Restricted-range bird species** occur only within a contiguous area of $< 50{,}000$ km^2 (Mills & Melo 2023). A **centre of endemism** is an area in which restricted-range species overlap, or is a localised area which has a high occurrence of endemics. A **hotspot** refers to an area common to endemic species of one or more – usually many – taxa and taxonomic groups.

The biological and ecological conditions in the physiographically diverse highland system often differ from those in the broader, more generalised biomes and ecoregions of southern Africa. As a consequence, the biota of these geographically restricted highland systems often represent depauperate outliers of broader regions. The relict forests of the Afromontane regional centre of endemism is a good example.

A **biome** is the largest category of structurally and functionally similar habitats and their biota which share climate, soil and disturbance factors. Four widely ranging biomes (*sensu* Dinerstein *et al.* 2017) fall within the HEAN, from Guinea-Congolian rainforests, through Afromontane forests and grasslands, and mesic and arid savannas and woodlands, to the Namib Desert. An **ecoregion** is a large unit of land that contains a distinct assemblage of species, habitats and ecological processes, and whose boundaries attempt to depict the original extent of natural communities before major land-use change. Twelve ecoregions are described within the HEAN (Huntley 2023a).

Landscape units are differentiated by their topographical, geomorphological, ecological and climatic characteristics. Eleven landscape units are recognised in the HEAN (Mendelsohn & Huntley 2023). **Socioeconomic zones** are defined by their human population distribution, density and dynamics, economic resources and livelihoods. Four socioeconomic zones are described within the HEAN (Mendelsohn & Gomes 2023). The contrast between the human population size of Angola (27.8 million) and of Namibia (2.7 million) is stark, with Angola having 10 times the population in 1.5 times the land area of Namibia. More people live in urban than rural areas in both countries.

THE CHALLENGES OF A WEAK INFORMATION BASE

With few exceptions, authors of this volume have noted the challenges of the limited information base available on the fauna and flora of the HEAN. These challenges include problems of taxonomic resolution, of sparse or incompletely georeferenced data, of the near absence of local capacity in systematics, and weak museum facilities. Statements such as the following illustrate the situation:

> "Little is known about the ant fauna of Angola and Namibia." (Gomez *et al.* 2023)
>
> "It is apparent that our knowledge of the butterfly species of the Angolan highlands and Angola in general is lacking." (Gardiner & Williams 2023)
>
> "… our herpetological knowledge of southwest African highlands is rudimentary." (Bauer *et al.* 2023)
>
> "The neuropteran fauna of Angola is the most poorly known on the African continent ..." (Mansell 2023)
>
> "The fishes of the HEAN are, in general, not well known." (Skelton 2023)

However, most authors have noted the advances made in the biological survey of the HEAN, particularly of Angola, over the past two decades. Recent rodent surveys recorded at least five new species which might be endemic to the Angolan section of the HEAN, in a total of 12 candidate new species found across Angola, while another recent small-mammal survey in the Serra da Namba recorded four endemic species and perhaps three undescribed species of rodents and shrews, and perhaps three (or more) undescribed bat species (Palmeirim *et al.* 2023). Reptile surveys of Angola have led to the description of more than 30 new species in the past decade (Bauer *et al.* 2023), while a review of *Afroedura* geckos revealed six new endemic species in the HEAN (Conradie *et al.* 2023). Great progress has been made within the Odonata, where 25 species have been added to the Angolan checklist since 2017 (Kipping *et al.* 2023). In plants, some arid zone species records are based on rare appearances of species following episodic rainfall events that might occur once in a century (Craven & Kolberg 2023). Many endemic species of both animals and plants are based on holotype specimens of single collections, often from the 19th century. Important areas, such as Serra Canda and Serra Mocoti in Angola and the Paresis Mountains of Namibia have yet to be explored. Much awaits discovery, and an air of excitement prevails among the new generation of biologists working along the 2,700 km of the HEAN.

GEOGRAPHIC AND TAXONOMIC COVER OF THE REVIEWS

Given the varied depth and breadth of information available, and of specialists on many taxonomic groups, the geographic coverage of papers is not uniformly consistent within the delineation of the HEAN. Some papers draw on distribution patterns across tropical Africa (Weeks & Swanepoel 2023), southwest tropical Africa (Bruyns *et al.* 2023), the

Table 1: *Numbers of taxa and endemics, and the percentages of endemic taxa in selected groups recorded in Angola, Namibia, Angola and Namibia combined, and in the highlands and escarpments zone of Angola and Namibia (HEAN).*

	Angola			**Namibia**			**Angola and Namibia**			**HEAN**		
Taxon Reference	**Total species**	**Endemic species**	**Endemic species %**	**Total species**	**Endemic species**	**Endemic species %**	**Total species**	**Endemic species**	**Endemic species %**	**Total species**	**Endemic species**	**Endemic species %**
Higher plants* Huntley (2019), Craven & Kolberg (2023), P Craven (in litt.)	6,850	997	15	4,000[1]	708	18					101[2]	
Angolan geoxyles Meller *et al.* (2023)										133	42	32
Apocynaceae Bruyns *et al.* (2023), P Bruyns (in litt.)	234	24	10	153	19	12	326	59	18	132	24	18
Ceropegieae Bruyns *et al.* (2023), P Bruyns (in litt.)	56	16	29	90	13	14	117	41	35	78	20	26
Euphorbia Bruyns *et al.* (2023), P Bruyns (in litt.)	70	39	56	56	11	20	107	59	55	57	16	28
Petalidium Dexter *et al.* (2023), K Dexter (in litt.)	12	6	50	28	19	68	34	31	91	24	22	92
Commiphora Weeks & Swanepoel (2023), W Swanepoel (in litt.)	25	6	24	30	5	17	36	23	67	34	10	29
Odonata Kipping *et al.* (2023), J Kipping (in litt.)	288	34	12	130	0	0	305	34	11	168	18	11
Ants Gomez *et al.* (2023), K Gomez (in litt.)	308	63	20	194	36	19	440	106	42	36	1	3
Amblypygi Prendini & Bird (2023), L Prendini (in litt.)	2	0	0	4	1	25	4	3	75	3	2	67
Scorpions Prendini & Bird (2023), L Prendini (in litt.)	24	2	8	66	31	47	72	40	56	19	8	42
Solifugae Prendini & Bird (2023), L Prendini (in litt.)	27	15	56	120	75	63	138	90	65	16	12	75
Butterflies Gardiner & Williams (2023), A Gardiner (in litt.)	800	42	5	220	8	4	857	76	7		32	
Fish Skelton (2023), P Skelton (in litt.)					2					65	47	72
Amphibians Becker *et al.* (2023), F Becker (in litt.)	130	24	18	64	4	6	144	31	22	34	12	35
Reptiles Bauer *et al.* (2023), A Bauer (in litt.)	306	52	17	279	55	20	430	141	33	238	46[3]	19
Birds* Mills & Melo (2023), M Mills (in litt.)	970	24	2	639	1	0.2	1,060	39	4	233	112	48[4]
Mammals* Palmeirim *et al.* (2023), A Monadjem (in litt.)	290	34	12	169	3	2	316	50	16	166	45	27

* Species and subspecies.

[1] Craven and Kolberg (in litt.) recognise between 3,953 and 4,101 plant species and subspecies in Namibia.

[2] Number of taxa endemic to the HEAN in Namibia.

[3] Another 16 reptiles are largely but not strictly limited to HEAN.

[4] Mills and Melo (2023) note that 194 (83%) of the 233 bird taxa on the HEAN are endemic Evolutionary Significant Units (ESUs).

highland flora of Namibia (Craven & Kolberg 2023), the conservation areas of Angola (Vaz Pinto *et al.* 2023), the geoxyle flora of central Angola (Meller *et al.* 2023), the biodiversity of a region of fold mountains in Uíge (Lautenschläger *et al.* 2023) or on the flora of a single mountain (Goyder *et al.* 2023). Mills and Melo (2023) include moister habitats at the base of the escarpment, and where these extend into the arid lowlands along rivers, but they exclude Cabinda from their assessment of escarpment birds. Indeed, except for the papers on mammals (Palmeirim *et al.* 2023) and on Angolan conservation areas (Vaz Pinto *et al.* 2023), few reviews include Cabinda due to the dearth of information on the biota of this enclave. Such diversity in geographic coverage is inevitable given the constraints of the knowledge base but it limits comparative measures of species diversity and endemism across the HEAN (*sensu stricto*) or across taxonomic groups (Table 1).

RICHNESS AND ENDEMISM

Despite the general paucity of strong modern taxonomies and limited georeferenced distribution records for many taxa, patterns of richness and endemism are being revealed for many taxonomic groups (Table 1).

Plants

In Namibia, the indigenous seed plant flora of 4,000 species includes over 700 species endemic to that country, with a further 540 near-endemics occurring marginally into neighbouring countries (Table 1). Of the total flora, over 100 are known only from the highlands – and these ‘highland endemics’ occur on one or more of eight highlands, escarpments and plateaus (Craven & Kolberg 2023). Craven and Kolberg (2023) conclude that no noticeable concentration of highland plant endemics occurs, with many endemics being rare and with small habitats at specific elevations. An exception to this observation is the Brandberg, with over 480 indigenous seed plants, of which about 90 are Namibian endemics and 9 are limited to the mountain itself (Craven & Kolberg 2023). However, no endemic species of *Euphorbia* or Apocynaceae are known from this inselberg (Bruyns *et al.* 2023). By contrast, the ant fauna of the Brandberg stands out in terms of interest, with 30% of ant species collected there being potentially new to science (Gomez *et al.* 2023).

In Angola’s HEAN zone, the geoxyle growth form (suffrutices with woody rootstocks which are adaptations against recurrent fires and other disturbance factors) is represented by at least 133 different geoxyle species in the strict sense (geoxyles with close tree relatives), of which 42 are endemic (31.6%) (Meller *et al.* 2023). Geoxyles, representing many families displaying coevolved traits, are a characteristic feature in mesic/dystrophic savannas of the Zambezian phytochorion of Central Africa, and of the Cerrado of Brazil (Huntley 2023b). In Angola, they are abundant within the HEAN, especially on the Angolan Planalto and Marginal Mountain Chain landscapes. Outside of the HEAN, they are similarly abundant and rich in species in the mesic savannas of eastern Angola.

More broadly, several plant groups have been studied in detail across the HEAN and beyond, often supported with modern molecular phylogenies. These include the genus *Euphorbia* and the Ceropegieae within the Apocynaceae (Bruyns *et al.* 2023). Of 107 species of *Euphorbia* recorded within Angola and Namibia, 70 occur in Angola (of which 56% are endemic) and 56 in Namibia (of which 20% are endemic). *Euphorbia* diversity in the HEAN is richest in the arid zone, with notable diversity on the highlands–escarpment interface (Serra da Chela, often also called the Humpata Plateau), but also on lower coastal areas around Moçâmedes and northwards to Benguela. *Euphorbia* is essentially absent from the extensive Kalahari sands that lie to the east of the HEAN (Bruyns *et al.* 2023).

Like *Euphorbia*, Apocynaceae endemics are associated with the arid areas of the rocky escarpment and highlands, where moisture gradients are steep over short distances. The highest diversity of Ceropegieae occurs in the Serra da Chela and the coastal lowlands between Moçâmedes and Lucira. Several ‘hotspots’ common to both *Euphorbia* and Ceropegieae occur along the escarpment and adjoining lowlands of the HEAN (Bruyns *et al.* 2023).

Two further plant groups important in the arid regions of the HEAN have enjoyed intense collecting and review during recent years: *Commiphora* and *Petalidium*. Of the 36 species of *Commiphora* native to Angola and Namibia, the majority are endemic (23 spp.) or near-endemic (6 spp.) to Angola and/or Namibia and 22 species may be found at elevations of 1,000 masl or greater, but nearly all *Commiphora* endemics are also found at much lower elevations (Weeks & Swanepoel 2023). Similarly, while the majority of the 36 African species of *Petalidium* (22 of 36 or 61%) are endemics or near-endemics of the HEAN, many of these also occur at lower elevations (Dexter *et al.* 2023). Twenty-two of the 24 *Petalidium* species recorded in the HEAN occur nowhere else (Table 1).

Invertebrates

About 857 species of butterflies and skippers have been recorded from Angola (800 spp.) and Namibia (220 spp.). Of these, 76 species (6.5%) are endemics or near-endemics to these countries (Table 1). Gardiner and Williams (2023) map 32 butterfly species as endemic to the HEAN. More broadly, the mesic savannas of Angola and Namibia have 21 endemic or near-endemic butterfly species, and the arid savannas 23 endemic or near-endemic species (Gardiner & Williams 2023). No butterfly hotspots were identified by Gardiner and Williams.

The Odonata in Angola have received intense attention over the past decade, with surveys extending from the western highlands across to the peneplains of the province of Cuando Cubango and its extensive, largely treeless, wetlands and floodplains. Kipping *et al.* (2023) rank Angola as one of the foremost centres of Odonata diversity and endemism in Africa. Of the 168 species recorded thus far from the HEAN, 18 are endemic. Of these 18 endemics, 12 have been found on escarpments, 15 on inselbergs and 11 on plateaus of Angola; none is found in Namibia. Furthermore, Kipping *et al.* (2023) record 34 endemics out of 288 species in Angola, but no endemics in Namibia's 130 odonate taxa. These authors also note that about half of the Angolan endemics occur neither along the western escarpment nor on the high plateau, but in the oligotrophic habitats of the Kalahari sands which provide grassy bogs and clear streams draining the 'water towers' of central Angola.

Gomez *et al.* (2023) note 308 indigenous ant taxa for Angola and 194 for Namibia, with 440 species and subspecies for the two countries. Only 62 species are common to both. In comparison, South Africa, covering just over half the combined area of Angola and Namibia, has a far higher total with 764 species and subspecies of ants. It is apparent that much collecting remains to be done on the ant fauna of the HEAN (Gomez *et al.* 2023).

While species lists for the termites of Angola are scarce, with only a few surveys having been undertaken in limited areas and none of these from the highlands, 10 of 93 Angolan species were found to be endemic (Gunter *et al.* 2023). Recent molecular studies indicate high genetic diversity in the single Angolan species studied (Jürgens *et al.* 2021) indicating the need for more detailed reviews of the country's termite fauna. The survey data for Namibia are more comprehensive, with at least 8 of 54 recorded species being endemic (Gunter *et al.* 2023).

Vertebrates

Within the Amphibia of Namibia and Angola (totalling ca. 144 species) the highest species richness (~47 species) is found in moister central and northern escarpments of Angola (Becker *et al.* 2023). Most highland endemics are limited to small areas of a particular mountain, ridge or inselberg. Richness decreases southwestwards, with arid southwestern Namibia hosting only three to five amphibian species. Approximately 130 amphibian species are recorded for Angola, and 24 of these regarded as country endemics, of which 11 are highland associated. There are at least five amphibian species that are strict endemics to the HEAN, with several more species described from the escarpment, but they are poorly known and their taxonomy remains unresolved. Ongoing studies are expected to increase the number of highland endemics.

A total of 430 reptile species have been recorded for Angola and Namibia. Approximately 238 species of these occur in the HEAN (Bauer *et al.* 2023). Of these, 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, plus nine cordylids, six skinks, four lacertids and one chameleon, as well as nine snakes (in five families) and a single tortoise comprising the remainder. The greatest diversity is present in the more extensive highland areas of the Khomas Hochland and Angolan Planalto, but many mountains, escarpments and inselbergs support at least some regional highland endemics (Bauer *et al.* 2023). These authors remark that there is a high north–south turnover of species, many highland endemics having small distributions and no species occurring throughout the highlands.

Palmeirim *et al.* (2023) in their paper on mammals recorded 12 endemic, 13 possible endemic and 20 near-endemic taxa in the HEAN, of which 28 are species, 10 are possible undescribed (new) species, and 7 are subspecies. Rodents showed the highest endemism (28 taxa), followed by bats (6 taxa). Most endemic mammals have distributions concentrated in the Angolan section of the HEAN, occurring in limited areas of moist tropical forest, mesic and arid savannas, along the escarpment and on the Angolan Planalto. No coherent 'centre of endemism' within the HEAN could be identified for mammals.

ORIGINS OF HEAN DIVERSITY AND ENDEMISM

Any considerations of the origins and evolution of the HEAN biota need to be grounded on the geological history of the region. Miller (2023) provides a succinct overview of the geological and landscape evolution of Angola and Namibia, and how they were shaped by tectonic and climatic forces from the deep past to the present. The HEAN landscapes have been moulded by successive periods of rifting, continental drift, ocean formation, sedimentary deposition, mountain-building, erosion and both humid and arid palaeoclimates. Miller (2023) describes the escarpment as representing the remains of an elevated rift shoulder of the continental margin formed after the breakup of Gondwana.

Against this background, an outline of some aspects of the origins of HEAN biological diversity can be summarised based on the papers in this volume.

The bird fauna of Angola and Namibia is better documented than any other taxonomic group. Regarding HEAN biodiversity and evolution, the pioneer paper of Hall (1960) has been an intellectual stimulus for research on the fauna of the HEAN for many decades. Mills and Melo (2023) provide a succinct analysis of the HEAN avifauna and the relationship between escarpment and montane taxa. It is appropriate to foreground this taxonomic group before considering other taxa.

Mills and Melo (2023) analysed the distribution patterns of 'Evolutionary Significant Units' (ESUs) of the HEAN avifauna (excluding Cabinda). They included as ESUs species and subspecies for which two-thirds of their global range or population size fell within the study area. The 233 ESUs recognised in the study included four monospecific genera endemic to the HEAN, all from the arid southwest escarpments of Angola and Namibia. These genera represent divergence events predating the Plio-Pleistocene. Next, 37 full species were regarded as endemic taxa, followed by 71 endemic subspecies, with the isolated populations of the remaining 121 ESUs not regarded as differentiated subspecifically.

Mills and Melo (2023) defined any species absent from the main highlands (such as the Serra do Môco and Serra da Namba montane regions) as being an escarpment species, and any species that occurs in the main highlands but absent from the escarpment as a highland species. They categorised 170 ESUs as escarpment taxa, 50 ESUs as montane/highlands taxa, with only 13 ESUs occurring both on the escarpments and highlands. Most of the escarpment ESUs are separated from relatives by over 300 km through a break in the forest zone between Pingano and the Congo Basin. Although the gap is narrow, Mills and Melo (2023) consider that the distance is a significant barrier to gene exchange in highly sedentary forest birds. In contrast, the highland ESUs are typically isolated from the nearest vicariants by 1,800 km or more. Mills and Melo (2023) suggest that the escarpment and highlands have independent bird faunas and origins, although in some habitat complexes at the head of escarpments and inland areas in Cuanza-Sul and Benguela provinces, the separation is blurred. They observe that gene flow is likely to be inversely proportional to gap size, and they suggest that the taxonomic status of many highly isolated populations needs further evaluation.

Hall (1960) and Fjeldså and Lovett (1997) noted the uniqueness of the Angolan escarpment due to the association of moister and cooler highlands, and hotter and drier lowlands, above and below the main escarpment, as factors in the radiation of the avifauna. Mills and Melo (2023) refer to allopatric speciation as a key driver in the speciation of birds, and emphasise the importance of disjunct patches of similar habitat – such as the forests of the escarpments and mountains of Angola. Based on molecular phylogenies, ecological niche modelling and bioclimatic histories of six Angolan escarpment and montane species, Vaz da Silva (2015) supported Hall's earlier proposal in 1960 that long-term habitat and climatic stability, induced by the orographic clouds formed along the escarpment, contributed to the high levels of endemism.

While the patterns of distribution and processes of evolution of the HEAN avifauna described by Mills and Melo (2023) are of relatively recent (Plio-Pleistocene) times, that of the Arachnida is much more ancient. The scorpion fauna of the HEAN includes some ancient lineages descended from the oldest evidence of terrestrialisation, dating from the Silurian, 435 mya (Prendini & Bird 2023). The monophyletic lineage of palaeoendemic scorpion species of the family Bothriuridae, which diverged from South America and Australian taxa with the separation of Gondwana 140 mya, is represented in the HEAN by two highland endemics occupying refugia with higher humidity than their surroundings. However, the diverse endemic arachnid fauna of southwestern Africa is richest in the arid lowlands of the Namib Desert, falling outside the HEAN *sensu stricto*.

Weeks and Swanepoel (2023) provide a detailed outline of the molecular phylogeny of *Commiphora.* This genus diverged from the predominantly American genus *Bursera* in the early Eocene, long after the separation of the continents, and these authors suggest that long-distance dispersal cannot be ruled out as important in the group's diversification. Furthermore, the crown radiations of both *Bursera* and *Commiphora* occurred well before Miocene aridification, indicating an early pantropical radiation of the Burserinae. Miocene aridification and uplift of the African continent may have caused vicariance between western and eastern distributions of the genus and other succulent and woody taxa. *Commiphora* species in southwestern Africa, rather than being evolutionary relicts, arose during the Miocene, Pliocene or far more recently during the Quaternary. Weeks and Swanepoel (2023) suggest that closely related *Commiphora* species might have been stratified by elevation and latitude, rather than by biotic factors – and that genetic isolation and diversification in *Commiphora* was driven by the topography of southwestern Africa.

Details on the evolution and monophyletic radiation of *Petalidium* include evidence that the 36 species of the genus in Africa arose in the last 4.3–1.6 million years, with the suggestion that adaptation to different pollinators, such as bees, sunbirds and long-tongued flies, was a driving force in speciation (Dexter *et al.* 2023). These authors also consider the rugged topography, diverse geologic and edaphic substrates, common in the HEAN, to present barriers between small populations with allopatric isolation, thus playing a role in the speciation of the genus.

Bruyns *et al.* (2023) note that neither *Ceropegia* nor *Euphorbia* are monophyletic but radiated as offshoots of many separate lineages. Bruyns *et al.* (2023), and Craven and Kolberg (2023), mention several cases of related species pairs on western (HEAN) and southeastern and southern (Highveld grasslands, Cape fynbos) reaches of Africa. More extreme disjunctions between the Afromontane forest biota of southern, western and eastern Africa and the arid zones of southwestern Africa and the Horn of Africa are known in diverse taxa (Mills & Melo 2023, Weeks & Swanepoel 2023).

Many authors (Becker *et al.* 2023, Conradie *et al.* 2023, Mills & Melo 2023, Palmeirim *et al.* 2023, Prendini & Bird 2023) refer to the role of refugia, altitudinal migration and vicariance during climatic changes as factors driving speciation. The *Afroedura* study provides an excellent case of Plio-Pleistocene vicariant speciation across the HEAN (Conradie *et al.* 2023). By contrast, Craven and Kolberg (2023) suggest that plant species diversity of the Namibian highlands did not increase in response to isolation during climatic changes.

Many taxa are adapted to the aridity of the southern reaches of the HEAN. Weeks and Swanepoel (2023) refer to the morphological characteristics of the majority of the 36 *Commiphora* species recorded – thin bark, spine-tipped, short-shoot branches and drought-deciduous leaves – that give them the ability to withstand extreme heat and water deficits. Similar traits are found within *Euphorbia*. Many succulent woody species found in the arid base to the HEAN in southern Angola, especially inland of Lucira, have short stocky pachycaul growth forms, a trait found in several families occurring in the area.

Among the Odonata, patterns of speciation are still being interpreted (Kipping *et al.* 2023). They note that many odonate taxa are distinct phylogenetically, but have unclear origins. Some HEAN taxa, as found in the avifauna, have disjunct links to Central and East Africa, and one with links to the Cape provinces of South Africa. Kipping *et al.* (2023) make the interesting observation that while the isolation of Angola's highlands and escarpments contributed to the evolution of their endemic fauna, the unusual oligotrophic ecological conditions (of the eastern peneplains) may have contributed more than vicariance factors.

Among the mammal fauna, murid rodents have the highest level of endemism in the HEAN, with 15 endemic or near-endemic taxa. The genus *Mus* has radiated since its arrival in Africa, ca. 3 mya, with about 20 endemic taxa recorded in the HEAN (Palmeirim *et al.* 2023).

The role of hydrological evolution across southern Africa is described by Skelton (2023) in relation to the speciation of the HEAN fish fauna. The impact of tectonic, climatic and erosional processes, especially river capture between the major river basins of central and southern Africa, have been primary drivers of fish speciation in the region. Skelton (2023) concludes that the highlands of southwestern Africa have served as a geoclimatic sanctuary or refuge for fishes since at least the Miocene.

CONCLUSION: IS THE HEAN A CENTRE OF DIVERSITY AND ENDEMISM?

This brief synopsis of the diversity and endemism of the HEAN biota provides a first impression of the biological richness of the belt of escarpments, mountains and plateaus stretching across the 2,700 km from Cabinda to the Orange River. In the six decades since the publication of Hall's insightful paper on the faunistic importance of the Angolan escarpment (Hall 1960), an ever-increasing body of work has addressed the question: Is the HEAN a centre of diversity and endemism?

The available evidence is provided in this volume. A cynic might suggest that endemism is an artefact best visible to the eye of the beholder. The beholding is also very uneven, with some groups of plants and animals more thoroughly studied than others. The various plant and animal groups presented in Table 1 contribute at least 570 known taxa that are endemic to the HEAN. However, this review excludes such speciose groups as plants on Angolan highlands, or coleopterans, dipterans, crustaceans, platyhelminths, nematodes, annelids, molluscs, diplopods, bryophytes, algae and others across the HEAN. The number of endemics in the highlands of Angola and Namibia would then be quite different if these other groups were taken into account.

A fairer assessment of endemism might be based on the proportions of taxa recorded in the HEAN that are endemic to that area. For example, of the 18 groups of taxa in Table 1, the rate of endemism in the HEAN is higher than 25% for 12 of them and higher than 67% for four of them. Furthermore, of the 24 *Petalidium* species found in the HEAN, 92% are endemic to it, with only two species also known from elsewhere. It is also likely that most invertebrates found in the highland caves are endemic to those isolated refugia (de Matos *et al.* 2023).

The diversity of examples of congruent distribution patterns of restricted-range species thus indicates that the HEAN is home to a wide diversity of endemic species of multiple taxonomic groups, from scorpions, ants, termites and butterflies to fishes, amphibians, reptiles, birds and mammals. Their evolution and speciation reflect multiple processes and origins. These endemics together do not form a single hotspot or centre of endemism but occur as disjunct pockets of richness and rarity along the full 2,700 km of the HEAN, where environmental conditions, substrates and history have resulted in speciation. As such, the whole of the HEAN deserves accelerated research through multidisciplinary partnerships.

All contributors to this volume would agree on several priorities. Particular emphasis should be placed on exploring neglected regions and habitats within the HEAN, and of developing robust phylogenies using modern technologies. Many taxonomic groups that have not been reviewed, especially within invertebrate and lower plant taxa, need attention. The most urgent priority is for effective conservation measures to be efficiently implemented, before the fragments of relict forests, grasslands and savannas that carry the products and evidence of many millions of years of evolution are lost, as emphasised by Vaz Pinto *et al.* (2023).

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The highlands and escarpments of Angola and Namibia: orientation maps

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-jarvis

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ABSTRACT

Five maps are presented which serve as orientation maps for the monograph on the highlands and escarpments of Angola and Namibia. The maps depict elevation, rivers, major topographical features and a selection of settlements.

Keywords: Angola, escarpments, highlands, Namibia, orientation maps

INTRODUCTION AND METHODS

Five orientation maps (Figures 1A–1E) showing a range of settlements and topographical features, such as elevation, highland areas and rivers, of the highlands and escarpments of Angola and Namibia (HEAN) were compiled using data from multiple sources including Instituto Geográfico e Cadastral de Angola (1982), Irish (2002) and Atlas of Namibia Team (2022). The maps are accompanied by a legend and an overview map which indicates the relative location of each orientation map within Angola and Namibia. The process that was used to define and delineate the HEAN for this monograph is described in Mendelsohn and Huntley (2023).

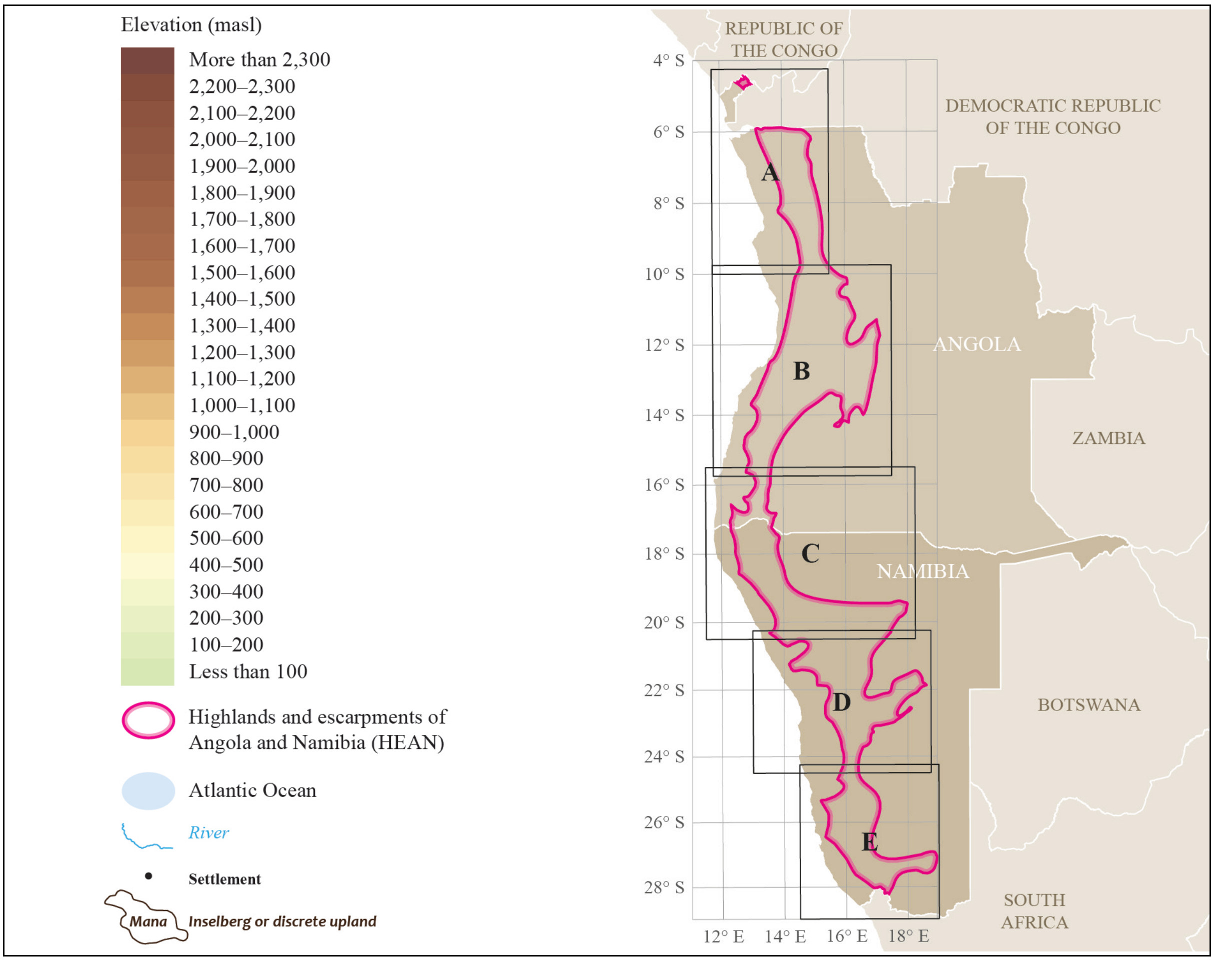

Figure 1: *Left: legend for the five orientation maps (Figures 1A–1E, pages 2–6). Right: relative location of the five orientation maps (Figures 1A–1E) of the highlands and escarpments of Angola and Namibia (HEAN).*

Figure 1A: *See page 1 for the legend and the relative position of this map within Angola and Namibia.*

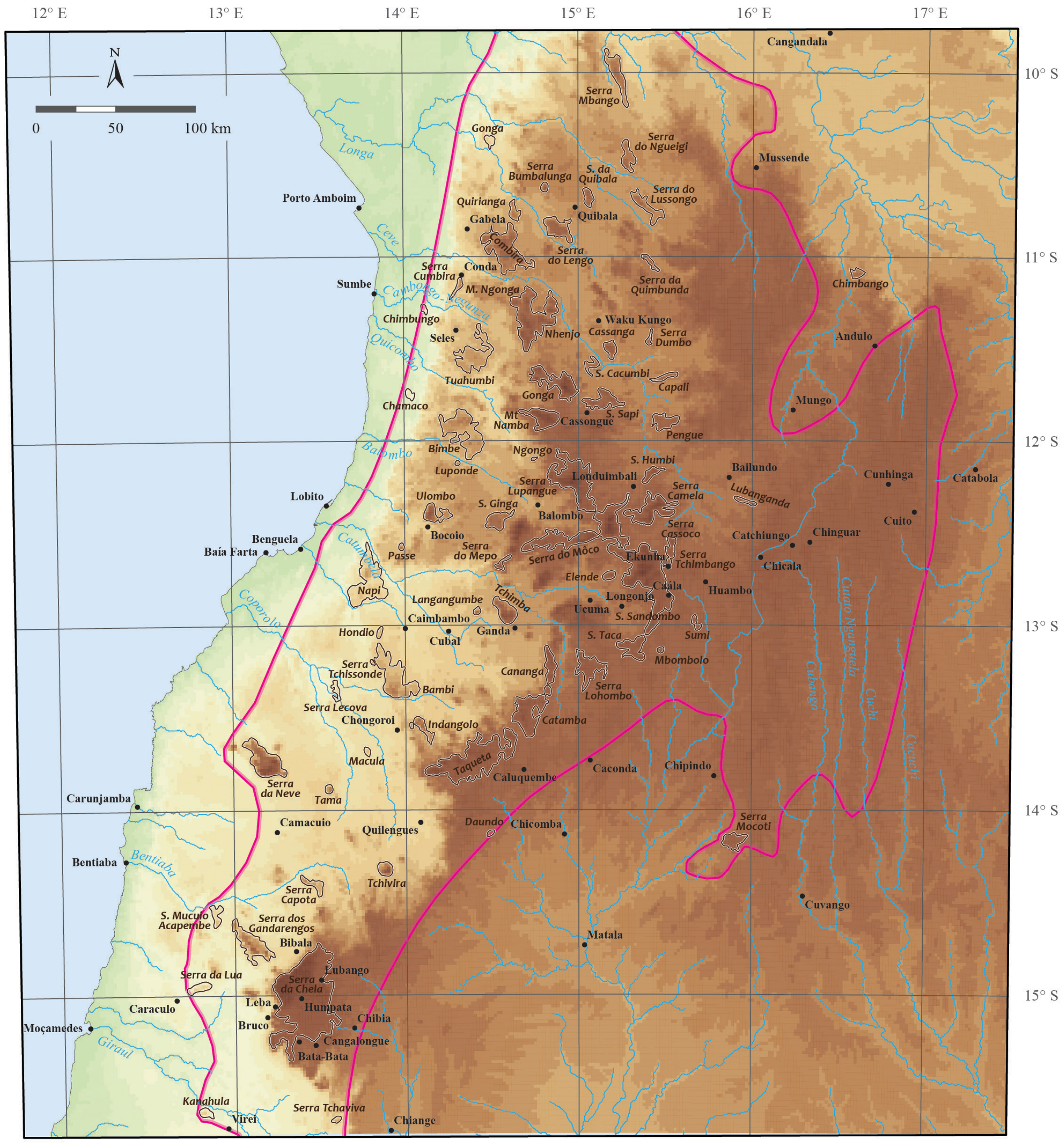

Figure 1B: *See page 1 for the legend and the relative position of this map within Angola and Namibia.*

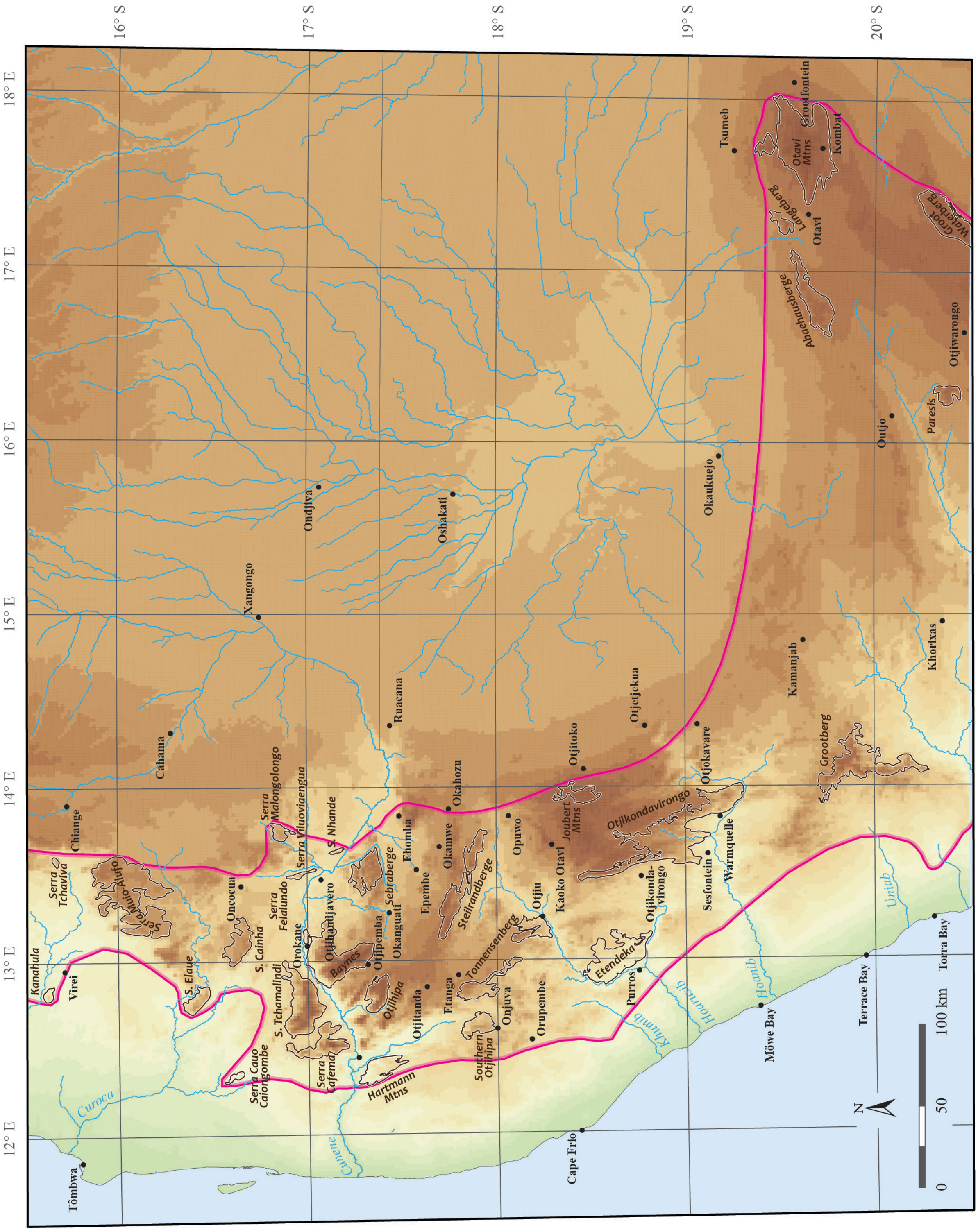

Figure 1C: *See page 1 for the legend and the relative position of this map within Angola and Namibia.*

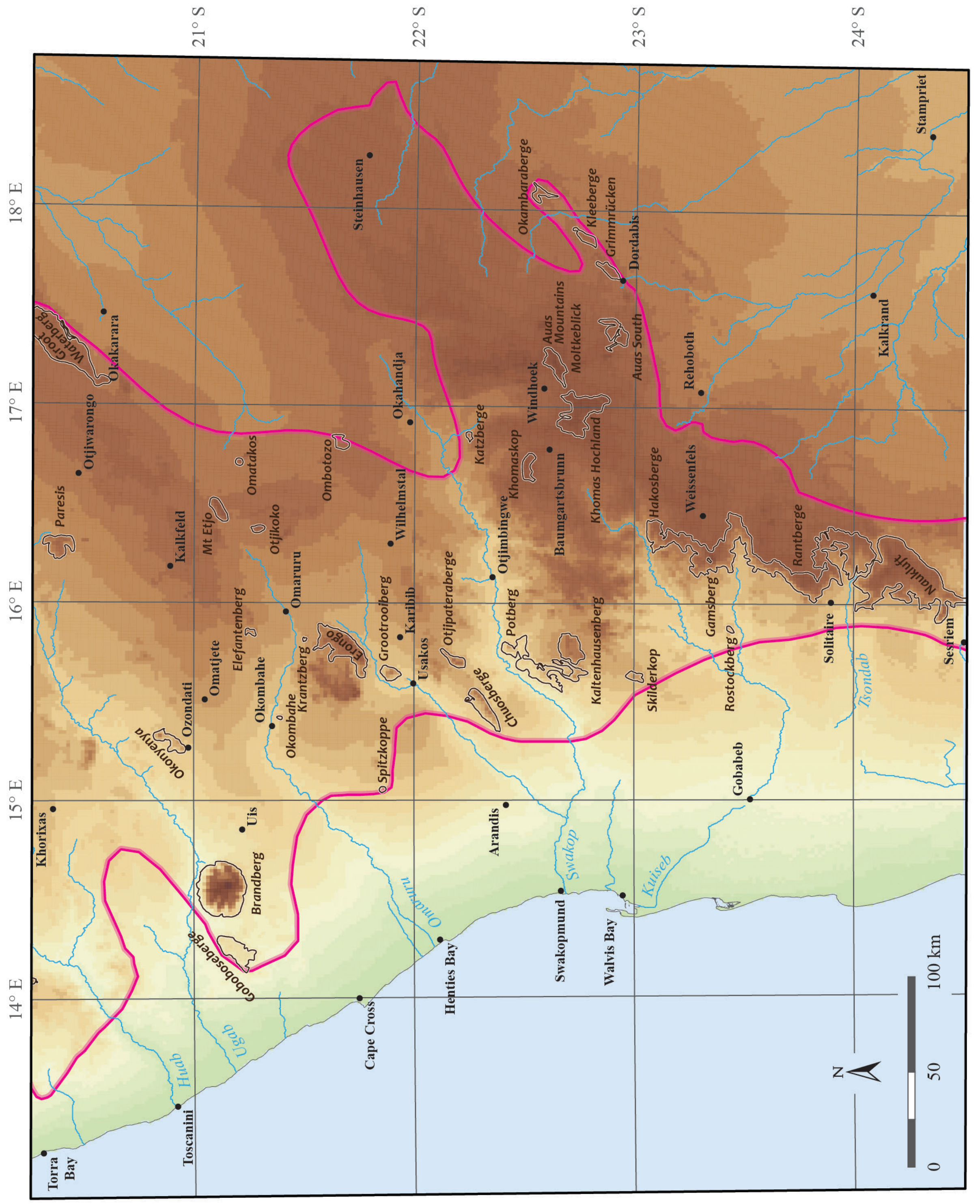

Figure 1D: *See page 1 for the legend and the relative position of this map within Angola and Namibia.*

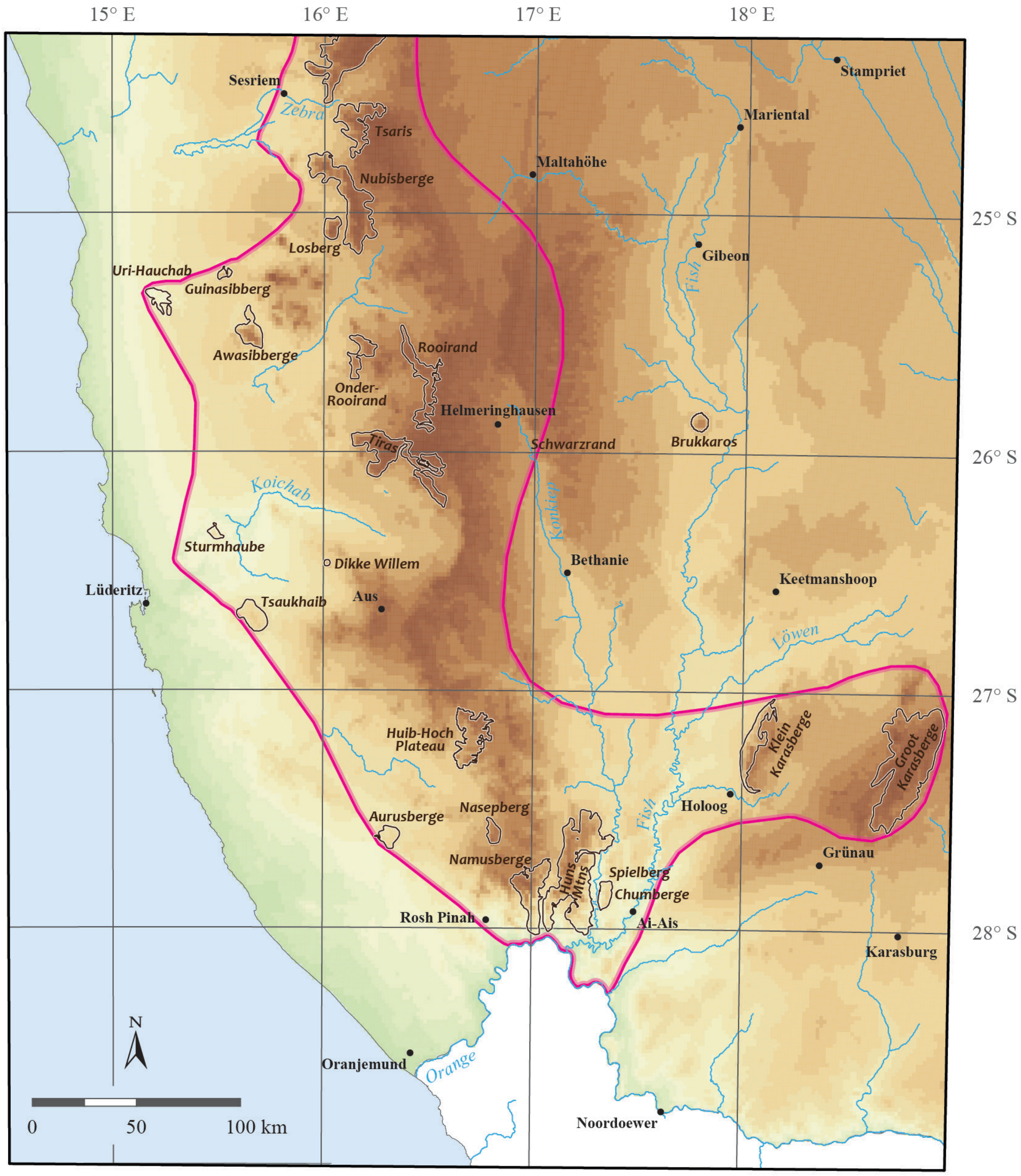

Figure 1E: *See page 1 for the legend and the relative position of this map within Angola and Namibia.*

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Introducing the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-mendelsohn1

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ABSTRACT

Our paper outlines the key features that characterise and define the highlands and escarpments of Angola and Namibia (HEAN) and their topography, origins, drainage, landscapes, soils and climate. The highlands and escarpments stretch some 2,700 km from Cabinda and the Congo River southwards to the Orange River on Namibia's border with South Africa. Two plateaus above 1,700 masl cover large areas: the Angolan Planalto and Namibia's Khomas Hochland. Numerous inselbergs rise above the landscape, and many scarps form sharp margins between lower, western and higher, eastern areas. The highest peaks rise above 2,500 masl. As part of the Great Escarpment along the margins of southern and stretches of eastern Africa, the HEAN probably rose isostatically as the erosion of coastal crust reduced the mass of coastal Africa following the breakup of Gondwana. Three groups of rivers are associated with the HEAN: erosive rivers that flow rapidly off the highlands westwards to the coast; rivers that flow north or southwards, hugging the eastern flanks of the highlands until they turn west towards the coast; and rivers that flow eastwards and away from the highlands. Rivers in the northern third of the HEAN have perennial flows, those in the central third are ephemeral, and those in the southern third seldom carry water. The 11 landscape units defined in the HEAN are differentiated based on their topographical, geomorphological, ecological and climatic characteristics. Cambisols, Ferralsols, Leptosols and four other soils cover over 99% of the area. Most soils have limited plant nutrients, organic carbon and water-holding capacity. Average annual rainfall ranges from about 1,200 mm in the north of Angola and on the Angolan Planalto to less than 100 mm in the far south of Namibia. Rainfall is most variable in the southern and western areas. There are two peaks of rainfall in the northern half of Angola: in November and December and then in March and April. Within the HEAN, the southern areas are far more arid than those in the north because of the combined effects of high evapotranspiration and low rainfall.

Keywords: Angola, climate, drainage, escarpments, geomorphology, highlands, landscapes, Namibia, soils

INTRODUCTION

The highlands and escarpments of Angola and Namibia (HEAN) form a swathe of elevated land stretching approximately 2,700 km from Cabinda, just north of the Congo River, to the Orange River. The swathe is between 150 and 250 km in width for most of its length. The total area is around 488,000 km^2.

The HEAN is part of the much larger Great Escarpment of southern Africa, which stretches from northern Angola anticlockwise around the subcontinent to the eastern highlands of Zimbabwe (Figure 1). This Great Escarpment and its associated highlands are estimated to host over 8,500 plant species, of which 1,460 species are endemic, and among many endemic animals are at least 126 endemic vertebrate species (Clark *et al.* 2011). Viewed as a whole, the Great Escarpment is characterised by its simplicity: a conspicuous upland where narrow coastal plains of 50–200 km skirt rising foothills and sharp escarpments that lead to rugged mountain chains, with peaks frequently rising to elevations of over 2,500 masl. Inselbergs are also prominent features of the highlands, standing high above the coastal plains or the rolling hills of the

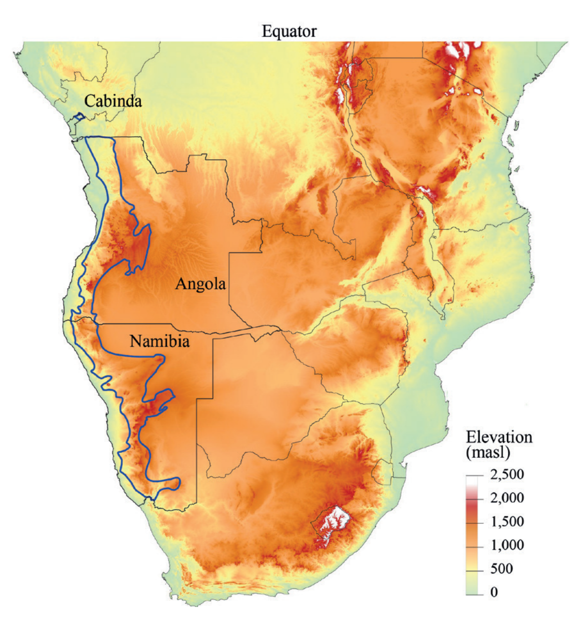

Figure 1: *Africa south of the equator, showing elevation, highlands (darker brown and white) and the area of the highlands and escarpments of Angola and Namibia (HEAN) demarcated by a blue outline. Black lines indicate the borders of Angola and Namibia.*

uplands. Inland of the mountain belts, elevations first drop quite steeply and then imperceptibly across interior peneplains that are drained by the great rivers of central and southern Africa (Moore & Larkin 2001).

On a grander scale, the HEAN and the Great Escarpment are part of the African Superswell, a feature that sets much of Africa apart from other continents (Nyblade & Robinson 1994). This is the broad tableland of elevated Africa stretching southwards from the Abyssinian Highlands in Ethiopia and across most of eastern and southern Africa. The tableland typically stands above 1,000 masl, whereas most other continental plains are below 500 masl (Figure 1).

Across the HEAN from about 5° South in Cabinda to 29° South along the Orange River, the climate ranges from tropical summer rainfall in the north to some temperate winter rainfall in the south, and from 1,300 mm of precipitation per year in the north to less than 100 mm in the south. The physiographic diversity and steep precipitation gradient from north to south have given rise to the extraordinary variety of biomes, ecoregions and vegetation types described by Huntley (2023) and animal and plant species found along the upland landscapes that extend across western Angola and Namibia, as described in many of the papers in this volume.

DEFINITION AND DELINEATION OF THE HEAN

The HEAN is an obvious physical feature on most maps (in Figure 1, for example), and to travellers on the ground or in the air because the inselbergs, scarps, escarpments, mountains and plateaus that constitute it are conspicuous. Figure 2 illustrates a selection of scarps, plateaus and inselbergs. However, defining a boundary that collectively encompasses these elements is challenging. The approach and terms adopted for this volume are explained below.

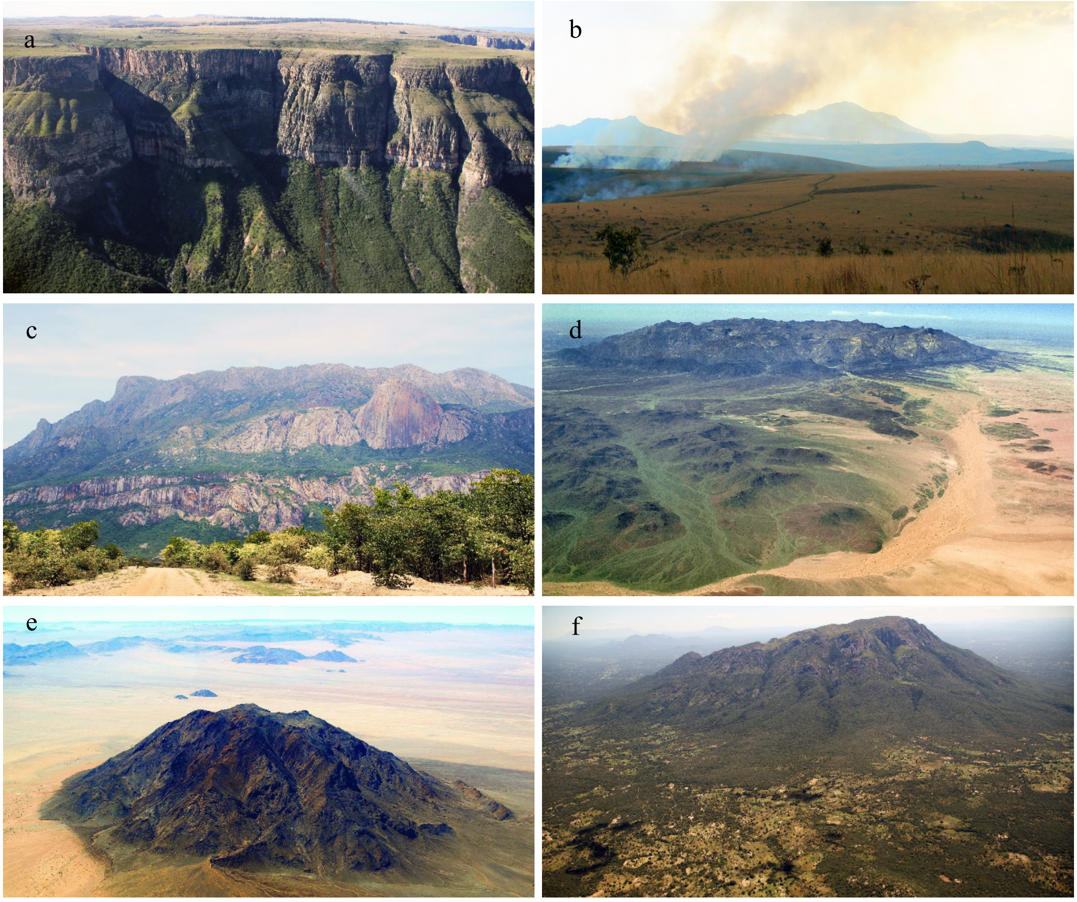

Figure 2: *A selection of scarps, plateaus and inselbergs in the highlands and escarpments of Angola and Namibia (HEAN): (a) the tallest scarp and escarpment and the plateau grasslands of Serra da Chela, just west of Lubango, Angola; (b) grasslands and human-caused dry-season fires around Serra do Môco typify the rolling hills of the Angolan Planalto; (c) Serra da Neve and (d) Brandberg are Angola's and Namibia's largest and tallest free-standing massifs, respectively, and both are located on the coastal plain; and (e) Namibia's Dikke Willem and (f) Angola's Serra Tchivira are typical of many isolated inselbergs on the lower western flanks of the highlands and escarpments, many of which rise 500 m or more above the surrounding lowlands. Photos: H Baumeler (Dikke Willem); T Figueira (Brandberg); others, J Mendelsohn.*

Highlands and plateaus

Two large blocks that lie between 1,700 and 1,800 masl make up and dominate much of the HEAN. One is often known as the Huambo highlands, Bié highlands or Huíla highlands, or Bié swell or dome (Knight & Grab 2016) or more practically – and in this volume – as the Angolan Planalto (*Planalto de Angola* in Portuguese). This forms an upland orientated NE–SW between Mussende and Lubango. The Namibian block is known colloquially, and in this volume, as the Khomas Hochland. It, too, stretches along a NE–SW axis, between Steinhausen and the Naukluft Mountains. Gently rolling hills and plateaus interspersed with inselbergs, many rising above 2,000 masl, cover large expanses of the two blocks. Grasslands, sparse shrubs and small trees dominate the vegetation. Plateaus were delimited as areas with gentle slopes and elevations greater than 1,700 masl (Figure 3).

West of the highlands, the landscape drops across steep escarpments, scarps or gently graded hills and valleys, descending to the coastal lowlands at about 600 masl, and to the coastal plain of the Atlantic Ocean. Rainfall over the coastal plain and lowlands is lower, and the vegetation generally sparser, than that on the highest elevations and to the east (see section on climate below). On the opposite and east side of the highland plateaus, landscapes gradually descend into the wooded plains of the Kalahari Basin.

Scarps and escarpments

Several escarpments and scarps form sharp boundaries to the highlands, some long and high, others shorter or lower. The most prominent and well-known in Angola are those forming the escarpment of Serra da Chela, which extends in a broken wall of tablelands from north of Humpata south towards Oncócua; the long scarp that runs from inland of Benguela for about 400 km north towards Calulo; and the scarp between Quilengues and Gabela.

In Namibia, the escarpment abruptly separates the coastal plain from higher ground to the east in many areas. It is best developed in central and southern Namibia from Usakos southwards to the flat-topped Gamsberg (2,350 masl), Naukluft Mountains, the Tiras and associated mountains that overlook the Namib, and to Aus. In central and northern Namibia the escarpment is not as well defined. Between Usakos and Khorixas erosion has largely removed the highlands and escarpment, resulting in a much gentler slope inland. The perennial Cunene and Orange rivers cut through the escarpment, as do the ephemeral Huab, Ugab, Omaruru and Swakop rivers. Environmental conditions change rapidly between the relatively wetter and more vegetated top of the escarpment and the arid, sparsely vegetated areas below.

Inselbergs

While large parts of the HEAN have been eroded away, many free-standing highland blocks of more resistant rock remain, overlooking their lower surrounds. The largest are close to or on the Angolan Planalto and Khomas Hochland, while many other smaller inselbergs are at lower altitudes farther west. Some inselbergs formed long after the main highlands. Most of these are composed of intrusive igneous rocks, and several are impressive features of the landscape, notably Serra da Neve, Brandberg and the Erongo and Paresis mountains. Features that rise sharply by 200 metres or more above their immediate surroundings were mapped as inselbergs.

In places, tall mountains rise above the plateaus as massifs to form, for example, Angola's highest peak (Serra do Môco on the Angolan Planalto at 2,620 masl), and Namibia's second-highest point (Moltkeblick on the Khomas Hochland which overlooks Windhoek from 2,479 masl). The elevations of both are similar to those of their large inselberg counterparts on the coastal plain where Serra da Neve at 2,489 masl is one of the highest peaks in Angola, and the Brandberg at 2,573 masl is Namibia's highest mountain. Many of the highest inselbergs on the Angolan Planalto support patches of forest, an effect of higher orographic precipitation. These forests are home to many endemic organisms, as described in the papers on plants (Goyder *et al.* 2023) and birds (Mills & Melo 2023) in this volume.

While drawing the boundary of the HEAN was often easy, for example along the margins of plateaus and along major scarps, elsewhere a more cautious approach had to be adopted, especially where we sought a boundary that encompassed most major inselbergs scattered on lower elevations to the west of the highland blocks and scarps (Figure 3).

ELEVATIONS AND SLOPES

Variation in elevation within the highlands and escarpments is largely related to their major components: plateaus, inselbergs on top of plateaus and at lower elevations, and scarps, as described above. Thus, most large inselbergs rise by at least 200 m above their surrounds; plateaus are above 1,700 masl on relatively flat ground, while the major highlands are in two large blocks, the Angolan Planalto and the Khomas Hochland, respectively in Angola and Namibia (Figure 3).

The transects in Figure 3 are as follows:

A – This transect runs from the coast just north of Ponte-Noire in the Republic of the Congo along

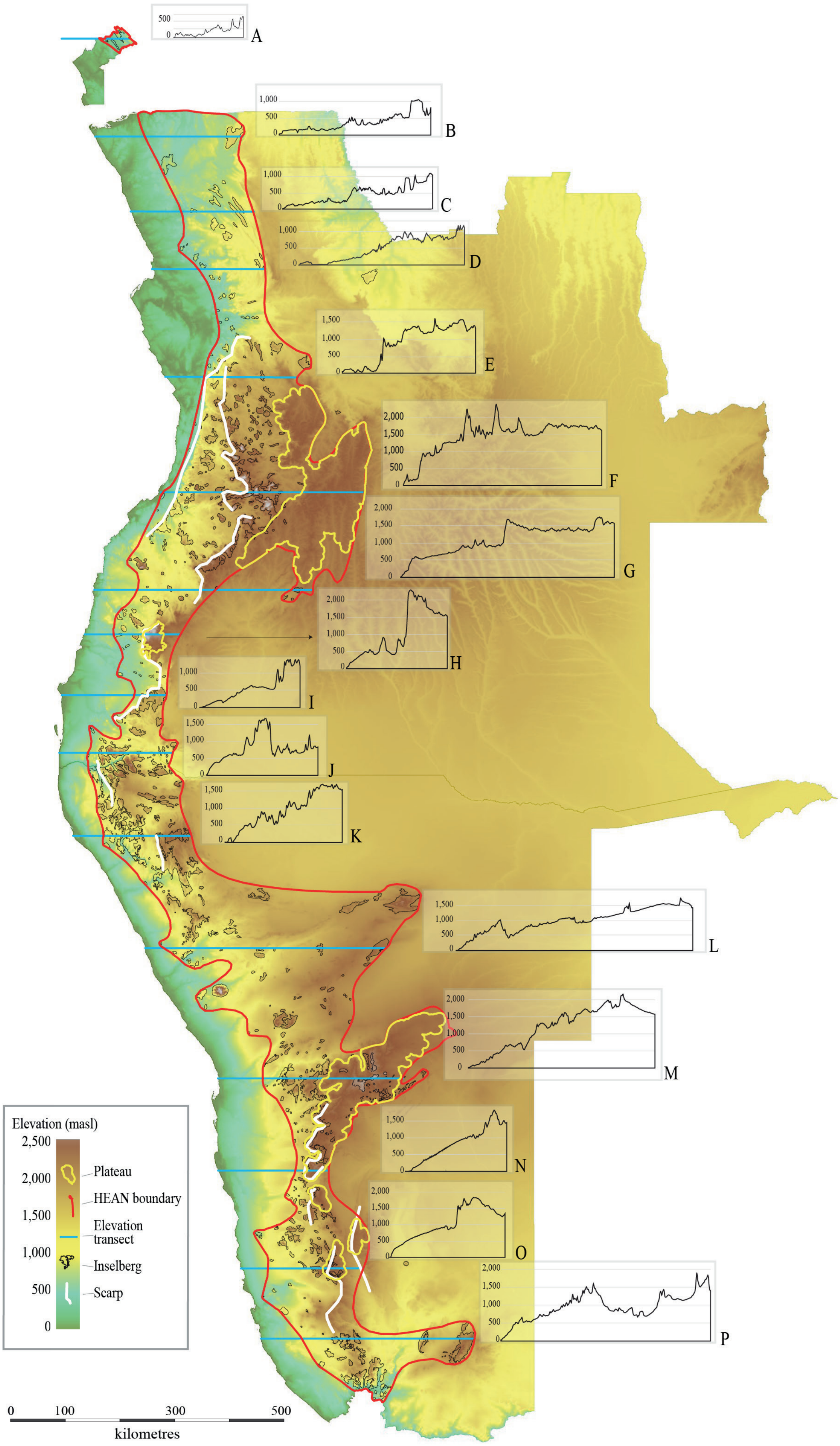

Figure 3: *Elevations in Angola and Namibia, and their highlands and escarpments (HEAN) together with scarps, plateaus and inselbergs, and profiles along select lines of latitude. The elevation profiles are described from west to east in the text.*

4.6° South to the northern border of Cabinda, and then cuts across the parallel ridges that run NW–SE through the Mayombe National Park. Elevations rise by about 500 metres from just west of Mayombe and the HEAN border up to the highest hills in the east.

B – The transect line along 6.3° South climbs from the coast through the hilly landscape of Angola's Zaire Province and then rises sharply by 500–600 m on to the relatively flat-topped Serra Canda.

C – Elevations are along 7.6° South between the coast and city of Uíge. The line traverses several parallel narrow ranges of sedimentary and carbonate rocks, among them Serra Calambinga, Serra do Pingano and Serra Uíge.

D – The transect along 8.6° South runs through Caxito, then climbs gradually across a broad ridge between Quibaxe and Bula Atumba and ends along the lower slopes of Serra do Combe.

E – From the Atlantic coast the transect along 10.47° South crosses about 80 kilometres of coastal plain between 200 and 300 masl. A sharp rise across the north–south escarpment that runs the length of Cuanza-Sul and Benguela provinces is followed by gently rolling countryside interrupted only by Serra do Ngueigi that rises some 600 metres from its surrounds.

F – From the coast along 12.48° South, the profile first ascends a small scarp and then transects the tall highlands of Serra do Mepo, Serra do Môco and Serra Cassoco. Eastwards, the profile crosses the gently rolling plateau grasslands of the Angolan Planalto.

G – Along 14.51° South, the profile rises gradually from the coast, and then climbs sharply over a moderate escarpment east of Quilengues. Elevations then drop slightly across the broad catchment of the Cunene River before rising over Serra Mocoti, an isolated inselberg largely covered in pristine miombo woodland.

H – About 110 km from the coast, elevations increase rapidly over the HEAN's highest scarp – in some places over 1,500 m – to the grassland plateau of Serra da Chela. To the west, the profile transects the Serra da Lua which rises several hundred metres above its surrounds. The profile line follows 14.94° South.

I – This profile transects a less prominent remnant of the Serra da Chela chert and dolomite plateau, again rising steeply up to a relatively flat tableland between 1,100 and 1,400 masl. The profile is along 16.0° South.

J – The profile along 17° South rises gradually across the Namib coastal plain in Angola, climbs part of the Serra Cafema massif and then the Serra Tchamalindi. Both mountains rise more than 1,000 metres above the surrounds and the nearby Cunene River which follows an ancient glacial valley (Martin 1965). The transect then follows the Cunene River valley upstream before crossing the smaller massifs of Serra Viluoviaengua.

K – From the coast, the profile along 18.44° South crosses several stretches of Etendeka basalt tablelands, as well as a major dip into the Hoarusib River valley. Farther east, the elevations record the northern ridge of the Otjikondavirongo range and then the Joubert Mountains.

L – After a sharp rise from the coast, elevations drop into the Huab River valley, then climb before a lesser drop into the Ugab River valley. It then follows the peaks of the intrusive granite Paresis Mountains, which rise several hundred metres above the surrounding landscape. In the far east, the elevations profile the sandstone Waterberg Plateau. The line follows 20.39° South.

M – Along 22.65° South, the line stretches across much of central Namibia, reaching the highest point in the Khomas Hochland. This is Moltkeblick, just south of Windhoek. The trough just west of this peak is the rift valley in which Windhoek lies.

N – After the flat coastal plain, the land rises steadily across the Namib Sand Sea before reaching the Naukluft, a dolomite massif which stands an average of 500 metres above its surrounds. The line of elevations is along 14.25° South.

O – Elevations rise gradually across the Namib Sand Sea along 25.95° South, and then climb steeply up the escarpment formed by the Tirasberge. The transect ends just south of Helmeringhausen and just west of another scarp known as the Schwarzrand.

P – The line runs from the coast along 27.17° South to the eastern border of the basalt-capped Karas Mountains. Elevations rise gradually from the west reaching about 2,000 masl on the Huib-Hoch Plateau before dropping into lower ground in the Fish River Canyon. The ground then rises to form the Klein Karasberge before reaching the higher Groot Karasberge.

The gentlest slopes (Figure 4) in the HEAN are on the plateaus of the Angolan Planalto and Khomas Hochland, the Central-Western Plains and in the landscape zones (see Figure 5) that flank the major highland blocks: Northern Escarpment, Central Escarpment, Southern Escarpment, the Nama Karoo Basin and Pro-Namib. By contrast, the steepest

Figure 4: *Slopes or gradients in the highlands and escarpments of Angola and Namibia (HEAN).*

slopes and vertical cliffs are the scarps and associated hillsides between the highland blocks and flanking the landscapes listed above, and on inselbergs. The dark colours, which depict steep slopes, highlight the rapid changes in elevation of the Serra da Neve, Brandberg and other major inselbergs. This map also demonstrates the substantial differences in landform between the rugged, broken surfaces within 300 km of the coast and the relatively level surface of the eastern interior.

MAJOR LANDSCAPES

The ecological importance of the major physiographic divisions in Angola was recognised as early as the 1850s by the pioneer Austrian botanist Friedrich Welwitsch who categorised the 5,000 plant species he collected in Angola within three regions: *região litoral*, *região montanhosa*, and *região alto-plano* (Welwitsch 1858). Welwitsch also prepared detailed geological profiles across the landscapes inland of Luanda and Moçâmedes (Albuquerque & Figueirôa 2018), probably the first of such analyses in western Africa. A further detailed and indeed classic study of Angola's geomorphology and local ecology was published in 1936 by the German geographer Otto Jessen (Jessen 1936). He defined a series of 11 transects from the coast inland, traversing the escarpment to the interior plateau from Moçâmedes and thereafter at intervals northwards to Luanda. Describing, illustrating and mapping selected vegetation communities, geological exposures, landscapes, land use and ethnological features of the country, Jessen's Angolan work remains unique in its diversity of interest and originality (Huntley *et al.* 2019). Geomorphological studies in Angola continued during the 1950s to 1970s and are summarised by Costa (2006).

Based on extensive field surveys of the agroecological potential of Angolan landscapes, Castanheira Diniz produced a series of maps illustrating the key features of Angola's topography, geomorphology, geology, climate, soils, and phytogeographic and bioclimatic zones (Diniz & Aguiar 1966, Diniz 1973, 1991, 2006). Diniz's landscape (mesological) units provide a useful framework for discussions on Angola's ecology and biodiversity. Indeed, his mesological concept closely corresponds with current perceptions of ecoregions (Huntley 2023).

By contrast, Namibia has not enjoyed the benefits of early extensive surveys of soils, climate and other ecological zones and landscapes. The first country-wide assessments of geology were published in 1965 (Martin 1965) and of vegetation in 1966 (Volk 1966, Giess 1971), while the first comprehensive atlas of the country was published in 1983 (van der Merwe 1983). To our knowledge, the first assessment of Namibian landscapes – based substantially on the unpublished understanding of landscapes of geologist Roger Swart (pers. comm.) – appeared in Mendelsohn *et al.* (2002). Goudie and Viles' *Landscapes and landforms of Namibia* was published in 2015.

For the purposes of this volume, 11 landscape units are recognised within the HEAN (Figure 5). In Angola, these include Diniz's (1973) Escarpment Zone, which we subdivided into Northern Escarpment, Central Escarpment and Southern Escarpment, and his Marginal Mountain Chain and Ancient Plateau; the Ancient Plateau is renamed here as the Angolan Planalto. In Namibia, the HEAN includes seven landscape units, of which one is a continuation of the Southern Escarpment. For each of the 11 HEAN landscape units, outlines of their constituent biomes, ecoregions, fauna and vegetation are given below, using the enumeration of ecoregions of Dinerstein *et al.* (2017) as used by Huntley (2023).

1. Cabinda Escarpment (Ecoregion 5). From Gabon southwards through the Republic of the Congo, and inland of the coast, low hills give way to steep ridges of a narrow escarpment belt which ends just north of the Congo River (Figure 6). The geology of the Escarpment Zone, of which Cabinda Escarpment is the northernmost section is complex, comprising plutonic and metamorphic gneisses, schists, quartzites and amphibolites of Palaeoproterozoic age (2.5–1.6 giga-annums [Ga]) (Miller 2023, this volume). Few people live in the area.

2. Northern Escarpment*,* from the Congo River to the Cuanza River (Ecoregions 35, 63). South of the Congo River, the landscape comprises a highly dissected relief with hills and low mountains rising eastwards to 1,300 masl. The area is largely dominated by plutonic and metamorphic gneisses, schists, quartzites and amphibolites of Palaeoproterozoic age (2.5–1.6 Ga). Smallholders farm maize, beans, sweet potatoes, melons, cassava and bananas as major staples for domestic consumption. Incomes are mainly earned from the sale of charcoal, bushmeat and vegetables.

3. Central Escarpment, from the Cuanza River to the Coporolo River (Ecoregions 35, 77, 104). The Central Escarpment forms a low, narrow but stepped landscape from about 200–400 masl along the base, rising within 50 km from the coast to 1,000 masl (and to 1,690 masl at the highest point on Serra Njelo). It is of Ryacian age (2.4–2.05 Ga), with basement plutonic and metamorphic rocks. Crops and commodities sold for incomes here are similar to those in the Northern Escarpment zone.

4. Angolan Planalto (Ecoregions 36, 77). This extensive plateau (the *Planalto Antigo* or *Planalto Central*) encompasses the headwaters of the south-flowing Cunene, Cubango, Cuchi, Cacuchi and Cutato Nganguela rivers, the west-flowing Queve, and the north-flowing Cutato River. The landscape consists of gently rolling grasslands, *anharas de ongote* geoxyle grasslands (see Meller *et al.* 2023, this volume), wetlands and low ridges with scattered granitic inselbergs. The plateau drops from 1,800 masl in the west to 1,400 masl in central Angola. These flat to gently undulating landscapes, together with the Congo and Zambezian peneplains, are part of the African and Post-African planation. Maize, pumpkins and cassava are grown on dry soils while vegetables are grown in moist fields around tributaries, known as *olanaka*.

5. Marginal Mountain Chain (Ecoregions 35, 77). These mountain lands, known as the Benguela and Huambo highlands, and Humpata Plateau or Serra da Chela, are underlain mostly by Precambrian rocks such as gneisses, granites and migmatites and lie above the escarpment along the western margin of Angola's extensive interior plateau at 1,800–2,620 masl. The highest peaks are Serra do Môco (2,620 masl), Serra do Mepo (2,582 masl) and Serra Lupangue (2,554 masl). The mountains are of biogeographic importance for their montane grasslands, with some elements of the Cape flora, and relict patches of Afromontane forests with endemic bird assemblages (Goyder *et al.* 2023, Mills & Melo 2023, both in this volume). Land uses are similar to those on the Angolan Planalto.

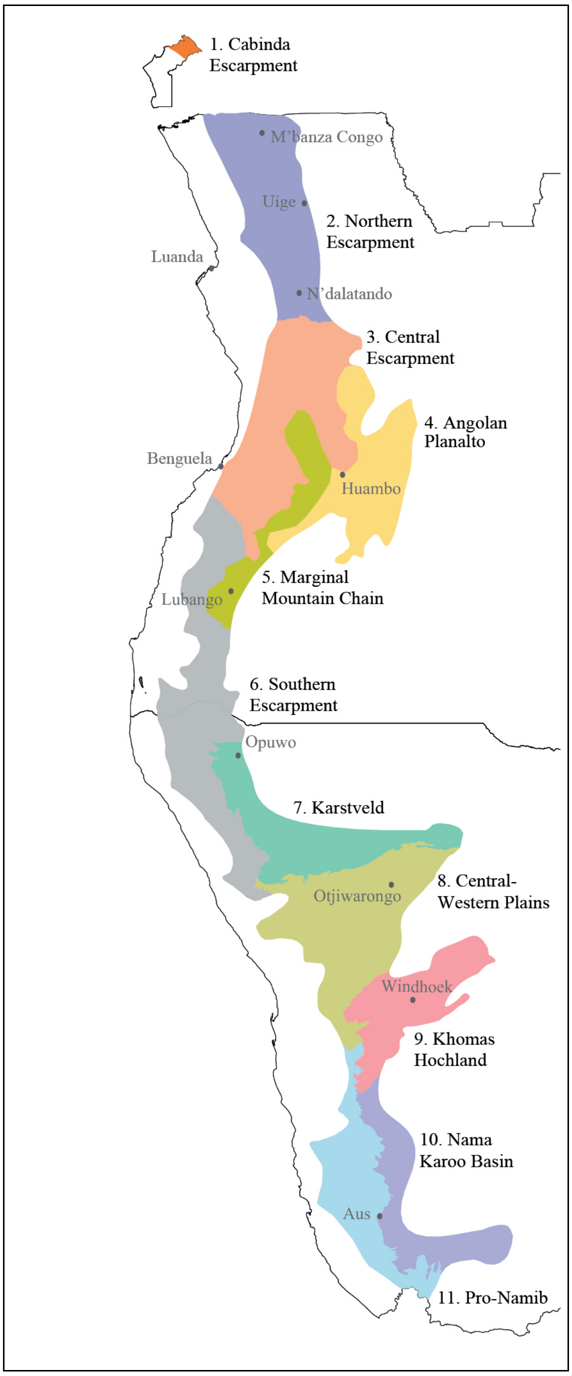

Figure 5: *The 11 major landscape units of the highlands and escarpments of Angola and Namibia (HEAN). The units are described in the text. Some towns are shown for orientation purposes.*

6. Southern Escarpment, from the Coporolo River in Angola southwards to about the Huab River in Namibia (Ecoregions 34, 98, 104). The escarpment becomes increasingly narrow, steep and high southwards from the Coporolo River and 100 km inland of the coast at Moçâmedes. Over much of the escarpment, the transition advances up a complex series of steep steps of between 100 and 600 m height. Between Moçâmedes and Lubango, the escarpment of the Serra da Chela is very sharp, rising 1,000 m in relief at Tundavala and Bimbe, where it is well defined by the Chela dolomites and cherts. The highlands above the escarpment form the Humpata/Huíla Plateau, within the Marginal Mountain Chain landscape unit.

To the south, a variety of substantial mountains protrude above this area, much of which is low lying. The best known are the Serras Cafema, da Lua, Capota, Viluoviaengua and Tchamalindi of southwest Angola, and the Baynes, Hartmann, Zebra, Otjihipa and Joubert mountains of northwest Namibia. These constitute the most rugged landscapes of both Angola and Namibia. The high carbonatite inselberg, Serra da Neve, lies in this landscape, rising to 2,489 masl. Similarly, some of the highlands between Lubango and Oncócua are capped with cherts belonging to the Serra da Chela formation. The landscape includes the Etendeka Basalts which form a distinctive landscape of flat-topped mountains underlain by layers of solidified lava that erupted during the breakup of Gondwana 132 mya (million years ago).

Few people live here, and there are only a few small towns in the area, such as Virei, Oncócua, Bibala, Camacuio, Orupembe, Purros and Okanguati. Livelihoods are based largely on remittances, social grants, tourism revenue, small stock and cattle.

7. Karstveld (Ecoregion 34). The Karstveld’s hills and ridges are underlain exclusively by dolomites or limestones formed from sediments deposited 750–600 mya, and metamorphic and sedimentary products of dolomites, in particular calcretes and cherts. Extensive aquifers underlie the permeable dolomite formations. Fossils are abundant in tufa deposits, and endemic insects and fish occur in some of the Karstveld’s many caves and underground lakes. Much of the hilly landscape is used for livestock and game farming and tourism, while crops are grown commercially in the lowlands around the hills.

8. Central-Western Plains (Ecoregions 34, 97). Much of the topography of this landscape unit is gentle in slope, rising gradually from the coastal lowlands in the west at about 500 masl to approximately 1,000 masl in the east at the western edge of the Kalahari Basin of aeolian sands. Acacia woodlands dominate the area. Many of the inselbergs that punctuate the area are intrusive granites formed during the breakup of Gondwana. The biggest of these are the Brandberg, and the Erongo and Paresis mountains. Many of the plants and animals that occur in these isolated highlands are restricted to them. Other prominent inselbergs are the Waterberg and other hills capped with Etjo sandstones. Most farms are used to produce or keep livestock, and for game farming and tourism.

9. Khomas Hochland (Ecoregions 97, 104). This plateau has a foundation of schists formed from sand and mud deposited on an ocean floor. The marine sediments were heated and folded into the rock formations of this plateau during the formation of Gondwana about 550 mya. The Auas Mountains form a conspicuous ridge which rises to over 2,000 masl. South of the mountains are the Rehoboth highlands of basement granites and complexes of metamorphic rocks. Livestock and game farming and tourism are the main rural economic activities. Windhoek, with its large population and various economic activities, is at the heart of these highlands which are largely covered in grasses and a sparse cover of shrubs and small trees. The tallest trees grow along drainage lines.

10. Nama Karoo Basin **(**Ecoregions 94, 104). This broad basin is underlain by horizontal layers of sediments. Some highlands protrude in the western margins of the basin, close to and above the prominent escarpment, such as the Huib-Hoch Plateau and Nasepberg. Other highlands below the escarpment are included here even though their geological compositions are different. These include the Huns Mountains, Chumberge and Namusberge. To the east are the two Karasberge mountain blocks which are uplifted metamorphic basement rocks overlain by a thin cover of basalts. Orographic processes provide the highlands with slightly more rain than the rest of southeastern Namibia. Soil and vegetation in these highlands are concentrated in valleys among large blocks of rock. Sheep and goat production and conservation on large farms are the main economic activities.

11. Pro-Namib (Ecoregions 103, 104). The Pro-Namib forms an apron below and west of the escarpment. Much of the surface is low-lying and underlain by gravel and shallow sand, as well as dunes of the Namib. The landscape includes vegetation communities dominated by karroid succulents in the south. Highlands include inselbergs of varying origins, such as the Klinghardt Mountains, Dikke Willem, Aurusberg and Uri-Hauchab, as well as highlands alongside the escarpment, such as the Tirasberge, Losberg and Nubisberge. Much of the area is managed for conservation and wildlife.

ORIGINS OF THE HIGHLANDS

While the topography of the HEAN uplands is clearly visible, their history is by no means clear. Two aspects seem to be agreed among geologists, however. First, the hills, mountains, escarpments and plateaus of Angola and Namibia are underlain by a much larger plateau that stretches between eastern and southern Africa (Figure 1). This raised plateau, designated as the African Superswell by Nyblade and Robinson (1994), has markedly higher elevations (on average > 1,000 masl) relative to other continents (~500 masl).

Second, the uplands of Angola and Namibia, and the wider expanse of African Superswell highlands, probably formed after the breakup of Gondwana 180–120 mya. Additionally, Gondwana's breakup led to a phase of rapid erosion of Africa's then recently formed continental margin. The removal through erosion of 2–4 km of soft crust material above and adjacent to the surrounding coast probably triggered a rapid isostatic rebound, with uplift of the continental margin resulting in the development of the Great Escarpment on the margins of the African Superswell surrounding an inland depression or basin (King 1963, Gilchrist & Summerfield 1990). The escarpment divided, and continues to divide, most river catchments draining to the coast from those which drain inland (see Figure 6).

Two other aspects of the highlands' history are more contested. The first concerns the processes that caused the uplift of the HEAN and other highlands of the African Superswell. One widely held view is that plumes of hot magma pushed the mantle and crust upwards (Nyblade & Robinson 1994, Fishwick & Bastow 2011). One broad and massive plume may have forced up the entire African Superswell and/or smaller plumes may have separately raised more localised uplands such as the Angolan Planalto and Khomas Hochland (Paul *et al.* 2014, Klöcking *et al.* 2020), perhaps during the breakup of Gondwana (R Miller pers. comm.). Another view is that uplift occurred along anticlinal flexures (in effect, buckled ridges or axes) caused by stresses within tectonic plates. These axes formed the major watersheds in southern Africa (du Toit 1933, Moore 1999). As noted earlier, the Great Escarpment which formed the axis that separated coastal and inland rivers has been ascribed to the isostatic rebound linked to deep erosion along the coastal plain. Two other axes transect the interior of the subcontinent of southern Africa. Uplift along one, called EGT (Etosha–Griqualand–Transvaal axis), is thought to have formed the Orange–Limpopo watershed and initiated the Kalahari Basin where fluvial sediments of the Kalahari Group were first deposited followed by the aeolian deposition of sands during episodes of Plio-Pleistocene aridity (Moore *et al.* 2009). The other axis, termed OKZ (Ovambo–Kalahari–Zimbabwe Axis), probably separated the Limpopo from the Kalahari Basin and impounded other major rivers, such as the Zambezi, within the Kalahari Basin.

The other contention concerns the timing of uplift. Proponents of the plume theory suggest that uplift occurred about 30 mya (Burke & Gunnell 2008, Klocking *et al.* 2020). By contrast, advocates of the tectonic plate buckling theory hold that uplift along the three axes occurred at different times: about 120 mya along the axis forming the southern African escarpment, about 85 mya along the EGT axis of the Orange–Limpopo watershed and Kalahari Basin, and about 40 mya along the OKZ axis (Moore *et al.* 2009).

DRAINAGE

Rivers associated with the HEAN can be grouped into three distinct categories. First, there are those that drain the western slopes of the highlands. They are relatively short and steep, with rapid flows to their nearby base levels on the Atlantic coast. Thus these are the most erosive rivers and many have cut back into the highlands where they formed distinct amphitheatre-like catchments. Cumulatively, rivers have done much to move the escarpment and spine of the HEAN steadily eastwards (Miller 2023, this volume). Twenty-two of these short, fast-flowing rivers are mapped schematically and named in Figure 6. Fourteen rivers are in Angola and eight are in Namibia (to avoid clutter, a similar number of other short, coastal rivers were not mapped). Between Angola's Coporolo River and Namibia's Kuiseb River all the coastal drainage lines are now ephemeral rivers which at times flood energetically after heavy rain. South of the Kuiseb River there are no local ephemeral or other rivers, except the Orange River which obtains its water in the South African interior and from the Fish River. The decrease in regularity of coastal flow and drainage from north to south reflects the corresponding decline in rainfall and increase in evaporation (Figures 8 & 9).

Second, is the category of rivers that drain the eastern areas and flanks of the highlands. Their large catchments are elongated from north to south. There are four such rivers, the Cuango, Cuanza, Cunene and Fish. They too have their base levels on the coast, but their river mouths are much farther from their catchments than the short, western rivers. Just why these four rivers seemingly hug the eastern flanks of the HEAN is not clear. It is likely that each of these four rivers turned west as a result of river capture by, respectively, the Congo, the coastal antecedents of the present Cuanza and Cunene, and perhaps the Orange River.

Third, are several rivers that drain the lower flanks of the HEAN including the elevated Angolan Planalto and Khomas Hochland Plateau in the east. Three of these rivers take an even longer route to their coastal base levels: the Zambezi, which flows eastwards into the Indian Ocean in Mozambique, and the Chicapa and Cassai which flow northwards to join the Congo River. Eight others never reach the coast: the perennial Cubango, Cuito and Cuando, and the ephemeral Cuvelai, Omatako, Eiseb, Nossob and Auob. Their base levels are between 900 and 1,000 masl in the Kalahari Basin, and their flows are thus slow and non-erosive.

Major rivers and their tributaries have eroded and bisected the HEAN in four areas: the Congo River between Cabinda and the Northern Escarpment landscape (see Figure 5), the Cuanza River in the southern area of the Northern Escarpment, the Cunene River between Angola and Namibia, and the Ugab, Omaruru and Swakop rivers across the Central-Western Plains landscape in Namibia. The southern extreme of the HEAN has also been truncated by erosion of the Orange River.

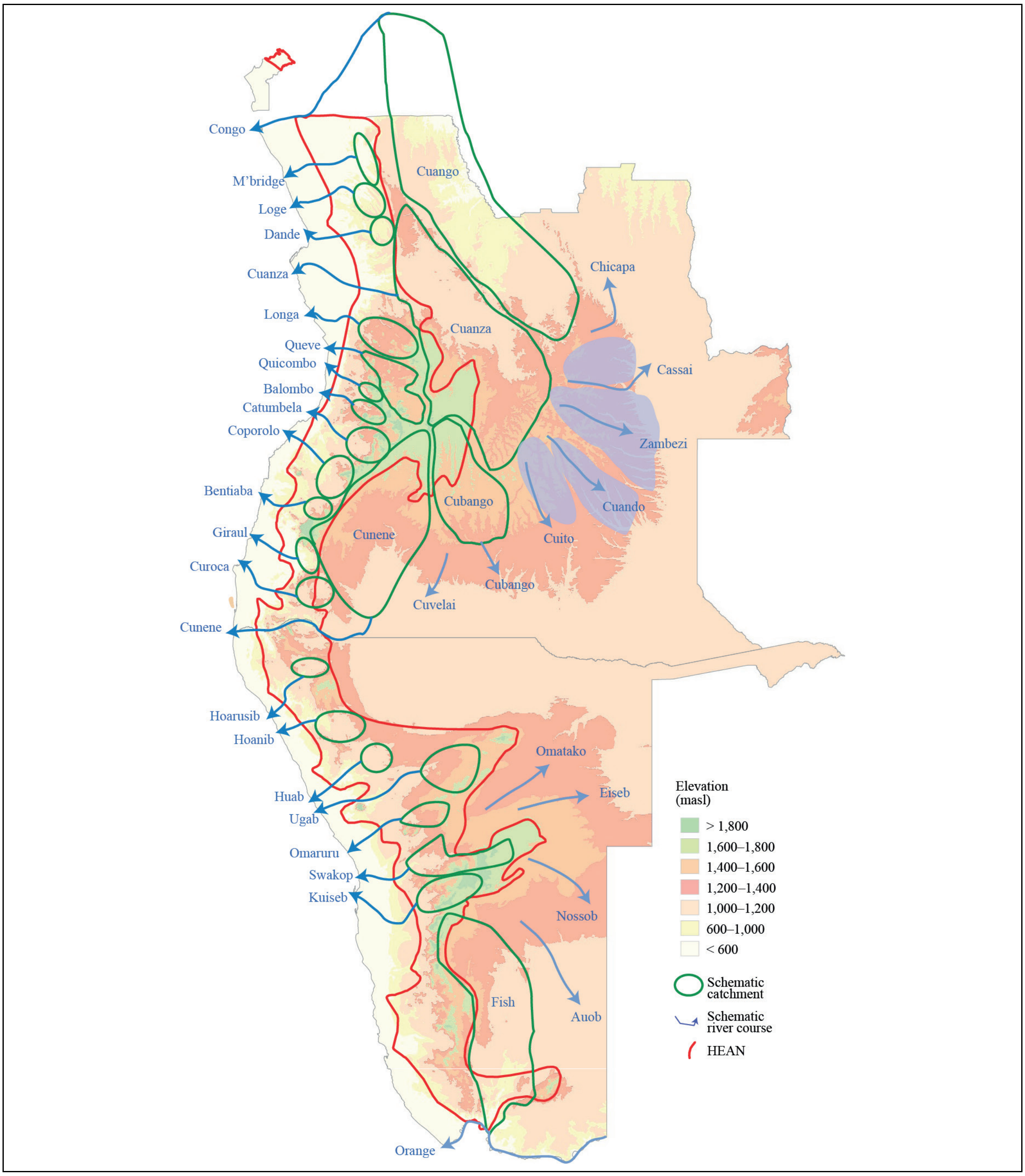

Figure 6: *Schematic portrayal of the major rivers and their catchment basins on and around the highlands and escarpments of Angola and Namibia (HEAN).*

SOILS

Only seven soil families cover more than 1% each of the HEAN area (Table 1). The two largest soil units dominate the surfaces of Angola (Ferralsols) and Namibia (Leptosols), respectively (Figure 7). Most Cambisols, Calcisols and Regosols are in Namibia, where the soils are less diverse than in the highlands of Angola, which is where most Luvisols, Phaeozems, Nitisols, Lixisols, Gleysols, Acrisols and Fluvisols are found. Arenosols cover much of the Kalahari Basin east of the HEAN in Angola and Namibia. The dominant soils in the HEAN have limited potential for arable agriculture, often because they were derived from rocks formed hundreds of millions of years ago. Such old soils are therefore well-weathered, leached and considerably deficient in nutrients. This is particularly true of Ferralsols. While they are usually deep, stable and easy to work with, Ferralsols have limited value for cultivation because of their low water-storage capacity and low natural fertility. They are used mostly for shifting cultivation of maize, sorghum, millet and cassava. Leptosols cover much of the hilly areas of Namibia and southern Angola. They are stony and often extremely shallow soils that hold little water and offer limited rooting space for plants. Cambisols are younger soils that form in recently deposited or exposed colluvial, alluvial and aeolian parent materials. They are often present in semiarid areas and can be relatively productive. Regosols are undeveloped, their formation often having been inhibited by aridity.

Arenosols occur on the eastern margins of the HEAN, particularly the Angolan Planalto and Khomas Hochland, and in areas adjacent to the coastal plain. These are deep windblown sands, consisting largely of quartz, and they hold little water and few nutrients. Calcisols are widespread in arid and semiarid environments that have distinct dry seasons. They form from deposits rich in calcium and magnesium.

***Table 1:** Areas covered by major soil families in the highlands and escarpments of Angola and Namibia (HEAN). (Derived from Jones* et al. *2013.)*

Soil family	Area (km^2)	Percentage (%) of HEAN
Leptosols	154,723	31.7
Ferralsols	125,125	25.6
Cambisols	67,624	13.9
Regosols	45,534	9.3
Calcisols	33,069	6.8
Arenosols	26,427	5.4
Luvisols	19,743	4.0
Other soils	15,903	3.3
TOTAL	**488,147**	**100**

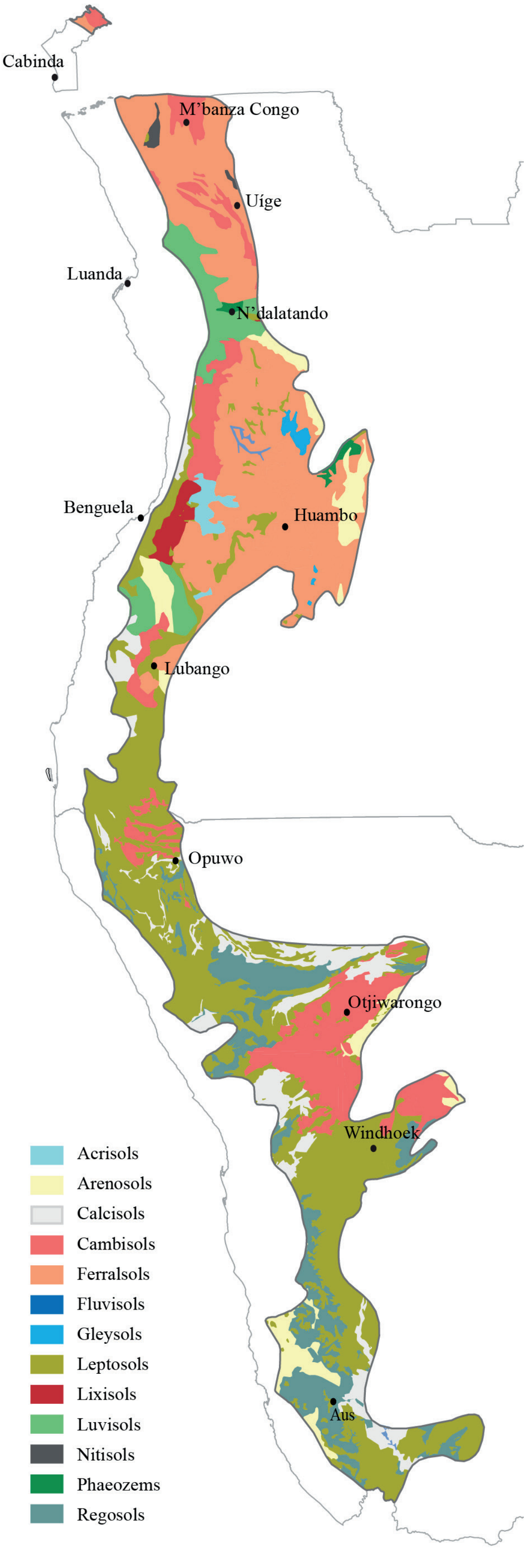

***Figure 7:** Distribution of major soil families in the highlands and escarpments of Angola and Namibia (HEAN). (Adapted from Jones* et al. *2013.)*

Significant amounts of calcium carbonate (lime) form below the surface where it may be concentrated into calcrete.

More fertile, deeper soils are limited to smaller areas of such soil families as Luvisols, Fluvisols, Gleysols, Nitisols and Phaeozems. The degree to which they are used for agriculture depends on factors such as rainfall, appropriate management and access to markets, for example. These enabling conditions are absent in certain areas.

CLIMATE

Most aspects of the climate in the HEAN vary along two axes: latitude and altitude. Thus, rainfall is highest in the northern, low latitudes and at high altitudes, especially over the Angolan Planalto. The lowest rainfall is in the extreme south of Namibia, where annual totals are many times lower than in the wettest areas of the highlands in Angola (Figure 8a). Annual variance in rainfall increases several-fold from north to south, and from east to west, but is less affected by elevation (Figure 8b). It is close to the coastal plain and the Namib Desert between southern Namibia and southern Angola that rainfall is most variable, and therefore least predictable.

The timing of rainfall also varies from low to high latitudes (Figure 9). In the northern half of Angola there are two distinct peaks: in November and December and then in March and April. From about Lubango south there is a single peak, usually in March but also in February in northern and central Namibia. In the southern quarter of Namibia rain falls in similar, small amounts throughout the year.

The antithesis of rainfall is the loss of water through evaporation and transpiration, known as potential evapotranspiration (PET). PET is about twice as high in the south than in the north, thus having a disproportionate effect on moisture availability. For example, annual PET is slightly lower than annual rainfall in northern Angola but more than ten times greater than annual rainfall in southern Namibia (Figure 10a). Aridity in the HEAN is therefore much greater in the south than in the north (Figure 10b).

Temperatures on the uplands of the HEAN are usually and on average lower than those to their west and east (Figure 11). However, minimum temperatures recorded early in the morning are somewhat higher than those to the east. In general, air temperatures are mild in the HEAN.

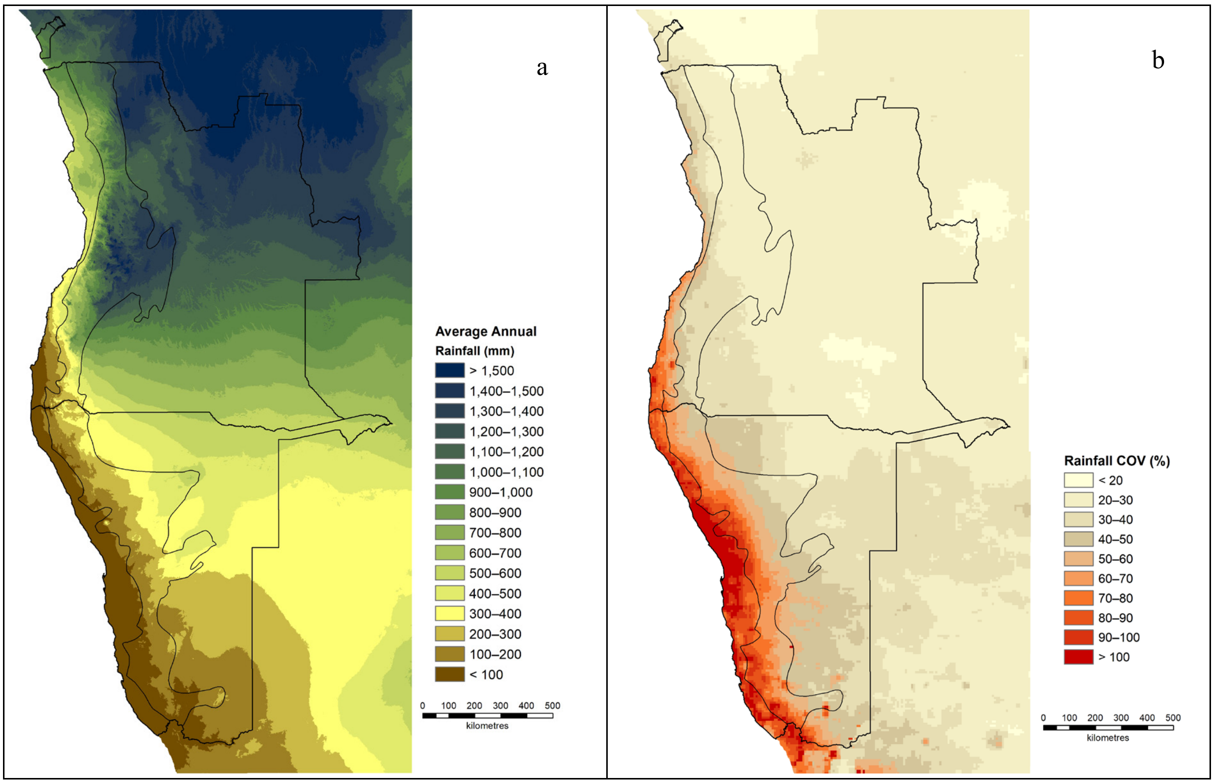

Figure 8: *Rainfall in Angola and Namibia: (a) average annual rainfall in millimetres and (b) average rainfall variance as the coefficient of variation (COV). Data from Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) data for the period 1981–2022. Annual rainfall totals were aggregated by rainfall season (July–June). Rainfall estimate (RFE) dekadal data from the Famine Early Warning Network (FEWS NET) were used for rainfall variance estimates.*

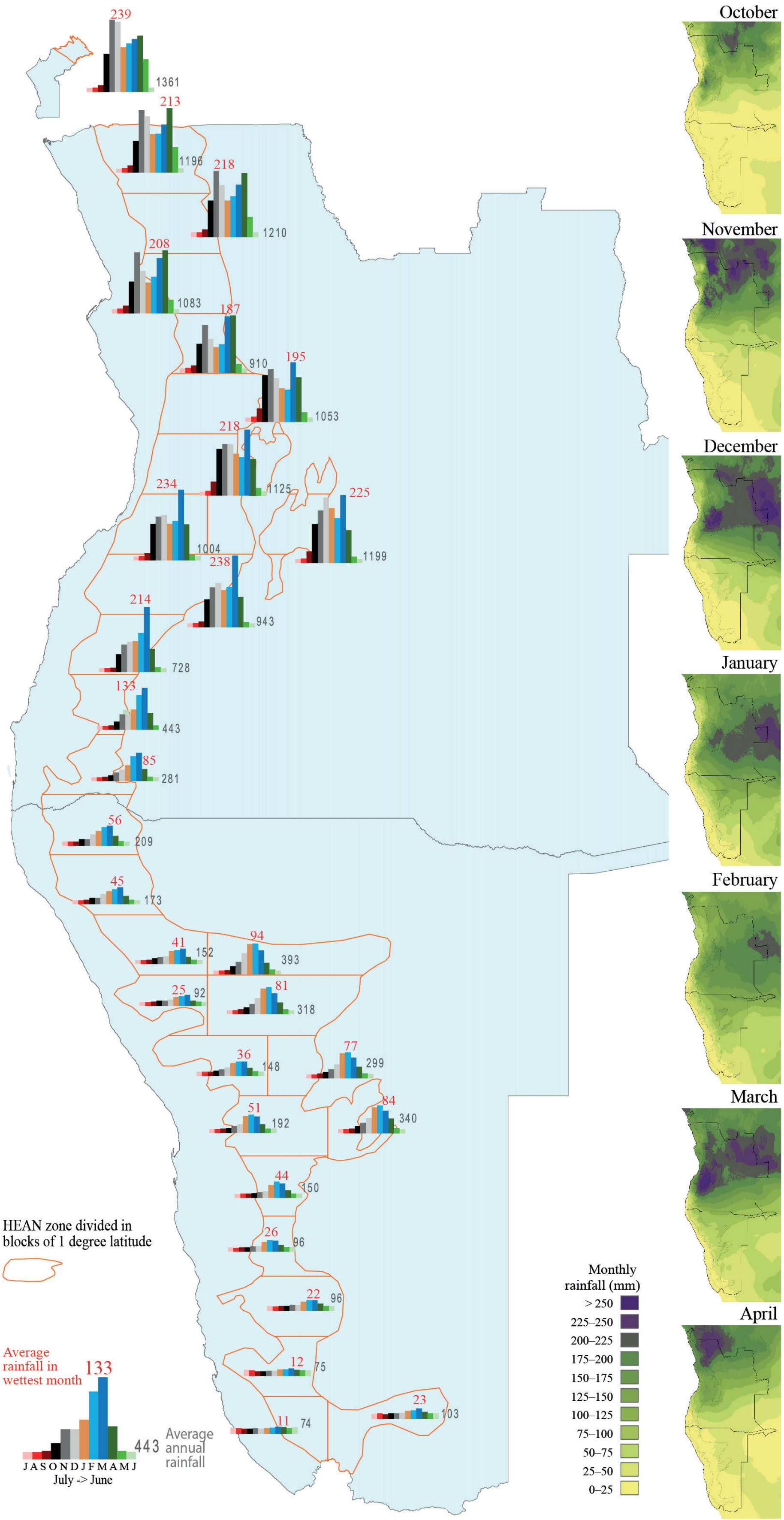

Figure 9: *Average monthly rainfall in millimetres per one-degree latitude block within the highlands and escarpments of Angola and Namibia (HEAN) (left) and average monthly rainfall in Angola and Namibia in the wet season between October and April (right). Data from Climate Hazards Group InfraRed Precipitation with Station (CHIRPS) data for the period 1981–2022.*

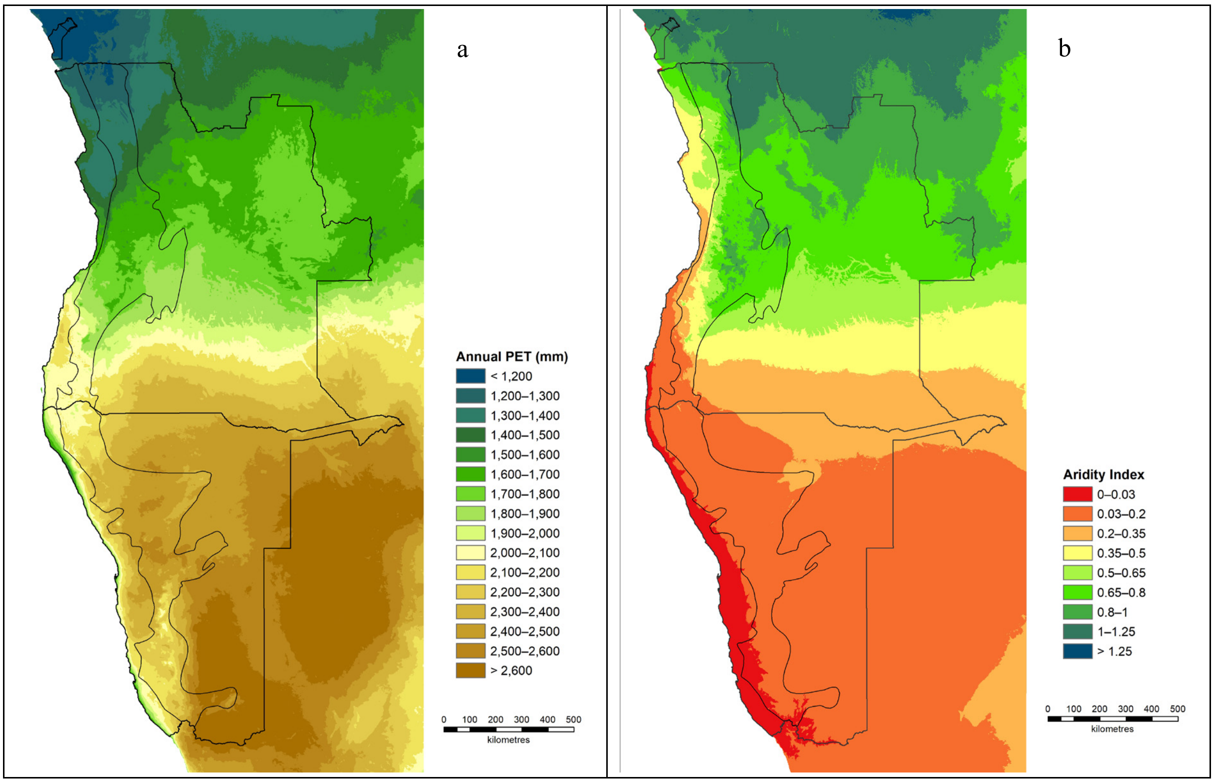

Figure 10: *Annual potential evapotranspiration (PET) in Angola and Namibia as millimetres of water lost (a) and an index of aridity calculated as annual average rainfall (Figure 8) divided by PET (b). Data from the Global Reference Evapotranspiration (Global-ET0) and Global Aridity Index (Global-Aridity_ET0) Version 2 dataset downloaded from CGIAR (2023).*

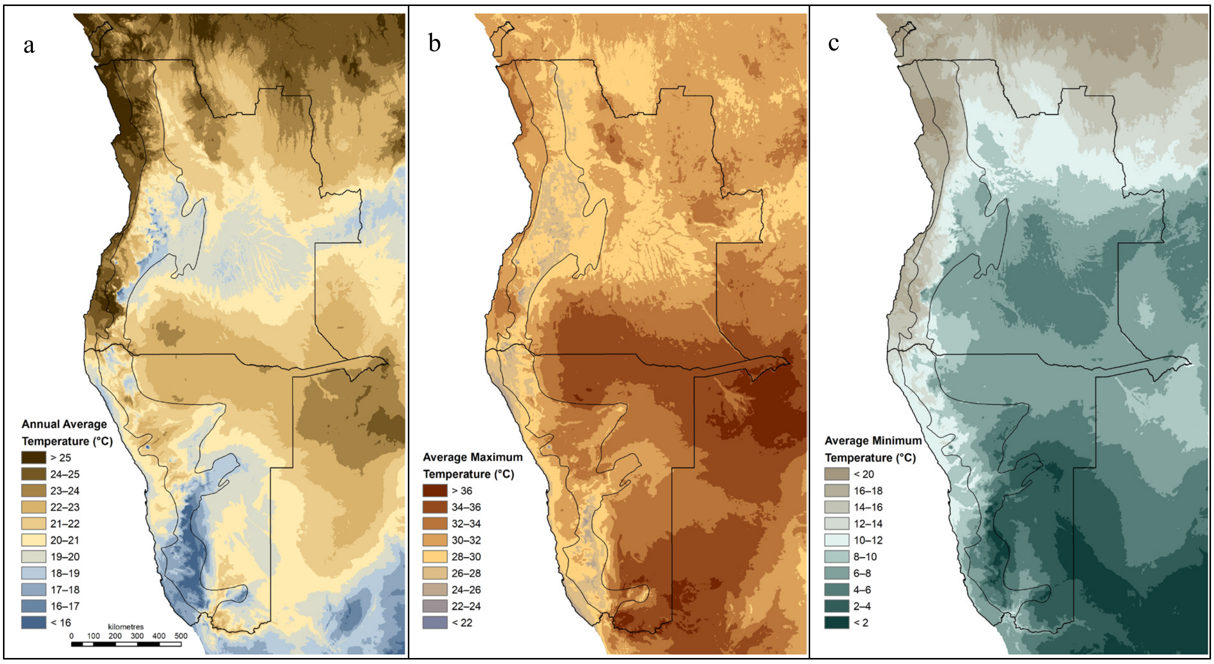

Figure 11: *Temperatures in Angola and Namibia: (a) average annual temperature; (b) average maximum temperature in the warmest month; and (c) average minimum temperature in the coldest month. Data from WorldClim http://worldclim.org (June 2016). The averages are created from monthly averages, maximums and minimums between 1970 and 2000.*

ACKNOWLEDGEMENTS

The manuscript benefited from comments and advice provided by Roy Miller, Andy Moore, KD Dijkstra and Pedro Vaz Pinto. Tony Robertson helped source and process some of the spatial data.

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Geology and landscape evolution of the highlands and escarpments of western Angola and Namibia

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ABSTRACT

The bedrock geology of Angola and Namibia has been built by rifting, continental drift, ocean formation, sedimentary deposition in both marine and continental environments, continental collision and mountain building since the Archaean. The palaeo-climates that followed, particularly during humid periods lasting tens of millions of years, have shaped the surface morphology. Erosion, removal of the humid-climate regoliths and gradual exposure of the present landscape started approximately 70 million years ago. The elevated escarpment regions of western Angola and Namibia are the result of scarp retreat after the breakup of Gondwana. They are underlain by igneous, sedimentary and metamorphic rocks ranging in age from Archaean to early Cretaceous. Inselbergs consist of weather-resistant igneous rocks of highly variable compositions such as granite, syenite, gabbro, basalt, rhyolite and carbonatite. Soils derived from the variable chemistry of these rocks in combination with the microclimates at different elevations and different locations provide the basis for the evolution of endemism.

Keywords: Angola, escarpments, geology, highlands, landscape evolution, Namibia

TECTONIC SETTING, CRUSTAL EVOLUTION AND REGIONAL GEOLOGY

The geology of Angola and Namibia today is the culmination of around 2.8 billion years (2.8 Ga) of geological history involving several plate tectonic cycles of breakup of supercontinents, sedimentation, continental collision and mountain building followed by successive cycles of denudation and erosion (Miller 2008 and references therein). Plastered around the old Archaean (> 2.5 Ga) cores are broad belts of Proterozoic gneisses and granites, some with associated acid and basic metavolcanic and metasedimentary successions. The oldest, with Palaeoproterozoic ages of 2.0–1.8 Ga, occur as inliers of gneiss surrounded by younger Mesoproterozoic (1.6–1.0 Ga) and Neoproterozoic successions (0.88–0.54 Ga). Younger Phanerozoic (0.54 Ga to present) rocks form an obscuring cover in places.

The oldest rocks, the Archaean metavolcanic, metasedimentary and granitic rocks of eastern and western Angola (Units 1–5 in Figure 1) probably formed part of the supercontinent of Ur (2.8–2.4 Ga). As rifting began to break up Ur during the Palaeoproterozoic, ocean basins formed between its fragments. Continent-derived sediments with interbedded acid and basic volcanic rocks that accumulated along the basin margins or along oceanic island arcs from about 2.3 to 2.0 Ga (Units 6–8) became folded and metamorphosed as continental fragments began to collide with each other to form the next supercontinent of Colombia (also known as Nuna) by about 1.8 Ga. Associated granites intrusive into these Palaeoproterozoic metasedimentary and metavolcanic rocks range from 2.0 to 1.7 Ga in age. Such metamorphic rocks and intrusive granites occur in western Angola and northwestern Namibia, named the Epupa Metamorphic Complex in the latter area. Occurring along the Orange River is an island-arc succession of andesitic volcanic rocks about 2.0 Ga in age, the Orange River Group, that is intruded by an associated suite of calc-alkaline rocks ranging from gabbro to quartz porphyry in composition and between 1.9 and 1.7 Ga in age.

At about 1.6 Ga the plate tectonic cycle began to repeat itself. Colombia started to break up, but by 1.0 Ga continental amalgamation had built the next supercontinent, Rodinia. Two belts of rocks formed during this period in Namibia (Unit 9). The belt in the south is the Namaqua Metamorphic Complex which consists of high-grade ortho- and paragneisses. It extends in a southeasterly direction from Lüderitz and is exposed in the escarpment cliffs west of Aus. The other belt is the low-grade, lithologically variable Sinclair Supergroup of the Sinclair–Rehoboth Magmatic Arc which extends from the Helmeringhausen area to Gamsberg and thence in a northeasterly direction through Rehoboth into Botswana. Suggestion of a third but highly deformed belt in the Cunene River area is provided by the 250-km long, north–south trending Angola Anorthosite, also known as the Kunene Anorthosite Complex, with an age of 1.37 Ga. Anorthosite, gabbro and norite in the western part of the complex form highlands and inselbergs in the highlands and escarpments of Angola and Namibia (HEAN).

Disruption of Rodinia began at about 880 million years (880 Ma) ago, again with intracontinental rifting followed by the separation of continental fragments and the formation of oceans, one trending north–south between Africa and South America, and one extending northeast through Namibia from the Swakopmund area. Sedimentary rocks of the Damara Supergroup (Units 10–12) were deposited in the oceans and on the continental margins with only very limited associated volcanism. As this plate tectonic cycle progressed, the oceans closed and evolved into three orogenic belts, two between Africa and South

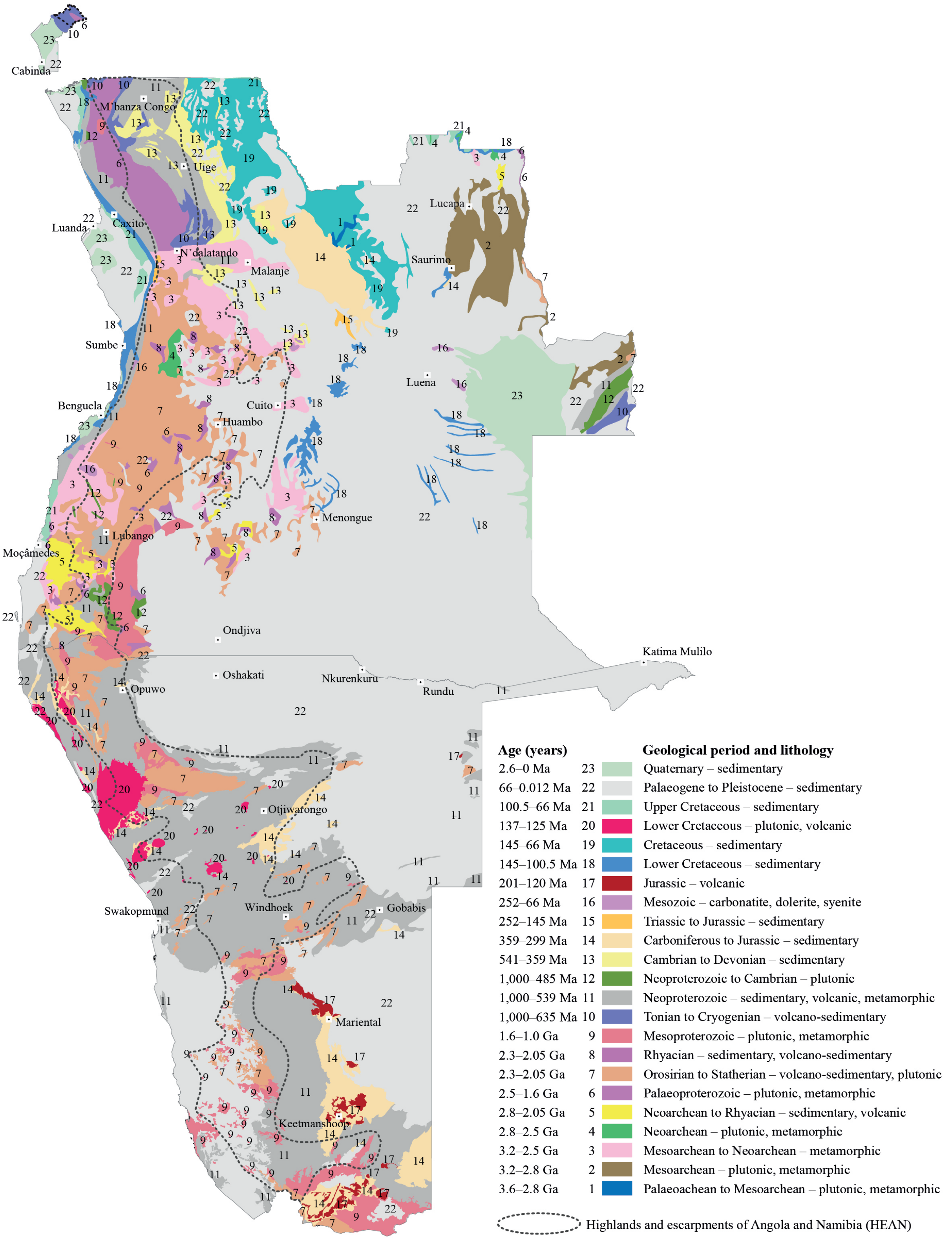

***Figure 1:** Major geological units in Namibia and Angola (Adapted from https://portal.onegeology.org/OnegeologyGlobal/ and Atlas of Namibia Team (2022)).*

America, the Gariep Belt in the south and the Kaoko Belt in the north, with the third being the northeast-trending Damara Belt through central Namibia. Damara Belt metagreywacke forms the Khomas Hochland, and quartzite forms the Auas and Hakos mountains. The centres of the Kaoko and Damara Belts are characterised by high-temperature metamorphic rocks and many granite intrusions. The margins of these belts were only weakly metamorphosed. Dolomites, limestones and shales of the Otavi Group occur in the north, forming some of the northwestern highlands as well as the dolomite belt that connects them to the Otavi Mountain highlands. Shales, sandstones and limestones of the Nama Group occur in the south. The Gariep Belt consists of low-grade schists, quartzites, limestones and oceanic metabasalts. Final continental amalgamation formed the Gondwana Supercontinent at 539 Ma but granite intrusion into the central Damara Belt continued until 460 Ma.

By 350 Ma Gondwana had drifted southwards, was located at the South Pole and was covered in ice. Glacial deposits form the base of the Karoo Supergroup (Units 14–15). Early, westerly flowing Karoo glaciers cut deep canyons into the bedrock of northwestern Namibia (Martin 1981). As drifting continued, Gondwana moved slowly northwards and the climate changed progressively from glacial to arid tropical. Much of the supercontinent was covered by an extensive, post-glacial shallow sedimentary basin in which muds and sands were deposited. These lithified to shale and sandstone but are poorly exposed in several subbasins. Accumulation of dune fields during the Triassic followed gentle uplift and exposure of earlier sediments. These aeolianites form the weather-resistant cappings of the Waterberg, Mount Etjo and the Gamsberg.

The breakup of Gondwana was initiated along the eastern margin of South Africa by a deep mantle plume rising from the core-mantle boundary at 183 Ma. Evidence of this are the 183 Ma basalts of Lesotho, the Kalkrand basalts (the top unit of the Karoo Supergroup) and the dolerite sills that form the Taantjiesberge in the Keetmanshoop area (Unit 17). A second, even larger mantle plume, the Tristan Plume, initiated the separation of southern Africa and South America at 134 Ma in the early Cretaceous. Its surface expression consists firstly of the Etendeka basalts that cap the Etendeka highlands with the thick interbedded and mountain-capping layers of ignimbritic quartz latite (Unit 20) (Erlank *et al.* 1984, Milner *et al.* 1992, 1995, Ewart *et al.* 2004a, 2004b) and secondly of scattered inselbergs which are the remnant roots of several large inland volcanoes: Cape Cross, Messum, Brandberg, Doros, the two Spitzkoppes, Okenyenya, Otjohorongo, Ozongombo, Etaneno, Ondurakarume, Eisenberg, Okaruzu, Paresis, Omatako and Erongo (Unit 20). Rock types forming these inselbergs include gabbro, granite, syenite, carbonatite, basalt, dolerite and/or alkali lava, some with rims of the older Karoo sediments and Etendeka basalts that they intruded.

The eroded cores of two other volcanoes form prominent inselbergs, the 77 Ma Brukkaros south of Mariental and the 49 Ma Dikke Willem northeast of Aus, and the carbonatite Serra da Neve (91 Ma; Jerram *et al.* 2019) (Unit 16). The alkaline Klinghardt phonolites form a scattering of small black hills south of Lüderitz. Areas of marine Cretaceous sediment occur in coastal Angola and further inland (Units 18, 19, 21). Various unconsolidated to semi-consolidated sands, clays and associated calcretes ranging in age from about 80–70 Ma to the present cover much of Namibia and Angola (Units 22, 23).

Orogenic belts mark the sites of continental collision as supercontinents grow. They erode to form old palaeo-surfaces before the next cycle of continental breakup starts. Small remnants of the post-Rodinia–pre-Gondwana peneplain occur in the vicinity of Duwisib and Helmeringhausen, atop the escarpment from west of Helmeringhausen to well south of Aus, and on the Karas Mountains, commonly with outliers of basal Nama on them (Miller 2008). Similarly, erosion between 540 and 300 Ma resulted in the development of a vast post-Gondwana peneplain, the pre-Karoo surface. This was broken by high, weather-resistant mountain ranges or inselbergs of the Damara mountain belts in western Angola, the Kaokoveld and central Namibia. Remnants of this surface are present west of Khorixas. Some of the present-day bevels such as that of the Khomas Hochland, the Eros Mountains and high ridges with uniform elevations south of Windhoek may be partially reworked remnants of the pre-Karoo surface (Miller 2008).

Palaeo-climates, particularly during the Cretaceous (135–65 Ma) and Cenozoic (last 65 million years), have exerted a strong influence on the present-day geomorphology of western Angola and Namibia. This includes broad, fluvially incised highlands, weather-resistant ridges and inselbergs surrounded by lower-lying plains, as well as the Great Escarpment separating the elevated interior from the low bedrock bevel of the Namib Desert. Geology, present-day climate and relative elevation determine the composition and volume of soil cover and the ecosystems that they support (Burke 2001, 2002).

During the 50–60 million years that followed the breakup of Gondwana, Africa's Cretaceous climate was humid. The resulting African Erosion Cycle culminated in the formation of an Africa-wide peneplain, the African Surface (King 1963, Partridge & Maud 1987), which, depending on the weather resistance of the bedrock, occurs at different elevations in Namibia: 1,800–2,000 masl, 1,200 masl and 0–800 masl. In the latter case, it forms the lithologically variable bedrock bevel of the Namib Desert as erosion cut deeply down and landwards into the elevated rift shoulder of the early Cretaceous continental margin. The present-day Great Escarpment, some 100 km inland from the coast, is all that remains of this rift shoulder. Older planation surfaces were reworked (Burke & Gunnel 2008) but the remnants described above have remained intact. An intensely weathered regolith about 50 m thick underlaid the African Surface. This is only preserved where it has been protected by an overlying layer of weather-resistant calcrete, such as in the Weissrand and north of Kamanjab, or by silcrete in the southern Namib. Deep river systems were incised during the humid Cretaceous. Most obvious are the re-incised, early Karoo glacial valleys of northwestern Namibia, but Kalahari sands now cover two others. One, trending northeast, arose southeast of the Waterberg, curved around to the northwest as it skirted the Otavi mountainland and disappeared into the Owambo Basin. The other is the palaeo Aranos River of southeastern Namibia that flowed in a southeasterly direction in a valley 300 m deep cut into the sub-Kalahari Karoo rocks of the Stampriet Artesian Basin. Sediments transported by this river washed down into the palaeo Molopo River in Botswana and then joined the sediments of the Orange–Vaal system as they built out the offshore, 7-km thick Orange River delta. Areas of marine Cretaceous sediment also occur in coastal Angola.

The supply of sediment from inland southern Africa down the Orange River to the offshore Orange Basin dropped dramatically between 80 and 70 Ma (Muntingh 1993, Brown *et al.* 1995) as the climate changed from humid to semiarid. With reduced flow in the inland rivers, the sands, clays and calcretes of the Kalahari Group began to slowly fill up the river systems and the great inland Kalahari Basin throughout the Tertiary by means of fluvial deposition and periodic aeolian reworking of the fluvial sediments. Sediment transport into the basin ceased at 4–3 Ma when Africa became hyperarid (deMenocal 2004, Miller *et al.* 2010). Approximately three million years of hyperaridity resulted in accumulation of the Kalahari dunes before a more humid climate returned at about 1.2 Ma; at this time the valleys of Namibia's eastern rivers were incised (Miller 2014).

The weathered remnants of the syn-Etendeka volcanoes were already inselbergs by the end of the African Erosion Cycle. Tertiary erosion and weathering rates have been slower since then but the relative elevation of the inselbergs has been enhanced by a greater degree of removal of the surrounding lithologies. Furthermore, the deeply weathered regolith below the African Surface, where not protected by weather-resistant cappings, has been totally removed leaving only hard bedrock. Dating of the African Surface reveals that it was periodically reworked during wetter periods up to about 30 Ma (Partridge & Maud 1987, Burke & Gunnel 2008).

During the Tertiary and Quaternary, i.e. since 65 million years ago, the global climate has fluctuated between cold glacial and warm interglacial periods which consequently caused huge changes in sea level (Haq *et al.* 1987). In contrast to the limited evidence of climate variation we have been able to glean from the Kalahari Group sediments, the Namib Desert and the immediate offshore do record a – somewhat different – history. Minor marine deposits in the southern Namib Desert dating from around 40 Ma and diamonds at Kolmanskop indicate that sea level during the upper Eocene was up to 175 m higher than at present. A sea level fall of possibly as much as 500 m during the extremely cold upper Oligocene (30–25 Ma) initiated the incision of V-shaped valleys 90 m deep into the bedrock of the Namib plain. The coastline was approximately 200 km west of its present position. As sea level rose again, fluvial gravels filled the Oligocene valleys. Since the beginning of the Miocene (23 Ma) there have been repeated glacial events during which the sea level fell by as much as 130 m. Each fall of sea level exposed vast expanses of marine sediment which the strong southwesterly winds began to blow onshore. An early, partly consolidated erg (area of shifting dunes) was deposited throughout the Namib between about 21 Ma and 5 Ma. Fluvial sediments were deposited by very sporadic flooding of westerly-flowing escarpment rivers and larger rivers further inland which were either trapped by the dune fields or occasionally broke through them to reach the sea (Ward *et al.* 1983, Brain *et al.* 1990). Deposition of the present unconsolidated sand seas in the Namib began at about 5 Ma and continues today (see Miller 2008 for references). Raised beaches along the coast record just a few of the many warm interglacial marine high stands, i.e., at 90 m (19–17 Ma), 50 m (7–5 Ma), 30 m (3–2.5 Ma), and 10 m and below (200,000 to > 10,000 years ago) (Pickford & Senut 2000).

GEOMORPHOLOGICAL EVOLUTION OF ANGOLA AND NAMIBIA

The western Angolan highlands within the boundaries of the HEAN contain highly deformed and metamorphosed basement rocks ranging in age from Mesoarchaean (3.2–2.8 Ga) to Neoproterozoic (1,000–635 Ma) with some significantly less deformed and metamorphosed Neoproterozoic to Ediacaran (635–539 Ma) platform successions, some remnant patches of Cambrian to Devonian (539–360 Ma) rocks and Mesozoic alkaline intrusions of carbonatite, syenite and dolerite. Younger Palaeogene to Holocene (66 Ma–present day) cover encroaches from the east.

Repeated episodes of plate tectonic accretion progressively amalgamated highly deformed and metamorphosed terranes of metasedimentary, metavolcanic and intrusive granitic and mafic rocks of Mesoarchaean to Neoproterozoic age onto each other to build the Precambrian Angolan/Congo Craton, an integral part of Gondwana.

An understanding of the post-Gondwana sedimentary succession offshore of Namibia and Angola helps to elucidate the concomitant evolution of the continental onshore from which the sediments were derived. The Gondwana breakup between Africa and South America opened like a zip with the opening starting in the south at about 134 Ma and progressing northwards. It was initiated by the hot, mantle-sourced, early Cretaceous Tristan Plume that generated the Paraná basalts of Brazil and the chemically identical Etendeka basalts of Namibia. Breakup took place through stages of rifting, sag of the incipient continental margins and then drifting apart of the now separated continents. Rifting between Angola and Brazil began at about 123 Ma resulting in the development of a deep, north–south, low-elevation rift basin with high rift shoulders similar to today's East African rifts. Tristan Plume volcanism produced the Cape Fria High which separated the rift into contrasting northern and southern parts. That to the south was a narrow, open ocean basin. The section to the north was initially a closed lacustrine rift lake in which basal, organic-rich, sapropelic muds were deposited. Overlying thick salt accumulations point to periods of seawater influx followed by evaporation.

As rifting evolved to final continental breakup and spreading, both basins separated into eastern and western parts and continent-sourced clastic sediments began to cover the developing continental margins. Shallow reef limestones accumulated locally just south of the Walvis Ridge and more extensively further north. The Angolan margin and its South American equivalent became the oil-rich Angolan and Campos basins.

Africa was very humid throughout the Cretaceous (135–65 Ma). Deep chemical weathering and intense erosion produced a gently undulating Africa-wide peneplain, the African Erosion Surface, which by the end of the Cretaceous was located inland of the Great Escarpment that encloses most of southern Africa. Large river systems dissected this surface and fed the erosion products into the expanding Atlantic and Indian oceans. Concomitantly, scarp retreat induced by short, high-energy rivers originating along the elevated and steep western edges of the Namibian–Angolan rift shoulder physically cut this back eastwards forming a much lower-elevation continental margin peneplain time-equivalent to the inland African Erosion Surface. This is the bevel west of the HEAN. Archaean, Proterozoic, Cretaceous and Cenozoic rocks and sediments form the outcrops on this bevel. The highlands and escarpments that comprise the HEAN are the remnants of the rift shoulder.

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Biomes and ecoregions of the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-huntley

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ABSTRACT

This paper outlines the extraordinarily rich diversity of biomes and ecoregions found within the highlands and escarpments of Angola and Namibia (HEAN). Across 2,700 km of latitude, the climate ranges from tropical summer rainfall averaging at 1,200 mm per year in the north to warm temperate non-seasonal rainfall of 100 mm per year in the extreme southwest. Biomes range from Guinea-Congolian rainforests, Afromontane forests and grasslands, arid and mesic savannas and woodlands, to the Namib Desert. The concepts of biomes, ecoregions and endemism are discussed, and these terms applied to the four biomes and twelve ecoregions falling within the HEAN.

Keywords: Angola, biomes, ecoregions, escarpments, highlands, Namibia, vegetation types

INTRODUCTION

Across the 2,700 km latitudinal extent of the highlands and escarpments of Angola and Namibia (HEAN), from Cabinda to the Orange River, climates range from tropical summer rainfall in the north to warm temperate non-seasonal or mildly winter rainfall in the extreme southwest, and from 1,200 mm to 100 mm precipitation per year from north to south across this range (see Figures 8 and 9 in Mendelsohn & Huntley 2023). The physiographic diversity and steep precipitation gradient from north to south account for the extraordinary richness of biomes, ecoregions and vegetation types, and animal and plant species, found along this spine of landscapes that extends across western Angola and Namibia.

In northern Angola, Guineo-Congolian rainforests clothe the sea-facing hills and escarpments of Cabinda, Zaire, Uíge, Bengo and Cuanza-Norte provinces, with remnants or elements in Cuanza-Sul, Benguela, Huambo and Huíla, within a matrix of fire-tolerant tall grasslands and open woodlands. On the highest peaks of Cuanza-Sul, Benguela, Huambo and Namibe provinces, isolated patches or elements of Afromontane forests survive in fire-protected mountain valleys, surrounded by short grasslands and open miombo *Brachystegia* woodlands. See Mendelsohn and Gomes (2023: Figure 2) for a map of provinces. Southwards, *Acacia*, *Commiphora*, *Colophospermum* and *Combretum* woodlands and shrublands occupy the arid plains, hills and mountains of Namibe and Cunene provinces. The savanna floras of Angola are dominated by Zambezian taxa. The arid ecoregions of southern Angola continue across the highland plateaus, escarpments and inselbergs of Namibia. Increasing proportions of Nama Karoo plant affinities appear in the shrublands of southern Namibia. The northern outliers of the Succulent Karoo biome of South Africa appear on the hills surrounding the Orange River valley and southern coastal plains of the Pro-Namib.

BIOMES, ECOREGIONS AND ENDEMISM: CLASSIFICATION AND NOMENCLATURE

The classification and mapping of the biomes and ecoregions of Africa received much attention in the decades following the establishment of the Convention on Biological Diversity (CBD) in 1992, specifically in efforts to design and implement biodiversity conservation strategies and programmes. Preceding the CBD, White (1983) provided a useful ‘big picture’ framework of African vegetation and floristic relations within his phytochoria, without referencing these to biomes or ecoregions. Influenced by this pioneering work and following wide consultation, WWF-US led the preparation of a series of classifications and maps that serve as templates for studies at global, regional and national levels (Olson *et al.* 2001, Olson & Dinerstein 2002, Burgess *et al.* 2004). For the purposes of this outline, the global ecoregions map and its nomenclature (Dinerstein *et al.* 2017) is used and is applied here referencing the more recent syntheses of the Atlas of Namibia Team (2022) for Namibia, and Huntley (2023) for Angola.

While the highlands and escarpments include representatives of four African biomes and 12 ecoregions (*sensu* Dinerstein *et al.* 2017), biological and ecological conditions in the physiographically diverse highland system often differ from those in the broader, more generalised biomes and ecoregions of southern Africa of which they form part. Thus many endemics reported from within the HEAN occur in specialised habitats, such as rock outcrops, wetlands, the spray zone of waterfalls or isolated forest fragments. An endemic is defined here as a species that only occurs in the area of concern (e.g., HEAN, Angolan Planalto, Khomas Hochland). Near-endemics are species with a limited distribution outside the core area which defines the endemic. A centre of endemism is an area in which restricted-range species overlap, or a localised area which has a high occurrence of endemics. Within the HEAN, areas with appreciable levels of endemism are mostly subsets of wider centres of which they are relatively depauperate outliers, such as the isolated fragments of the Afromontane archipelago-like regional centre of endemism of White (1983) which occur in the Angolan highlands.

The biome concept has become widely applied in the ecological and biodiversity literature, and has been comprehensively reviewed by Mucina (2019). Although increasingly understood as the largest category of structurally and functionally similar habitats and their biota which share climate, soil and disturbance factors, the use of the term 'biome' varies widely between authors. In relation to the HEAN, three different applications are worth noting. The HEAN area includes four biomes and 12 ecoregions as defined by Dinerstein *et al.* (2017). However, the Atlas of Namibia Team (2022) includes four biomes (Tree-and-Shrub Savanna, Nama Karoo, Succulent Karoo and Namib Desert) within the single 'Deserts and Xeric Shrublands Biome' of Dinerstein *et al.* (2017). Huntley (2023) distinguishes between Arid and Mesic Savanna biomes, which fall within the Tropical and Subtropical Grasslands, Savannas and Shrublands Biome of Dinerstein *et al.* (2017) (Table 1).

Table 1: *Biomes, ecoregions and vegetation types represented in the highlands and escarpments of Angola and Namibia (HEAN). Classifications and terms follow Dinerstein* et al. *(2017), Huntley (2023) and Atlas of Namibia Team (2022). Ecoregion numbers in the first column refer to numbered ecoregions in Figure 3 and accompanying text.*

Global biome and ecoregion number and name (Dinerstein *et al.* 2017)	**Angolan biome** and ecoregion number and name (Huntley 2023)	**Namibian biome** and vegetation type number and name (Atlas of Namibia Team 2022)
Tropical and Subtropical Moist Broadleaf Forests/Tropical and Subtropical Grasslands, Savannas and Shrublands Biome	**Guineo-Congolian Rain Forest Biome and Forest/Savanna Mosaics**	**(Not represented)**
5. Congolian Coastal Forest	1. Congolian Rain Forest	
63. Western Congolian Forest–Savanna	2. Western Congolian Forest/Savanna Mosaic	
Montane Grasslands and Shrublands Biome	**Afromontane Forest and Grassland Biome**	**(Not represented)**
77. Angolan Montane Forest–Grasslands	4. Afromontane Forest 5. Montane Grassland	
Tropical and Subtropical Grasslands, Savannas and Shrublands Biome	**Mesic Savanna Biome**	**Tree-and-Shrub Savanna Biome**
35. Angolan Scarp Savanna and Woodlands	6. Angolan Escarpment Savannas	
36. Angolan Wet Miombo Woodlands	7. Angolan Wet Miombo Woodlands	
	Arid Savanna Biome	
34. Angolan Mopane Woodlands	12. Angolan Mopane Woodlands	20. Western Highlands 16. Karstveld
Deserts and Xeric Shrublands Biome		
104. Namibian Savanna Woodlands	13. Namib Savanna Woodlands	
		Nama Karoo Biome
		6. Central-Western Escarpment and Inselbergs 7. Desert – Dwarf Shrub Transition 12. Northwestern Escarpment and Inselbergs
97. Kalahari Xeric Savanna		19. Thornbush Shrubland 15. Highland Shrubland
94. Gariep Karoo		8. Dwarf Shrub Savanna 11. Karas Dwarf Shrubland
		Succulent Karoo Biome
102. Namaqualand–Richtersveld Steppe		4. Succulent Steppe
	Namib Desert Biome	**Namib Desert Biome**
98. Kaokoveld Desert	15. Angolan Namib Desert	1. Northern Desert
103. Namib Desert		2. Central Desert 3. Southern Desert

Greater consensus is found regarding the ecoregions of the HEAN. An ecoregion is defined by Dinerstein *et al.* (1995) as: "A large unit of land or water that contains a distinct assemblage of species, habitats and processes, and whose boundaries attempt to depict the original extent of natural communities before major land use change." The varied application of the biome concept and constituent ecoregions within the HEAN, and their nomenclature, is summarised in Table 1.

The vegetation types of Angola and Namibia were mapped and described respectively by Barbosa (1970) and Giess (1971) using their extended field experience and expert knowledge of the flora, in addition to drawing on earlier studies. These early studies are summarised by Revermann and Finckh (2019) for Angola and Westinga *et al.* (2020) for Namibia. Given the succession of maps, interpretation of patterns, and use of terms, their integration is not simple. Indeed, as the multiple maps of Namibia's vegetation presented by Westinga *et al.* (2020) demonstrate (Figure 1), the student might have difficulty in 'seeing the wood for the trees'. If one adds the phytochoria of White (1983) and natural floristic groups of Craven (2009) and Craven and Kolberg (2023) one can visualise a succession of the past (phytochoria, floristic groups) and present (vegetation types, green vegetation biomass); a palimpsest of changing concepts and patterns over time. Such inconsistencies reflect the rapidly evolving and expanding biodiversity studies in the region.

BIOMES AND ECOREGIONS REPRESENTED IN THE HEAN

Within the constraints of successive vegetation maps, ecoregion delineations and biome definitions, the following outlines of the biomes (Figure 2) and ecoregions (Figure 3) within the HEAN provide a general background to the taxon-focused chapters of this monograph. The ecoregion numbers and nomenclature follow Dinerstein *et al.* (2017), while the vegetation type numbers of Barbosa (1970), Giess (1971), Atlas of Namibia Team (2022) and Huntley (2023), and the landscape unit numbers used in Mendelsohn and Huntley (2023: Figure 5) are added for ease of cross-referencing. For each of the biomes represented within the HEAN, the ecoregions it encompasses are described and illustrated, and a selected listing of vertebrate species typical of the broader biome – within Angola, and over much of Namibia – is given to help characterise the biome.

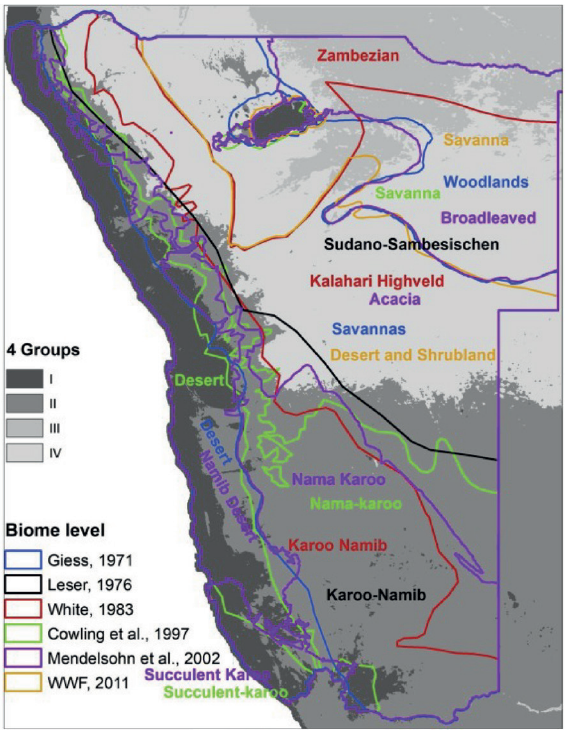

Figure 1: *A compilation of the six published biome level maps of Namibia and NDVI-profile cluster-groups (shades of grey) of Westinga* et al. *(2020). The names given to each unit are those of the authors of the maps. Reproduced from Westinga* et al. *(2020).*

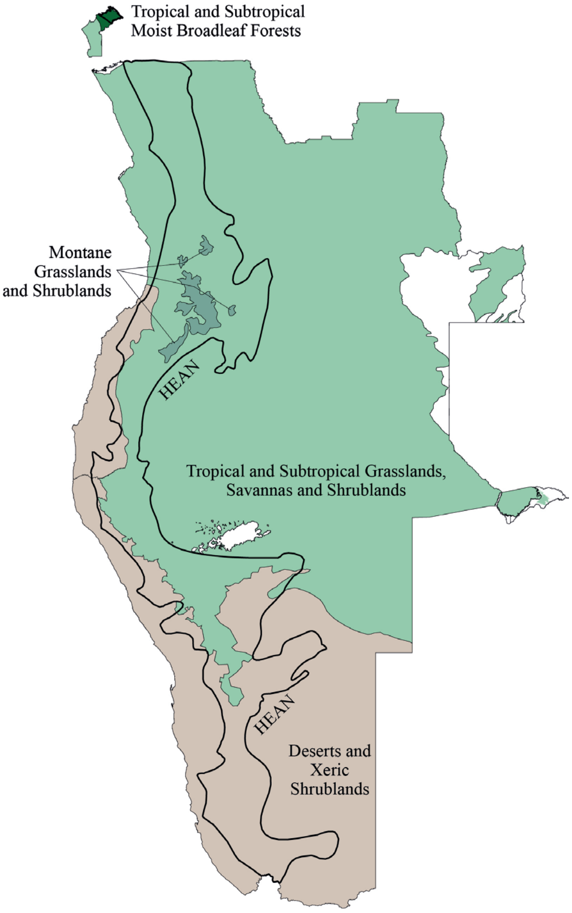

Figure 2: *Biomes (Dinerstein* et al. *2017) of the highlands and escarpments of Angola and Namibia (HEAN).*

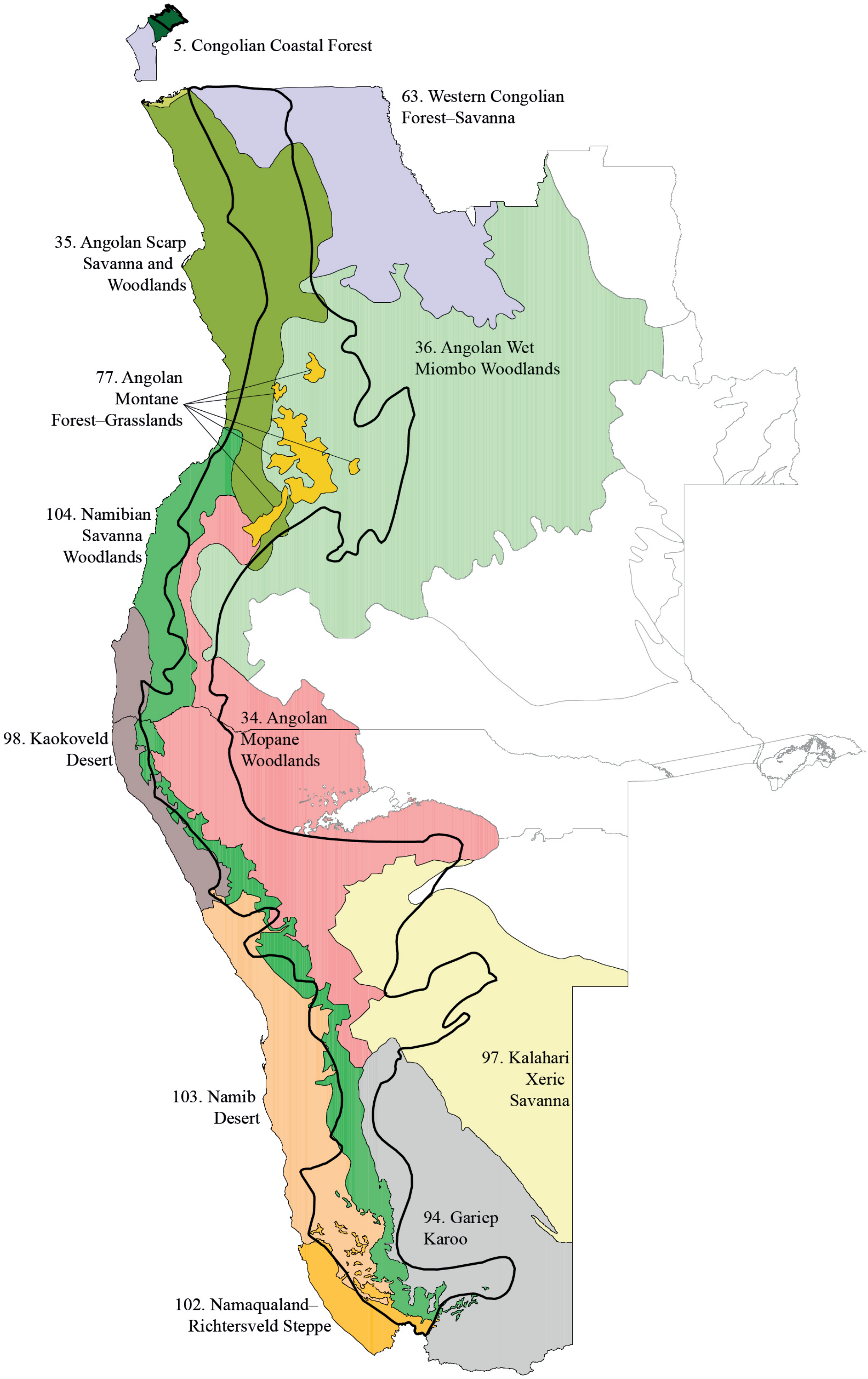

***Figure 3:** Ecoregions (Dinerstein* et al. *2017) of the highlands and escarpments of Angola and Namibia (HEAN).*

Tropical and Subtropical Moist Broadleaf Forests Biome

Across northern Angola, the rich Guineo-Congolian flora and fauna of African rainforests are represented in the moist forests found along the low mountains (400–1,200 masl) and escarpments of Cabinda, Zaire, Uíge, Cuanza-Norte, Cuanza-Sul and Malanje provinces. The biome comprises two ecoregions within the HEAN, Congolian Coastal Forest (5) and Western Congolian Forest–Savanna (63). Table 2 provides a synopsis of vertebrate species found within these forests, reflecting the species richness, in particular, of the remaining forests of Cabinda.

Ecoregion 5. Congolian Coastal Forest (Barbosa 1–3; Huntley 1; Landscape Unit 1).
These forests occur most extensively in Cabinda (Figures 4 and 5), where a continuation of the narrow belt of Lower Guinean evergreen to semi-evergreen broadleaf forest extends from central Cameroon to just north of the mouth of the Congo River. Outliers of Guineo-Congolian rainforest floristic and faunistic elements follow the Angolan escarpment in isolated blocks in Cuanza-Sul, and as tiny forest fragments in the seaward-facing ravines of the Chela Escarpment. The Alto Mayombe forests of Cabinda receive 1,200–1,400 mm of rain per annum, with fog a regular phenomenon. The canopy of mature forest in Mayombe may reach 50 m in height, but generally the canopy is 30–40 m in height. Important genera include *Gilbertiodendron*, *Julbernardia*, and *Tetraberlinia* in climax forest and *Milicia*, *Musanga*, *Piptadeniastrum*, *Ricinodendron* and *Terminalia* in disturbed, secondary forest. These forests are of great conservation importance (see Vaz Pinto *et al.* 2023).

Figure 4: *Ecoregion 5. Congolian Coastal Forest. A subsistence farm in Alto Mayombe Forest, Cabinda. Tall trees include forest margin pioneer* Terminalia superba *with erect white trunks, and the branched crowns of* Musanga cecropioides *at left and right of the scene. Photo: Brian Huntley.*

Figure 5: *Ecoregion 5. Congolian Coastal Forest. Forest canopy, Alto Mayombe, Cabinda. Photo: Brian Huntley.*

Table 2: *Vertebrate species typical of the Guineo-Congolian rainforests of Angola, including those areas of Ecoregions 5 and 63 falling within the highlands and escarpments of Angola.*

Amphibians	Congolese clawed frog, large-spotted reed frog, Benito river reed frog, Vilhena's reed frog, Carqueja's squeaker, Lameer's squeaker, Gabon forest tree frog
Reptiles	western forest feylinia, Owen's chameleon, variable bush viper, Gabon adder, forest night adder, Jameson's mamba, ringed water cobra, emerald snake, yellow-throated bold-eyed tree snake, forest twig snake
Birds	black guineafowl, afep pigeon, grey parrot, red-fronted parrot, great blue turaco, Guinea turaco, black bee-eater, African pied hornbill, black-and-white-casqued hornbill, piping hornbill, red-rumped tinkerbird, yellow-crested woodpecker, grey-green bushshrike, Angola white-throated greenbul, red-tailed loveleaf, banded prinia, forest chestnut-winged starling, dusky-blue flycatcher, Bannerman's sunbird
Mammals	African golden cat, Ansorge's cusimanse, African palm civet, bay duiker, white-bellied duiker, black-fronted duiker, blue duiker, sitatunga, red river hog, water chevrotain, white-belled (tree) pangolin, red-tailed monkey, moustached monkey, blue monkey, black-footed crowned monkey, De Brazza's monkey, putty-nosed monkey, Angola colobus, black-crested mangabey, northern talapoin, southern talapoin, Demidoff's dwarf galago, Thomas's dwarf galago, western lowland gorilla, central chimpanzee, golden potto, Milne-Edwards's potto, forest elephant, Beecroft's scaly-tailed squirrel

Ecoregion 63. Western Congolian Forest–Savanna (Barbosa 7–10; Huntley 2; Landscape Unit 2).
A large block of mixed forest and tallgrass savanna extends the reach of rainforests as gallery forests in valleys, and isolated forest fragments on hillsides and plateaus, southwards from the Congo Basin (Figure 6). The landscapes range 800–1,500 masl in the mountainous regions of Zaire and Uíge provinces (Lautenschläger *et al*. 2023). Precipitation of 1,000–1,400 mm falls per annum with fog being an important factor. Forest covers less than 5% of this mosaic, including species of *Entandrophragma*, *Milicia*, *Musanga*, *Piptadeniastrum*, *Raphia* and *Xylopia.* Trees of the fire-prone tallgrass savannas include genera such as *Annona*, *Erythrophleum*, *Hymenocardia*, *Piliostigma* and *Strychnos*, mesic woodlands include *Brachystegia*, *Julbernardia*, *Burkea* and *Isoberlinia* and drier woodlands include *Dialium*, *Daniellia*, *Cryptosepalum* and *Marquesia.*

Figure 6: *Ecoregion 63. Western Congolian Forest–Savanna. This forest and savanna mosaic is near Camabatela, Cuanza-Norte. Tall grasses of* Hyparrhenia *and* Trachypogon *species, with a fire-tolerant* Hymenocardia acida *in left foreground. Photo: Brian Huntley.*

Montane Grasslands and Shrublands Biome

Angola’s most isolated and vulnerable biome comprises forests and grasslands of White’s (1983) archipelago-like regional centre of endemism. The highest areas of the Angolan plateau and mountains have small areas of montane grassland on the Cuanza-Sul, Huambo, Huíla, Benguela and Bié highlands, much of it forming the Angolan Planalto. Very small remnants of Afromontane flora survive in the forests and shrublands along the Marginal Mountain Chain – specifically on Serra do Môco, Mount Namba and in ravines of the Chela Escarpment and the Humpata Plateau. They are important areas of biotic richness and endemism, although they occupy only 1.1% of Angola. Afromontane forests and grasslands are absent from Namibia. Vertebrate species typical of the Afromontane forests and grasslands of Angola are listed in Table 3.

Ecoregion 77. Angolan Montane Forest–Grasslands (Barbosa 6, 32; Huntley 4, 5; Landscape Units 3, 5).
The Afromontane forests of Angola are the most fragmented and isolated of all representatives of the Afromontane centre of floristic endemism in Africa, being over 2,000 km from related forests in Cameroon, South Africa and East Africa. With a total area of less than 1,000 ha across their entire range in Angola, they occur as small forest patches that are provided some shelter from fire in deep valleys and by rock outcrops (Powell *et al*. 2023). These highland sites receive between 800 and 1,600 mm of rainfall per annum, lying at 1,800–2,400 m elevation. The weakly stratified forests have a broken canopy of up to 20 m in height. Trees include Afromontane genera such as *Apodytes*, *Cassipourea*, *Erythroxylum*, *Halleria*, *Ilex*, *Maesa*, *Myrica*, *Nuxia*, *Pittosporum* and *Podocarpus* (Figures 7 and 8). The montane grasslands of the Angolan Marginal Mountain Chain and Angolan Planalto extend across the highlands of Cuanza-Sul, Benguela, Huambo, Bié and Huíla (Figures 9–11). Lying mostly between 1,500 and 1,800 masl, the rolling hills rise to 2,620 masl on

Table 3: *Vertebrate species typical of the Afromontane forests and grasslands of Angola, including those areas of Ecoregion 77 falling within the highlands and escarpments of Angola.*

Amphibians	Chela mountain reed frog, Anchieta’s tree frog, Udzungwa ridged frog
Reptiles	Benguela gecko, mountain day gecko, Angolan rough-scaled lizard, Marx’s rough-scaled lizard, Angolan girdled lizard, Anchieta’s chameleon, Angolan adder, link-marked sand racer
Birds	Finsch’s francolin, Swierstra’s francolin, Ruwenzori nightjar, Fernando Po swift, naked-faced barbet, Margaret’s batis, Perrin’s bushshrike, Angola lark, black-collared bulbul, Brazza’s martin, black-and-rufous swallow, Laura’s woodland warbler, Huambo cisticola, Salvadori’s eremomela, orange ground thrush, Angola slaty flycatcher, Bocage’s sunbird, Ludwig’s double-collared sunbird, Oustalet’s sunbird, bronzy sunbird, black-chinned weaver, dusky twinspot, Angola swee waxbill, Fulleborn’s longclaw, black-faced canary, thick-billed seedeater
Mammals	common duiker

Serra do Môco, the highest point in Angola. In many areas, seasonally waterlogged soils result in the near absence of trees but an abundance of grass, forb, geophyte and geoxyle species, including many orchids. (See Goyder *et al.* 2023 and Meller *et al.* 2023).

Figure 7: *Ecoregion 77. Angolan Montane Forest–Grasslands. Fire-cut margin of Afromontane Forest on Serra do Môco, with* Podocarpus milanjianus *of 25 m height. Note the person standing at the base of the* Podocarpus, *for scale. Photo taken in 1972. Photo: Brian Huntley.*

Figure 8: *Ecoregion 77. Angolan Montane Forest–Grasslands. Isolated patch of Afromontane forest near Caluquembe, Huíla Province. Photo: Pedro Vaz Pinto.*

Figure 9: *Ecoregion 77. Angolan Montane Forest–Grasslands.* Aloe grata *on the slopes of Serra do Môco, overlooking montane grasslands of the Huambo highlands. Photo: Brian Huntley.*

Figure 10: *Ecoregion 77. Angolan Montane Forest–Grasslands. Fire-resilient* Protea *and* Philippia *shrubs scattered through short grassland on the summit of Serra do Môco, Huambo Province. Photo: Brian Huntley.*

Figure 11: *Ecoregion 77. Angolan Montane Forest–Grasslands. Moist montane short grassland at 2,000 masl, Humpata, Huíla Province. Photo: Brian Huntley.*

Tropical and Subtropical Grasslands, Savannas and Shrublands Biome

The Zambezian flora of this biome dominates the highlands of Angola and Namibia, occupying over 90% of the HEAN in Angola and 37% in Namibia. Huntley (1982, 2023) and Owen-Smith (2021) have emphasised the distinction between the mesic-dystrophic and arid-eutrophic savannas of Africa, the structural and functional distinctions of which are highly relevant to the savanna ecoregions of the HEAN that extend from the moist equatorial forests of Cabinda to the hyperarid Namib Desert.

The mesic-dystrophic savannas, typical of the Zambezian centre of endemism, occupy over 80% of Angola, predominantly on the interior plateau, above 1,000 masl, and on freely draining nutrient-poor and acidic (dystrophic) soils. Fire is the key driving force that maintains the mix of grasses and trees that constitute the woodlands, savannas, shrublands and grasslands of mesic savannas. Although mesic savannas – including the Broadleaved Tree-and-Shrub Savannas of the Atlas of Namibia Team (2022) – occupy much of northwest Namibia, they do not extend into the HEAN other than on the Waterberg Plateau, a sandstone inselberg that rises above the surrounding arid acacia savannas. Vertebrates typical of the miombo woodlands of Angola, and mesic-dystrophic savannas of central Africa, are listed in Table 4.

Arid-eutropic savannas cover 13% of Angola and 61% of Namibia where they are termed Acacia Tree-and-Shrub Savanna (Atlas of Namibia Team 2022). These savannas and shrublands are characterised by low rainfall (less than 650 mm per annum) and generally occur on richer (eutrophic) soils than the leached, nutrient-poor (dystrophic) Ferralsols and Arenosols of the mesic savannas of central Africa. Arid savannas skirt the HEAN, typically along the base of escarpments and inselbergs and river valleys, but reaching 2,000 masl on the summits of the arid mountains of Iona National Park in southwest Angola and the mountains of Namibia. Vertebrates typical of the arid-eutrophic savannas of Angola (and parts of Namibia) are listed in Table 5.

Ecoregion 35. Angolan Scarp Savanna and Woodlands (Barbosa 15, 18a, 22; Huntley 6; Landscape Units 2, 3).
South of the Congo River and along Angola’s Central Escarpment, this narrow band of mixed savannas lies between the arid savannas of the coastal lowlands and miombo savannas of the high plateaus. A mosaic of tall grasslands and woodlands constitutes the Angolan Scarp Savanna and Woodlands. Trees include species of *Brachystegia*, *Burkea*, *Cochlospermum*, *Combretum*, *Cussonia*, *Pterocarpus*, *Terminalia* and *Uapaca.* Grasses are mostly species of the Andropogoneae (Figure 12).

Table 4: *Vertebrate species typical of Angolan miombo woodlands, savannas and grasslands, including those areas of Ecoregions 35 and 36 falling within the highlands and escarpments of Angola.*

Amphibians	Peter’s clawed frog, Merten’s striped toad, banded rubber frog, Guinea snout-burrower, Angolan reed frog, Benguela long reed frog, Senegal kassina, Bocage’s burrowing tree frog, Angola ornate frog, sharp-nosed grass frog
Reptiles	African dwarf mud turtle, Queen Nzinga’s gecko, Iven’s skink, Bayão’s skink, Angola tree agama, Anchieta’s cobra, spotted boomslang
Birds	pale-billed hornbill, miombo barbet, western black-headed batis, Souza's shrike, miombo tit, red-capped crombec, short-winged cisticola, miombo wren warbler, black-necked eremomela, yellow-bellied hyliota, sharp-tailed starling, white-winged babbling starling, miombo scrub robin, Congo moor chat, Anchieta’s sunbird, chestnut-backed sparrow-weaver, Bocage’s weaver, bar-winged weaver
Mammals	side-striped jackal, spotted hyaena, miombo genet, common duiker, greater galago

Table 5: *Vertebrate species typical of the arid savannas of Angola and Namibia, including those areas of Ecoregions 34, 97 and 104 (of the Deserts and Xeric Shrublands Biome), within the highlands and escarpments of the two countries.*

Amphibians	Dombe toad, Grandison’s pygmy toad, marbled rubber frog, African bullfrog
Reptiles	leopard tortoise, Ansorge’s leaf-toed gecko, Angola banded thick-toed gecko, Huntley’s sand lizard, Sundevall’s writhing skink, horned adder, western banded spitting-cobra
Birds	ostrich, secretary bird, Monteiro’s hornbill, white-tailed shrike, Benguela long-billed lark, rockrunner, Benguela long-tailed starling, rufous-tailed palm thrush, Cinderella waxbill
Mammals	black-backed jackal, bat-eared fox, Cape fox, cheetah, caracal, lion, leopard, spotted hyaena, brown hyaena, aardwolf, black-faced impala, springbok, Kirk’s dik-dik, klipspringer, gemsbok, steenbok, greater kudu, plains zebra, Hartmann’s mountain zebra

Ecoregion 36. Angolan Wet Miombo Woodlands (Barbosa 16–19; Huntley 7; Landscape Unit 4).

These woodlands, savannas and grasslands typically receive more than 1,000 mm of rainfall per year and lie at elevations of 900–1,500 masl. The deep, moist, dystrophic soils support a woodland canopy height of 15–25 m. *Brachystegia spiciformis* occurs in varying densities and robustness throughout the Angolan miombo, with other *Brachystegia* species. *Julbernardia paniculata* is also widespread across the miombo, together with *Burkea*, *Cryptosepalum*, *Guibourtia* and *Pterocarpus* species (Figures 13 and 14). On the edges of drainage-line grasslands (*mulolas*, *dambos*) species of *Monotes*, *Protea* and *Uapaca* occur as short trees. Grasses include species of *Andropogon*, *Digitaria*, *Elionurus*, *Eragrostis*, *Hyparrhenia*, *Loudetia*, *Monocymbium* and *Setaria*, with *Panicum* becoming prominent under woodland.

Ecoregion 34. Angolan Mopane Woodlands (Barbosa 20, 21, 27; Huntley 12; Giess 5; Atlas of Namibia Team 20, 21; Landscape Units 6– 8).

The leguminous tree *Colophospermum mopane* occurs across the interior of the southern coastal lowlands and lower Cunene valley in Angola and extends southwards across the Western Highlands and Karstveld of Namibia, as the dominant species of woodlands, savannas and shrublands (Figures 15 and 16). *Colophospermum mopane* is typically found on heavy soils and stony hills receiving less than 650 mm rainfall per annum and mostly below 1,000 masl in Angola and 1,200 masl in Namibia, but occurs at higher elevations on inselbergs and escarpment mountains. Although often found as a single dominant species in woodlands, *C. mopane* also forms mixed communities with species of *Adansonia*, *Albizia*, *Boscia*, *Combretum*, *Commiphora*, *Sclerocarya*, *Senegalia*, *Terminalia* and *Vachellia*.

***Figure 12:** Ecoregion 35. Angolan Scarp Savanna and Woodlands. Fire-tolerant* Cochlospermum angolense *trees are typical of the tall grasslands covering the rolling hills of this ecoregion. Photo: Brian Huntley.*

***Figure 13:** Ecoregion 36. Angolan Wet Miombo Woodlands. Typical wet miombo in the Quibala hills, Cuanza-Sul Province. Photo: António Martins.*

***Figure 14:** Ecoregion 36. Angolan Wet Miombo Woodlands. Typical mature open miombo woodland of* Brachystegia *and* Julbernardia*, near Serra Mocoti. Note the continuous cover below the woodland canopy. Photo: John Mendelsohn.*

***Figure 15:** Ecoregion 34. Angolan Mopane Woodlands. Mixed mopane woodlands and thicket below granite domes and inselbergs of the Angolan escarpment, between Lubango and Caraculo. Photo: Brian Huntley.*

***Figure 16:** Ecoregion 34. Angolan Mopane Woodlands. Open mopane woodland in the foreground with karstveld hills in the background, all flushed green after recent rain.* Commiphora, Combretum, Kirkia *and* Steganotaenia *species dominate the karstveld woodland. Photo: John Mendelsohn.*

Deserts and Xeric Shrublands Biome

Six of the ecoregions of the Deserts and Xeric Shrublands Biome as defined by Dinerstein *et al.* (2017) are represented in the HEAN (Table 1). These are Namibian Savanna Woodlands, Kalahari Xeric Savanna, Kaokoveld Desert, Namib Desert, Gariep Karoo and Namaqualand–Richtersveld Steppe. As noted above, this mix of arid ecoregions has been classified variously and differently by African biologists, especially those working in Angola, Namibia and South Africa. Mucina and Rutherford (2006) recognise, *inter alia*, Savanna, Nama Karoo, Succulent Karoo, and Desert biomes, each of which is represented in the single Deserts and Xeric Shrubland Biome of Dinerstein *et al.* (2017). Huntley (2023) places the Namibian Savanna Woodlands in his Arid Savanna Biome, while the Atlas of Namibia Team (2022) recognise a Nama Karoo Biome and a Succulent Karoo Biome, which are both represented within the Deserts and Xeric Shrublands Biome of Dinerstein *et al.* (2017) and which partially fall within the HEAN. The diversity of interpretations of the biome concept can hardly be more explicitly demonstrated. At a lower hierarchical level, the ecoregion concept is nevertheless useful. Vertebrate species typical of the Namibian Savanna Woodlands are listed in Table 5, and those of the Namib Desert are listed in Table 6.

Figure 17: *Ecoregion 104. Namibian Savanna Woodlands. Namibian Savanna Woodlands dominated by* Acacia *species on the Talamajamba plateau, 40 km inland of Benguela. Rich grasslands are present following summer rain. Photo: António Martins.*

Figure 18: *Ecoregion 104. Namibian Savanna Woodlands. Mixed woodlands south of Serra da Neve, which rises to 2,489 masl. The dark green line of tall trees in the middle distance marks the Bentiaba River. Photo: Brian Huntley.*

Table 6: *Vertebrate species typical of the Namib Desert, including those areas of Ecoregions 98 and 103 falling within the highlands and escarpments of Angola and Namibia.*

Reptiles	feathered-tailed gecko, Namib web-footed gecko, common Namib day gecko, Anchieta's dune lizard, Kaokoveld girdled lizard, desert plated lizard, speckled sand skink, dotted blind dart skink, Namaqua chameleon, Namib rock agama, Anchieta's dwarf python, Peringuey's adder, western sand snake
Birds	lappet-faced vulture, Ludwig's bustard, Rüppell's korhaan, Burchell's courser, Gray's lark, tractrac chat
Mammals	bat-eared fox, meerkat, brown hyaena, aardwolf, springbok, Kirk's dik-dik, gemsbok, Hartmann's mountain zebra

Ecoregion 104. Namibian Savanna Woodlands

(Barbosa 27; Huntley 13; Giess 5; Atlas of Namibia Team 6, 7, 12; Landscape Units 3, 6, 8– 10).

This ecoregion occupies a narrow belt of coastal lowlands and escarpment foothills and inselbergs which extend across 2,000 km from Sumbe in the north to the proximity of the Orange River in the south, as woodlands, scrubland and thickets wedged between the Namib Desert to the west and the Angolan Mopane Woodlands and Gariep Karoo ecoregions to the east. The landscapes include a mix of gravel and sandy plains, rolling stony hills and arid escarpments, mostly between sea level and 1,000 masl, but rising to 2,000 masl on Serra Cafema in Iona National Park, Angola, and in the Baynes and Gamsberg Mountains of Namibia. Rainfall decreases from north to south, from an annual average of 400 mm to 100 mm. Low trees and shrubs of the genera *Acacia*, *Balanites*, *Boscia*, *Catophractes*, *Combretum*, *Commiphora*, *Euphorbia*, *Maerua*, *Rhigozum*, *Sesamothamnus*, *Sterculia* and *Terminalia* form open savannas and shrublands (Figures 17–19).

Figure 19: *Ecoregion 104. Namibian Savanna Woodlands. Open savanna and shrublands in the Hakos Mountains north of the Gamsberg with their sparse cover of* Acacia, Boscia, Catophractes, Commiphora *and other small trees and shrubs.* Tribulus *flowers adorn the foreground. Photo: John Mendelsohn.*

Figure 20: *Ecoregion 97. Kalahari Xeric Savanna. The Auas Mountains just south of Windhoek are dominated by grass cover in between scattered shrubs and small trees. Moltkeblick is the highest peak in the area and the second highest point in Namibia, rising to 2,479 masl. Photo: John Mendelsohn.*

Figure 21: *Ecoregion 97. Kalahari Xeric Savanna. Dense* Acacia *and* Dichrostachys *bush cover much of the Central-Western Plains landscape. Photo: John Mendelsohn.*

Figure 22: *Ecoregion 94. Gariep Karoo. Open grassland and scattered small shrubs characterise much of the Gariep Karoo in Namibia. Photo: Peter Cunningham.*

Figure 23: *Ecoregion 102. Namaqualand–Richtersveld Steppe. There is a great variety of succulents in the hills of the Aurusberge. Photo: John Pallett.*

Ecoregion 97. Kalahari Xeric Savanna (Giess 7, 8; Atlas of Namibia Team 15, 19; Landscape Units 8, 9). The deciduous woodlands and shrublands of the Kalahari extend westwards to the central highlands of Namibia, including the Khomas Hochland, which lies at 1,700–2,000 masl. The highlands comprise rolling hills covered by shrubs and low trees (Figure 20), with species of *Acacia*, *Boscia*, *Combretum*, *Euclea*, *Searsia*, *Tarchonanthus* and *Ziziphus* being prominent. To the east, the elevation drops and the plateau is covered by deep Kalahari sands and open tree savannas and grasslands (Figure 21).

Ecoregion 94. Gariep Karoo (Giess 9; Atlas of Namibia Team 8, 11; Landscape Unit 10).

The Gariep Karoo is a northwestern extension of the vast Nama Karoo Biome of low shrublands that covers more than a third of South Africa's arid interior plateau. The Nama Karoo Basin of southeast Namibia is a large, flat plateau at 900–1,400 masl, underlain by sedimentary rocks and covered by dwarf shrubs, sparse grasses and scattered short trees (Figure 22). Shrubs include species of *Aizoon*, *Eriocephalus*, *Pentzia*, *Pteronia* and *Salsola*. Low trees and shrubs include species of *Acacia*, *Boscia*, *Catophractes*, *Euclea*, *Rhigozum*, *Searsia* and *Tamarix*.

Ecoregion 102. Namaqualand–Richtersveld Steppe (Giess 4, Atlas of Namibia Team 4; Landscape Unit 11).

This ecoregion represents a northern outlier of the Succulent Karoo Biome of South Africa. The primary ecological feature of this ecoregion, distinct from all others in the HEAN, is the weakly seasonal winter rainfall regime, with less than 150 mm per annum, supplemented by fog and dew. Strong, cool southwesterly winds alternating with hot, dry northeasterly winds also influence life in this desert. Lying mostly below 500 masl, isolated inselbergs and mountains rise to 2,000 masl. The characteristic plant growth forms of this ecoregion include stem-, leaf- and root-succulents belonging to the families Apocynaceae, Crassulaceae, Geraniaceae, Portulacaceae and Zygophyllaceae (Figure 23). Grasslands cover extensive plains and intermontane basins towards the interior, with species of *Stipagrostis* dominating.

Ecoregion 98. Kaokoveld Desert (Barbosa 28, 29; Giess 1; Huntley 15; Atlas of Namibia Team 1–3*;* Landscape Units 6, 11).

The Namib Desert extends from the Carunjamba River in Angola to the Orange River. On the basis of its rich floral endemism, a northern (Kaokoveld Desert) ecoregion has been distinguished from the species-poor southern (Namib Desert) ecoregion. These ecoregions form a narrow (20–100 km) wedge between the Atlantic Ocean and the coastal plains, hills and inselbergs that skirt the escarpment

(Figures 24–26). They fall peripherally within the HEAN area, as minor outliers on inselbergs and the slopes of escarpments. Characterised as a hyperarid desert, these two ecoregions receive less than 150 mm rainfall per annum, with much of the area receiving half of this amount. Mobile dunes and hard calcrete, gypsum and gravel plains lie between the sea and intermittent sandy plains and rocky hills of the interior. The dunes have little if any vegetation. Inland, succulent shrubs, thorny bushes and low trees of *Acacia*, *Commiphora*, *Euphorbia*, *Rhigozum*, *Sesamothamnus* and *Sterculia* are scattered across a matrix of sparse, short grasses of *Stipagrostis* species. The iconic gymnosperm *Welwitschia mirabilis* is locally common in the Kaokoveld Desert. Despite its aridity, the desert is home to a rich diversity of vertebrate and invertebrate species, many of these demonstrating complex adaptations to life in an almost waterless environment.

Figure 24: *Ecoregion 98. Kaokoveld Desert. Large-leaved deciduous trees such as* Cyphostemma currorii *succeed in the most arid parts of the Namib by exploiting infrequent rain through rapid photosynthesis via their large leaves and water storage in their fleshy trunks. Photo: Ernst van Jaarsveld.*

Figure 25: *Ecoregion 98. Kaokoveld Desert. Intermontane plains on the margins of the Serra Tchamalindi, Iona National Park. Photo: Merle Huntley.*

Figure 26: *Ecoregion 98. Kaokoveld Desert. Mixed* Commiphora *and* Acacia *savanna at the interface between the Namibian Savanna Woodlands and Namib Desert ecoregions, Iona National Park, Namibe. Photo: Ernst van Jaarsveld.*

Ecoregion 103. Namib Desert (Giess 2, 3; Atlas of Namibia Team 3; Landscape Unit 11).

The vegetation includes a mix of Karoo-Namib and Zambezian floristic elements. Vegetation-less dunes occur along the coast, with gravel plains occupied by dwarf shrublands to the interior, succeeded by ephemeral grasslands on the sandy plains of intermontane basins. The rocky hills to the east have mixed open woodlands and a light cover of grasslands (Figure 27). Following rare rainfall events, annual forbs proliferate, including species of *Aizoanthemum*, *Helichrysum*, *Mesembryanthemum*, *Senecio* and *Zygophyllum* and species of both annual and perennial grasses. The plains of the southern Namib have a thin mantle of sands, gravel and calcrete, interrupted occasionally by rocky outcrops and hills, with inselbergs rising to over 1,000 masl.

Figure 27: *Ecoregion 103. Namib Desert.* Stipagrostis *grasses dominate the plains of the Pro-Namib as they meet the western scarp of the Naukluft Mountains.* Acacia *riverine woodland demarcates a linear oasis through the desert. Photo: John Mendelsohn.*

ACKNOWLEDGEMENTS

My thanks to John Mendelsohn for his valuable contributions to this chapter and to leading the conceptualisation and production of the monograph, and to him and to Peter Cunningham, Merle Huntley, António Martins, John Pallett, Pedro Vaz Pinto and Ernst van Jaarsveld for the use of photographs.

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The human environment in the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-mendelsohn2

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ABSTRACT

The distribution and density of people in the highlands and escarpments of Angola and Namibia (HEAN) is largely a product of proximity to urban areas, climate and soil fertility. The highest rural densities in HEAN are in central Angola, and the lowest in southern Namibia. In northern and central Angola most rural households grow crops for domestic consumption and sale, whereas pastoralism prevails in the HEAN areas of southern Angola and northern Namibia. Remittances, social grants and revenues from tourism provide most household income in northern Namibia. Angola is divided and administered via provinces, *munícipios* and *comunas*, whereas Namibia is administered through regions and local authorities for urban areas. Shifting cultivation has led to the clearing of large areas of forest, woodland and grassland. Other major human impacts are the harvesting of trees for charcoal and timber, the hunting of wildlife for the sale of bushmeat, soil erosion, and the loss of forests and woodlands and soil nutrients as a result of frequent fires.

Keywords: Angola, cultivation, deforestation, escarpments, fire, highlands, land uses, livelihoods, Namibia, people

INTRODUCTION

The distribution of people, land uses and sources of income in the highlands and escarpments of Angola and Namibia (HEAN) vary considerably, in particular from north to south. In the northern areas, rainfall is highest, evaporation is lowest, soils are more fertile and access to urban markets is relatively easy. This is where most people live and grow crops, and where the loss of natural resources is greatest. Many people there also live in large towns such as Uíge, Gabela, Cuito, Huambo and Lubango. By contrast, few crops are grown in the southern arid areas where soil nutrients are scarce. With the exception of Otjiwarongo and Windhoek, towns and settlements are small, and the majority of rural people make a living from livestock, labour on farms and mines, and tourism.

DISTRIBUTION OF PEOPLE

The major differences in climate and soil types between Angola and Namibia have significant effects on their populations: Angola's population census in 2014 counted 25,789,024 people (Instituto Nacional de Estatística 2016), about 12 times more than the 2,113,007 people counted in Namibia's 2011 census (Namibia Statistics Agency 2011), yet Angola's land mass of 1,246,700 km² is only 1.5 times larger than Namibia's 824,300 km². Population densities are therefore much greater in Angola than in Namibia, but both countries have enormous variation in population density, ranging between the massive city of Luanda with close to 10 million people to the vast expanses of desert and mostly inert Kalahari sands which are virtually devoid of humans (Figure 1).

Urban populations in Angola and Namibia have grown rapidly, with the majority of growth being in unserviced informal settlements. The rates of annual urban population growth in Angola over the past 60 years is estimated to be 4.8% (Instituto Nacional de Estatística 2016), and about 4% over the same period in Namibia (Atlas of Namibia Team 2022). Angola's urban residents accounted for 73% of the national population in 2014, while the corresponding proportion in Namibia was 52% in 2020. A range of conditions prompt people in both countries to leave rural areas, especially the lack of incomes, services and basic goods, while other conditions attract them to urban areas, in particular jobs and other potential sources of incomes, services and the allure of modern 'civilisation' (Jenkins *et al.* 2002, Gomes 2012, Calunga *et al.* 2015).

ADMINISTRATIVE AREAS

Angola is divided into three administrative levels, from biggest to smallest: *província* (Figure 2), *município* and *comuna*. Namibia is split into regions for purposes of local administration, which are further divided into constituencies; these are political rather than administrative units. Urban areas are administered by local authorities in both countries. Namibian rural areas are divided into surveyed freehold land and communal land. Rights to land and its natural resources in both Angola and Namibia are theoretically controlled by traditional authorities.

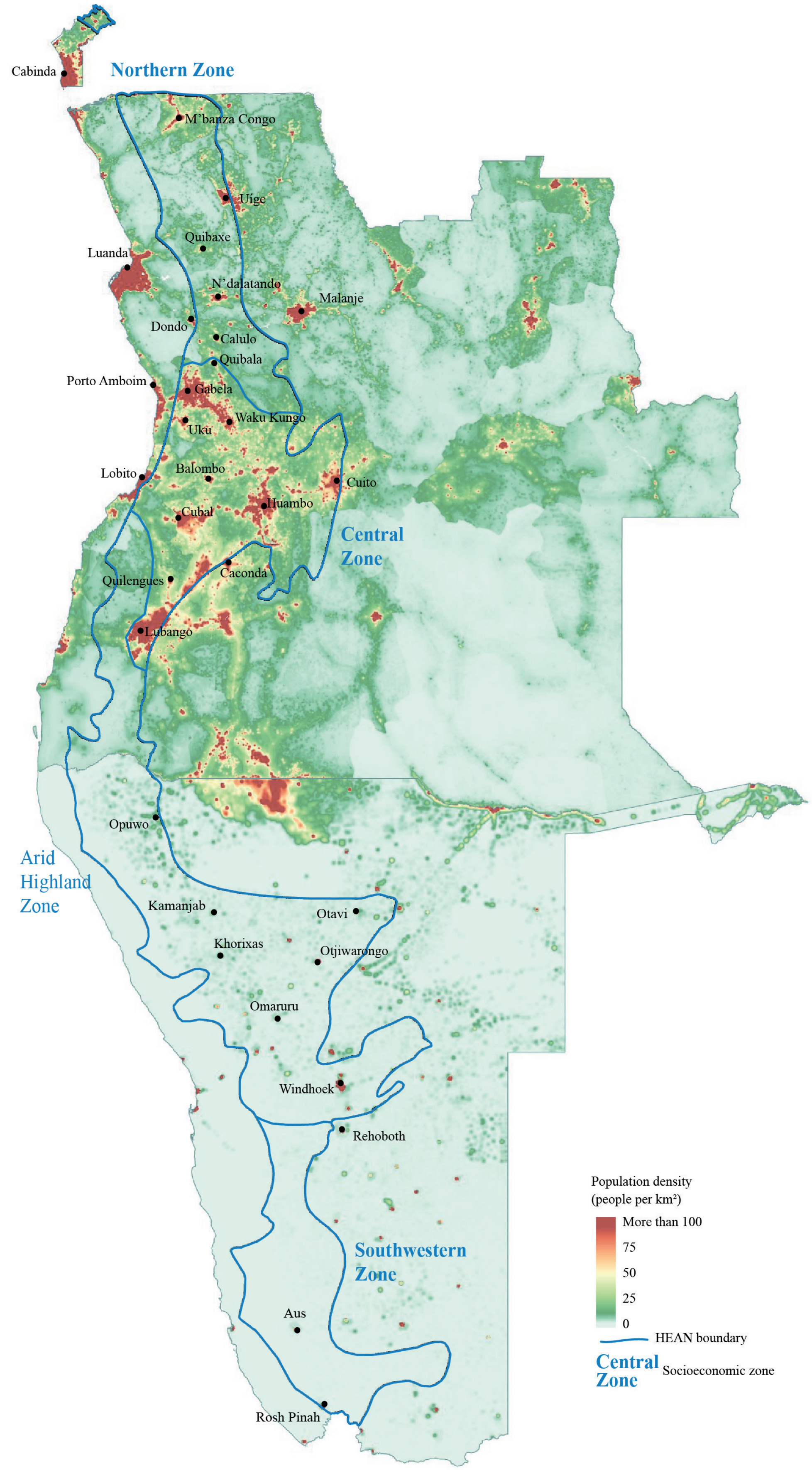

Figure 1: *Human population density and four socioeconomic zones in Angola and Namibia. The highlands and escarpments of Angola and Namibia (HEAN) and socioeconomic zones are in blue. Sources: Angola population density for 2020 from WorldPop (2023), and for Namibia from Atlas of Namibia Team (2022).*

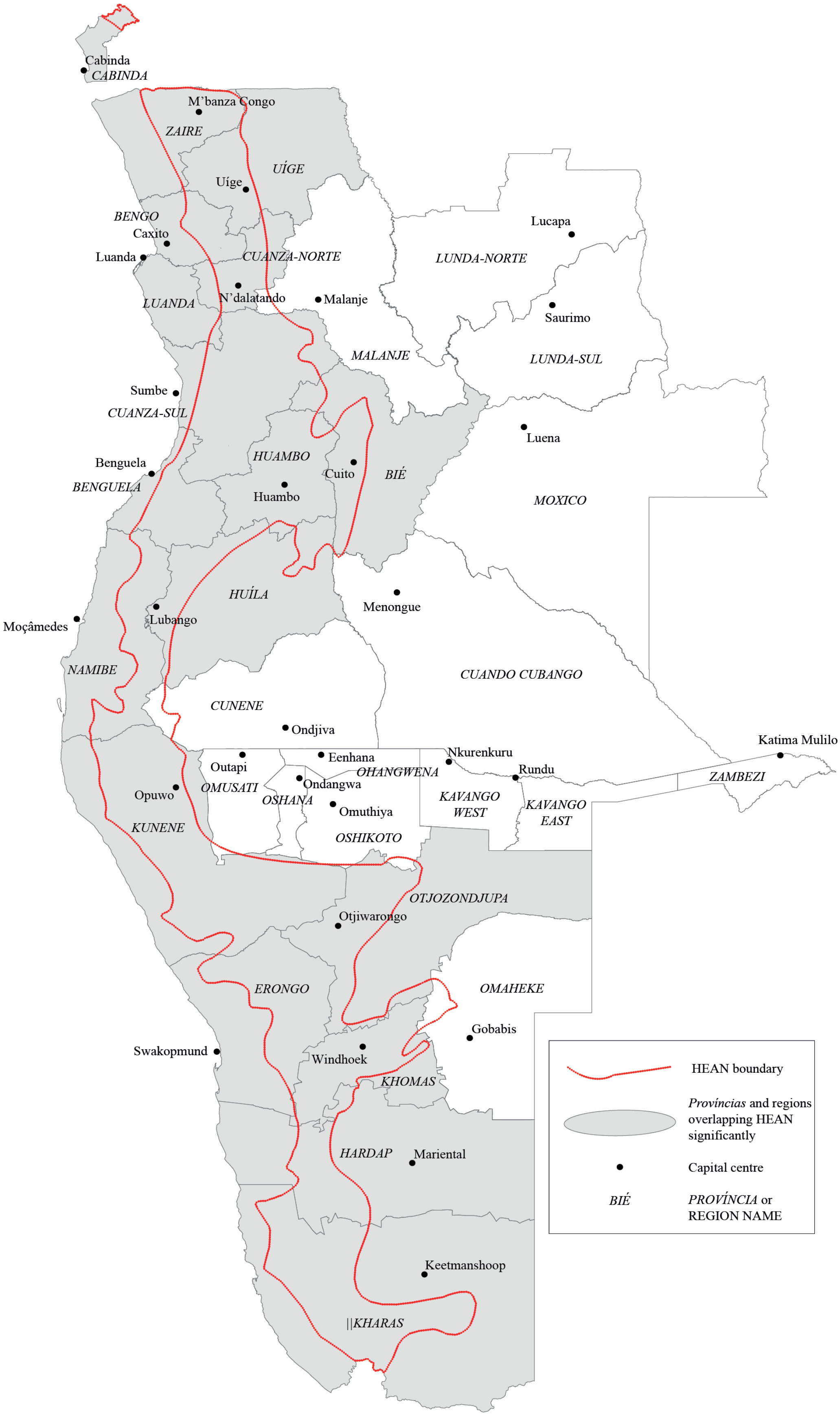

Figure 2: *The highlands and escarpments of Angola and Namibia (HEAN) in relation to Angola's* províncias *and their capitals, and Namibia's regions and their capitals. Administrative areas that overlap significantly with HEAN are shaded grey.*

However, the extent and nature of control is often weak with the result that large areas of land have been appropriated for grazing or expropriated for exclusive use by people who live in urban areas (Cain 2019, Atlas of Namibia Team 2022).

RURAL ECONOMIES, LAND USES AND SOCIOECONOMIC ZONES

Types of livelihoods across the highlands and escarpments can be grouped into four rather distinct socioeconomic zones which are described below: Northern Zone; Central Zone; Arid Highland Zone; Southwestern Zone (Figure 1). The four socioeconomic zones described here correspond largely to the physical landscapes described by Mendelsohn & Huntley (2023). Thus:

- *Northern Zone* ≡ Northern Escarpment
- *Central Zone* ≡ Marginal Mountain Chain, Central Escarpment and Angolan Planalto
- *Arid Highland Zone* ≡ Southern Escarpment, Karstveld, Central-Western Plains and Khomas Hochland
- *Southwestern Zone* ≡ Pro-Namib and Nama Karoo Basin.

Throughout the HEAN on average, rural households are larger and poorer than their urban counterparts, and adults in rural areas have had fewer years of formal education than adults in urban areas. In Angola, most household income in rural areas comes from the sale of charcoal, bushmeat, fish, crops (especially vegetables) and poultry. By contrast, most rural households in Namibia derive their incomes from social grants, remittances, local retail trade and wildlife and livestock products. Smallholder crop farmers usually retain staple foods that can be stored for long periods for domestic consumption, whereas soft vegetables and other products that decay quickly are normally sold to generate income.

Several major changes in rural economies – and therefore land uses – have occurred during the past 60 years. These include the introduction of incomes from wildlife and tourism and the concurrent reduction in livestock production in many parts of Namibia. In Angola exports of coffee and maize have declined, but local trade and sales of charcoal, vegetables and bushmeat have increased. Extraction of timber by commercial companies has contributed to the rapid deforestation of mature tropical rainforest and biodiversity loss in Bengo, Uíge and Cuanza-Norte provinces (see below, and Lautenschläger *et al.* 2023).

With increasing demands for income security – rather than just food security – rapid and efficient transport connections between rural homes and urban areas are increasingly important, giving rural producers access to markets for their crops and natural commodities, such as charcoal and bushmeat (Figure 3), as well as providing rural residents the added ease of purchasing necessities in towns.

Prior to the introduction of cash economies and trade in urban areas, rural populations were largely concentrated along rivers where they had access to water, fish and comparatively fertile alluvial soils. Nowadays, many people continue living near rivers in remote areas of the HEAN, especially in the Arid Highland Zone (Figure 1) where they grow crops in these ephemeral rivers' fertile silt.

Land uses and the distribution and densities of people are strongly related to soil fertility and aridity (Mendelsohn & Huntley 2023), and proximity to roads and urban areas (Figure 1). Thus, densities of

Figure 3: *Informal trade in Angola. Left: The roadside market at Mangueiras below the escarpment of Serra da Chela on the main road between Moçâmedes and Lubango. Right: A leopard skin for sale along the same road just west of Humpata. Photos: J Mendelsohn.*

people in the central areas of Angola's HEAN are highest because of the wetter and cooler climate, presence of relatively fertile soils and reasonable access to roads and urban markets. Lubango and Huambo, both in this Central Zone (Figure 1), are the largest urban areas in the HEAN. Conditions for farming and human habitation are less conducive in the warmer and more tropical area north of Gabela (Northern Zone), as well as in the increasingly arid area south of Lubango (Arid Highland Zone and Southwestern Zone). The highlands and escarpments of Namibia are divided into a northern arid area and a southern hyperarid area by an approximate boundary between Windhoek and Walvis Bay.

Northern Zone

Much of this zone is in the provinces of Zaire, Uíge, Bengo and Cuanza-Norte. (Technically, the zone also includes Cabinda, but few people live in the forests of Mayombe.) Bakongo people predominate in Zaire and Uíge, and Ambundu people in Cuanza-Norte. Most residents live in rural villages where their farm produce is used for domestic consumption or sold along roads and in local towns. Cassava, maize, beans, sweet potatoes and pumpkins are major staples, supplemented by other cultivated vegetables, and fruit and mushrooms gathered in the wild. In the past coffee was an important cash crop but its cultivation was steadily abandoned due to low prices and high production costs (Bernardo 2012).

Wooded and forested areas in the vicinity of their villages provide rural residents with timber for construction, firewood and medicinal products. Although some areas of forest remain in a relatively undisturbed state, it is likely that timber resources will become scarce in the long term if current rates of depletion continue.

In addition to the clearing of forests and woodlands for shifting cultivation, large-scale timber harvesting occurs in Uíge Province in the municipality of Quitexe and in adjacent municipalities which still have areas of virgin forest (see Lautenschläger *et al.* 2023). Large-scale logging also occurs in Bengo Province in the areas of Nambuangongo, Quibaxe and Bula Atumba (pers. obs.).

Vegetable fields and plantations of beans, maize, banana and other fruits tend to be located on fertile soils along watercourses. Livestock consist mainly of goats, pigs and poultry with their numbers being significantly limited, largely by disease.

Severe soil loss due to erosion gullies has occurred in Uíge Province in the municipalities of Sanza-Pombo, Quimbele and Milunga.

Central Zone

This zone is bounded by Cuito in the east, Gabela in the north, Lubango in the south and coastal lowlands to the west. Apart from Lubango and Huambo previously mentioned, other substantial urban areas are Cachiungo, Caconda, Caluquembe, Cubal and Waku Kungo. Most of Angola's major rivers derive much of their flow from upper catchments in this zone (Lourenco & Woodborne 2023).

Average rainfall ranges between 1,000 and 1,600 mm per year, largely falling in December and March (Mendelsohn & Huntley 2023). Temperatures in these highlands are comparatively moderate (Mendelsohn & Huntley 2023), but often drop to freezing levels – with associated frost – in the early mornings of July and August.

The clearing of woodlands and forests for crops, charcoal and firewood is the most severe environmental problem in the Central Zone. For example, the greater part of Huambo Province and Angola's central plateau, the Angolan Planalto, was originally wooded, with 78.4% of Huambo Province being covered in miombo woodland in 2002. Thirteen years later that proportion had dropped to 48.3%, amounting to the loss of some 1,265,000 ha of woodland cover (Palacios *et al.* 2015).

Significant areas were planted with exotic eucalyptus and pine plantations for timber production during the colonial period, and new areas have been planted in the last decade (pers. obs.).

Other major problems are the loss of soil to erosion, often now evident in gullies big enough to be mapped from satellite images (for example, see Mendelsohn & Mendelsohn 2018).

While most people in this zone live in towns or large villages, many households and smallholder farms are clustered along the major roads that bisect the zone from west to east and from north to south. Agricultural production focuses on dryland crops, mostly of maize, millet, cassava, sorghum and pumpkins. Most vegetables are grown in irrigated *olunaka* fields on patches of fertile, moist Gleysol soils along rivers and their tributaries (Figure 4) and marketed along roads and in nearby towns.

Prior to independence much of Angola's commercial agriculture was concentrated in the Central Zone. This included the production of beef, milk, poultry, fruit, vegetables and maize, the latter being produced largely by smallholders. Most of those commercial ventures ceased during the civil war between 1975 and 2002, but an increasing number have been restarted or developed afresh during the past 15 years, many of them resulting in the clearing of wooded areas or the conversion of grasslands into fields.

Figure 4: *An irrigated* olunaka *field in dark, moist, fertile Gleysol soils alongside a tributary, Huambo Province. Photo: J Mendelsohn.*

The largest ethnic groups present in the Central Zone are the Ambundu in the north, the Ovimbundu in the central areas, and the Nyanyeka Humbe people in the southern areas. Portuguese is the lingua franca in urban areas, as is the case throughout Angola.

Arid Highland Zone

This large zone extends from the Humpata Plateau in the east, to the area inland of Dombe Grande in the west, and south into Namibia where it includes a broad area to the east as far as Otjiwarongo and Windhoek. The southern boundary of the zone is approximately east of Walvis Bay (Figure 1). Sub-groups of Herero and Damara people predominate in this area of the HEAN, their principal areas of occupation respectively being north and south of approximately 19° South. Average rainfall varies between about 600 mm per year south of the Humpata Plateau and 300 mm in the southern parts of the zone in central Namibia. The reliability or predictability of rain declines similarly from north to south (Mendelsohn & Huntley 2023).

Except for Windhoek, urban centres in this area are small, such as Oncócua, Virei, Opuwo, Khorixas, Otjiwarongo and Karibib. Cattle and goats are kept on both communal lands and large, private farms. Charcoal and firewood are sold along major roads and in towns, and are processed for international export. Wildlife has considerable commercial value – for tourism, trophy hunting and venison – in Namibia where many areas are proclaimed conservancies or game farms (Atlas of Namibia Team 2022). Maize, pumpkins, squashes and many other vegetables are grown along larger ephemeral rivers for domestic consumption and sale.

Water is limiting throughout the zone. The west-flowing Cunene River provides the only substantial natural, permanent fresh water. Elsewhere, people, livestock and wildlife obtain water from springs, wells and boreholes.

Rural populations are scattered and small throughout the zone. Permanent settlements are usually located along ephemeral rivers or near boreholes and major springs, almost always in the lowlands that cover much of the area. The few people to be found in the mountain lands are mostly herders of cattle and goats. Livestock in communal areas are moved seasonally or sporadically from depleted to new or more productive grazing. These movements occur within and between Namibia and Angola.

In Namibia, almost the entire western half of the zone is communal land, while the eastern segment largely consists of surveyed, privately tenured farms. Commercial livestock production here has declined in recent decades as increasing numbers of farmers turned to wildlife and tourism, or to holding farms and livestock as capital assets (Atlas of Namibia Team 2022). Rangeland pastures in this area have also shrunk as a result of bush encroachment, a consequence of management and limited fuel loads that curtail the occurrence and frequency of intense wildfires.

Southwestern Zone

Very few people live in this extremely arid area, the great majority of which is conserved in national parks and private nature reserves. These conservation areas generate considerable revenues through tourism.

The reserves were previously farms on which sheep and goats were raised and sold, a farming system that now seldom generates viable incomes. The few farms that continue to produce livestock are large, typically over 10,000 hectares.

Average rainfall ranges between 300 mm per year in the northeastern area of the zone and 100 mm per year further south, but it is always extremely variable. Unlike other areas of the HEAN, the south of the zone receives some rain in winter.

The only urban settlements in this zone are very small: Aus, Helmeringhausen, Rosh Pinah and Sesriem being amongst the biggest. Rural residents typically reside at farmsteads on large farms and at tourist lodges where they are employed. Most residents originate from other areas of Namibia, and only a small number of traditionally resident Nama people continue to live here.

ENVIRONMENTAL CONCERNS

Losses of woodland and forests due to clearing for agriculture (Figure 5) and the harvesting of trees for charcoal are most severe along roads and close to towns in Angola (Mendelsohn 2019). These effects are particularly conspicuous in analyses of woodland and forest loss this century which show how cleared areas around towns have expanded (Schneibel *et al.*

Figure 5: *Shifting cultivation in Cumbira, a forested area rich in endemics and proposed for conservation (Vaz Pinto* et al. *(2023), Cuanza-Sul Province. Photo: A Gomes.*

2013, 2018). Other negative environmental effects are also concentrated along roads and around urban areas but seldom documented, such as the clearing of natural grasslands, concentrations of waste and the contamination of rivers.

Most clearing of woodland and forest that has occurred in recent decades has been in the Northern Zone, especially in Cabinda and between Uíge town and N'dalatando, and in large areas of the Central Zone. These areas originally had the highest percentage of forest cover in Angola (Figure 6a). Clearing in the Central Zone has largely been for shifting agriculture and charcoal production, whereas woodland and forest loss in the Northern Zone was also caused by timber harvesting. Little clearing is apparent in the southern zones where there is little forest or woodland to clear (Figure 6b).

Rates of clearing for new fields are exacerbated where soils have limited fertility (Asanzi *et al*. 2006, Ucuassapi & Dias 2006, Wallenfang *et al.* 2015) which require farmers to shift their crops to virgin soil once nutrients in existing fields are depleted (Mendelsohn 2019). The relative lack of nutrients and moisture in soils is arguably the most important factor driving the loss of Angolan woodlands and forests. Poor soil quality also slows the rate of plant growth and thus forest recovery.

Fires are frequent and widespread, particularly in the Northern and Central zones where they are most prevalent and influential on plant communities in grasslands and floodplains (Catarino *et al*. 2020, Meller *et al*. 2022). Additionally, intense fires year after year reduce the extent of the woodlands and forests by killing trees on the margins of wooded areas because there is relatively little fuel within woodlands to sustain the intensity of fires. These frequent hot fires have indeed destroyed significant areas of Afromontane forests (Powell *et al*. 2023). The extent to which fires lead to further losses of soil fertility should also be a concern, given the low base of nutrients in most areas of Angola.

The conservation of Angola and Namibia's highlands and escarpments is another concern. Little of the HEAN area in Angola is formally protected, although proposals are being pursued to proclaim several protected areas (Vaz Pinto *et al*. 2023). In Namibia, land managed for conservation falls into five categories: national parks managed by the government; tourism concessions on state land allocated to private enterprises; conservancies and community forests on communal land managed by local residents; and privately owned farms used for wildlife and tourism (Atlas of Namibia Team 2022). Significant localised environmental threats in Namibia are due to prospecting and mining, and the collecting and sale of special, protected plants, such as *Lithops*.

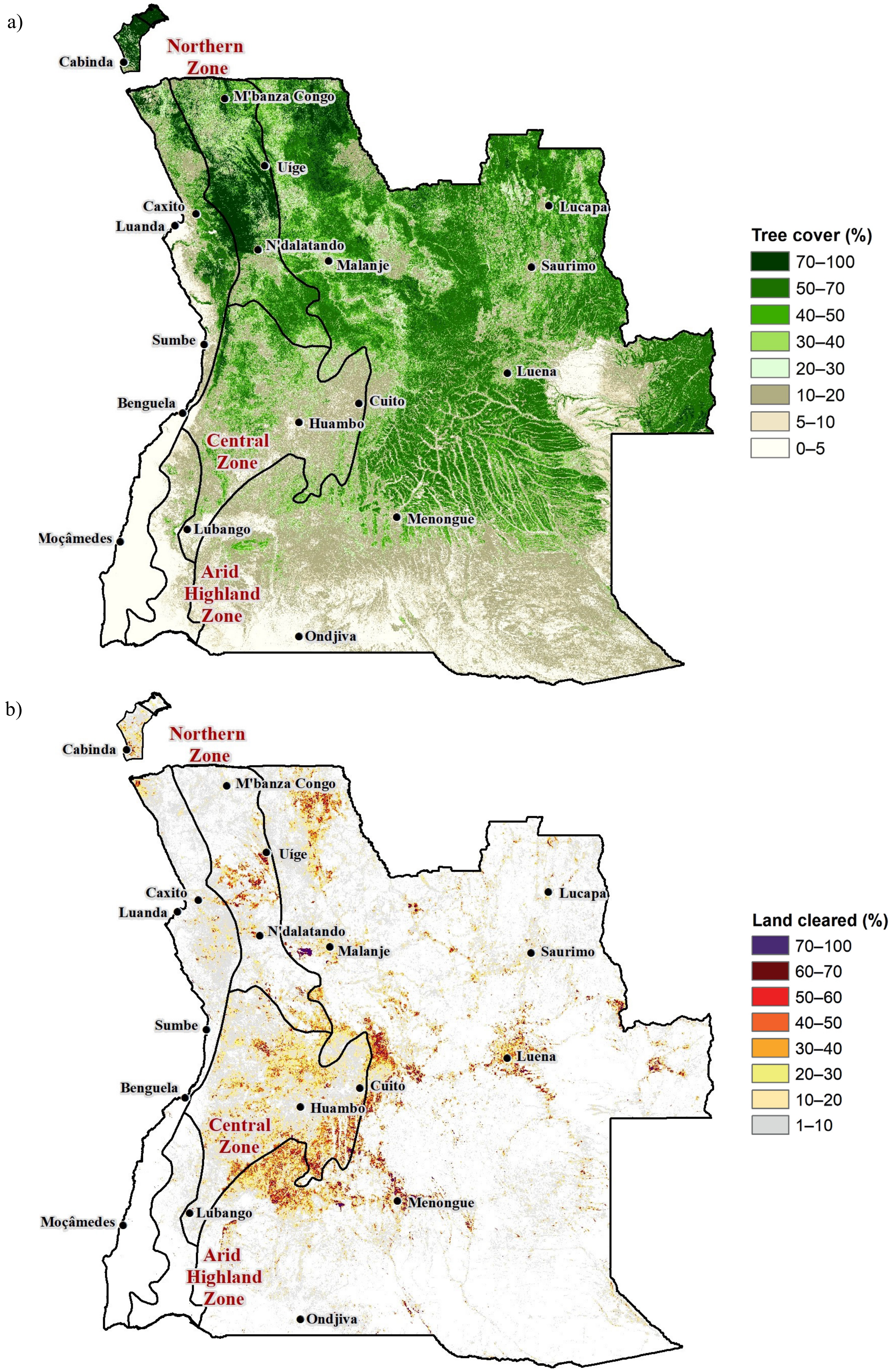

Figure 6: *Woodland and forest cover and loss in Angola. a) Cover in 2000. b) Areas cleared of woodland and forest between 2001 and 2021. From the data set developed by Hansen* et al. *(2013) and updated annually.*

Conservancies and community forests have been declared over much of the Namibian part of the Arid Highland Zone, where there are transboundary connections to Angola's Iona National Park. Substantial areas of national parks are present in the Southwestern Namibia Zone.

Regardless of the way land for conservation is promulgated, the effectiveness of conservation management is often limited, especially where rights to land and its natural resources are either vague and/or poorly controlled.

ACKNOWLEDGEMENTS

Tony Robertson kindly processed data on population densities and woodland clearing and Alice Jarvis and Carole Roberts improved the manuscript.

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The highlands in Angolan conservation areas

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ABSTRACT

Angola has an unbalanced assemblage of conservation areas that cover few key ecosystems and, despite expert recommendations and recent efforts to expand the protected area network, the highlands remain poorly represented. This paper lays out the context behind the creation of Angola's protected areas, while exploring some of the existing constraints and attempts to overcome these limitations. Two existing national parks and one partial reserve incorporate some of Angola's highlands, and are briefly described. In addition, some important highland ecosystems proposed for protection are briefly discussed; these highlands are either part of protected areas under current consideration by the Government of the Republic of Angola or are flagged based on biodiversity assessments. In addition to being poorly represented in the protected area network, current inadequate management and limited scientific knowledge of Angola's highlands are highlighted as important components that need to be addressed in order to better conserve these ecosystems.

Keywords: Angola, biodiversity hotspots, escarpment, highlands, protected area network, national parks

INTRODUCTION

The roots of the Angola's protected areas network can be traced back to the mid-1930s when the Portuguese authorities established the first game-hunting reserves in the country. At the time, this decision was framed within the recommendations derived from the 1933 London Convention – *Convention Relative to the Preservation of Fauna and Flora in their Natural State* – encouraging European powers to set aside protected areas in their African colonies (Huntley 2019). During the decades that followed under Angola's colonial rule, several reserves were proclaimed and a total of six were upgraded to 'national parks'. At that time the main rationale behind identifying suitable areas to conserve was the abundance and diversity of large mammals found there and the perceived threats to those populations within regions of little economic development potential, rather than a broader focus to protect different biomes and ecosystems. As a result of this narrow approach, the Angolan protected area network was unbalanced, with critical assemblages of ecosystems, such as Tropical and Subtropical Moist Broadleaf Forests, and Montane Grasslands and Shrublands biomes (see Huntley 2023), seriously underrepresented. This limitation was duly recognised and highlighted, notably by Brian Huntley, the senior ecologist and advisor to Angola's government on protected areas prior to the country's independence and who identified key areas that should be additionally demarcated for conservation (Huntley 1974a, 1974b, 1974c). Due to the Angolan Civil War and resulting civil unrest that followed Angola's independence, little to no progress was achieved on this front until 2010, when a new framework assessment was produced recommending the expansion of the protected area network (Huntley 2010). This culminated in 2011 with the proclamation of three new national parks by the Angolan government. More recently, a further three key areas have been proposed for subsequent demarcation, including two within the Angolan highlands. Table 1 provides a list of Angola's parks.

Throughout this chapter we refer to the highlands *sensu lato* to include the montane regions across the central and southern Marginal Mountain Chain, as well as some inselbergs and the entire escarpment zone. The escarpment can be roughly defined as a broad section of broken, often rugged topography at varying elevations, orientated north–south and separating the lowlands of the coastal plain from the marginal mountain chain and inland plateau. Within the escarpment zone we consider four sections, namely, Cabinda, Northern, Central and Southern (Figure 1). We also briefly discuss the relevance of specific areas in terms of their endemism of plants and/or of terrestrial vertebrates.

PROTECTED AREAS THAT INCLUDE HIGHLANDS

As there is not one clear definition of what formally constitutes a conservation area in Angola, we follow the latest Angolan legislation and policy documents (e.g., Ministério do Ambiente 2018, Russo *et al.* 2022), which recognises within Angola's protected area network nine national parks, one regional park, two integral nature reserves and two partial reserves.

***Table 1:** Updated list of Angolan protected areas, including sites currently under consideration by government (October 2023), indicating the year when they were gazetted, area covered, whether they include areas within the boundaries of the highlands and escarpments of Angola (Mendelsohn & Huntley 2023), and a brief mention of main vegetation types represented.*

Protected area Gazetted	**Province**	**Area (km^2)**	**Highlands**	**Main vegetation types**
Bicuar National Park First established as a hunting reserve in 1938, elevated to national park status in 1964; its boundaries were redefined in 1972	Huíla	6,748	No	Miombo woodlands, and woodland–thicket mosaic (mesic)
Cameia National Park Created as a hunting reserve in 1935; established as national park in 1957	Moxico	14,688	No	Floodplains–grasslands, Zambezian savannas and woodlands, wetlands
Cangandala National Park Established as an integral nature reserve in 1963; elevated to national park in 1970	Malanje	637	No	Miombo woodland (humid)
Iona National Park First established as a hunting reserve in 1937; elevated to national park status in 1964 with new boundaries	Namibe	15,190	Yes	Kaokoveld desert, including sand dunes, gravel plains and xeric savannas; montane habitats; and higher elevation grassland–shrubland (sub-desert)
Luengue-Luiana National Park Established as a national park in 2011	Cuando Cubango	47,913*	No	Savanna–woodland (mesic), and wetlands
Mavinga National Park Established as a national park in 2011	Cuando Cubango	42,483*	No	Mixed woodlands and savannas (mesic), wetlands
Mayombe National Park Established as a national park in 2011	Cabinda	2,074	Yes	Humid evergreen and semi-deciduous forests
Mupa National Park Created as a hunting reserve in 1938; established as national park in 1964	Cunene	6,039	No	Mopane woodlands, woodland-thicket mosaic (mesic)
Quiçama National Park Created as a hunting reserve in 1938; reclassified as national park in 1957	Luanda	9,227	No	Arid savanna–thicket mosaic, and wetlands
Chimalavera Regional Nature Park Created as a special reserve in 1971; revised as regional nature park in 1974	Benguela	102	No	Savanna–grassland mosaic (arid)
Búfalo Partial Reserve Established as a partial reserve in 1974	Benguela	405	Yes	Semi-arid savanna, and woodland–thicket mosaic (mesic)
Namibe Partial Reserve Created as a partial reserve in 1959; boundaries revised in 1960 and 1973	Namibe	4,642	No	Grassland–shrubland (sub-desert) and savanna–grassland mosaic (arid)
Ilhéu dos Pássaros Integral Nature Reserve Established as an integral nature reserve in 1973	Luanda	1.5	No	Mangroves
Luando Integral Nature Reserve Established as a hunting reserve in 1938; upgraded to integral nature reserve status in 1957	Malanje, Bié	9,930	No	Miombo woodlands (humid), wetlands
Cumbira Proposed; still under consideration	Cuanza-Sul	n/a	Yes	Humid semi-deciduous forest
Serra do Môco Proposed; still under consideration	Huambo	n/a	Yes	Afromontane grasslands and forests
Pingano Proposed; still under consideration	Uíge	n/a	Yes	Humid semi-deciduous forest

* Area based on new revised boundaries under consideration for re-gazetting.
n/a = not available

Following guidelines set by the International Union for Conservation of Nature (IUCN), national parks constitute the basic legal tool to ensure the conservation of valuable natural landscapes and their biodiversity (Muhumuza & Balkwill 2013). National parks in Angola aim to protect biodiversity while also promoting and benefiting from related services, such as tourism, thereby contributing to socioeconomic development to achieve long-term sustainability. Historically, and in comparison with neighbouring countries, Angola has adopted and maintained a lenient approach in enforcing regulations. For example, human presence and even urban development has been permitted inside national parks, which has recently been worsened by legislation allowing for the industrial exploitation of natural resources in national parks, partial nature reserves and special nature reserves. At least in theory, integral nature reserves enjoy a much stricter mandate, contemplating scientific research as one of its main goals, and not allowing for any exploitation of natural resources. The use of various types of natural resources is permitted in partial reserves, making them more lenient in terms of regulations, while regional parks are intended to be managed at a provincial level, rather than by central government.

For the reasons detailed earlier, Angola's highlands are poorly represented in existing conservation areas. Currently, only two national parks (Iona and Mayombe) and one partial reserve (Búfalo) of Angola's 14 protected areas (Ministério do Ambiente 2018) include small sections of the highlands and escarpments of Angola (Figure 1).

Iona National Park

Situated in the southwest corner of Angola, Iona was the first conservation area to be proclaimed in the country, as a national game park in 1937. Subsequently, it was changed to a game reserve in 1944 and finally upgraded to a national park in 1957. Covering 15,196 km^2 it was, until recently, the largest protected area in the country. Iona National Park (INP) contains a diverse array of desert and semi-arid ecosystems and spectacular landscapes, spanning from a pristine Atlantic coastline under the influence of the cold Benguela Current, to a vast sand sea of massive dunes, extensive gravel plains, tall

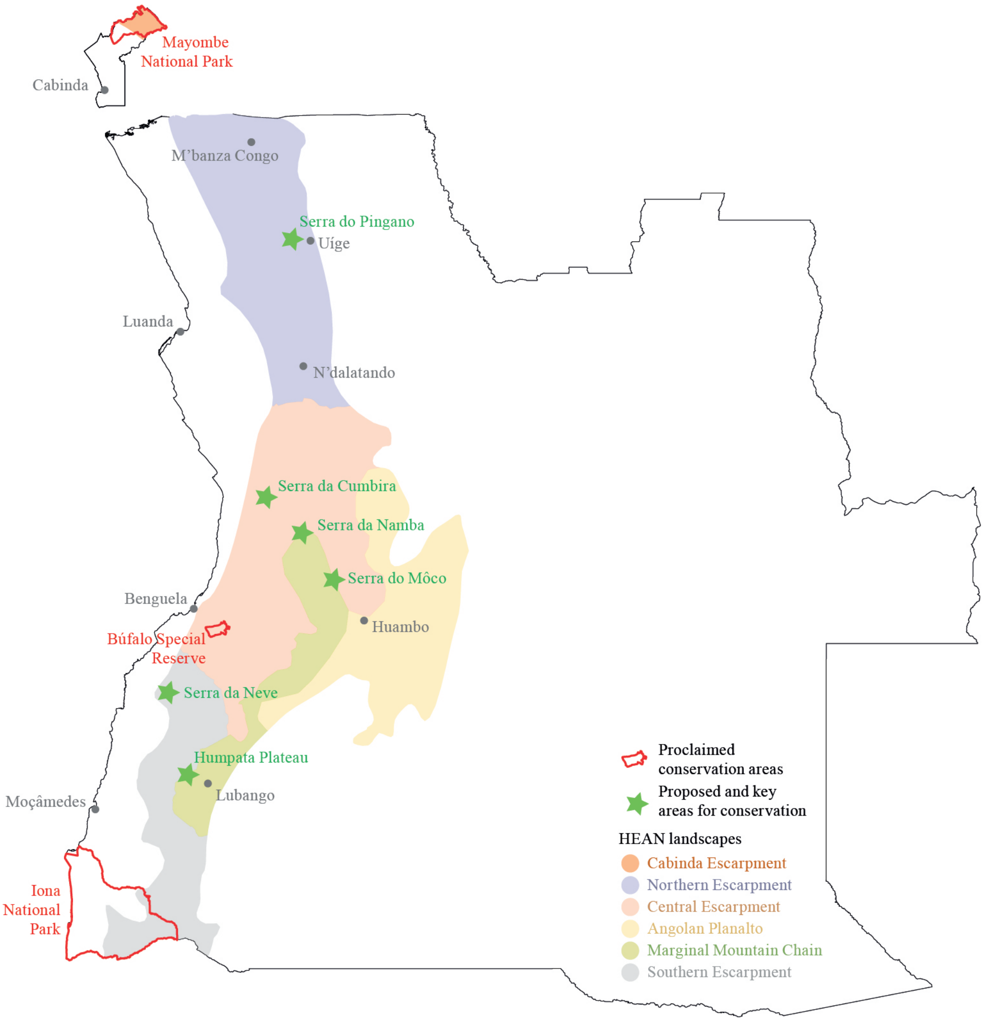

Figure 1: *Proclaimed, proposed and key areas for conservation in the highlands and escarpments of Angola. Landscapes are adapted from Mendelsohn and Huntley's (2023) mapping of the highlands and escarpments of Angola and Namibia (HEAN).*

mountains and dramatic geological formations. The park was formerly famous for its rich biodiversity, ranging from the iconic plant *Welwitschia mirabilis*, large numbers of oryx, mountain and plains zebras and springbok, to the presence of desert-adapted black rhino, elephant and lion (all three species now locally extinct), and the park's very rich coastal marine life.

Although the better-known sections of INP are relatively flat or covered by dunes, the eastern regions are very rugged and mountainous, and include some remarkable highlands. These highlands constitute the southern tip of the Great Escarpment in western Angola, and are represented here by two major orographic features, Serra Tchamalindi and Serra Cafema. Rising just east of Iona village, Serra Tchamalindi consists of a chain of quartzite and dolomitic limestone mountains which stretches about 40 km southwards, reaches 1,944 masl at its highest peak and is surrounded by numerous vertical cliffs of several hundred metres. West of Serra Tchamalindi, Serra Cafema is mainly structured by granites and granodiorites. It is somewhat shorter in length and less steep than Serra Tchamalindi, but has a higher plateau that towers more than 2,000 masl.

Despite constituting some of the most notable highlands in Angola and arguably situated in the best protected and more thoroughly studied conservation area in the country, very little is known about the biodiversity of these mountains because of their remoteness and lack of access routes which have prevented researchers from surveying them. The relatively arid climate on these Iona highlands does not allow for the development of Afromontane forest or moist montane grasslands, yet they may still hold many endemic or restricted-range species, especially plants. Only very recently a biodiversity survey was carried out when a team of scientists was flown to the top of the highlands by helicopter (de Cauwer 2021, de Cauwer *et al*. 2023). Even though the survey was a rapid assessment and most of the data were, at the time of writing this paper, still being analysed, at least two plants previously considered as Namibian endemics, *Sesamothamnus leitneri* and *Commiphora otjihipana*, were found on Tchamalindi and Cafema, respectively, and the rare and vulnerable *Euphorbia leistneri* was recorded for the first time in Angola. In addition, five woody and one succulent taxa may prove to be new species to science (de Cauwer 2021, de Cauwer *et al*. 2023). As a result of this survey, two bird species were also added to the Angolan list, the Cape eagle-owl (*Bubo capensis*) and Layard's warbler *Curruca layardi*, in addition to the Herero chat *Namibornis herero*, a poorly known Kaokoveld endemic. Finally, the herpetofauna found in both these highlands included one of the most spectacular and enigmatic African geckos, the southwestern Angolan endemic *Kolekanos plumicaudus*, and possibly still-undescribed species of *Pachydactylus* and *Trachylepis* (Vaz Pinto *et al*. 2021, Lobón-Rovira *et al*. 2022).

Mayombe National Park

Located in the northern enclave of Cabinda, this is one of the more recently established conservation areas in Angola (proclaimed in December 2011) and covers approximately 2,074 km^2. The creation of Mayombe National Park (MNP) was a late response to protect the unique and highly biodiverse moist rainforest ecosystems present in Cabinda, a priority identified decades earlier (Huntley 1973, 1974a, 2010). The park is part of a transfrontier conservation area (TFCA) proposed to cover most of the Mayombe forest across four countries: Angola, Republic of the Congo, Democratic Republic of the Congo and Gabon. The TFCA encompasses several protected areas, such as national parks, biosphere reserves and marine parks, with a total area of about 36,000 km^2. By integrating MNP into a broader transfrontier initiative it is hoped that it might conserve some of its critical biodiversity components. The park contains a series of mountainous ridges reaching elevations above 900 masl which together with their proximity to the equator and coastline translate into a very moist climate, and lush cloud forests covering the slopes. In contrast to its richness in biodiversity, and because of its remoteness and persistent civil unrest, MNP is also one of the least known national parks. For example, the main publication on the vegetation of the Angolan Mayombe is outdated, focusing on the area from a forestry perspective (Monteiro 1962).

The park is mostly famous for the presence of threatened apes, being the only site in Angola where they occur, namely, the critically endangered western lowland gorilla, *Gorilla gorilla gorilla*, and the chimpanzee, *Pan troglodytes*. These apes are likely threatened by extinction locally due to habitat destruction and poor law enforcement, but viable populations of the critically endangered African forest elephant, *Loxodonta cyclotis*, may still be present in the park. An ongoing study of the mammal communities in MNP, based on a network of trap cameras, has confirmed the presence of both species of apes, forest elephants and a rich diversity of antelopes (Fundação Kissama in prep.).

Although poorly known and probably lacking in strict endemics, the avifauna in MNP is extremely rich and the Angolan Mayombe has been defined as an Important Bird and Biodiversity Area (Dean 2001). Recent ornithological surveys in the park have added 23 new species to Angola's country list (Mills *et al*. in press). Subsequently, pictures of one of the most iconic African birds, the grey-necked rockfowl (*Picathartes oreas*) were retrieved from trap cameras in the rainforest, thus extending the distribution of this threatened passerine southwards into Cabinda (pers. obs.). Other faunistic groups remain less studied, and the local herpetofauna is virtually unknown even though it may well hold many endemics and undescribed species.

Búfalo Partial Reserve

Covering approximately 405 km^2, the Búfalo Partial Reserve (BPR) was one of the last protected areas to be proclaimed by the Portuguese colonial authorities in April 1974. The main rationale behind the creation of this reserve seems to have been the need to preserve an isolated population of Cape buffalo *Syncerus caffer caffer* which at that time was the most western and isolated population of this subspecies in Angola. The BPR is situated in the first elevational range in western Angola's orographic relief, presenting rugged terrain and a series of hills rising to 1,400 masl. The local climate is semi-arid, and the area is densely covered with spiny savanna and mixed woodlands. This reserve has never benefited from any sort of management, and it has never been surveyed. Its biodiversity is unknown. Given the location, it is likely that the area could have a rich herpetofauna and, pending future investigation, may include several endemics.

HIGHLAND AREAS PROPOSED FOR PROTECTION

Following preliminary and ongoing multidisciplinary studies (Lautenschläger & Neinhuis 2020, Holísticos 2021a, 2021b, 2021c, 2021d), three highland areas have been proposed for protection and are being considered by the government for formal proclamation.

Serra do Môco

Rising abruptly from the surrounding plateau to reach 2,620 masl, Serra do Môco (more commonly known as Morro do Môco) is the highest peak in Angola. It comprises some of the most important montane grassland patches and remnants of Afromontane forest left in the country. In 2009 it was estimated that there were only about 30 Afromontane pockets larger than 0.5 ha in size, totalling just 85 ha left in the whole region (Mills *et al*. 2011, Powell *et al*. 2023). These relict forest patches are found in deep ravines and narrow gorges above 2,000 masl and have high levels of endemism in addition to rare species shared with a few other forest 'islands' scattered across Africa (Huntley & Matos 1992). The need to conserve Serra do Môco had long been recognised, and it was flagged as a priority area to become a reserve even before the country's independence (Huntley 1974a, 1974b, 2010). Although it could not be included as one of the new protected areas created in 2011, a proposal was recently submitted for the demarcation of 138.5 km^2 as the Morro do Môco Partial Nature Reserve, following a public tender and request by the Government of Angola (Holísticos 2021d).

The mountain and its surrounds have been the focus of several biodiversity surveys since the 1950s, at least, and is comparatively better studied than most other Angolan highlands, despite the paucity in botanical data. Nevertheless, recent preliminary vegetation surveys found some of the characteristic floristic elements of these relict Afromontane forests, including *Erythroxylum emarginatum*, *Ficus* spp., *Ilex mitis*, *Newtoni buchananii*, *Pittosporum viridiflorum* and *Podocarpus milanjianus* (Gonçalves 2009, Holísticos 2021b).

In contrast, the avifauna of the massif is relatively well known (e.g., Hall 1960, Mills *et al*. 2011, Mills & Dean 2021) and the area has been identified as an Important Bird and Biodiversity Area as it holds a third of all Angolan endemic species (Dean 2001, Mills & Dean 2021). Of special note, a minimum of c. 75 pairs of the endangered Swierstra's spurfowl *Pternistis swierstrai* may persist at Serra do Môco, making this one of the most important populations worldwide (Mills *et al*. 2011, Mills & Dean 2021). The other endemics are the red-backed mousebird *Colius castanotus*, pale-throated barbet *Gymnobucco vernayi*, Huambo cisticola *Cisticola bailunduensis*, Angola slaty flycatcher *Malaenornis brunneus*, Ludwig's double-collared sunbird *Cinnyris ludovicensis*, Landana firefinch *Lagonosticta landanae* and Angola waxbill *Coccopygia bocagei*. The Môco area may also be important for the preservation of many other montane birds, including rare forms and endemic subspecies (Mills *et al*. 2011, Mills & Dean 2021).

At least four species of endemic reptiles have already been reported from Serra do Môco (Gonçalves *et al*. 2019, Branch *et al*. 2021, Holísticos 2021b). Three of these endemic reptiles have distributions restricted to the Angolan highlands, such as the recently described gecko, *Afroedura wulfhaackei*, the lizard *Agama* cf. *schacki* and the viper *Bitis heraldica*. A fourth species is a mysterious lizard only known from this massif, *Ichnotropis microlepidota*. Even though few studies have focused on amphibians within Môco, the presence of two endemic species has been confirmed recently, namely *Leptopelis anchietae* and *Breviceps ombelanonga* (Holísticos 2021b). In terms of mammals, the region currently holds few large mammals and almost no studies have focused on the most speciose groups such as rodents and bats. The endemic shrew *Crocidura erica* and the mouse *Otomys anchietae* are likely present, and recently another mouse species, *Hylomyscus heinrichorum* was described from a museum series obtained both at Môco and nearby Serra Soque (Carleton *et al*. 2015).

Serra da Cumbira

Serra da Cumbira (sometimes spelled as Kumbira) is the name given to an escarpment ridge situated southwest of the town of Gabela. The ridge is north–south oriented, stretching for about 20 km and reaching just over 1,600 masl at the peak of Engelo. This mountainous ridge holds some of the more extensive remnants of the Central Escarpment forests which can be considered as impoverished outliers of Guineo-Congolian rainforests (Mills 2010). The region of Gabela had been identified as a centre of endemism and underlined as a priority for conservation at least since the 1960s (Hall 1960, Huntley 1974a, 2010, Huntley & Matos 1992, Dean 2001, Cáceres *et al.* 2015). In response, a formal proposal for the creation of Cumbira Partial Nature Reserve, covering 224.5 km^2, was recently submitted to the government (Holísticos 2021c).

A recent botanical survey identified four main vegetation types in Cumbira: moist high forest; submontane forest/woodland; coffee plantations dominated by exotic *Inga*; and agricultural and secondary/disturbed habitats (Gonçalves & Goyder 2016). This short survey found three new Guineo-Congolian species for Angola – *Ficus saussureana*, *Justicia paxiana* and *Tarenna pavettoides*, the latter possibly a new subspecies – and one potentially undescribed species of Rubiaceae within the genus *Rytigynia* (Gonçalves & Goyder 2016).

The area is especially relevant for the conservation of birds, and most biodiversity studies conducted have focused on the ornithological communities (e.g., Mills 2010, 2019, Cáceres *et al.* 2015, 2016, 2017). A total of 227 bird species have been recorded at Cumbira, which holds the highest number of Angola endemics of any site in the country, with 11 endemic species and 20 endemic subspecies (Mills 2019). Significantly, it is also the only site where three of the rarest and most endangered avian endemics are found together, namely the Gabela akalat *Sheppardia gabela*, Gabela bushshrike *Laniarius amboimensis* and Pulitzer's longbill *Macrosphenus pulitzeri* (Mills 2019). Other rare and threatened endemics present include the pale-throated barbet *Gymnobucco vernayi* and Monteiro's bushshrike *Malaconotus monteiri*.

In comparison to the birdlife, mammals have been studied less in the region so far. However, a new and endemic species of nocturnal primate was recently found and described from Cumbira, the Angolan dwarf galago *Galagoides kumbirensis* (Svensson *et al.* 2017), and a poorly known endemic subspecies of the mongoose, Ansorge's cusimanse *Crossarchus ansorgei ansorgei*, was rediscovered in Cumbira which represents the southernmost global record for the forest genus *Crossarchus* (Vaz Pinto *et al.* 2020). Cumbira also holds populations of poorly known primates such as the near-endemic southern talapoin *Miopithecus talapoin*, the endemic subspecies of blue monkey *Cercopithecus mitis mitis*, and the forest nocturnals, Demidoff's bushbaby *Galagoides demidovii* and Central African potto *Perodicticus edwardsi* (Svensson *et al.* 2017, Holísticos 2021a). Due to the lack of herpetological surveys until very recently, only two endemic species of reptiles, *Rhoptropus benguellensis* and *Agama* cf. *schacki*, have so far been recovered from Cumbira, in addition to one amphibian, *Leptopelis jordani*, but definitive identification of these and several other taxa are pending ongoing taxonomic studies.

Serra do Pingano

The need to protect a significant section of the forest biome in northwestern Angola and, more specifically, the mountain ridges of Uíge Province was stressed in the Angolan Protected Area Planning Strategy (Huntley 2010). As a result, a proposal for the creation of protected area to include the Serra do Pingano Forest Ecosystem has been submitted to the Government of Angola and is being considered. Lautenschläger *et al.* (2023) provide a detailed description of the area.

OTHER KEY HIGHLANDS NOT PROTECTED

Several other highlands in Angola are not yet protected by legislation and not included in areas which are currently under consideration to become conservation areas, even though they were prioritised in earlier assessments (e.g., Huntley 1974a, 2010, Huntley & Matos 1992). Here, we briefly discuss three such sites which contain important highland areas in Angola: Humpata Plateau, Serra da Namba and Serra da Neve. There are potentially other important areas, which might be virtually unstudied and have not been mentioned previously or have received much less attention, such as Chongorói, Tchivira Mountain and Serra Mocoti, to name just a few.

Humpata Plateau

The Humpata–Bimbe plateau sits on top of the Chela Escarpment, just west of the town of Lubango in southwestern Angola. The elevation in the area ranges from about 1,900 masl to over 2,300 masl, with its western edges marked by spectacular precipitous cliff faces, and gorges, often more than 1,000 m high, marking the abrupt transition to the coastal plain of Namibe Province, such as at Tundavala or Bimbe. The altitudinal gradient and diversity of ecosystems – Zambezian woodlands, arid savannas, montane grasslands and Afromontane forests – make this area a biogeographic unit of great interest (Huntley 2010). The local vegetation is probably rich in endemism, which can be illustrated by a recently described, new plant species from

Tundavala, *Stomatanthes tundavalaensis* (Hind & Goyder 2014). This site is also recognised as an Important Bird Area (Dean 2001), and among the local avifauna there are at least eight endemic or near-endemic taxa, including the endangered Swierstra's spurfowl *Pternistis swierstrai* and possibly the rarest Angolan endemic, only recently rediscovered in Tundavala, the Angolan white-headed barbet *Lybius leucocephalus leucogaster* (Baptista & Mills 2018, Dean *et al*. 2019). Although the larger mammal populations have long been extirpated from the area, a very short recent survey in Tundavala discovered five unique genetic lineages among rodents, which possibly represent endemic taxa (Krasova *et al*. 2021), and thus suggest a high endemism rate. At least six endemic reptiles occur on the Humpata Plateau, including three geckos and two very rare snakes only recently rediscovered in Tundavala, *Psammophis ansorgii* and *Psammophylax ocellatus* (Baptista *et al*. 2018, Branch *et al*. 2019a, 2019b). Three endemic amphibians are known to occur in the area (Baptista *et al*. 2018), but these include arguably one of the rarest African frogs, the Serra da Chela reed frog *Hyperolius chelaensis*, a montane species only known from two specimens collected in a forest stream down a deep gorge near Bimbe (Conradie *et al*. 2012).

Serra da Namba

Situated in Cuanza-Sul Province, Serra da Namba reaches 2,420 masl at its highest peak; it may well be one of the most important highlands in Angola in terms of biodiversity. The ecosystems of the Serra da Namba share a lot of similarities with those of Serra do Môco, presenting Zambezian woodlands and savanna on the lower slopes, extensive montane grasslands, and Afromontane forest in deep valleys above 2,000 masl. A botanical assessment of Mt Namba, as it is often named, has recently been published (Goyder *et al*. 2023). Although recognised as an Important Bird Area (Dean 2001) and proposed as a potential strict nature reserve for many years (Huntley 1974a, 2010, Huntley & Matos 1992), recent surveys have found that Mt Namba may actually hold, by far, the most extensive and best-preserved remnants of Afromontane forest in Angola (Mills *et al*. 2013), making it the most critical area for the preservation of this highly endangered ecosystem and its associated fauna and flora (Powell *et al*. 2023). An ornithological study confirmed the presence of eight endemic birds at Mt Namba, including the endangered Swierstra's spurfowl *Pternistis swierstrai* and, significantly, two rare montane birds which were only previously known to occur at Môco in Angola but then feared extinct, the bar-tailed trogon *Apaloderma vittatum* and the orange ground-thrush *Zoothera gurneyi*. At least two endemic geckos and one tree frog are known to occur at Serra da Namba, but ongoing studies are expected to lead to the description of new species, some of which might be limited to a highly restricted local range.

Serra da Neve

The intrusive alkaline complex of Serra da Neve constitutes one of the most remarkable inselbergs of southwestern Africa. Situated in the north of Namibe Province, Serra da Neve rises abruptly from the coastal lowlands and resembles, in shape, a huge extinct volcano with a central flat crater at approximately 1,600 masl. It is well framed by cliffs and a mountainous, almost circular ridge consistently above 2,000 masl and reaching 2,489 masl at its highest peak. The inselberg is completely surrounded by acacia savanna and mopane woodlands in the arid coastal plain but contains extensive rich and well-developed Zambezian woodlands dominated by *Brachystegia* spp. and *Julbernardia paniculata*; some escarpment mixed woodlands; savannas dominated by *Cussonia angolensis* and *Peltophorum africanum*; and riverine forest patches with *Ficus* spp. in moister valleys (Barker *et al*. 2015). The local climate appears to be too dry to sustain Afromontane forests, but some elements are present. The montane grasslands at the highest elevations are extensive, while succulent plants are also well represented on Serra da Neve, including the endemic *Euphorbia teixeirae* (Barker *et al*. 2015).

This is arguably one of the most exciting biodiversity hotspots in Angola, fully justifying its inclusion in proposals to extend the protected area network (Huntley 1974a, 2010, Huntley & Matos 1992). Unfortunately, it is also one of the least studied highlands in Angola, and only recently a few biodiversity surveys have been successfully conducted. Almost nothing is known of the local mammal fauna, while it is assumed to have a rich avifauna which includes a combination of rare and endemic birds, including, for example, the grey-striped spurfowl *Pternistis griseostriatus* and the Angolan white-headed barbet *Lybius leucocephalus leucogaster*. Providing more support to consider the site as a regional centre of endemism, recent herpetofauna assessments have already recovered five new species as strict endemics to Serra da Neve: two geckos, *Lygodactylus baptistai* (Marques *et al*. 2020) and *Afroedura praedicta* (Branch *et al*. 2021); one girdled lizard, *Cordylus phonolithos* (Stanley *et al*. 2016); one limbless skink, *Acontias mukwando* (Marques *et al*. 2023); and a toad, *Poyntonophrynus pachnodes* (Ceríaco et al. 2018).

THE WAY FORWARD

Angolan highlands include some of the most unique, endemism-rich and highly threatened montane ecosystems in southern Africa, while also supporting some of the highest human densities in Angolan rural areas (Mendelsohn & Gomes 2023). Unfortunately, these highlands have long been neglected in terms of conservation and the most sensitive areas have not yet been legally protected. The most obvious priority is for the Government of Angola to follow up on previous recommendations and ongoing initiatives to designate as conservation areas some of the already identified sites with critical highlands, such as Serra do Môco, Serra da Cumbira, Serra do Pingano, Humpata Plateau, Serra da Namba and Serra da Neve. Even though designating conservation areas is a necessary step to protect these ecosystems, it does not guarantee that these ecosystems will be successfully conserved. Recent experience in Angola has shown that formally protected areas can be abused as much as community or private lands, since most national parks and reserves have received little or no management and can be considered ‘paper parks’ – parks that feature in legislation and official maps but are abandoned on the ground. Currently, the government is trying to step-up management practices in some areas and are exploring co-management initiatives in others, which may hold the key for more effective conservation and hopefully can be successfully implemented in Angola’s highlands. Furthermore, the regulations around protected areas are, in most cases, inherited from the colonial period and need to be revised and updated to align with up-to-date good practices used elsewhere in southern Africa.

Much of the biodiversity of Angola’s highlands is still poorly known, and therefore it is crucial to conduct biodiversity inventories in these areas and report new endemic taxa, especially in cryptic or less-studied groups such as invertebrates, fossorial reptiles, rodents and bats. Finally, our current knowledge of the highlands derives mostly from surveys and expeditions conducted decades ago; there are still large sections of the Angolan escarpment and remote and almost inaccessible mountain peaks and ridges that remain virtually unexplored. Therefore, the identification and surveying of potentially unknown highland hotspots of biodiversity should also be a priority for future work.

ACKNOWLEDGEMENTS

We thank the Ministry of Environment of the Republic of Angola and the INBC, the Instituto Nacional da Biodiversidade e Conservação, for allowing us frequent access to the protected areas and other relevant sites discussed in this chapter over several years. John Mendelsohn and Brian Huntley provided many useful insights throughout various stages of the manuscript, and Carole Roberts’ meticulous edits much improved the final version of this chapter.

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An overview of plant endemism on the highlands of Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-craven

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ABSTRACT

Over 700 of Namibia's nearly 4,000 seed plants are endemic to the country and, of these endemics, the distributions of more than 100 were found to be restricted to highlands with elevations over 1,500 masl. The families with the most highland endemics are Apocynaceae, Asteraceae, Leguminosae and Scrophulariaceae with life forms varying from herbs and shrublets to succulents. Species restricted to specific mountain ranges are listed and the highlands of importance to plants are mapped. No noticeable concentration of endemic highland plants occurs, with many being rare with restricted habitats at specific elevations.

Keywords: endemism, highlands, Namibia, plants

INTRODUCTION

The number of taxa in Namibia, and especially the recorded number of endemics is constantly changing as research progresses. To date, over 700 of Namibia's nearly 4,000 indigenous species of seed plants are endemic to the country. When taxa that occur marginally into neighbouring countries (near-endemics) are added, this number rises to over 1,400 species. Mapping the distributions of individual taxa show discernible range patterns and over 100 endemics were found to be restricted to highlands at elevations over 1,500 masl. Only plants occurring on highlands, and not on plains or lower-lying areas, were included in this analysis.

METHODS

There is sufficient information on the taxonomy and distribution of the Namibian endemic flora to allow a provisional assessment of geographical ranges and affinities because the information is housed on Craven and Kolberg (ongoing), a BRAHMS8 database (University of Oxford 2023) which is partly online. The data include lists of plants endemic or near-endemic to Namibia, as well as occurrence records from literature and specimens housed in many herbaria. The database needed some updating and additions for this evaluation.

Our taxonomic decisions are based on morphological and distributional data, and only phylogenetic analyses that are linked to these data. Our accepted names allow for identification within the Namibian context and are practical for our work and that of other users. Worksheets accompanying Irish (2002) were used to identify mountains and mountain groups with elevations over 1,500 masl within the area of highlands and escarpments defined in Mendelsohn and Huntley (2023). QGIS, which is incorporated into BRAHMS8, was used to overlay specimen records with shapefiles of highlands and specific mountains. Overlapping ranges were evaluated. Relationships, gaps, life forms and the status – threat, protection, listing under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2023) – of highland endemics were documented. Mountain names and shapefiles follow the Atlas of Namibia Team (2022).

Results are discussed under eight highland areas, each with a map showing the specific highlands, mountains and inselbergs within the general area of highlands and escarpments (Mendelsohn & Huntley 2023). Species endemic to highlands in Namibia, their protection and international recognition are listed in Appendix 1, while the complement of endemic species of each highland area, mountain and inselberg is listed in Appendix 2.

HIGHLAND AREAS IN NAMIBIA

Seven groups of highlands with co-occurring endemic plant species, as well as their own complement of endemic plants, have been identified. An eighth group of highlands comprises those without known endemic flora. Each group is discussed, on the pages that follow, alongside a map that illustrates the highlands included in the group.

1. Central and southeastern highlands: Auas Mountains, Brandberg, Erongo Mountains, Gamsberg, Groot Karasberge, Khomas Hochland, Naukluft Mountains, Otjihaveraberge (also known as the Neudamm Hochland), Spitzkoppe and Tirasberge

2. Highlands with restricted endemic flora associated mainly with the central and southern highlands: Awasibberge, Central Group, Hakosberge, Naos, Nubib and Tsaris Mountains

3. Baynes, Otjihipa and Zebra mountains

4. Huns Mountains – Orange River valley

5. Waterberg and Otavi Mountains

6. Inselbergs in the southwest: Aurusberg, Klinghardt Mountains, Kowisberge and Obib

7. Escarpment and plateaus

8. Highlands and inselbergs without known endemic flora: Brukkaros Mountain, Dikke Willem, Etendeka Mountains, Huab Outliers, Middle Ugab, Otjikondavirongo, Paresis Mountains, Rantberge, Rooirand and Swakop–Khan ranges.

Group 1: Central and southeastern highlands

Some of the highest mountains in Namibia share range-restricted species, first documented by Hilliard (1994) after a study of the *Manuleae*. Subsequent research and fieldwork by the two authors (Craven and Kolberg) confirmed that mountains in central and southeastern Namibia with co-occurring species include the Auas Mountains, Brandberg, Erongo Mountains, Gamsberg, Khomas Hochland, Groot Karasberge, Naukluft Mountains and Tirasberge (Figure 1). A few range-restricted plants may also occur on Mount Etjo or Nubisberge and, due to more recent targeted fieldwork and recent literature, additional records of localities and species have been added to this list.

One species, known from most of these highlands is *Lightfootia dinteri*. Two taxa, one published in 1910 and the other in 1922, were given this name by different authors. One taxon is a synonym of *Wahlenbergia denticulata* (Lammers 1995) which occurs from Kenya to South Africa, while the other is an intriguing, taxonomically unresolved species only found in Namibia. This is not the first time a Namibian endemic species has been excluded from a taxonomic treatment and, although it would be easy to transfer the name, this plant may not even be a *Wahlenbergia* as it differs in many aspects and needs taxonomic study.

The genus *Namacodon* is endemic to Namibia and the one species *N. schinzianum* is known from the Auas, Erongo and Naukluft mountains and from the Gamsberg. Like *Lightfootia*, it belongs to the Campanulaceae, a family that is not species rich or generally noteworthy in Namibia. The Apocynaceae and Scrophulariaceae families have the most endemic taxa on these highlands, with each having about seven co-occurring species. Most of the Apocynaceae endemics are localised succulents. The endemic taxa belonging to the Scrophulariaceae are more likely to be herbs or dwarf shrubs and some are relatively widespread, even being found on other highlands or at lower elevations as well. This brings to light some of the challenges in determining a strict division of taxa according to highlands, as some species such as *Jamesbrittenia heucherifolia* are montane in Namibia but occur near sea level in Angola (Hilliard 1994). The monogeneric *Manuleopsis*, was previously associated with these central and southeastern highlands of Namibia, but the species *M. dinteri* is now known to be common and more widespread and is found as far north as the Omavanda Mountain in the Baynes–Otjihipa mountain group. The only indigenous *Nicotiana* species in southern Africa is limited to the Brandberg, Spitzkoppe and Erongo Mountains. A species of *Tetradenia* from the central highlands, presently included in *T. brevispicata*, may be a distinct highland endemic taxon. The bryophyte flora of the Namibian highlands also showed the distribution to be concentrated on these central and southern highlands (Russell & van Rooy 1986).

Notes on endemic plant species specific to each of the mountains making up the central and southeastern highlands area follow below.

Brandberg

Over 480 indigenous seed plants occur on the Brandberg with about 90 Namibian endemics of which nine are limited to the mountain itself. Another ten are also found on other mountains in the central and southern highlands area, particularly the Erongo

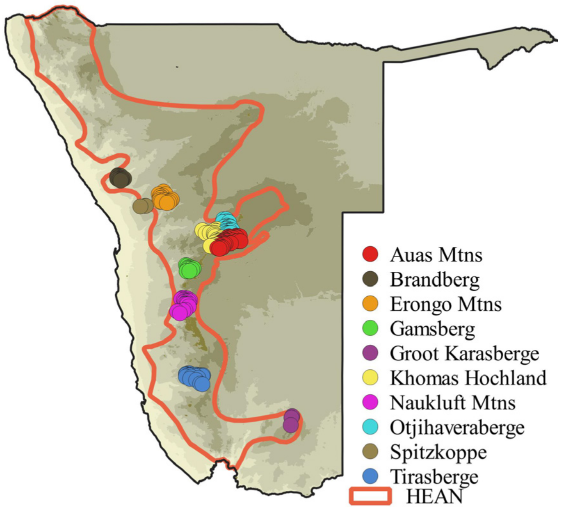

Figure 1: *Central and southeastern highlands of Namibia making up Group 1 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

Mountains and the Gamsberg escarpment. Four members of the Asteraceae family are restricted to the Brandberg and are found at the summit: *Anisopappus brandbergense*, *Felicia gunillae*, *Nidorella nordenstamii* and *Pentzia tomentosa*. The last three have only been collected in a few years of high rainfall (1963, 1974 and 2000) with decades between collections. That Nordenstam, a specialist on the Asteraceae, collected all the type specimens in years of abnormally high rainfall, poses the question as to whether collecting by specialists in favourable conditions would not yield more localised endemics? *Anisopappus brandbergense* has been found at elevations from about 1,850 masl to the Amis River which is below 900 masl.

The different peaks of the Brandberg – Horn, Numas Spitz, Aigub and Königstein – although isolated from one another by some distance, may have the same endemic species, such as *Euphorbia monteiroi* subsp. *brandbergensis* and *Plumbago wissii* known from Königstein and on Aigub (2,550 masl), as well as a possible new species of *Cyathula*. Unfortunately, no taxonomic research is currently being undertaken on genera that may have endemic species on these highest peaks. A subspecies of *Lithops gracilidelineata* occurring at 2,300–2,400 masl and previously recorded as endemic is now, according to recent taxonomic work (Jainta 2019), considered part of a more widespread species.

A Brandberg endemic not at the summit, but at high elevations is *Adromischus schuldtianus* subsp. *brandbergensis. Hermannia merxmuelleri* and the more common *Ruellia brandbergensis* can be found lower down. Another endemic almost at the base is *Eragrostis aristata* and although few specimens have been collected to date, they are restricted to the mountain.

Moisel (1982) noted altitudinal variations of plants in Orabeswand and Craven and Craven (2000) expanded this survey to other parts of the mountain. Certain species, for example *Ruellia brandbergensis*, were found to occur at higher elevations on the northern side of the mountain (e.g., at Sonsusib) than on the southern side.

Erongo Mountains

A geophyte *Afrosolen erongoensis*, only known from the type collection, and a succulent *Lithops werneri* are the only two species endemic to the Erongo Mountains on Farm Ameib. The dwarf shrub *Corchorus merxmuelleri* also occurs on the Brandberg, while the shrub *Dombeya rotundifolia* var. *velutina* is probably only found here and on the Naukluft Mountains. Eight other highland endemics on the Erongo Mountains co-occur with a few other mountains.

Spitzkoppe

There are no endemic species restricted to the Spitzkoppe. This is possibly because Spitzkoppe is mainly a granite rock unable to support many plants. It does share *Nicotiana africana* and *Euphorbia monteiroi* subsp. *brandbergensis* with the Brandberg and Erongo Mountains.

Gamsberg

The Gamsberg is most well known for having an endemic shrub *Euryops walterorum* that occurs in numbers only on the plateau. Species diversity varies with aspect and elevation and the plateau is not as diverse as the slopes. More endemic species, like *Othonna brandbergensis*, are recorded on the Gamsberg Pass which runs down the escarpment, a little distance from the actual mountain tabletop. Highland endemics that occur here are also found mostly on the Brandberg to the west and the Auas Mountains to the east.

Naukluft Mountains

There are probably five plants endemic to the Naukluft range. *Anginon streyi* is found just below the plateau, while *Commicarpus squarrosus* var. *fruticosus* has also only been found once on the mountain slope and *Aloe argenticauda* is also not on highest areas. *Jamesbrittenia pilgeriana* and *Sisymbrium dissitiflora* appear to be limited to this mountain at about 1,500 masl. Another 14 species endemic to the highlands of Namibia also occur here.

Tirasberge

Two of the three plants restricted to the Tirasberge are stem succulents of the Apocynaceae family, namely *Larryleachia tirasmontana* and *Huernia plowesii*, while *Hoodia ruschii* is also found at Tsaris. *Namaquanula bruynsii*, a geophyte in family Amaryllidaceae, has rarely been collected and then from 1,850 masl. Four other woody highland endemics occur here and co-occur on the Gamsberg and the Naukluft and Auas mountains. There are more succulent species here than on other highlands and interestingly none of these occurs on the Brandberg or Groot Karasberge as well.

Groot Karasberge

There are five taxa endemic to the Groot Karasberge: *Adromischus schuldtianus* subsp. *juttae, Hoodia juttae, Panicum pearsonii, Stapelia pearsonii* and *Tulbaghia karasbergensis. Nemesia karasbergensis* has only been collected twice and possibly further south, while the collecting data for *Crassula ausensis* subsp. *giessii* may be erroneous. There are also very few collections of *Euphorbia baliola*, for which no mention of elevation is given.

Auas Mountains, Khomas Hochland and Otjihaveraberge (Neudamm Hochland)

There are a few highland endemics restricted to this area. However, the plateau needs further evaluation which is likely to increase the numbers of endemics here. *Hibiscus discophorus* is on the Auas Mountains and in the Otjihavera area, while *Caroxylon mirabile* (although probably at lower elevations) and *Afrosolen avasmontanus* seem to be only on the Khomas Hochland and plateau. *Heteromorpha papillosa* collections need to be verified, but it appears this species also only occurs here. *Ebracteola montis-moltkei* is also found on the Gamsberg.

Group 2: Awasibberge, Central Group, Hakosberge, Naos, and Nubib and Tsaris Mountains

Most of these highlands (Figure 2) have their own restricted endemic species. For example, *Jamesbrittenia giessii* only occurs on Mount Etjo in the Central Group, and *Jamesbrittenia fimbriata* is on Nubib Mountains. There are also some that are on other central and southern highlands, like *Ruschia axthelmiana* which grows on the Naos and on the Gamsberg escarpment. *Cucumis clavipetiolatus* is found on the Nubib Mountains and on Brandberg, while *Othonna brandbergensis* which is recorded as growing at elevations above 1,640 masl, occurs on Satanskop, the Awasibberge, the Brandberg and the Gamsberg. *Searsia volkii* and *Commicarpus squarrosus* var. *fruticosus* also occur on the Tsaris Mountains, as well as the Naukluft Mountains. The widespread but key central highland species, *Lightfootia dinteri*, is also found on Etjo and Naos mountains. Some species on the Etjo Mountains are also found on the Waterberg.

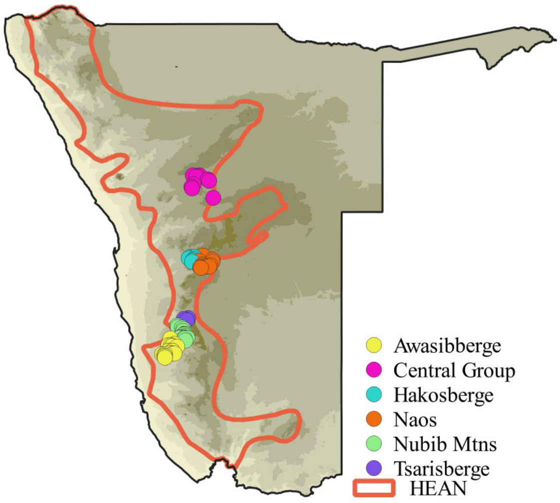

Figure 2: *Awasibberge, Central Group, Hakosberge, Naos, Nubib and Tsaris Mountains making up Group 2 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

Group 3: Baynes, Otjihipa and Zebra mountains

Eight range-restricted species have been recorded for this mountain group (Figure 3). No endemics from here are found further south in Namibia, but two have been found in Angola and more are expected. Recent research on Omavanda Mountain has increased the number of range-restricted plants, however, more fieldwork in Angola is needed for a proper evaluation of the taxonomy and ranges. Growth forms of plants include succulents, such as *Baynesia lophophora, Stapelia remota, Aloe huntleyana* and *A. omavandae*, to perennials, like *Aeollanthus rydingianus.* The shrub, *Hibiscus merxmuelleri* has only been collected twice and might occur only at lower elevations. *Maerua kaokoensis* is included in this group, but it may be found at lower elevations.

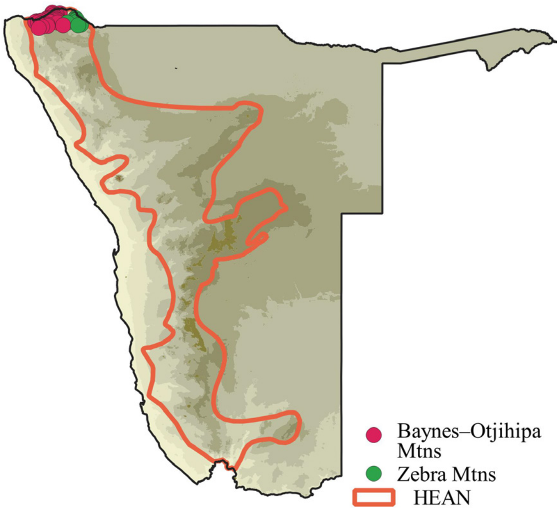

Figure 3: *Baynes, Otjihipa and Zebra mountains making up Group 3 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

Group 4: Huns Mountains – Orange River valley

There are several interesting endemic species around the Huns Mountains and, to the east, the arid mountains along the Orange River (Figure 4). A few monocotyledons have been found on Sonberg, with an elevation of nearly 1,000 masl, but the highest recorded is *Xenoscapa grandiflora* on Hohenzollern, at about 1,500 masl. Very few monocotyledons occur at high elevations in this area, although some are also found in the Aus vicinity and on the Huib-Hoch Plateau, but these need to be verified as highland endemics. On the western side of the Huns Mountains, plants may be influenced by mist from the sea, while the eastern side is drier and very rugged with low rainfall. Most of the species here are woody, but often with succulent leaves. They are mostly dwarf shrubs and shrubs, with some geophytes and herbs. Many may remain leafless for years, but the vegetation transforms completely after rain, especially after an abnormally good rainy season when a completely different complement of species may grow. Succulent species from the succulent desert in the west have even been recorded on the summit of the Huns Mountains after exceptionally high rains.

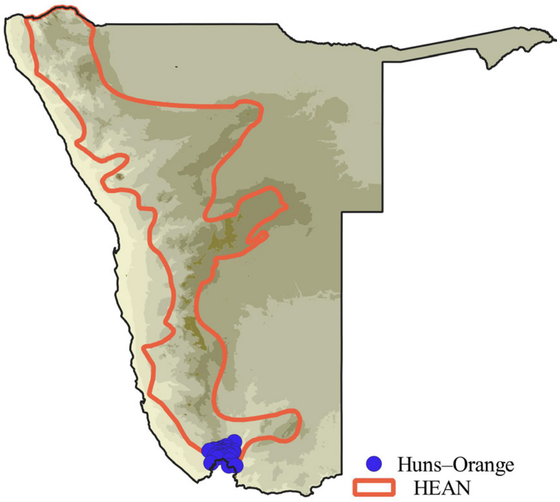

Figure 4: *Huns Mountains and the Orange River valley making up Group 4 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

Group 5: Waterberg and Otavi Mountains

There are at least four endemics occuring only on the Otavi Mountains (Figure 5), namely *Jamesbrittenia dolomitica, Elephantorrhiza schinziana, Brachystelma recurvatum* and *Euphorbia otavibergensis.* Three plants are endemic to the Waterberg: *Eriospermum citrinum, Jamesbrittenia acutiloba* and *Helichrysum fleckii* subsp. *volkii*. These two areas also share a few endemics such as *Dintera pterocaulis*, *Barleria jubata*, *Decorsea dinteri*, *Eriosema harmsiana* and *Crassocephalum coeruleum*. Genus *Jamesbrittenia* is significant, and some extend into Angola.

Although a few wide-ranging highland endemics found on the Waterberg (Figure 5) and Otavi Mountains may also be found further south on the Brandberg, Groot Karasberge and Tiras Mountains, there are notably more co-occurrences on the Auas mountains, such as *Lobelia hereroensis*, which may also be in the Erongo Mountains. No Otavi Mountains or Waterberg endemics have been found on the Baynes Mountains, Khomas Hochland or Naukluft Mountains.

Group 6: Southwestern inselbergs

Mountains in the former Sperrgebiet – Aurusberg, Boegoeberg, Klinghardt Mountains, Kowisberge and Obib (Figure 6) – are more botanically diverse than the surrounding plains and, although excluded from the highlands and escarpments of Angola and Namibia (HEAN) defined by Mendelsohn and Huntley (2023) due to their low elevations, they are worth mentioning. No endemic is confined to just one mountain, but there are localised endemic plants on Aurusberg, Boegoeberg and the Klinghardt

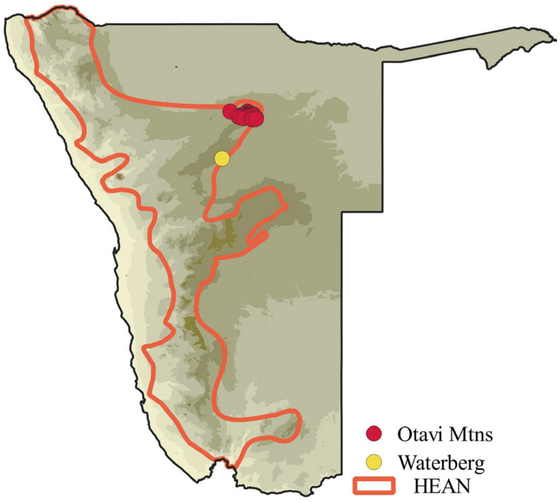

Figure 5: *Waterberg and Otavi Mountains making up Group 5 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

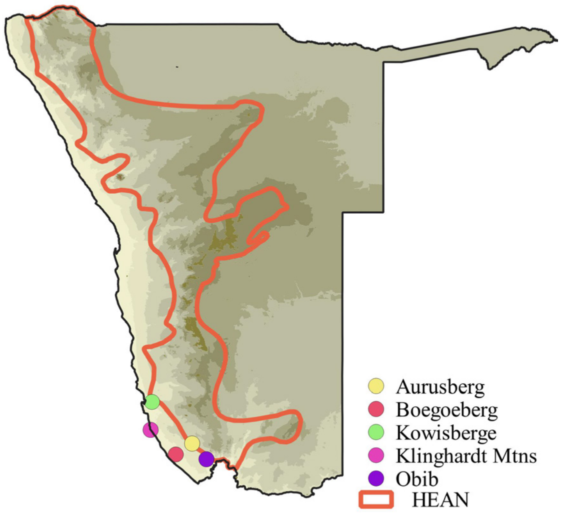

Figure 6: *Inselbergs in the southwest making up Group 6 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

Mountains. Unfortunately, despite a great deal of botanical research in the area, elevation records are limited, and certain mountains still need to be better explored to compare the floras. At the summit of Aurusberg, *Crassula aurusbergensis* occurs, but it is not limited to this mountain. *Senecio herreianus* seems to be restricted to Boegoeberg, but this may be because of limited collecting on other mountains.

Group 7: Escarpments and plateaus

Some endemic species are known to be restricted to escarpments and plateaus (Figure 7), but these areas need further study before species can be listed. Evaluation of possible endemics is hampered by a lack of precise location and especially elevation data.

Some known endemics include *Lotononis pallidirosea* in the Schwarzrand and *Leobordea mirabilis* that has only been collected three times in the Aus vicinity. This latter area has several localised endemics, probably because of the combined effects of substrate, coastal mist and cool air preventing plants here from reaching further inland.

Group 8: Highlands without known endemic flora

Between the Otjihipa–Baynes mountains in the north and the Brandberg in the south there are scattered smaller mountains and inselbergs with numerous western-flowing rivers and tributaries in between. These include those shown in Figure 8 – Brukkaros Mountain, Dikke Willem, the Etendeka Mountains, the Paresis Mountains, Rantberg, Rooirand, and the Huab River outliers, those around the middle Ugab River, Otjikondavirongo and Swakop and Khan rivers. Collection data for many Namibian endemic species in the area were analysed and the results show that the endemics grow on the slopes of the mountains, as well as on the plains. No endemics have been recorded from the highest peaks – Okonjeje (in the middle Ugab group) and Omuhiva (in the Otjikondavirongo Mountains) – even though they are over 1,800 masl. The most probable explanation for this is that the scattered individual highlands making up the groups are relatively low and the many catchment areas allow for dispersal of plants from higher ground to the surrounding lower elevations. This is in stark contrast to the area south of the Gamsberg where there are few rivers and localised endemics do occur.

The Etendeka range is made up of basalts and, like the basalt on the Brandberg, they bear no range-restricted species. No highland endemics have been found on Brukkaros, Dikke Willem or Omatako inselbergs, or co-occurring elsewhere.

The Klein Karasberge were well collected by Dinter in the early 1920s and several interesting species occur here, but his locality data are limited and imprecise, and no information on elevation was given. This area needs more fieldwork to evaluate its flora and assess whether any are endemic to highlands.

Noteworthy mountains

Some mountains mentioned in the text are mapped separately because they are of importance, either for having an interesting complement of species or, in three cases mentioned in Group 8 (Okonjeje and Omuhiva) for having no endemic taxa collected there yet, despite their high elevations. See Figure 9.

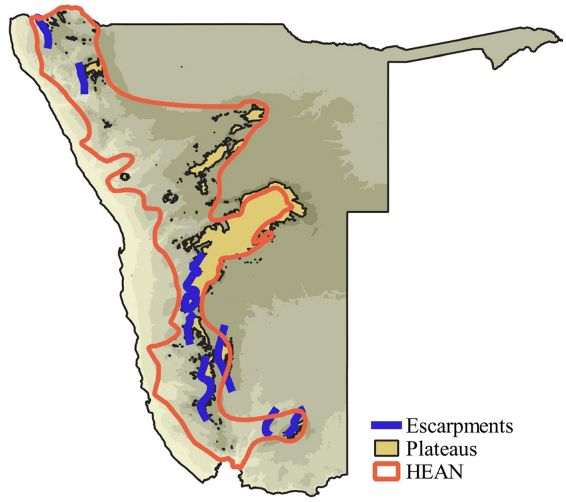

Figure 7: *Escarpments and plateaus making up Group 7 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

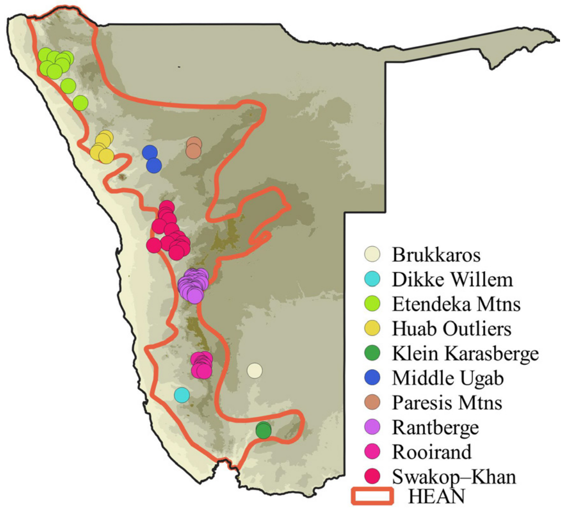

Figure 8: *Highlands without known endemic flora making up Group 8 of the highland areas of Namibia. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

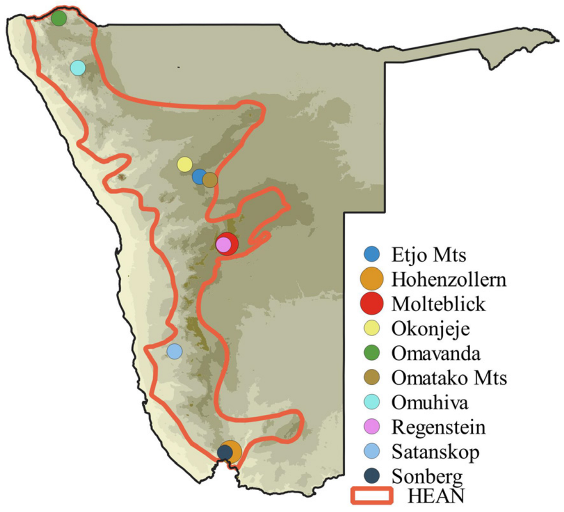

Figure 9: *Noteworthy mountains mentioned in the text. (HEAN is the area of highlands and escarpments defined by Mendelsohn and Huntley (2023).)*

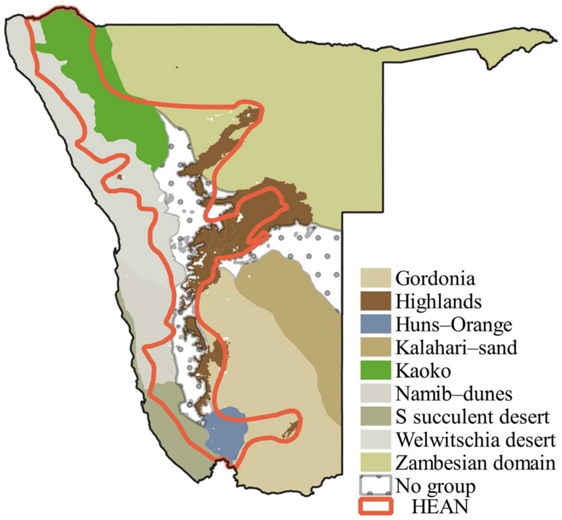

Figure 10: *The floristic groups of Namibia, of which three fall within Namibia's highlands and escarpments (HEAN) defined by Mendelsohn and Huntley (2023).*

FLORISTIC GROUPS

Three of the nine floristic groups identified (Craven 2009) fall within the HEAN (Figure 10). Each group is defined by having endemic taxa and co-occurring species found here and not elsewhere in Namibia, and by climatic and topographical features. The Highlands group is made up of taxa occurring over a disjointed landscape over 1,500 masl with summer rainfall. The Huns–Orange group is 900–1,500 masl, rainfall is low and erratic, and the area is crossed by the Konkiep, Fish and Orange rivers. The Kaoko group is mainly 1,200–1,500 masl and has annual summer rainfall up to 350 mm in the eastern parts.

Taxa only endemic to higher elevations in these highlands are discussed in this paper. Many more species are endemic to these floristic groups, but they are not included here as they also occur at lower elevations; they will, however, be useful in understanding possible movements and relationships of the endemic species. See Figure 10.

ORIGINS AND EVOLUTIONARY RELATIONSHIPS AND PATTERNS

There is some evidence for the relationships and the age of the flora of Namibia's highlands from studies of present plant localities and palaeopalynological research. Studies of fossil pollen by Scott *et al.* (1991) suggest a close connection between the flora of the Khomas Hochland and the Highveld of South Africa. This is confirmed by present locality data, for example *Passerina montana* and *Seriphium plumosum*. Although not endemic, both are only found at the summit of Moltkeblick on the Auas Mountains, with *Seriphium plumosum* (previously *Stoebe*) also on Regenstein in Namibia but they also occur on the eastern escarpment in South Africa and maybe on the Angolan Planalto. The occurrence of *Passerina* in Namibia was considered to represent a relict of the Cape Floristic Region (Rennie 1936) until Bredenkamp and van Wyk (2006) identified specimens as *P. montana*, a species not found in the Cape. They postulated that both species originated in the Cape Floristic Region and formed part of a previously wider northern temperate Afromontane grassland-dominated vegetation during the Quaternary of which relicts remained (Bredenkamp & van Wyk 2006). The disjunctions observed today are believed to be due to environmental changes. *Passerina* pollen has also been identified in hyrax middens in the Brandberg (Scott *et al.* 2004) although there are no extant plants now.

While taxa at elevations above 1,700 masl are related to the Great Escarpment of southern Africa, those above 1,500 masl are related to the highlands of the eastern parts of South Africa (Bredenkamp & van Wyk 2006). For example, *Chasmatophyllum musculinum* which occurs on the Groot Karasberge is disjunct to the Free State Province of South Africa. The distribution of genus *Cineraria*, which stretches from the mountainous areas of Namibia and southern Angola, to much higher elevations in the mountains of tropical East Africa and the Drakensberg in South Africa (Cron *et al.* 2008) may also provide some interesting insights into the origins of highland taxa. However not all taxa found only on one mountain in Namibia and then outside the country may provide clues to the evolutionary past as some may be present due to human use, for example, *Erythrophysa alata* in the Naukluft Mountains and *Trema orientalis* in the Erongo Mountains.

One study that did show patterns of endemism that point to the concept of highland refugia is that of the genus *Lotononis*. Subsequent speciation in and around the centres identified in the study are thought to explain the localised distribution of the species and most of the sections (van Wyk 1991).

The *Nicotiana* genus is known from semi-arid habitats in Australia and South America, and the species in Namibia is now considered to be most closely related to a group from Australia and New Caledonia and may be an endemic relict of considerable age (Knapp *et al*. 2004). Tobacco is also a *Nicotiana* species, and the genus has been well researched, however, this species, *N. africana*, has caused some headaches and information about its origins in Namibia are still debated.

Not many molecular studies have included Namibian taxa and no highland endemics have been evaluated. Although research on a few widespread genera points to the oldest taxa in Namibia occurring in the vicinity of the Huns Mountains (Craven 2009), none of these are highland species.

Plant species distributions contribute greatly towards understanding origins and evolutionary relationships, especially in the absence of other mechanisms. It is possible that the Groot Karasberge would have been included in the study of the Great Escarpment of southern Africa (Clark *et al*. 2011) if the authors had considered the co-occurring taxa.

CONSERVATION, AND THREATENED AND PROTECTED SPECIES

Highland species protected by the Forest Act (No. 21 of 2001) and/or the Nature Conservation Ordinance (No. 4 of 1975) and amendments, CITES and/or have IUCN threat categories are listed in Appendix 1. Over 22 species are protected. One plant has been evaluated as 'Endangered' and three as 'Vulnerable' using the IUCN categories. About 14 are of 'Least Concern', but 12 are listed as being 'Data Deficient'.

Fires are possibly the most serious threat to endemic highland plants. Fires reach the highest areas and directly affect the diversity and structure of the surroundings. One of the biggest problems is the misplaced belief that fires are natural and good for the veld in all areas of Namibia. The reality is that some species, like *Dichrostachys cinerea*, the well-known encroaching sickle bush spreads rapidly after fire and can take over the habitats of local species, including endemics. No research has to date been carried out on the effects of fire on seed germination, establishment, resprouting or recovery of indigenous plants and there are no studies on monitoring burnt areas for taxa diversity changes.

Some highland endemics are sought after by collectors, but many are not charismatic and are at risk rather because of a lack of appreciation of their value. Fences preventing game movements and overstocking of livestock and game, as well as the use of helicopters to supply water, food and equipment so that increased numbers of people can reach the summit of sensitive areas, like the Brandberg and Otjihipa Mountains, threaten the endemic flora.

Mountaintops are commonly used for tele-communication stations and even water reservoirs. Environmental impact assessments, which are often based on desk-top studies, usually miss the highland endemics because they seldom include a well-trained botanist that can correctly identify taxa and threats.

GAPS AND PRIORITIES

Further studies are needed to verify information and fill in knowledge gaps about Namibia's highland plant endemics. This will require sound taxonomy and accurate and complete locality data. This overview has highlighted the lack of elevation data on many herbarium specimens, as well as accurate locality and habitat data, especially for the escarpments and plateaus.

Following further examination of taxa, specimens and literature, targeted fieldwork identified from this review is required. Closer examination of collections and identifications made in years of outstanding rainfalls in Namibia, e.g., in 1963, 1974, 2000, 2010 and 2022, is important. Some endemics have only been collected after episodic rain events which may occur once a decade or century. These conditions may also have resulted in variations of true species that are now described as new taxa.

Very little is known about mosses and ferns restricted to highlands, and the number of endemics is not known. Furthermore, although lichens are not plants, they are very diverse and important organisms that need to be highlighted for further study. In Namibia, lichen investigations have focused on the Namib Desert, and the Waterberg is the only mountain that has been considered in more detail. Lichens may have been the first organisms to colonise the Waterberg sandstone and could be centuries old (Wessels 1989). At least one, *Acarospora elegans* is known to be endemic. It grows on south-facing vertical cliffs in an unusually shaded spot for this genus. Although most lichens known are cosmopolitan, more endemic species are expected to be added to the list after further study.

The relationships and origins of some plant species have been suggested based on distribution patterns inside and outside the country. Possible reasons for the evolution of other species on highlands still need to be explored and defined. The view that species evolved on these highlands when climatic changes occurred that divided existing populations may not be true for plants. It is important that the differences between the biota in a multidisciplinary study of this nature be acknowledged.

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***Appendix 1:** Plant species endemic to highlands in Namibia.*

Taxon	Family	Life form	Protection[a]	IUCN[b]	CITES[c]	Status[d]	Highland[e]
Adromischus schuldtianus subsp. *brandbergensis*	Crassulaceae	shrublet	P			E	BB
Aeollanthus rydingianus	Lamiaceae	shrublet				N	BO, Huila
Afrosolen avasmontanus	Iridaceae	geophyte				E	KH
Afrosolen erongoensis	Iridaceae	geophyte				E	E
Aloe argenticauda	Asphodelaceae	aloe	P	LC	II	E	N
Aloe huntleyana	Asphodelaceae	aloe	P		II	E	BO
Aloe kaokoensis	Asphodelaceae	aloe	P		II	E	BO
Aloe meyeri	Asphodelaceae	aloe	P		II	N	HO
Aloe omavandae	Asphodelaceae	aloe	P		II	E	BO
Aloe pavelkae	Asphodelaceae	aloe	P		II	E	HO
Aloe viridiflora	Asphodelaceae	aloe	P	LC	II	E	A, BB, G
Anginon streyi	Apiaceae	shrub				E	N
Anisopappus brandbergensis	Asteraceae	shrublet				E	BB
Barleria jubata	Acanthaceae	shrublet		VU B2		E	OW
Barleria lanceolata subsp. a	Acanthaceae	shrublet		LC		E	AV
Baynesia lophophora	Apocynaceae	stem succulent				E	BO
Brachystelma pruniosum	Apocynaceae	geophyte				N	BO
Brachystelma recurvatum	Apocynaceae	geophyte		DD		N	OW
Calobota obovata	Leguminosae	shrub		DD		E	A, G, TI
Caroxylon mirabile	Amaranthaceae	shrublet		DD		E	KH
Commiphora otjihipana	Burseraceae	tree				E	BO
Commicarpus squarrosus var. *fruticosus*	Nyctaginaceae	shrublet				E	N, TS
Corchorus merxmuelleri	Malvaceae	shrublet				E	BB, E
Cordylogyne argillicola	Apocynaceae	geophyte		EN		E	A, E
Crassocephalum coeruleum	Asteraceae	herb				E	OW
Crassula aurusbergensis	Crassulaceae	succulent	P			E	SW inselbergs
Crassula ausensis subsp. *giessii*	Crassulaceae	succulent	P			E	K
Crotalaria aurea	Leguminosae	herb		DD		E	A, G
Crotalaria kolbergii	Leguminosae	suffrutex		DD		E	KH, TI, Escarp
Cucumis clavipetiolatus	Cucurbitaceae	creeper				E	BB, G, Nubib
Cyphostemma bainesii	Vitaceae	tree	F	LC		E	G, T
Cyphostemma juttae	Vitaceae	tree	F	LC		N	O, Angola
Decorsea dinteri	Leguminosae	twiner				E	OW
Dintera pterocaulis	Scrophulariaceae	herb		NT		E	OW
Dombeya rotundifolia var. *velutina*	Malvaceae	shrub or tree		LC		E	E, N
Ebracteola montis-moltkei	Aizoaceae	succulent	P			E	A, G
Elephantorrhiza schinziana	Leguminosae	shrub		DD		E	OW
Eragrostis aristata	Poaceae	graminoid				E	BB
Eriocephalus klinghardtensis	Asteraceae	shrublet				E	SW inselbergs
Eriosema harmsiana	Leguminosae	geophyte				E	OW
Eriospermum citrinum	Eriospermaceae	geophyte				E	OW
Eriospermum strachaniae	Eriospermaceae	geophyte				E	HO
Eriospermum volkmanniae	Eriospermaceae	geophyte		DD		E	OW
Euphorbia baliola	Euphorbiaceae	stem succulent		DD	II	E	K
Euphorbia cornelliae	Euphorbiaceae	herb			II	E	HO
Euphorbia monteiroi subsp. *brandbergensis*	Euphorbiaceae	stem succulent		LC	II	E	BB, E, SP
Euphorbia otavibergensis	Euphorbiaceae	tree			II	E	OW
Euryops walterorum	Asteraceae	shrub				E	G
Felicia gunillae	Asteraceae	shrublet				E	BB
Haemanthus avasmontanus	Amaryllidaceae	geophyte		NT		E	A
Helichrysum fleckii subsp. *volkii*	Asteraceae	shrublet				E	OW

Taxon	**Family**	**Life form**	**Protection**[a]	**IUCN**[b]	**CITES**[c]	**Status**[d]	**Highland**[e]
Hermannia merxmuelleri	Malvaceae	shrub				E	BB
Heteromorpha papillosa	Apiaceae	shrub				E	OW, KH, A
Hibiscus discophorus	Malvaceae	herb				E	A, Otjihavera
Hibiscus merxmuelleri	Malvaceae	shrub				E	BO
Hoodia juttae	Apocynaceae	stem succulent	P	LC		E	K
Hoodia ruschii	Apocynaceae	stem succulent	P			E	TI, TS
Huernia plowesii	Apocynaceae	stem succulent	P	LC		E	TI
Hymenodictyon kaokoensis	Rubiaceae	shrub		VU D1D2		E	BO
Indigofera merxmuelleri	Leguminosae	shrub				E	HO low
Jamesbrittenia acutiloba	Scrophulariaceae	shrublet				E	OW
Jamesbrittenia dolomitica	Scrophulariaceae	shrublet				E	OW
Jamesbrittenia fimbriata	Scrophulariaceae	shrublet				E	Nubib
Jamesbrittenia fragilis	Scrophulariaceae	herb				E	OW, A, E
Jamesbrittenia giessii	Scrophulariaceae	shrublet				E	Central group
Jamesbrittenia heucherifolia	Scrophulariaceae	shrublet				N	BO
Jamesbrittenia lyperioides	Scrophulariaceae	herb				E	A, G, N
Jamesbrittenia pilgeriana	Scrophulariaceae	herb				E	N
Larryleachia tirasmontana	Apocynaceae	stem succulent	P	LC		E	TI
Lavrania haagnerae	Apocynaceae	stem succulent	P			E	Escarp
Lightfootia dinteri	Campanulaceae	shrublet				E	BB, E, G, KH, N, K
Lithops werneri	Aizoaceae	succulent	P	VU D2		E	E
Lobelia hereroensis	Campanulaceae	herb		VU B1ab (iii)c(iv)		E	E, OW
Lotononis pallidirosea	Leguminosae	herb		DD		E	A, N, Escarp
Maerua kaokoensis	Capparaceae	tree				E	BO
Microloma hereroense	Apocynaceae	twiner				E	BB, G, N, S
Moraea graniticola	Iridaceae	geophyte				E	AV
Namacodon schinzianum	Campanulaceae	shrublet		LC		E	A, E, G, N
Namaquanula bruynsii	Amaryllidaceae	geophyte				E	TI
Nemesia karasbergensis	Scrophulariaceae	herb				E	K
Nicotiana africana	Solanaceae	shrub		LC		E	BB, E, SP
Nidorella nordenstamii	Asteraceae	herb				E	BB
Ocimum sebrabergensis	Lamiaceae	shrub		VU D1		E	BO
Othonna brandbergensis	Asteraceae	suffrutex				E	BB, G, KH, Awasib
Oxalis schaeferi	Oxalidaceae	geophyte				E	AV
Panicum pearsonii	Poaceae	graminoid				E	K
Pelargonium vanderwaltii	Geraniaceae	shrublet				E	BO
Pentatrichia rehmii subsp. *avasmontana*	Asteraceae	shrublet		LC		E	A, KH, G, W
Pentatrichia rehmii subsp. *rehmii*	Asteraceae	shrublet		VU D1		E	O
Pentzia tomentosa	Asteraceae	suffrutex				E	BB
Plumbago hunsbergensis	Plumbaginaceae	shrub				E	HO
Plumbago wissii	Plumbaginaceae	suffrutex				E	BB
Ruellia brandbergensis	Acanthaceae	shrub				E	BB
Ruschia axthelmiana	Aizoaceae	succulent	P			N	A, KH, K, Naos
Schizostephanus gossweileri	Apocynaceae	shrub				N	BO
Searsia volkii	Anacardiaceae	shrub or tree				E	N, Rantberg
Senecio herreianus	Asteraceae	herb				E	SW inselbergs
Senecio windhoekensis	Asteraceae	herb				E	A, G, KH
Sisymbrium burchellii var. *dinteri*	Brassicaceae	herb		DD		E	A, N

Taxon	Family	Life form	Protection[a]	IUCN[b]	CITES[c]	Status[d]	Highland[e]
Sisymbrium dissitiflora	Brassicaceae	herb		DD		E	N
Stachys dinteri	Lamiaceae	herb				E	N, TI
Stapelia pearsonii	Apocynaceae	stem succulent	P			E	K
Stapelia remota	Apocynaceae	stem succulent	P			E	BO
Strumaria speciosa	Amaryllidaceae	geophyte				N	HO
Tetradenia kaokoensis	Lamiaceae	shrublet				E	BO
Thesium xerophyticum	Thesiaceae	parasite or hemi-				E	OW, A, G
Trachyandra ensifolia	Asphodelaceae	geophyte				E	HO, Escarp
Tulbaghia karasbergensis	Amaryllidaceae	geophyte				E	K
Xenoscapa grandiflora	Iridaceae	geophyte				E	HO

Taxa mentioned in the text, but are not highland endemics:

Taxon	Family
Chasmatophyllum musculinum	Aizoaceae
Erythrophysa alata	Sapindaceae
Manuleopsis dinteri	Scrophulariaceae
Passerina montana	Thymelaeaceae
Seriphium plumosum	Asteraceae
Tetradenia brevispicata	Lamiaceae
Trema orientale	Cannabaceae

[a] Protection under: F = Forestry legislation; and P = Nature Conservation Ordinance.

[b] IUCN category: DD = Data Deficient; EN = Endangered; LC = Least Concern; NT = Not Threatened; and VU = Vulnerable.

[c] CITES: II = Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

[d] Status: E = endemic; and NE = near-endemic.

[e] Highland: A = Auas Mountains; AV = Aus vicinity; BB = Brandberg; BO = Baynes–Otjihipa; E = Erongo Mountains; Escarp = escarpment; G = Gamsberg; HO = Huns Mountains – Orange River valley; K = Karasberge; KH = Khomas Hochland; N = Naukluft Mountains; O = Otavi Mountains; OW = Otavi Waterberg; SP = Spitzkoppe; SW inselbergs = southwestern inselbergs; TI = Tirasberge; TS = Tsaris Mountains; and W = Waterberg.

Appendix 2: *Highlands in Namibia and their complement of endemic species. An asterisk (*) indicates that a species is restricted to the mountain indicated.*

Highland area	**Endemic species**	
1. Central and southern highlands		
Brandberg	*Adromischus schuldtianus* subsp. *brandbergensis** *Aloe viridiflora* *Anisopappus brandbergensis** *Corchorus merxmuelleri* *Cucumis clavipetiolatus* *Eragrostis aristata** *Euphorbia monteiroi* subsp. *brandbergensis* *Felicia gunillae**	*Hermannia merxmuelleri** *Lightfootia dinteri* *Microloma hereroense* *Nicotiana africana* *Nidorella nordenstamii** *Othonna brandbergensis* *Pentzia tomentosa** *Plumbago wissii** *Ruellia brandbergensis**
Erongo	*Afrosolen erongoensis** *Corchorus merxmuelleri* *Cordylogyne argillicola* *Dombeya rotundifolia* var. *velutina* *Euphorbia monteiroi* subsp. *brandbergensis*	*Jamesbrittenia fragilis* *Lightfootia dinteri* *Lithops werneri** *Lobelia hereroensis* *Nicotiana africana*
Spitzkoppe	*Euphorbia monteiroi* subsp. *brandbergensis* *Nicotiana africana*	*Microloma hereroense*
Gamsberg	*Aloe viridiflora* *Calobota obovata* *Crotalaria aurea* *Cucumis clavipetiolatus* *Cyphostemma bainesii* *Ebracteola montis-moltkei* *Euryops walterorum**	*Jamesbrittenia lyperioides* *Lightfootia dinteri* *Microloma hereroense* *Othonna brandbergensis* *Pentatrichia rehmii* subsp. *avasmontana* *Senecio windhoekensis* *Thesium xerophyticum*
Naukluft	*Aloe argenticauda** *Anginon streyi** *Commicarpus squarrosus* var. *fruticosus* *Dombeya rotundifolia* var. *velutina* *Jamesbrittenia lyperioides* *Jamesbrittenia pilgeriana** *Lightfootia dinteri*	*Lotononis pallidirosea* *Microloma hereroense* *Searsia volkii* *Sisymbrium burchellii* var. *dinteri* *Sisymbrium dissitiflora** *Stachys dinteri*
Tiras Mountains	*Calobota obovate* *Crotalaria kolbergii* *Cyphostemma bainesii* *Hoodia ruschii*	*Huernia plowesii** *Larryleachia tirasmontana** *Namaquanula bruynsii** *Stachys dinteri*
Karasberge	*Crassula ausensis* subsp. *giessii** *Euphorbia baliola** *Hoodia juttae** *Lightfootia dinteri* *Nemesia karasbergensis**	*Panicum pearsonii** *Ruschia axthelmiana* *Stapelia pearsonii** *Tulbaghia karasbergensis**
Auas Mountains, Khomas Hochland, Otjihaveraberge	*Afrosolen avasmontanus** *Aloe viridiflora* *Calobota obovata* *Caroxylon mirabile** *Cordylogyne argillicola* *Crotalaria aurea* *Crotalaria kolbergii* *Ebracteola montis-moltkei* *Haemanthus avasmontanus** *Heteromorpha papillosa*	*Hibiscus discophorus** *Jamesbrittenia fragilis* *Jamesbrittenia lyperioides* *Lotononis pallidirosea* *Namacodon schinzianum* *Othonna brandbergensis* *Pentatrichia rehmii* subsp. *avasmontana* *Ruschia axthelmiana* *Senecio windhoekensis* *Sisymbrium burchellii* var. *dinteri*
2. Group of highlands		
Tsaris Mountains	*Commicarpus squarrosus* var. *fruticosus*	*Cucumis clavipetiolatus*
Nubib	*Hoodia ruschii*	*Jamesbrittenia fimbriata**
Central Group, Etjo mountains	*Jamesbrittenia giessii*	

Highland area	**Endemic species**	
Awasibberge	*Othonna brandbergensis*	
Naos	*Ruschia axthelmiana*	
Rantberg	*Searsia volkii*	
3. Baynes, Otjihipa and Zebra mountains		
	Aeollanthus rydingianus *Aloe huntleyana** *Aloe kaokoensis** *Aloe omavandae** *Baynesia lophophora** *Brachystelma pruniosum** *Commiphora otjihipana** *Hibiscus merxmuelleri**	*Hymenodictyon kaokoensis** *Jamesbrittenia heucherifolia** *Maerua kaokoensis** *Ocimum sebrabergensis** *Pelargonium vanderwaltii** *Schizostephanus gossweileri** *Stapelia remota** *Tetradenia kaokoensis**
4. Huns Mountains–Orange River valley		
	*Aloe meyeri** *Aloe pavelkae** *Eriospermum strachaniae** *Euphorbia cornelliae** *Indigofera merxmuelleri*	*Plumbago hunsbergensis** *Strumaria speciosa** *Trachyandra ensifolia* *Xenoscapa grandiflora**
5. Otavi Mountains and Waterberg		
	*Acarospora elegans** *Barleria jubata** *Brachystelma recurvatum** *Crassocephalum coeruleum** *Cyphostemma juttae* *Decorsea dinteri** *Dintera pterocaulis** *Elephantorrhiza schinziana** *Eriosema harmsiana** *Eriospermum citrinum** *Eriospermum volkmanniae**	*Euphorbia otavibergensis** *Helichrysum fleckii* subsp. *volkii** *Heteromorpha papillosa* *Jamesbrittenia acutiloba** *Jamesbrittenia dolomitica** *Jamesbrittenia fragilis* *Lobelia hereroensis* *Pentatrichia rehmii* subsp. *avasmontana* *Pentatrichia rehmii* subsp. *rehmii** *Thesium xerophyticum*
6. Southwestern inselbergs		
	*Crassula aurusbergensis**	*Senecio herreianus**
7. Escarpments		
	Barleria lanceolata subsp. a * *Crotalaria kolbergii* *Lavrania haagnerae*	*Lotononis pallidirosea* *Moraea graniticola** *Trachyandra ensifolia*

A botanical assessment of Mt Namba, Cuanza-Sul, Angola: an isolated mountain towards the northwestern limits of the Great Escarpment of southern Africa

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-goyder

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ABSTRACT

A rapid assessment of Mt Namba recorded 271 plant taxa including six new records for Angola and 22 new records for the province of Cuanza-Sul. The mountain has the most extensive tracts of intact Afromontane forest in the country amid a mosaic of species-rich montane rocky grassland and miombo woodland at lower elevations. Range extensions of two shrubby species of Compositae reveal floristic affinities with the discrete elevated escarpment to the west of Lubango in Huíla Province nearly 400 km south of Mt Namba. We suggest that the largely intact ecological units we observed on Mt Namba might inform speculation as to the potential vegetation of the Serra da Chela which, due to local population pressures, is now mostly devoid of woody vegetation. The extent of threatened Afromontane forest vegetation in Angola and the presence of local endemic *Barleria namba* described from the mountain, qualify Mt Namba as an Important Plant Area for Angola. It has already been designated an Important Bird Area for the country. *Araujia sericifera*, an alien species of conservation concern due to its potential as an invasive, is recorded from Angola for the first time.

Keywords: Angola, endemism, floristic diversity, highland, Important Bird Area, Important Plant Area, invasive plants, Mt Namba

INTRODUCTION

Mt Namba is located c. 30 km west of Cassongue in Cuanza-Sul Province and around 80 km to the north of Angola's highest mountain, Serra do Môco, in neighbouring Huambo Province. Huntley (2019, Mendelsohn & Huntley 2023) refers to this region as the Marginal Mountain Chain which comprises, "residual mountain lands, mostly at 1,800–2,200 m, underlain mostly by Precambrian rocks such as gneiss, granites and migmatites." Mt Namba reaches an elevation of 2,420 masl at its highest point, rising abruptly from the surrounding land which is about 1,600–1,800 masl (Figures 1–5). The Marginal Mountain Chain falls within the Angolan Montane Forest–Grasslands mosaic ecoregion (WWF 2021, Huntley 2023), an isolated portion of the Afromontane archipelago regional centre of endemism or phytochorion of White (1978, 1983), some 2,000 km to the west of Africa's eastern mountain chain.

Mt Namba lies within the northwestern limits of the Great Escarpment of southern Africa (Clark *et al.* 2011), which stretches from western Angola, through Namibia, South Africa, Lesotho and eSwatini to the Eastern Highlands of Zimbabwe and neighbouring Mozambique. Plant diversity and endemism of the northeastern limit of the Great Escarpment have been recently documented (Chimanimani: Wursten *et al.* 2017, Cheek *et al.* 2018; Nyanga: Clark *et al.* 2017; and Bvumba: Timberlake *et al.* 2020), but corresponding documentation of the Angolan portion of the escarpment is still lacking. The presence of Afromontane forest relicts in the Angolan highlands was noted by Barbosa (1970), Huntley (1974, 2011), White (1978, 1983) and Huntley and Matos (1994), but there have been no detailed surveys of these forests or regions. Indeed, the whole of Angola is poorly documented botanically in comparison to surrounding territories (Sosef *et al.* 2017, Goyder & Gonçalves 2019). Botanical surveys that have been published have focused on environments at lower elevations, such as the Serra do Pingano coffee forests of Uíge Province and other areas of neighbouring Cuanza-Norte (Lautenschläger *et al.* 2020, 2023, Mezonda *et al.* 2020); the Guineo-Congolian Cumbira Forest nestled beneath the Serra Njelo in Cuanza-Sul (Gonçalves & Goyder 2016); the upper reaches of the Okavango system centred on the high-rainfall Kalahari sand plateau of Moxico Province (Goyder *et al.* 2018); and the woody vegetation of Huíla Province (Gonçalves *et al.* 2017, 2021, Chisingui *et al.* 2018). The present contribution is an attempt to rectify that omission.

MATERIAL AND METHODS

Botanical surveys were conducted by authors Gonçalves, Goyder and Luís on and around the Namba massif in the rainy (8–16 January) and dry

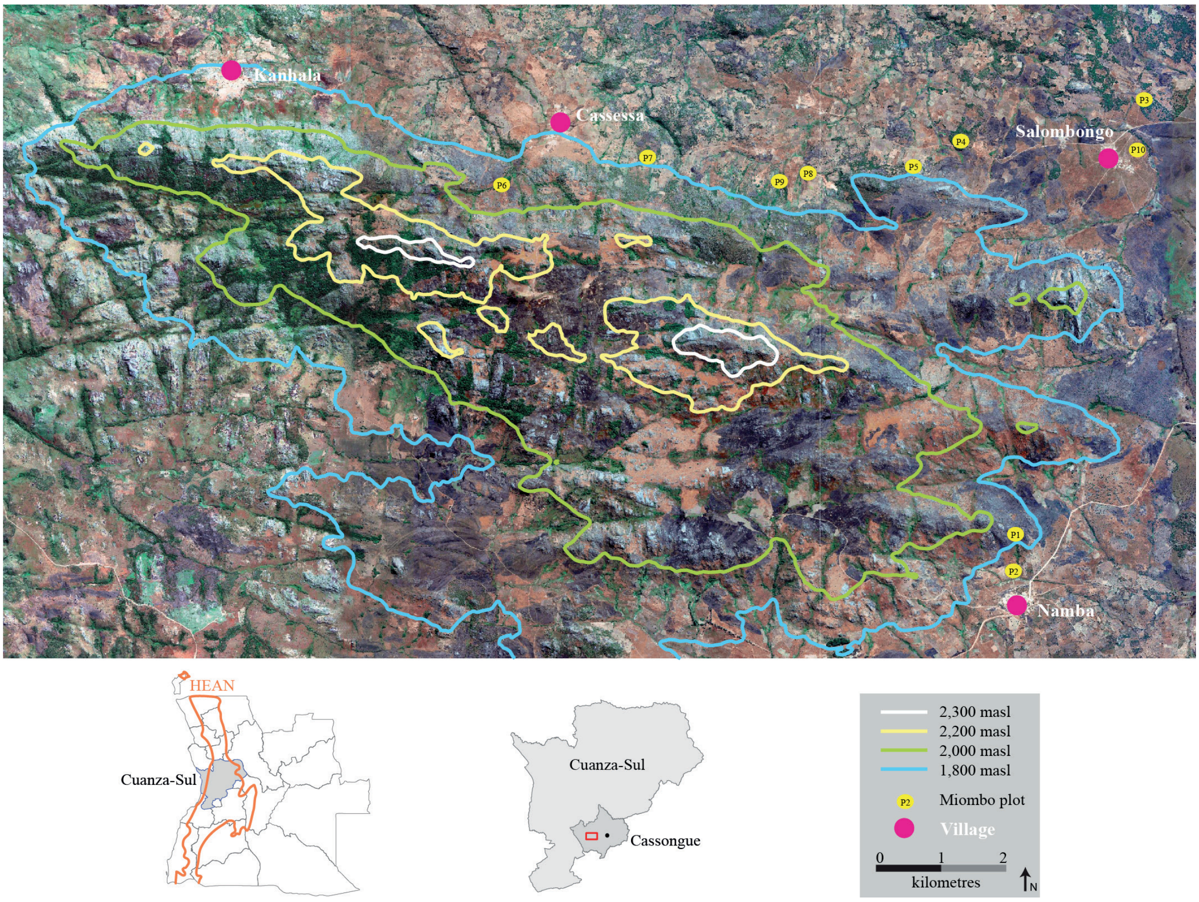

Figure 1: *Map showing the elevation and position of Mt Namba in Cuanza-Sul Province, Angola, and the positions of the vegetation plots in the low-elevation miombo woodlands. HEAN (lower left) is the area designated as the highlands and escarpments of Angola and Namibia (Mendelsohn & Huntley 2023).*

(10–18 June) seasons of 2016 in order to maximise the recording of plant diversity. Plant diversity was mostly assessed through walk-over surveys of each habitat. Higher elevations on the mountain (Vegetation Types 6 and 32; Barbosa 1970), and the lower slopes and surrounding areas (Vegetation Type 16; Barbosa 1970) were surveyed. The major vegetation types encountered generally formed discrete, readily observable units and were categorised informally.

Herbarium collections were made, mostly in sets of two, and deposited in the Lubango Herbarium (LUBA) at the Instituto Superior de Ciências de Educação da Huíla (ISCED-Huíla) in Angola and at the Herbarium of the Royal Botanic Gardens, Kew (K), United Kingdom. Herbarium acronyms follow Thiers (ongoing). Species covered by regulations of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), such as *Aloe* and Orchidaceae, were deposited only in Angolan institutions and identified from photographs.

Author Gomes visited the southern and eastern flanks of the mountain in June 2022, making voucher collections and field observations. In addition, António Martins and Chris Hines kindly shared their photographs of plants taken on the mountain over several days in April and May 2018 and January 2019. Collections and photographs were identified principally by Goyder at Kew, with expert opinion sought from specialists in particular plant families: Susan Carter (*Aloe*), Iain Darbyshire (Acanthaceae and Orobanchaceae), Nicholas Hind (Compositae), Alan Paton (Lamiaceae), Andre Schuiteman (Orchidaceae), Gideon Smith (*Kalanchoe*), Marie Claire Veranso-Libalah (Melastomataceae) and Martin Xanthos (Cyperaceae, Gramineae).

Angiosperm classification and nomenclature follows APG IV *et al.* (2016) at family level, and the African Plant Database (Version 3.4.0) or Plants of the World Online (POWO 2021) in most cases at lower taxonomic levels, while fern and lycopod names follow Roux (2009). Occasionally, accepted names may diverge from these resources where expert opinion suggests otherwise. Where new country or provincial records are reported, Figueiredo and Smith (2008) with updates from Lautenschläger *et al.* (2020) and Mezonda *et al.* (2020) have been used as the baselines for comparison. Recent

Figure 2: *Mt Namba from the east. Photo: D Goyder.*

Figure 3: *Southern slopes of Mt Namba showing rock slabs, montane grassland and fingers of Afromontane forest. Photo: C Hines.*

Figure 4: *Afromontane forest surrounded by montane rocky grassland above Kanhala village. Photo: D Goyder.*

Figure 5: *View of Mt Namba from Cassessa village. Photo: D Goyder.*

taxonomic revisions and searchable online herbarium catalogues, principally those for the Natural History Museum (BM), University of Coimbra (COI), Royal Botanic Gardens, Kew (K), and Instituto de Investigação Científica Tropical (LISC), were also consulted.

Additionally, two of the authors (Gonçalves and Luís) set up a vegetation plot of 20 m × 20 m in each of ten woodland patches (Figure 1) to assess the woody species composition and diversity of the miombo woodlands below the mountain. The species were ranked by Importance Value Index (IVI) through the summation of their relative values of frequency, density and dominance (Freitas & Magalhães 2012).

RESULTS

Around 200 plant collections were made with many additional unvouchered photographic or visual observations. An annotated checklist is presented in Appendix 1. As this represents plants collected and observed on only a few brief visits, it is by no means exhaustive. It records 271 taxa. Six new records for Angola, one of which is a potential invasive, and 22 new records for Cuanza-Sul are highlighted.

Afromontane forest patches (Figure 4) occur at high elevations within a mosaic of fire-prone montane rocky grasslands, with miombo woodland and ruderal vegetation at lower elevations (Figure 3).

Afromontane forest

We were able to access closed-canopy Afromontane forest patches above the villages of Cassessa and Kanhala on the northern slopes of the mountain (Figure 4). Patches of forest are restricted to rocky gullies at high elevation (2,000–2,200 m, generally). The principal tree species are *Bersama abyssinica* Fresen. subsp. *abyssinica*, *Nuxia congesta* R.Br. ex Fresen., *Pittosporum viridiflorum* Sims, *Podocarpus milanjianus* Rendle and *Syzygium afromontanum* (F.White) Byng. Understorey shrubs included several species of *Psychotria* (Rubiaceae), while *Elatostema monticola* Hook.f. (Urticaceae) found growing on rocks in a forest stream represents a new record for Angola. The epiphytic fern *Drynaria volkensii* Hieron. (Figure 6a) and the Apocynaceae climber *Periploca linearifolia* A.Rich are also recorded from Angola for the first time.

Montane rocky grassland

Cussonia angolensis (Seem.) Hiern and *Erythrina abyssinica* Lam. ex DC. occur among larger rock slabs, along with scattered individuals of *Phoenix reclinata* Jacq., *Faurea discolor* Welw., *Rotheca myricoides* (Hochst.) Steane & Mabb. var. *discolor* (Klotzsch) Verdc. and *Aloe littoralis* Baker. The resurrection plant *Myrothamnus flabellifolius*

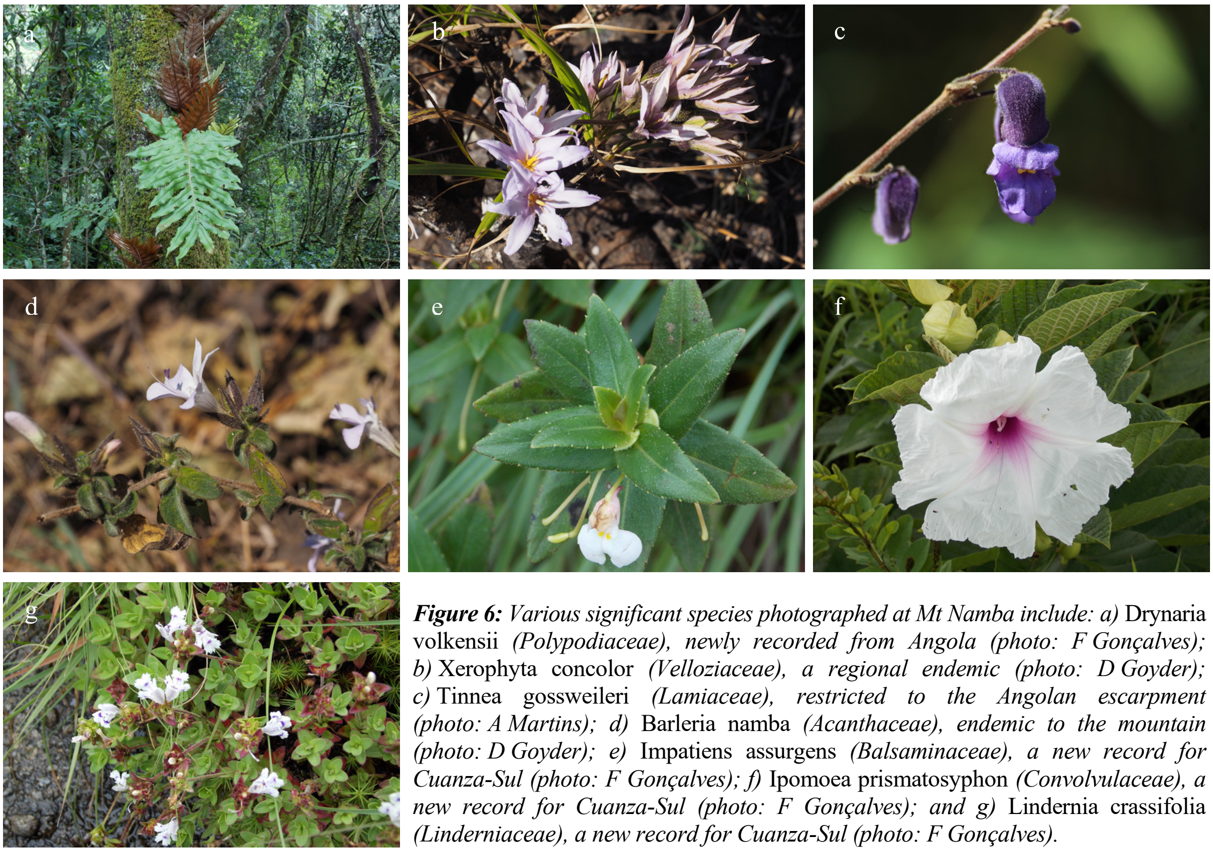

***Figure 6:** Various significant species photographed at Mt Namba include: a)* Drynaria volkensii *(Polypodiaceae), newly recorded from Angola (photo: F Gonçalves); b)* Xerophyta concolor *(Velloziaceae), a regional endemic (photo: D Goyder); c)* Tinnea gossweileri *(Lamiaceae), restricted to the Angolan escarpment (photo: A Martins); d)* Barleria namba *(Acanthaceae), endemic to the mountain (photo: D Goyder); e)* Impatiens assurgens *(Balsaminaceae), a new record for Cuanza-Sul (photo: F Gonçalves); f)* Ipomoea prismatosyphon *(Convolvulaceae), a new record for Cuanza-Sul (photo: F Gonçalves); and g)* Lindernia crassifolia *(Linderniaceae), a new record for Cuanza-Sul (photo: F Gonçalves).*

Welw. was also observed. There are extensive populations of *Xerophyta concolor* L.B.Sm. & Ayensu (Figure 6b), a species described from Serra de Candungo, west of Huambo in Benguela Province, that is also known from an inselberg in Cuanza-Sul close to the Queve River (Behnke *et al.* 2013).

We report significant range extensions for *Othonna huillensis* Welw. ex Hiern and *Lopholaena decurrens* (Hutch.) E.Phillips & C.A.Sm. These species were previously known only from the Serra da Chela close to Lubango, an area of considerable plant endemism, although this has not been adequately analysed to date (Goyder & Gonçalves 2019). We note that de Cauwer *et al.* (2023) have recently recorded *Othonna huillensis* from the remote Otjihipa Mountains of northwestern Namibia, extending its known distribution to the south as well. Compositae, Lamiaceae and Rubiaceae are all well represented in open habitats. *Tinnea gossweileri* Robyns & Lebrun (Figure 6c) is restricted to the Angolan escarpment, occurring on the Serra da Chela, through Huambo Province and into Cuanza-Sul.

A wide range of perennial herbs and subshrubs includes *Berkheya angolensis* O.Hoffm., *Droogmansia megalantha* (Taub.) De Wild. var. *pilosa* (Taub.) De Wild., *Gnidia kraussiana* Meisn. var. *mollissima* (E.A.Bruce) A.Robyns, *Hibiscus rhodanthus* Gürke, *Humularia welwitschii* (Taub.) P.A.Duvign. var. *gossweileri* (Baker f.) P.A.Duvign., *Pentanisia rubricaulis* (K.Schum.) Kårehad & B.Bremer and *Pseudognaphalium luteo-album* (L.) Hilliard & B.L.Burtt.

Tripteris monocephala Oliv. & Hiern represents a new record for Angola, while new provincial records include *Cephalaria retrosetosa* Engl. & Gilg, *Isodon ramosissimus* (Hook.f.) Codd and *Triumfetta welwitschii* Mast. An endemic species of Acanthaceae, *Barleria namba* I.Darbysh. (Figure 6d) was described from material collected during the June surveys and is known only from Mt Namba (Darbyshire *et al.* 2019).

Unfortunately, at the time of our brief visits, Gramineae were not in flower, so we are unable to comment on grass diversity.

Miombo woodland

The miombo woodlands below the mountain were comprised of detarioid legumes such as *Brachystegia floribunda* Benth., *B. gossweileri* Hutch. & Burtt Davy, *B. spiciformis* Benth. and *Isoberlinia angolensis* (Welw. ex Benth.) Hoyle & Brenan var. *lasiocalyx* Hoyle & Brenan., with *Pericopsis angolensis* (Baker) Meeuwen (Papilionoideae), *Uapaca kirkiana* Müll. Arg. var. *benguelensis* (Müll. Arg.) Meerts, *U. nitida* Müll. Arg., *Bridelia micrantha* (Hochst.) Baill. and *Hymenocardia acida* Tul.

(Phyllanthaceae), *Monotes* spp. (Dipterocarpaceae) and *Parinari curatellifolia* Planch. ex Benth. (Chrysobalanceae) also present. Several species of Combretaceae were also recorded.

Four hundred and twenty-eight individual trees were recorded and measured from the ten vegetation plots. The ten most dominant species ranked by their IVI were: *Isoberlinia angolensis* (29.2%), *Brachystegia gossweileri* (26.9%), *Monotes* sp. (15.4%), *Uapaca nitida* (11.8%), *Parinari curatellifolia* (8.8%), *Bridelia micrantha* (8.4%), *Hymenocardia acida* (7.0%), *Uapaca kirkiana* (6.7%), *Brachystegia floribunda* (5.7%) and *Brachystegia spiciformis* (5.4%).

Vernonia nestor S.Moore, found in a patch of miombo close to Namba village, represents a new record for Angola.

DISCUSSION AND THREATS TO BIODIVERSITY

Mills *et al.* (2013) designated Mt Namba an Important Bird Area, principally on the basis of the twenty Afromontane-forest bird taxa found there. Many of these are now rare or extinct on Serra do Môco, the only other mountain in the region with significant patches of Afromontane forest (Mills *et al.* 2011). This reflects the more extensive and largely intact tracts of forest on Mt Namba whose extent was estimated at around 590 ha (Mills *et al.* 2013), an order of magnitude larger than equivalent forest patches on Môco, which are heavily impacted by the local population (Gonçalves 2009).

The mountain would also qualify as an Important Plant Area under Criterion A(i) of Darbyshire *et al.* (2017) on the basis of *Barleria namba* which is endemic to the mountain and which was assessed as Vulnerable under Criterion D2 of the International Union for Conservation of Nature (IUCN) Red List (Darbyshire *et al.* 2020), and under Criterion C as home to the largest extent of threatened Afromontane forest habitat in the country.

We observed no timber extraction or significant damage to trees in the Afromontane forest, and there was little evidence of charcoal production in the surrounding woodlands, although we did see a few miombo trees that had been cut. Excavations to harvest roots of the leguminous herb *Eminia benguellensis* Torre were spotted in one patch of miombo; the roots of a related species *Pseudeminia muxiria* (Welw. ex Baker) Verdc. are used to sweeten a traditional drink (*kissangua*) in south-central parts of Angola made from cornflour and water (Sanfilippo 2014).

Grasslands on the mountain are burnt annually, but this probably has little effect on species composition. The forest itself is resistant to fire. Only in a few areas were large stands of bracken, *Pteridium aquilinum* (L.) Kuhn subsp. *centrali-africanum* Hieron. ex R.E.Fr., observed. One of these was at the margin of a patch of Afromontane forest above Cassessa village. Extensive stands of *Pteridium* can be an indicator of disturbance or excessive fire frequency. Rather worryingly, Powell *et al.* (2023) have reported fires within closed-canopy forest on the mountain in recent years, which they link to increased human pressure. A potentially invasive South American species *Araujia sericifera* Brot. was found only once, close to a cattle ranch on the plateau. Two forms are in cultivation: one, originating in the environs of Buenos Aires, has become a significant problem in Mediterranean biomes including the Cape Fynbos in South Africa; the other more tropical form originating in southeastern Brazil seems to be less of a problem. The plant found on Mt Namba was in fruit and not in flower so the variety could not be determined, but Goyder believes that the local environment would be more conducive to the tropical form than the Buenos Aires form of the species. This is the first report of *Araujia sericifera* from Angola (Figueiredo & Smith 2008, Rejmánek *et al.* 2017).

We recorded evidence of blue duiker (*Philantomba monticola* Thunberg, 1789) on the mountain on a camera-trap set up in the forest above Kanhala village. However, this was the sole observation of a mammal recorded by this method, suggesting that the population may have been reduced due to poaching. We also saw recent diggings made by aardvark (*Orycteropus afer* Pallas, 1766). Many artisanal traps were encountered in both forest and woodland environments. These were probably intended to catch small mammals and edible game birds (Swierstra's spurfowl (*Pternistis swierstrai*) and Finsch's francolin (*Scleroptila finschi*) were spotted on and around the mountain).

CONCLUSIONS

Mt Namba retains the largest extent of intact Afromontane forest in Angola and despite some conservation concerns, the forest seems to be largely intact but vulnerable to a recent increase in fires. Miombo woodland at lower elevations is certainly more affected by human activity, however, there was little evidence of charcoal production in the region. The seasonally burnt montane rocky grassland harbours many plants of interest including the recently described *Barleria namba* (Acanthaceae), which is known only from this mountain, and large populations of the regional endemic *Xerophyta concolor*. Two shrubby Compositae species in this habitat, *Lopholaena decurrens* and *Othonna huillensis*, demonstrate floristic affinities with the much more intensively collected Serra da Chela, the high escarpment zone close to the city of Lubango. Indeed, the more natural condition of the forest-grassland-miombo mosaic habitat on Mt Namba gives potential insights into the former state of other upland regions such as the Serra da Chela on which almost all woody vegetation has been cleared for timber or charcoal production.

Mt Namba qualifies for recognition as both an Important Bird Area (Mills *et al.* 2013) following the criteria of Fishpool and Evans (2001), and an Important Plant Area as indicated here according to criteria laid out by Darbyshire *et al.* (2017).

ACKNOWLEDGEMENTS

Fernanda Lages (ISCED-Huíla) is gratefully acknowledged for her support and the staff of ISCED-Huíla for the logistics and permissions. We are extremely grateful to the former Angolan Ministry of Science and Technology, now the Ministry of Higher Education, Science, Technology and Innovation, for funding this project through the framework of a bilateral agreement signed between Angola and South Africa. We thank and acknowledge the Research Centre in Biodiversity and Genetic Resources (CIBIO) and the Kissama Foundation who funded and facilitated Amândio Gomes' visit to the mountain. We are also indebted to both António Martins and Chris Hines who generously shared their photographic records of plants from the mountain, which have added many additional records to our own collections and observations.

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Appendix 1: Annotated checklist of the vascular plants of Mt Namba

This checklist was based on field surveys conducted in January and June 2016 and June 2022 and photographic surveys by Martins and Hines in April/May 2018 and January 2019 of plants in Vegetation Types 6 (Afromontane forest relicts), 16 (submontane miombo woodland, savanna and geoxylic grassland) and 32 (montane geoxylic grassland) of Barbosa (1970). Two hundred and seventy-one taxa were recorded, including six new records for Angola, and 22 for the province of Cuanza-Sul.

Family	Species	Habitat	Vouchers	New records
LYCOPODIOPHYTA				
Lycopodiaceae	*Lycopodiella cernua* (L.) Pic.Serm.	Forest, woodland	Goyder *et al.* 8625; Maiato & Camôngua 1132	Cuanza-Sul
	Lycopodium clavatum L.	Forest	Gomes visual record	
PTERIDOPHYTA				
Anemiaceae	*Anemia angolensis* Alston	Grassland	Gomes visual record	
	Mohria vestita Baker	Grassland	Maiato & Camôngua 1120	
Aspleniaceae	*Asplenium aethiopicum* (Burm.f.) Bech.	Forest	Maiato & Camôngua 1121	Cuanza-Sul
	Asplenium friesiorum C.Chr.	Forest	Goyder *et al.* 8643	Cuanza-Sul
Cyatheaceae	*Alsophila dregei* (Kunze) R.M.Tryon	Woodland	Goyder *et al.* visual record 4	Cuanza-Sul
Dennstaedtiaceae	*Pteridium aquilinum* (L.) Kuhn subsp. *centrali-africanum* Hieron. ex R.E.Fr.	Forest, grassland	Goyder *et al.* visual record 27	
Dryopteridaceae	*Didymochlaena truncatulata* (Sw.) J.Sm.	Forest	Goyder *et al.* 8637	
Nephrolepidaceae	*Nephrolepis* sp.	Forest	Goyder *et al.* 8689	
Osmundaceae	*Osmunda regalis* L.	Woodland, wetland, grassland	Goyder *et al.* 8629; Maiato & Camôngua 1118	
Polypodiaceae	*Drynaria laurentii* (H.Christ ex De Wild. & T.Durand) Hieron.	Forest	Maiato & Camôngua 1115	
	Drynaria volkensii Hieron.	Forest	Maiato & Camôngua 1133; Goyder *et al.* visual record 7 (Figure 6a)	Angola
Sinopteridaceae	*Cheilanthes inaequalis* (Kunze) Mett.	Grassland	Maiato & Camôngua 1134	
GYMNOSPERMAE				
Podocarpaceae	*Podocarpus milanjianus* Rendle	Forest	Gomes 882; Goyder *et al.* 8642; Goyder *et al.* visual record 13	
ANGIOSPERMAE: MAGNOLIIDS				
Annonaceae	*Annona stenophylla* Engl. & Diels	Woodland	Gomes visual record	
Piperaceae	*Piper capense* L.f. var. *capense*	Forest	Gomes 925; Goyder *et al.* 8641	
ANGIOSPERMAE: MONOCOTS				
Amaryllidaceae	*Boophone disticha* (L.f.) Herb.	Grassland	Gomes visual record	
Asparagaceae	*Asparagus* sp.	Forest	Goyder *et al.* 8690	
	Albuca abyssinica Jacq.	Grassland	Photographic record (Martins s.n.)	

Family	Species	Habitat	Vouchers	New records
	Dracaena mannii Baker	Forest	Gomes visual record	
Asphodelaceae	*Aloe andongensis* Baker var. *andongensis*	Grassland	Photographic record (Hines CJHH-4561; Martins s.n.)	
	Aloe littoralis Baker	Grassland	Goyder *et al.* visual record 17	
	Aloe sp.	Grassland	Maiato & Camôngua 1098	
Burmanniaceae	*Burmannia madagascariensis* Mart.	Wetland	Photographic record (Hines CJHH-4129; Martins s.n.)	
Commelinaceae	*Cyanotis lanata* Benth.	Grassland	Maiato & Camôngua 1062	
	Cyanotis longifolia Benth.	Grassland	Maiato & Camôngua 1068	
Gramineae	*Hyparrhenia newtonii* (Hack.) Stapf	Grassland	Photographic record (Hines CJHH-4523)	
Iridaceae	*Gladiolus dalenii* Van Geel	Woodland, grassland	Goyder *et al.* 8662; Maiato & Camôngua 1123; Goyder *et al.* visual record 16	
	Gladiolus sp.	Grassland	Maiato & Camôngua 1125	
	Moraea textilis Baker	Grassland	Maiato & Camôngua 1124; photographic record (Hines CJHH-4715; Martins s.n.)	
Orchidaceae	*Bulbophyllum scaberulum* (Rolfe) Bolus	Woodland	Maiato & Camôngua 1114; photographic record (CJHH-4688; Martins s.n.)	
	Eulophia horsfallii (Bateman) Summerh.	Wetland	Goyder *et al.* 8628	
	Platycoryne micrantha Summerh.	Wetland	Photographic record (Hines CJHH-8490)	
Palmae	*Phoenix reclinata* Jacq.	Forest, woodland, grassland	Goyder *et al.* visual record 2; visual record 5; visual record 18	
Pandanaceae	*Pandanus welwitschii* Rendle	Grassland, wetland	Goyder *et al.* 8676 (photographic record only)	
Smilacaceae	*Smilax anceps* Willd.	Grassland	Gomes visual record	
Velloziaceae	*Xerophyta concolor* L.B.Sm. & Ayensu	Grassland	Goyder *et al.* 8627 (Figure 6b)	
ANGIOSPERMAE: EUDICOTS				
Acanthaceae	*Acanthus montanus* (Nees) T.Anderson	Woodland, forest	Goyder *et al.* 8612; Goyder *et al.* visual record 10; photographic record (Martins s.n.)	
	Barleria namba I.Darbysh.	Grassland	Goyder *et al.* 8660 (Figure 6d)	
	Blepharis buchneri Lindau	Grassland	Photographic record (Martins s.n.)	
	Blepharis cuanzensis S.Moore	Grassland	Gomes visual record	
	Hypoestes triflora (Forssk.) Roem. & Schult.	Forest	Goyder *et al.* 8639	Cuanza-Sul
	Justicia betonica L.	Forest	Gomes visual record	
	Neuracanthus gracilior S.Moore	Woodland, grassland	Photographic record (Martins s.n.)	
	Phaulopsis lankesterioides (Lindau) Lindau	Woodland	Goyder *et al.* 8680	Cuanza-Sul
Anacardiaceae	*Lannea edulis* (Sond.) Engl.	Grassland	Gomes visual record	
	Lannea rubra (Hiern) Engl.	Grassland	Gomes visual record	
Anisophylleaceae	*Anisophyllea boehmii* Engl.	Woodland	Goyder *et al.* 8675	
Apocynaceae	*Araujia sericifera* Brot.	Grassland, ruderal	Photographic record (Gomes DSCN1049)	Angola

Family	**Species**	**Habitat**	**Vouchers**	**New records**
	Gomphocarpus physocarpus E.Mey.	Forest, grassland	Goyder *et al.* 8620; photographic record (Martins s.n.)	
	Huernia volkartii Werderm. & Peitscher var. *volkartii*	Grassland	Photographic record (Hines CJHH-8498)	
	Landolphia buchananii (Hallier f.) Stapf	Forest	Goyder *et al.* 8645	
	Landolphia camptoloba (K.Schum.) Pichon	Forest	Gomes visual record	
	Periploca linearifolia A.Rich.	Forest	Goyder *et al.* 8650; Goyder *et al.* visual record 12	Angola
	Strophanthus welwitschii (Baill.) K.Schum.	Grassland	Gomes visual record	
Araliaceae	*Cussonia angolensis* (Seem.) Hiern	Grassland	Visual record 8; photographic record (Martins s.n.)	
	Polyscias fulva (Hiern) Harms	Forest	Gomes visual record	
Balsaminaceae	*Impatiens assurgens* Baker f.	Grassland	Maiato & Camôngua 1126 (Figure 6e)	Cuanza-Sul
Boraginaceae	*Trichodesma ambacense* Welw. [but leaves whorled like in *T. baumii*]	Woodland	Goyder *et al.* 8679	
Campanulaceae	*Lobelia xongorolana* E.Wimm.	Grassland	Gomes visual record	
	Wahlenbergia napiformis (A.DC.) Thulin	Grassland	Maiato & Camôngua 1104	
Cannabaceae	*Trema orientale* (L.) Blume	Forest	Gomes visual record	
Caprifoliaceae	*Cephalaria retrosetosa* Engl. & Gilg	Grassland	Goyder *et al.* 8694; photographic record (Hines CJHH-5034; Martins s.n.)	Cuanza-Sul
	Scabiosa columbaria L.	Grassland	Gomes visual record	
Caryophyllaceae	*Dianthus angolensis* Hiern ex F.N.Williams subsp. *angolensis*	Woodland	Goyder *et al.* 8661	
Celastraceae	*Gymnosporia acuminata* (L.f.) Szyszyl.	Forest	Goyder *et al.* 8688	
	Gymnosporia senegalensis (Lam.) Loes.	Grassland	Gomes visual record	
Chrysobalanaceae	*Parinari curatellifolia* Planch. ex Benth.	Woodland	Gomes 887; Goyder *et al.* visual record 28; photographic record (Martins s.n.)	
Clusiaceae	*Garcinia smeathmannii* (Planch. & Triana) Oliv.	Forest	Gomes 883	
Combretaceae	*Combretum argyrotrichium* Welw. ex M.A.Lawson	Woodland	Maiato & Camôngua 1135	
	Combretum collinum Fresen	Grassland, woodland	Gomes visual record	
	Combretum molle R.Br. ex G.Don	Woodland	Goyder *et al.* 8603	
	Combretum platypetalum Welw. ex M.A.Lawson	Woodland	Goyder *et al.* 8619; photographic record (Martins s.n.)	
	Combretum psidioides Welw.	Woodland	Maiato & Camôngua 1138b	
	Combretum sp.	Grassland	Maiato & Camôngua 1146b	
	Terminalia prunioides M.A.Lawson	Woodland	Maiato & Camôngua 1116	
Compositae	*Artemisia afra* Jacq. ex Willd.	Grassland, woodland	Gomes visual record	
	Berkheya angolensis O.Hoffm.	Grassland	Gomes 901; Goyder *et al.* 8633; Maiato & Camôngua 1140; Goyder *et al.* visual record 15	
	Berkheya carlinopsis Welw. ex O.Hoffm.	Grassland	Gomes 899	
	Berkheya welwitschii O.Hoffm.	Grassland	Gomes 900; Maiato & Camôngua 1079	

Family	Species	Habitat	Vouchers	New records
	Dicoma welwitschii O.Hoffm.	Woodland	Goyder *et al.* 8707	
	Helichrysum globosum A.Rich.	Grassland	Maiato & Camôngua 1084	
	Helichrysum odoratissimum (L.) Sweet	Grassland	Goyder *et al.* 8700	
	Helichrysum stramineum Hiern	Grassland	Maiato & Camôngua 1082	
	Inula glomerata Oliv. & Hiern	Woodland	Goyder *et al.* 8611	
	Lopholaena decurrens (Hutch.) E.Phillips & C.A.Sm.	Grassland	Goyder *et al.* 8652; photographic record (Martins s.n.)	Cuanza-Sul
	Othonna huillensis Welw. ex Hiern	Grassland	Gomes 902; Goyder *et al.* 8631; Goyder *et al.* visual record 19	Cuanza-Sul
	Pleiotaxis pulcherrima S.Moore	Grassland	Maiato & Camôngua 1087	
	Pseudognaphalium luteo-album (L.) Hilliard & B.L.Burtt	Grassland	Goyder *et al.* 8659	
	Senecio pachyrhizus O.Hoffm.	Woodland	Goyder *et al.* 8626	
	Stomatanthes africanus (Oliv. & Hiern) R.M.King & H.Rob.	Grassland	Gomes 903	
	Tagetes minuta L.	Grassland, woodland	Photographic record (Martins s.n.)	
	Tripteris monocephala Oliv. & Hiern	Grassland	Goyder *et al.* 8654	Angola
	Vernonia britteniana Hiern	Grassland	Goyder *et al.* 8696	Cuanza-Sul
	Vernonia filipendula Hiern	Grassland	Maiato & Camôngua 1091	
	Vernonia incompta S.Moore	Grassland	Maiato & Camôngua 1083	
	Vernonia karaguensis Oliv. & Hiern	Forest	Goyder *et al.* 8684	
	Vernonia nestor S.Moore	Woodland	Goyder *et al.* 8669	Angola
	Vernonia cf. *poskeana* Vatke & Hildebr.	Grassland	Goyder *et al.* 8655	
	Vernonia sclerophylla O.Hoffm.	Grassland	Maiato & Camôngua 1090	
	Vernonia turbinella S.Moore	Grassland	Maiato & Camôngua 1085; Maiato & Camôngua 1088	
	Vernonia sp. 1	Grassland	Maiato & Camôngua 1080	
	Vernonia sp. 2	Grassland	Maiato & Camôngua 1081	
	Vernonia sp. 3	Grassland	Maiato & Camôngua 1086	
Convolvulaceae	*Ipomoea involucrata* P.Beauv.	Grassland	Gomes visual record	
	Ipomoea prismatosyphon Welw.	Grassland	Maiato & Camôngua 1107 (Figure 6f)	Cuanza-Sul
Crassulaceae	*Crassula vaginata* Eckl. & Zeyh.	Grassland	Gomes 911	
	Kalanchoe teixeirae Raym.-Hamet ex R.Fern.	Grassland	Photographic record (Hines CJHH-4236; Martins s.n.)	
Dipterocarpaceae	*Monotes* sp. (?*M. hypoleucus* (Oliv.) Gilg var. *caloneurus* (Gilg) Meerts)	Woodland	Gomes visual record; Goyder *et al.* visual record 25	
Ebenaceae	*Euclea natalensis* A.DC. subsp. *natalensis*	Grassland	Goyder *et al.* 8699	
Ericaceae	*Erica benguelensis* (Welw. ex Engl.) E.G.H.Oliv.	Grassland	Goyder *et al.* 8651	
Gentianaceae	*Chironia angolensis* Gilg	Grassland	Gomes visual record	
	Swertia welwitschii Engl.	Grassland	Photographic record (Martins s.n.)	
Hydrostachyaceae	*Hydrostachys polymorpha* Klotsch	Submerged aquatic	Gomes visual record	
Hypericaeae	*Harungana madagascariensis* Lam. ex Poir.	Woodland	Goyder *et al.* 8670	

Family	**Species**	**Habitat**	**Vouchers**	**New records**
	Hypericum roeperianum Schimp. ex A.Rich.	Woodland, grassland	Goyder *et al.* 8613	Cuanza-Sul
	Psorospermum febrifugum Spach	Woodland	Gomes visual record	
Lamiaceae	*Aeollanthus buchnerianus* Briq.	Grassland	Maiato & Camôngua 1066	
	Aeollanthus engleri Briq.	Woodland	Goyder *et al.* 8609	
	Aeollanthus sp.	Grassland	Maiato & Camôngua 1142	
	Clerodendrum capitatum (Willd.) Schumach.	Forest	Goyder *et al.* 8640; photographic record (Gomes DSCN0542)	
	Clerodendrum formicarum Gürke	Grassland, woodland	Gomes visual record	
	Clerodendrum splendens G.Don	Forest, woodland	Gomes visual record	
	Coleus welwitschii Briq. [syn. Plectranthus dupiusii (Briq.) A.J.Paton]	Grassland	Maiato & Camôngua 1144b; Photographic record (Martins s.n.)	
	Endostemon membranaceus (Banth.) Ayob. ex A.J.Paton & Harley	Grassland	Maiato & Camôngua 1145	
	Endostemon tubulascens (Briq.) M.Ashby	Grassland	Maiato & Camôngua 1106	
	Endostemon villosus (Briq.) M.Ashby	Grassland	Maiato & Camôngua 1144a	
	Holostylon robustum (Hiern) G.Taylor [syn. *Plectranthus robustus* (Hiern) A.J.Paton]	Woodland	Goyder *et al.* 8681	
	Isodon ramosissimus (Hook.f.) Codd	Grassland	Goyder *et al.* 8698	Cuanza-Sul
	Leonotis nepetifolia (L.) R.Br. var. *nepetifolia*	Ruderal	Photographic record (Martins s.n.)	
	Platostoma strictum (Hiern) A.J.Paton	Wetland	Photographic record (Martins s.n.)	
	Plectranthus tenuicaulis (Hook.f.) J.K.Morton	Wetland	Photographic record (Martins s.n.)	
	Pycnostachys angolensis G.Taylor	Forest, grassland	Gomes 921; Goyder *et al.* 8621; photographic record (Martins s.n.)	
	Rotheca myricoides (Hochst.) Steane & Mabb. var. *discolor* (Klotzsch) Verdc.	Grassland	Goyder *et al.* 8697; Maiato & Camôngua 1139	
	Solenostemon niveus Hiern	Grassland	Goyder *et al.* 8701	
	Syncolostemon welwitschii (Rolfe) D.F.Otieno	Grassland	Maiato & Camôngua 1143	
	Tinnea eriocalyx Welw.	Grassland	Maiato & Camôngua 1129; Maiato & Camôngua 1130	
	Tinnea gossweileri Robyns & Lebrun	Grassland	Photographic record (Martins s.n.) (Figure 6c)	
	Vitex madiensis Oliv. subsp. *milanjiensis* (Britten) F.White	Woodland	Goyder *et al.* 8710	
Leguminosae	*Aeschynomene baumii* Harms	Grassland	Goyder *et al.* 8656	
	Albizia antunesiana Harms	Woodland	Gomes visual record	
	Albizia zygia (DC.) J.F.Macbr.	Woodland	Gomes visual record	
	Bobgunnia madagascariensis (Desv.) J.H.Kirkbr. & Wiersema	Woodland	Gomes visual record	
	Brachystegia floribunda Benth.	Woodland	Goyder *et al.* 8713	
	Brachystegia gossweileri Hutch. & Burtt Davy	Woodland	Goyder *et al.* 8712; Goyder *et al.* visual record 22	
	Brachystegia spiciformis Benth.	Woodland	Goyder *et al.* 8714; Goyder *et al.* visual record 21	
	Brachystegia tamarindoides Welw. ex Benth.	Woodland	Gomes visual record	

Family	**Species**	**Habitat**	**Vouchers**	**New records**
	Crotalaria sp. 1	Woodland	Photographic record (Martins s.n.)	
	Crotalaria sp. 2	Grassland	Photographic record (Martins s.n.)	
	Droogmansia megalantha (Taub.) De Wild. var. *pilosa* (Taub.) De Wild.	Grassland	Goyder *et al.* 8658	
	Droogmansia pteropus (Baker) De Wild.	Grassland	Gomes 906	
	Eminia benguellensis Torre	Woodland	Goyder *et al.* 8682	
	Entada abyssinica Steud. ex A.Rich.	Grassland	Gomes visual record	
	Entada gigas (L.) Fawc. & Rendle	Forest	Gomes 932	
	Erythrina abyssinica Lam. ex DC.	Woodland, grassland	Goyder *et al.* 8607; Goyder *et al.* visual record 9	
	Humularia welwitschii (Taub.) P.A.Duvign. var. *gossweileri* (Baker f.) P.A.Duvign.	Grassland	Goyder *et al.* 8623; Maiato & Camôngua 1108	
	Indigofera hofmanniana Schinz	Grassland	Maiato & Camôngua 1103	
	Isoberlinia angolensis (Welw. ex Benth.) Hoyle & Brenan var. *lasiocalyx* Hoyle & Brenan	Woodland	Maiato & Camôngua 1111; Goyder *et al.* visual record 1; visual record 20	
	Julbernardia globiflora (Benth.) Troupin	Woodland	Gomes visual record	
	Kotschya strigosa (Benth.) Dewit & P.A.Duvign.	Woodland	Goyder *et al.* 8672	
	Kotschya strobilantha (Welw. ex Baker) Dewit & P.A.Duvign.	Woodland	Goyder *et al.* 8671; photographic record (Martins s.n.)	
	Mucuna stans Welw. ex Baker	Woodland	Goyder *et al.* 8663; photographic record (Martins s.n.)	
	Pericopsis angolensis (Baker) Meeuwen	Woodland	Goyder *et al.* 8677	
	Pterocarpus angolensis DC.	Woodland	Gomes visual record	
	Tephrosia vogelii Hook.f.	Grassland	Maiato & Camôngua 1109	
	Tylosema fassoglense (Kotschy ex Schweinf.) Torre & Hillc.	Grassland, woodland	Gomes visual record	
Linderniaceae	*Crepidorhopalon schweinfurthii* (Oliv.) Eb.Fisch.	Grassland	Photographic record (CJHH-4229; Martins s.n.)	
	Lindernia crassifolia (Engl.) Eb.Fisch.	Grassland	Maiato & Camôngua 1127 (Figure 6g)	Cuanza-Sul
Loganiaceae	*Strychnos pungens* Soler.	Grassland, woodland	Gomes visual record	
Loranthaceae	*Globimetula anguliflora* (Engl.) Danser	Woodland	Photographic record (Martins s.n.)	Cuanza-Sul
Malvaceae	*Dombeya burgessiae* Gerrard ex Harv.	Forest	Gomes 892; Goyder *et al.* 8691	
	Dombeya rotundifolia (Hochst.) Planch.	Woodland	Goyder *et al.* 8678	
	Grewia sp.	Woodland	Maiato & Camôngua 1112	
	Hibiscus rhodanthus Gürke	Woodland, grassland	Goyder *et al.* 8604; Goyder *et al.* 8693	
	Hibiscus sp.	Grassland	Maiato & Camôngua 1137	
	Triumfetta macrocoma K.Schum.	Woodland	Goyder *et al.* 8615; Maiato & Camôngua 1113	Cuanza-Sul
	Triumfetta welwitschii Mast.	Grassland	Goyder *et al.* 8657	Cuanza-Sul
Melastomataceae	*Antherotoma naudinii* Hook.f.	Grassland	Photographic record (Martins s.n.)	
	Dissotis carrissoi A.Fern. & R.Fern.	Woodland	Goyder *et al.* 8602; Goyder *et al.* 8616	
	Dissotis princeps (Bonpl.) Triana	Grassland, woodland	Gomes visual record	
Meliaceae	*Ekebergia benguelensis* Welw. ex C.DC.	Woodland	Gomes visual record	

Family	Species	Habitat	Vouchers	New records
Melianthaceae	*Bersama abyssinica* Fresen. subsp. *abyssinica*	Forest	Goyder *et al.* 8692; Goyder *et al.* visual record 6	
Mensipermaceae	*Stephania abyssinica* (Quart.-Dill. & A.Rich.) Walp.	Grassland	Maiato & Camôngua 1105	
	Stephania cyanantha Welw. ex Hiern	Forest	Gomes visual record	
Moraceae	*Ficus craterostoma* Warb. ex Mildbr. & Burret	Woodland	Goyder *et al.* 8683	
	Ficus cyathistipula Warb.	Forest	Gomes visual record	
	Ficus sur Forssk.	Woodland	Goyder *et al.* 8608; Goyder *et al.* 8630	
Myrothamnaceae	*Myrothamnus flabelliformis* Welw.	Grassland	Maiato & Camôngua 1099	
Myrtaceae	*Syzygium afromontanum* (F.White) Byng	Forest	Goyder *et al.* 8647; Goyder *et al.* visual record 3; visual record 11	
	Syzygium cordatum Hochst. ex Krauss	Woodland	Goyder *et al.* 8605; photographic record (Martins s.n.)	
Ochnaceae	*Ochna afzelii* R.Br. ex Oliv.	Woodland	Gomes visual record	
Oleaceae	*Schrebera alata* (Hochst.) Welw.	Woodland	Gomes visual record	
	Schrebera trichoclada Welw.	Woodland	Gomes visual record	
Orobanchaceae	*Alectra rigida* (Hiern) Hemsl.	Wetland	Photographic record (Martins s.n.)	
	Buchnera sp.	Woodland	Goyder *et al.* 8610	
	Micrargeria filiformis (Schumach. & Thonn.) Hutch. & Dalziel	Wetland	Photographic record (Hines CJHH-4953)	
	Sopubia aemula S.Moore	Grassland	Photographic record (Martins s.n.)	
	Sopubia lanata Engl. var. *densiflora* (Skan) Hansen	Woodland	Goyder *et al.* 8706; photographic record (Martins s.n.)	Cuanza-Sul
Passifloraceae	*Adenia cissampeloides* Harms	Forest	Gomes visual record	
	Adenia lobata (Jacq.) Engl.	Forest	Gomes visual record	
Pedaliaceae	*Ceratotheca reniformis* Abels	Ruderal	Goyder *et al.* 8601; Maiato & Camôngua 1138a; photographic record (Martins s.n.)	
Penaeaceae	*Olinia huillensis* Welw. ex A.Fern. & R.Fern. subsp. *huillensis*	Forest	Gomes visual record	
Peraceae	*Clutia benguelensis* Müll.Arg.	Grassland	Maiato & Camôngua 1073	
Phyllanthaceae	*Bridelia micrantha* (Hochst.) Baill.	Woodland	Gomes 892; Goyder *et al.* 8664; Goyder *et al.* 8665; Goyder *et al.* 8705	
	Hymenocardia acida Tul	Woodland	Goyder *et al.* 8709	
	Uapaca kirkiana Müll. Arg. var. *benguelensis* (Müll. Arg.) Meerts	Woodland	Goyder *et al.* 8666; Goyder *et al.* visual record 23	
	Uapaca nitida Müll. Arg.	Woodland	Goyder *et al.* 8667; Goyder *et al.* visual record 24; photographic record (Martins s.n.)	
Picodendraceae	*Oldfieldia dactylophylla* (Welw. ex Oliv.) J.Léonard	Grassland	Gomes visual record	
Pittosporaceae	*Pittosporum viridiflorum* Sims	Forest	Goyder *et al.* 8648	
Polygalaceae	*Polygala albida* Schinz	Grassland	Gomes visual record	
	Polygala gomesiana Welw. ex Oliv.	Wetland	Photographic record (Hines CJHH-4996; Martins s.n.)	
	Polygala petitiana A.Rich.	Grassland	Photographic record (Martins s.n.)	

Family	**Species**	**Habitat**	**Vouchers**	**New records**
Primulaceae	*Maesa lanceolata* Forssk.	Woodland	Photographic record (Gomes DSCN0605)	
	Myrsine africana L.	Woodland	Goyder *et al.* 8668	
	Rapanea melanophloeos (L.) Mez	Forest	Gomes visual record	
Proteaceae	*Faurea discolor* Welw.	Grassland, forest	Goyder *et al.* 8632; Goyder *et al.* 8649	
	Faurea rochetiana (A.Rich.) Chiov. ex Pic.Serm.	Woodland	Goyder *et al.* 8614; photographic record (Martins s.n.)	
	Faurea saligna Harv.	Forest	Gomes visual record	
	Protea angolensis Welw. var. *angolensis*	Grassland	Photographic record (Martins s.n.)	
	Protea micans Welw. subsp. *trichophylla* (Engl. & Gilg) Chisumpa & Brummitt	Grassland	Gomes 905; Goyder *et al.* visual record 29; photographic record (Hines CJHH-8482)	
	Protea poggei Engl.	Grassland	Gomes visual record	
	Protea welwitschii Engl.	Grassland	Maiato & Camôngua 1110	
Ranunculaceae	*Clematis brachiata* Thunb.	Grassland	Gomes visual record	
	Clematis chrysocarpa Welw. ex Oliv.	Grassland	Photographic record (Martins s.n.)	
	Clematis villosa DC.	Grassland	Maiato & Camôngua 1141; photographic record (Martins s.n.)	
Rosaceae	*Rubus pinnatus* Willd.	Forest	Gomes visual record	
Rubiaceae	*Agathisanthemum globosum* (Hochst. ex A.Rich.) Klotzsch	Grassland	Maiato & Camôngua 1067	
	Anthospermum welwitschii Hiern	Woodland	Photographic record (Martins s.n.)	
	Ancylanthos rubiginosus Desf.	Grassland	Goyder *et al.* 8622	
	Fadogia cf. *lactiflora* Welw. ex Hiern	Grassland	Maiato & Camôngua 1078	
	Fadogia punctulata Robyns	Woodland	Goyder *et al.* 8618	
	Gardenia imperialis K.Schum.	Forest	Gomes visual record	
	Gardenia ternifolia Schumach. & Thonn. subsp. *jovis-tonantis* (Welw.) Verdc.	Grassland, woodland	Gomes visual record	
	Hymenodictyon floribundum (Hochst. & Steud.) B.L.Rob.	Woodland	Goyder *et al.* 8606; photographic record (Gomes DSCN0455)	
	Keetia gueinzii (Sond.) Bridson	Forest	Gomes visual record	
	Leptactina benguellensis (Welw. ex Benth. & Hook.f.) R.D.Good	Woodland	Goyder *et al.* 8673	
	Mussaenda arcuata Poir.	Grassland	Gomes visual record	
	Mussaenda rivularis Welw. ex Hiern var. *rivularis*	Woodland	Goyder *et al.* 8624; Maiato & Camôngua 1076	
	Otiophora caerulea (Hiern) Bullock	Grassland	Maiato & Camôngua 1097	
	Otomeria elatior (A.Rich. ex DC.) Verdc.	Grassland	Maiato & Camôngua 1094; photographic record (Martins s.n.)	
	Pentanisia rubricaulis (K.Schum.) Kårehad & B.Bremer [Syn. *Calanda rubricaulis* K.Schum.]	Grassland	Goyder *et al.* 8653; Maiato & Camôngua 1095; photographic record (Martins s.n.)	
	Psychotria articulata (Hiern) E.M.A.Petit	Forest	Goyder *et al.* 8635	
	Psychotria hypsophila K.Schum. & K.Krause	Forest	Goyder *et al.* 8634; Goyder *et al.* 8644; Maiato & Camôngua 1077	
	Psychotria ?succulenta (Schweinf. ex Hiern) E.M.A.Petit	Forest	Goyder *et al.* 8685	

Family	Species	Habitat	Vouchers	New records
	Psychotria welwitschii (Hiern) E.M.A.Petit	Forest	Goyder *et al.* 8687	Cuanza-Sul
	Psydrax subcordata (DC.) Bridson	Forest	Gomes visual record	
	Rothmannia engleriana (K.Schum.) Keay var. *engleriana*	Woodland	Goyder *et al.* 8674	
	Tarenna pallidula Hiern	Forest	Goyder *et al.* 8686	Cuanza-Sul
Santalaceae	*Osyris lanceolata* Hochst. ex Steud.	Grassland	Goyder *et al.* 8702	
Sapindaceae	*Dodonaea viscosa* Jacq.	Grassland	Goyder *et al.* 8703	Cuanza-Sul
	Pappea capensis Eckl. & Zeyh.	Forest	Gomes 913	
Sapotaceae	*Englerophytum magalismontanum* (Sond.) T.D.Penn.	Forest	Gomes 885	
Sladeniaceae	*Ficalhoa laurifolia* Hiern	Forest	Gomes 931	
Solanaceae	*Solanum aculeatissimum* Jacq.	Forest	Goyder *et al.* 8636	
	Solanum mauritianum Scop.	Grassland	Gomes visual record	
Stilbaceae	*Nuxia congesta* R.Br. ex Fresen.	Forest	Goyder *et al.* 8646; Goyder *et al.* visual record 14	
Thymelaeaceae	*Gnidia chrysantha* Gilg	Grassland	Maiato & Camôngua 1136	
	Gnidia kraussiana Meisn. var. *mollissima* (E.A.Bruce) A.Robyns	Grassland	Goyder *et al.* 8695; Maiato & Camôngua 1093	
Umbelliferae	*Centella asiatica* (L.) Urb.	Grassland	Gomes visual record	
	Diplolophium zambesianum Hiern	Woodland	Goyder *et al.* 8704	
	Heteromorpha stenophylla Welw. ex Schinz	Grassland	Maiato & Camôngua 1146a	
	Physotrichia muriculata (Welw. ex Hiern) S.Droop & C.C.Towns.	Grassland	Maiato & Camôngua 1072	
	Pimpinella huillensis Welw. ex Engl.	Woodland	Goyder *et al.* 8708	
	Steganotaenia araliacea Hochst.	Grassland, woodland	Gomes visual record	
Urticaceae	*Elatostema monticola* Hook.f.	Forest	Goyder *et al.* 8638	Angola
Verbenaceae	*Lippia abyssinica* (Otto & F.Dietr.) Cufod.	Grassland	Maiato & Camôngua 1100	
	Lippia plicata Baker	Woodland, grassland	Goyder *et al.* 8617; Maiato & Camôngua 1100A	
Vitaceae	*Cyphostemma* sp. 1	Grassland	Maiato & Camôngua 1101	
	Cyphostemma sp. 2	Grassland	Maiato & Camôngua 1102	
	Rhoicissus tridentata (L.f.) Wild & R.B.Drumm. subsp. *cuneifolia* (Eckl. & Zeyh.) Urton	Forest	Maiato & Camôngua 1074	

Diversity and endemism of geoxylic plants on the Angolan Planalto

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-meller

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ABSTRACT

The Angolan Planalto and adjacent areas are characterised by flammable grassy ecosystems. Within these old-growth grasslands, geoxyles are a dominant component and play a key role in the functioning, diversity and beauty of these ecosystems. Geoxyles are a plant life form characterised by having low aboveground biomass and massive belowground wooden structures from which they can draw stored reserves and resprout quickly after disturbances such as fire. The Angolan Planalto has a high number of geoxyle taxa of which many are endemic to the area. We give an overview of the number of geoxyle taxa in these highlands based on a compilation of all available data, discuss reasons for this remarkable diversity, and point out research and conservation priorities for this important life form that is threatened by upcoming land-use changes.

Keywords: Angola, Angolan Planalto, diversity, endemism, geoxyles, highlands, suffrutices

INTRODUCTION

Geoxylic suffrutices, also known as geoxyles, are woody plants with an eccentric growth form, earning them the name ‘underground trees’ because most of their woody biomass is underground (White 1976, Maurin *et al.* 2014, Pausas *et al.* 2018, Zigelski *et al.* 2019a). Figure 1 illustrates some endemic geoxylic plants of the Angolan Planalto. The underground biomass encompasses roots, woody rhizomes or xylopodia and serves as an underground storage organ and bud bank, which is essential for resprouting after disturbance (Pausas *et al.* 2018, Ott *et al.* 2019). By locating critical organs underground and restricting their aboveground biomass to short-lived flowering and fruiting shoots, species with this growth form are well adapted to rainfall seasonality and fire, herbivory and frost (Maurin *et al.* 2014, Finckh *et al.* 2016, Wigley *et al.* 2019).

Geoxyles grow in frost- and fire-prone tropical grasslands and savannas dominated by C4 grasses. They can cover the ground densely (Meller *et al.* 2022a) and reach ages of thousands of years (Alves *et al.* 2013, B van Wyk pers. comm.). Coexistence with grasses is possible because geoxyles begin to resprout and flower in the dry season, well before the grasses do; this asynchronicity in assimilation periods and generative propagation reduces competition between geoxyles and grasses (Zigelski *et al.* 2019a). Although geoxyles tend to be overlooked in grasslands due to their lower stature, they contribute to biodiversity, functionality, carbon stocks and the resilience of their habitats (Fidelis *et al.* 2014, Zaloumis & Bond 2016, Gomes *et al.* 2021).

Starting in the late Miocene around 10 mya, tropical forests in south-central Africa gave way to open vegetation types as the CO_2 levels dropped and the climate became drier and more seasonal (Zachos *et al.* 2001, Trauth *et al.* 2009, Bonnefille 2011, Herbert *et al.* 2016). In this context, the geoxylic growth form evolved convergently in response to seasonality in a multitude of plant families, particularly from savanna and tropical forest lineages (Meller *et al.* 2022b). Many geoxyles evolved from tree and shrub species (White 1976, Maurin *et al.* 2014), and many of them have remarkably similar morphological traits to closely related tree species, except for the growth height (Meerts 2017, Gomes *et al.* 2019).

Geoxyles occur in tropical regions that are affected by fire, herbivory and/or frost, and these types of periodical aboveground disturbances and biomass removal are regarded as a prerequisite for their occurrence (Fidelis *et al.* 2014). Globally, the Cerrado (Brazil) and south-central Africa represent hotspots of diversity and endemism for geoxyles (White 1983, Maurin *et al.* 2014, Pennington & Hughes 2014). In Angola, the Zambezian phytochorion, i.e., centre of endemism (White 1983; Figure 2A), with its mosaic of miombo woodlands and open vegetation types, and particularly the Angolan Montane Forest–Grasslands mosaic (Olson *et al.* 2001) provides ideal conditions for geoxyles: sufficient and seasonal precipitation combined with frequent abiotic disturbances like fire and frost which promote areas of low tree cover. Parts of South Africa, Zambia, Democratic Republic of the Congo, Zimbabwe, Mozambique and Malawi are also rich in geoxyles, whereas most parts of Namibia and Botswana are too

Figure 1: *Endemic geoxylic plants of the Angolan Planalto. A)* Leptactina prostrata *(Rubiaceae); B)* Thunbergia retefolia *(Acanthaceae); C)* Adenodolichos mendesii *(Fabaceae); D)* Protea ongotium *(Proteaceae); E)* Dolichos dongaluta *(Fabaceae); F)* Protea ongotium *excavated (lignotuber); G)* Clutia benguellensis *(Phyllanthaceae); H)* Eriosema albo-griseum *(Fabaceae); I) resprouting geoxyles (light green:* Brachystegia russelliae, *dark green:* Cryptosepalum *sp. nov. aff.* maraviense*) on the Bié high plain, end of dry season.*

arid. Several highland areas in Africa harbour endemic geoxyles, e.g., the Nyika Plateau in Malawi (Willis *et al.* 2001), and the Highveld (Davy 1922) and Cape Floral Region of South Africa (Grobler & Cowling 2021).

According to the catalogue of Angolan plants (Figueiredo & Smith 2008), our own compilations (Zigelski *et al.* 2019a, Meller *et al.* 2022b) and research for this paper, Angola is home to at least 133 different geoxyle species in the strict sense (i.e., species with close tree relatives), of which 42 are endemic (31.6%). When defining geoxyles in a broader sense, i.e., the majority of woody biomass is underground and species descriptions include phrases like “from a woody rootstock”, “with a woody tuber” or “suffruticose”, there are 229 different taxa in Angola, 83 of which are endemic (36.2%). The high number of endemic species and the floristic singularity of the Zambezian phytochorion (Clayton & Cope 1980, White 1983) is thus prominently shaped by Angolan geoxyles. Strikingly, the geoxyle communities of the Angolan Planalto, being part of the highlands and escarpments of Angola and Namibia (HEAN), are predominantly composed of different species and endemics than those of the Kalahari sands in the eastern, less elevated parts of Angola. In this paper, we focus on Angola’s endemic geoxyle species that are restricted to the Ancient Plateau (Angolan Planalto) and the Marginal Mountain Chain (see Mendelsohn & Huntley 2023) of the HEAN. By collating available data on those species and mapping their occurrences in Angola, we present hotspots of geoxyle endemism, and then discuss the current state of knowledge, as well as threats and conservation needs for geoxyles.

METHODS

The geoxyle taxa enumerated in this review were compiled based on the catalogue of Angolan plant species which indicates most endemic species (Figueiredo & Smith 2008), our own ongoing vegetation surveys conducted in Bié, Huíla, Moxíco and Cuando Cubango provinces since 2011, and a thorough search of geoxyle literature (White 1976, Maurin *et al.* 2014, Revermann *et al.* 2017, Goyder *et al.* 2018, Zigelski *et al.* 2019a). We furthermore checked whether newly described and revised species from Angola match the definition of a geoxyle (Robbrecht *et al.* 1996, Dessein *et al.* 2003, Darbyshire *et al.* 2019, 2021, Frazão *et al.* 2020). It was not always clear if a species is a geoxyle because species descriptions were often vague and insufficient with regard to belowground parts. In many cases information was limited to terms like “perennial”, “with a woody base” or “growing from a woody rootstock”. We thus applied a broader definition (species with a woody base) and a stricter definition (species with woody underground organs and with congeneric tree relatives) and categorised the species accordingly (Table 1). Taxa which also occur outside of Angola or are endemic to Angola but restricted to the lowlands (≤ 1,200 masl) were excluded, leaving a total of 126 highland taxa. Table 2 provides information on the plant families with geoxyle taxa in Angola, and Appendix 1 lists all endemic geoxyle taxa occurring on the Angolan Planalto. For these taxa we retrieved georeferenced occurrence data from the Vegetation Database of the Okavango Basin (ID AF-00-009) in the Global Index of Vegetation-Plot Databases (Dengler *et al.* 2011), vegetation databases from Angolan Biodiversity Observatories (SASSCAL ObservationNet 2023), collections stored at the herbarium LUBA in Lubango (Angola) and the Global Biodiversity Information Facility (GBIF 2021). For the latter two we manually georeferenced entries which had precise enough locality descriptions. A total of 1,630 georeferenced occurrence records were obtained and these were mapped using standard settings for kernel density estimation in QGIS 3.10.14 (QGIS.org 2023).

ENDEMIC GEOXYLE SPECIES

Figure 2 shows the distribution of the 126 highland geoxylic taxa in Angola. A similar number of taxa are known from the Nyika Plateau in Malawi, which is

Table 1: *Number of geoxyle taxa endemic to the Angolan Planalto, and endemic to Angola but also occurring beyond the Angolan Planalto at lower altitudes.*

	Taxa endemic to the Angolan Planalto		**Taxa endemic to Angola**	
Geoxyle characteristic*	Number of endemic taxa	Number of families represented	Number of endemic taxa	Number of families represented
i) Species with a woody base	91	23	126	23
ii) Species with a woody base and a woody underground storage organ	50	16	77	16
iii) Species with a woody base, woody underground storage and tree relatives	22	10	32	13

* As species descriptions are often vague and insufficient with regard to belowground parts, we compiled the table with increasingly strict definitions of geoxyles: (i) species with “a woody base” can be termed geoxyles in the broad sense, this group may also include perennial herbs; (ii) species with woody underground storage organs (USO) have a woody base and extended belowground woody structures; and (iii) species have a woody base, USOs and congeneric tree relatives which are geoxyles in the strict sense.

also part of the Zambezian phytochorion, though only 10 geoxylic species (in the broad sense) are endemic to the plateau (Meller 2022). Hotspots are evident on the Humpata plateau near Lubango, and on the Bié and Huambo high plains. Table 3 lists endemic geoxyle taxa occurring on the Angolan Planalto, and indicates which species are strict highland endemics. Although the high plain of southeastern Angola is also known to be particularly rich in geoxyles (Goyder *et al.* 2018, Zigelski *et al.* 2018, 2019a), its species pool differs from that of the Angolan Planalto because most highland geoxyles do not extend far into the eastern areas (Figure 2B). This concurs with the findings of Linder (2001), who identified two centres of plant endemism and diversity in Angola, one extending eastwards from central Angola across Katanga and Zambia, the other on the Humpata Plateau.

Meller *et al.* (2022b) have shown that multiple biogeographic origins and environmental heterogeneity promote geoxyle diversity in Angola. The high number of families that contribute geoxyle species also adds to the diversity (Tables 1 and 2), as

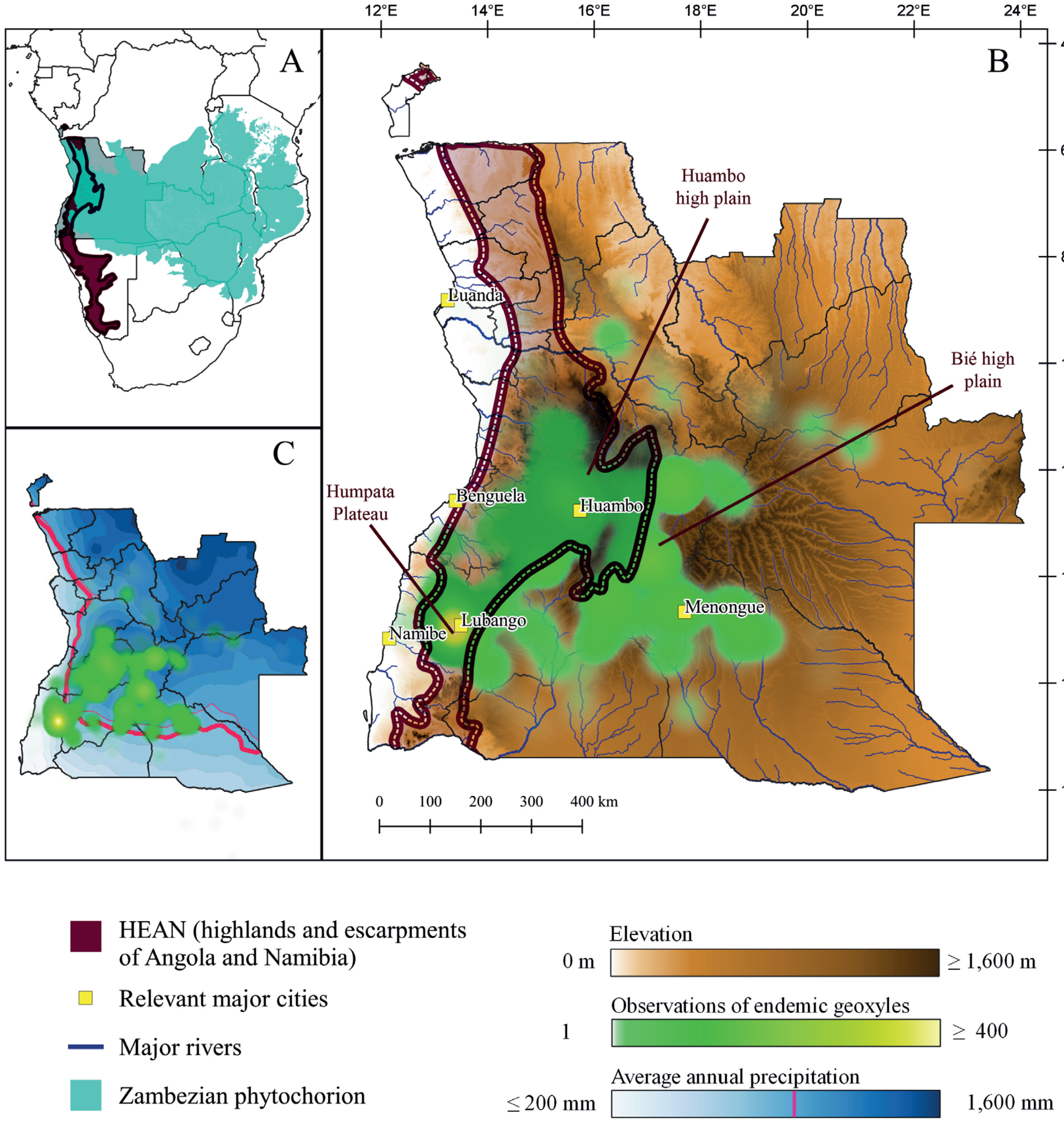

Figure 2: *Distribution of geoxyle taxa endemic to the Angolan Planalto. A) Location of the Zambezian centre of endemism (phytochorion) (cyan) in relation to Angola (shaded) and the highlands and escarpments of Angola and Namibia (HEAN). B) Angola in detail, showing topography with the HEAN boundary, and the density of collections and observations of 126 endemic geoxyle taxa. C) Distribution of average annual precipitation across Angola, overlaid with geoxyle density, showing that highland-specific geoxyles do not generally occur where average annual precipitation falls below 800 mm (pink line).*

Table 2: *Families with the most geoxyle taxa in Angola. The number of highland endemic geoxyles in families with at least five geoxyle taxa in the broad sense is given. For comparison, the total number of geoxyle taxa in these families that occur in Angola (including non-endemics) is given in brackets. USO = underground storage organ.*

	Number of highland endemic geoxyle species (total number of geoxyle species)		
Family	**With a woody base**	**With a woody USO**	**With congeneric tree relative**
Fabaceae	28 (69)	13 (49)	2 (11)
Rubiaceae	10 (45)	6 (40)	5 (38)
Acanthaceae	11 (15)	3 (7)	0 (0)
Lamiaceae	7 (17)	2 (13)	1 (3)
Euphorbiaceae	5 (12)	5 (11)	2 (10)
Malvaceae	5 (11)	5 (11)	1 (6)
Other*	25 (110)	16 (98)	11 (65)
Total	91 (279)	50 (229)	22 (133)

*Some important geoxyle families have fewer than five highland endemics and are therefore included in the group “other”; this group includes Anacardiaceae (three highland endemic taxa out of a total of eleven taxa), Apocynaceae (no highland endemic taxa out of a total of five taxa), Ochnaceae (no highland endemic taxa out of a total of six taxa) and Proteaceae (four highland endemic taxa out of a total of nine taxa).

phylogenetic diversity often is a prerequisite for overall species diversity (Enquist *et al.* 2002). Environmental differences between the higher- and lower-lying areas, particularly regarding edaphic conditions and disturbance regimes, could thus cause distinct geoxyle communities. Many geoxyle species have specific requirements with regard to substrates (Revermann *et al.* 2017). From the coastal plain in western Angola elevations increase, the topography is rugged and weathered plinthosols and shallow substrates on unweathered bedrock predominate (Huntley 2019). The southern and eastern parts of Angola, on the other hand, are characterised by gently undulating landscapes covered by deep and nutrient-poor deposits of Kalahari sands that extend eastwards into Zambia and southwards into Namibia and Botswana. In these sandy areas in southern and eastern Angola, quantity and seasonality of rainfall follows a north–south gradient, thereby forming a natural boundary for highland-specific geoxyles at the 800 mm isopleth of annual average rainfall (Figure 2C). Rainfall above 800 mm is enough for sufficient, continuous fuel loads (cured grasses) to support frequent fires (Govender *et al.* 2006, Archibald *et al.* 2010).

However, there are differences in the exposure to other aboveground disturbances along the east–west gradient. The higher lying areas of the Angolan Planalto and Humpata Plateau are prone to localised, frequent frosts in the dry season (up to 40 per year) which affect the open grasslands in the valleys, in particular, because the cold air can pool there (Finckh *et al.* 2016, 2021). During the Pliocene (5.3–2.6 mya), and particularly in the Pleistocene (2.6 million to 11,700 years ago), Angola had a cooler and more arid climate, and probably experienced more frequent and more severe nocturnal frost events (deMenocal 1995, Herbert *et al.* 2016). Strikingly, the highest areas along the western escarpment now receive very little frost and it only occurs in enclosed valleys (SASSCAL WeatherNet 2023, pers. obs. P Meller, M Finckh), probably due to the mild oceanic influence.

Several ecological theories may help to explain the high number of highland endemic geoxyle taxa, for example, plant and/or seed dispersal has been limited in the past (Freestone & Inouye 2006), climatic conditions have been stable over a long time (Lovett & Friis 1996) and/or soils in the highlands are heterogeneous at a small scale (Hulshof & Spasojevic 2020). A combined effect is probable, because the topography of the highlands leads to only slightly connected small-scale mosaics of forests, woodlands, grasslands and wetlands, an environment that seems to promote evolutionary processes. However, it should also be noted that historically the western part of Angola has been far better covered by collectors than the eastern part (Sosef *et al.* 2017, Goyder & Gonçalves 2019). Some of the geoxyle hotspots in Figure 2 reflect historical collection sites (e.g. Morro de Lopollo near Lubango) and expedition routes.

THREATS AND CONSERVATION

Inherently, most aboveground disturbances are not threatening to geoxyles because they are well-adapted to them. Their belowground storage organs and bud banks are vulnerable, however, because once these are critically damaged, geoxyles lose their carbon reserves and resprouting ability (Zaloumis & Bond 2016, Buisson *et al.* 2019). These critical parts are mostly located in the topsoil, in the first ~30 cm below the surface (Gomes *et al.* 2021), which is sufficient to buffer short thermal peaks caused by the passage of fire (Auld & Bradstock 1996), as well as nocturnal frost pulses lasting several hours (Revermann 2013); soil temperature at 5–10 cm deep only deviates slightly in both situations. However, the geoxyles' location in the topsoil might not protect them from physical impacts. Historically, the Angolan Planalto had low densities of meso- and megaherbivores (Huntley *et al.* 2019), which implies that geoxyle grasslands there were probably not heavily affected by grazing or trampling. In Cangandala National Park, herds of giant sable antelope (*Hippotragus niger variani*) have been seen

Table 3: *Endemic geoxyle taxa occurring on the Angolan Planalto. Only taxa with a congeneric tree relative are listed here; a full list of endemic geoxyle taxa is provided in Appendix 1. For each species, geoxyle category indicates whether it is a geoxyle in a broad sense (with a woody base), or strict sense (with a woody underground storage organ), and whether it is a strict highland endemic (Y = yes; N = no). Close tree relatives from south-central Africa are also provided, however, since phylogenetic studies are lacking for most geoxyle taxa, the tree taxa listed here should be regarded as examples and not necessarily as the actual closest tree relative. Distribution indicates if species are restricted to particular high plains, escarpments or localities; wider distributions within Angola are presented as an alphabetical list of provinces abbreviated as follows: BE – Benguela; BI – Bié; CC – Cuando Cubango; CS – Cuanza-Sul; CU – Cunene; HI – Huíla; HU – Huambo; MA – Malanje; MO – Moxico; and NA – Namibe.*

Taxon	**Family**	**Geoxyle category**	**Highland endemic**	**Close tree relative(s)**	**Distribution**
Baphia sp. nov.	Fabaceae	strict	N	*Baphia bequaertii*	BI, CC, MO
Clutia benguelensis Müll.Arg.	Euphorbiaceae	strict	Y	*Clutia abyssinica*	BE, BI, HI, HU
Combretum argyrotrichum Welw. ex M.A.Lawson	Combretaceae	strict	Y	*Combretum zeyheri*	Humpata Plateau, HU high plain
Combretum viscosum Exell	Combretaceae	strict	Y		BE, BI, HI, HU
Cryptosepalum sp. nov. aff. *maraviense*	Fabaceae	strict	Y	*Cryptosepalum exfoliatum*	BI high plain
Dissotis benguellensis A.Fern. & R.Fern.	Melastomataceae	broad	Y	*Dissotis melleri*	HU, Serra do Môco
Dissotis carrissoi A.Fern. & R.Fern.	Melastomataceae	broad	N		CS, HU
Erythrina pygmaea Torre	Fabaceae	strict	Y	*Erythrina abyssinica*	Humpata Plateau
Euclea angolensis Gürke	Ebenaceae	strict	Y	*Euclea divinorum*	Humpata Plateau
Euphorbia asclepiadea Milne-Redh.	Euphorbiaceae	broad	N	*Euphorbia matabelensis*	BI high plain
Euphorbia parifolia N.E.Br.	Euphorbiaceae	strict	Y		Humpata Plateau, Tundavala
Fadogia caespitosa Robyns	Rubiaceae	strict	N	*Fadogia erythroploea*	Humpata Plateau
Fadogia chrysantha K.Schum.	Rubiaceae	strict	Y		HU high plain
Fadogia graminea Wernham	Rubiaceae	strict	N		BI high plain
Fadogia punctulata Robyns	Rubiaceae	strict	Y		HU high plain
Fadogia stenophylla Welw. ex Hiern	Rubiaceae	strict	N		Humpata Plateau, Lubango
Gnidia fruticulosa Gilg	Thymelaeaceae	broad	Y	*Gnidia glauca*	Humpata Plateau
Gnidia newtonii Gilg	Thymelaeaceae	broad	Y		Humpata Plateau
Gnidia rendlei Hiern	Thymelaeaceae	broad	Y		Humpata Plateau, Mumpulla
Gnidia welwitschii Hiern	Thymelaeaceae	broad	Y		Humpata Plateau
Grewia suffruticosa K.Schum.	Malvaceae	strict	Y	*Grewia bicolor*	Humpata Plateau
Hypericum abilianum N.Robson	Hypericaceae	broad	Y		Humpata Plateau
Julbernardia gossweileri (Baker f.) Torre & Hillc.	Fabaceae	strict	N	*Julbernardia paniculatum*	CC, HI, HU, MA

Lannea gossweileri Exell & Mendonça	Anacardiaceae	strict	Y	*Lannea discolor*	BI high plain
Lannea rubra Hiern (Engl.)	Anacardiaceae	strict	Y		Humpata Plateau, Tundavala
Leptactina prostrata K.Schum.	Rubiaceae	strict	N	*Leptactina platyphylla*	BI high plain, MO
Ozoroa xylophylla (Engl. & Gilg) R.Fern. & A.Fern.	Anacardiaceae	strict	Y	*Ozoroa insignis*	BI high plain and Humpata Plateau
Pavetta nana K.Schum.	Rubiaceae	strict	Y	*Pavetta gardeniifolia*	Humpata Plateau, Tchivinguiro
Phyllanthus microdendron Müll.Arg.	Phyllanthaceae	strict	Y	*Phyllanthus muellerianus*	BI high plain
Protea dekindtiana Engl.	Proteaceae	strict	Y	*Protea gaguedii*	Humpata Plateau, Tchivinguiro
Protea ongotium Beard	Proteaceae	strict	Y		BI high plain and Humpata Plateau
Protea paludosa subsp. *paludosa* Hiern (Engl.)	Proteaceae	strict	Y		BI high plain and Humpata Plateau
Protea poggei subsp. *haemantha* (Engl. & Gilg) Chisumpa & Brummitt	Proteaceae	strict	N		BI high plain, MO
Protea poggei subsp. *heliophila* Chisumpa & Brummitt	Proteaceae	strict	Y		HU high plain
Psychotria moninensis (Hiern) E.M.A.Petit	Rubiaceae	strict	N	*Psychotria succulenta*	BE, BI, CC, HI, HU, MA
Psychotria welwitschii (Hiern) Bremek.	Rubiaceae	strict	Y		HU, HI and NA escarpment
Tricalysia angolensis A.Rich. ex DC.	Rubiaceae	strict	N	*Tricalysia elliotii*	BI, CC, CU high plains and Humpata Plateau
Vangueria cistifolia var. *cistifolia* (Welw. ex Hiern) Lantz	Rubiaceae	strict	N	*Vangueria infausta*	BI, HI, MA
Vangueria fulva (Robyns) Lantz	Rubiaceae	strict	Y		BI high plain and Humpata Plateau
Vitex caespitosa Exell	Lamiaceae	strict	Y	*Vitex ferruginea*	BI, BE, HU

feeding on geoxyles in grasslands after fire, when grasses have not yet resprouted in the dry season (pers. obs. A Gomes). However, it is unclear what effect modern herbivory and trampling by cattle has on geoxyles in Angola. Land-use changes and landscape transformations in Angola have accelerated in the past two decades and are currently happening without regulation (Mendelsohn 2019). In the Cerrado in Brazil, another biome characterised by a high geoxyle diversity, much damage has been done to the natural vegetation, including geoxyles, with the transformation from natural grasslands into intensively used rangelands or into agricultural fields (Grecchi *et al.* 2014, Velazco *et al*. 2019).

The biggest threat to geoxyles lies in the transformation of natural tropical grasslands to intensive land-use types. Once trampling or ploughing damages their belowground parts irreversibly, geoxyle species cannot easily recuperate. Their strategy is to grow slowly, to survive and live long (Alves *et al.* 2013, B van Wyk pers. comm.), whereas propagation via seeds seems only secondary and with a low rate of success, since geoxyle seedlings seem to be very rare (pers. obs. P Meller). This means that even after an agricultural field has been abandoned, it may take a very long time for geoxyles to recolonise the area. To date, agriculture in more remote parts of Angola is only starting to become industrialised, and most agricultural practices still rely on combinations of hard manual work, animal traction and/or fire. However, urbanisation and technical progress promote the mechanisation of agriculture, which in turn makes it easier to convert land pervaded by massive belowground woody structures, as seen for instance on the Bié and Huambo plateaus (Figure 3, pers. obs. M Finckh, A Gomes, P Meller).

Analogously, misguided attempts to afforest tropical grasslands in order to sequester atmospheric CO_2 (Bastin *et al.* 2019, Bond *et al.* 2019) endanger geoxyles and make little sense because intact geoxyle grasslands can store carbon amounts comparable to old-growth woodlands (Gomes *et al.* 2021). Even if the geoxyles' belowground structures are left unharmed,

Figure 3: *Tractor-ploughed fields in geoxyle grasslands near Chitembo, Bié, appeared in July 2021 (top photos). A plough pulled by a tractor is deep and strong enough to destroy the massive belowground geoxyle structures. Ploughed fields are then planted with crops like cassava, beans or maize (bottom photo). The maize field in the lower photo was ploughed in 2015 but had already been abandoned four years later because productivity decreases rapidly in these nutrient-poor soils.*

once they are overshadowed by trees, the shade-intolerant geoxyles rapidly become outcompeted (Zaloumis & Bond 2016, Buisson *et al.* 2019). Like intensified agriculture, this destroys biodiverse, old-growth natural grasslands (Bond 2016).

It is clear that geoxylic species face imminent threats in Angola due to accelerating land use change and intensification. For example, nearly 800,000 ha of miombo woodland, including geoxyle habitats, were converted to croplands on the Angolan Planalto between 2002 and 2015 (Palacios *et al.* 2015, Mendelsohn 2019). Lack of knowledge about geoxyle diversity makes it difficult to estimate specific conservation needs, because many geoxyle species are poorly known and/or described, and the range extent and population sizes of most species are still unknown. As a result, threat status assessments (IUCN Red List) are rarely available. Of the 126 taxa occurring on the Angolan Planalto, 119 taxa (94.4%) are either Data Deficient or not assessed. The high rate of localised endemics facing land-use intensification, however, indicates a substantial threat to at least some of the geoxyle species, such as *Barleria kacondensis* subsp. *glabrescens* which is classified as EN B1ab(iii), i.e., "Endangered, with extent of occurrence < 100 km² and further decline" (Darbyshire *et al.* 2021) and *Bolusia ervoides* which has been described as a "rare species and is known from only few collections" (van Wyk *et al.* 2010).

GAPS IN KNOWLEDGE AND PRIORITIES FOR RESEARCH

As described, several knowledge gaps and research priorities are already apparent: the impact of herbivory on geoxyle grasslands cannot be assessed without further research, and the same is true for the threats and conservation needs of individual geoxyle species and communities. The diversity, richness and multiple origins of geoxyle species make it difficult to study them as a whole (Meller *et al.* 2022b), so we advocate not to treat them across-the-board as a uniform plant growth form, but as a conglomeration of species that adapted convergently in response to similar environmental drivers.

Geoxyle grasslands are characterised by the low agricultural potential of the soils on which they occur, and the fact that different soil types bear different geoxyle communities (Revermann *et al.* 2017). Generally, these soils are weathered, well-drained, nutrient-poor and of high sand content (> 80%); they are acidic (~pH 4) with a low cation exchange capacity (< 20 cmolc/dm³) and low base saturation (71%–78%) (Gröngröft 2013, Gomes *et al.* 2021). This is also evident from other co-occurring plant species that are adapted to low nutrient contents, such as orchids. From pristine species-rich grassland ecosystems worldwide it is known that the application of nitrogen and phosphorus fertilisers leads to diversity losses and homogenisations in grasslands (Tilman & Downing 1994, Harpole & Tilman 2007). If industrial agriculture in Angolan geoxyle grasslands intensifies further, it is likely that the application of fertilisers will have a similar effect on geoxyle diversity in the long term. Research on these issues is urgently needed.

The high number of endemic species and their often localised ranges raise the question of genetic diversity and connectedness between populations. To our knowledge, there have been no studies on population genetics of Afrotropical geoxyles to date, except for one study on the widely distributed and polymorphic *Syzygium guineense* complex, which includes geoxylic forms, and where gene flow between geoxyle, shrub and tree forms occurs over wide ranges (Zigelski *et al.* 2019b). Detailed studies on the genetic diversity, or isolation, of specific geoxyle populations are missing, which is concerning because the influence of the geoxyles' supposedly limited sexual reproduction cannot be assessed. Furthermore, demographic studies of geoxyle species are practically non-existent, with one exception (Chidumayo 2019), making it hard to understand and counteract the observed rarity of seedlings. Such knowledge is crucial for conservation and restoration purposes, particularly in the light of impending grassland degradations and fragmentations.

There are manifold research deficiencies regarding African geoxyles, although Burtt Davy published the first comprehensive review 100 years ago (Davy 1922), followed by treatises from White (1976), Maurin *et al.* (2014) and Zigelski *et al.* (2019a). These articles, however, focus predominantly on ecological and evolutionary aspects rather than the complexity of the geoxylic growth form. Scientific information on the life cycle of geoxyles would make conservation and management plans more sustainable and holistic. Aspects such as animal–geoxyle interactions, plant–fungi and plant–microbe mutualisms, pollination and pollinators, dispersal mechanisms, growing rates, and success rates of generative reproduction (and how to improve it) need to be investigated. To conclude, we see imminent threats of destruction and loss of a landscape type which is home to unique plant evolution, before we even have started to grasp and comprehend its functioning, diversity, history, biotic interactions and ecosystem services.

ACKNOWLEDGEMENTS

This study was conducted within the framework of the Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL), funded by the German Federal Ministry of Education and Research (BMBF) (Grant No. 01LG1201N). The Studienstiftung des Deutschen Volkes supported livelihood and travels of PM. The Global Biodiversity Information

Facility (GBIF.org) provided valuable data on the occurrence of geoxylic species. Furthermore, we thank Ruth, Grece and Telmo from the Instituto Superior Politécnico Tundavala (ISPT), Lubango, and the Angolan permit authorities for their help and support.

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Appendix 1: *Full list of endemic geoxyle taxa occurring on the Angolan Planalto (extended version of Table 3). For each species, the geoxyle category indicates whether it is a geoxyle in a broad sense (with a woody base), or strict sense (with a woody underground storage organ); also indicated, is whether it is a strict highland endemic and whether it has a close congeneric tree relative (Y = yes; N = no). Distribution indicates if species are restricted to particular plateaus, escarpments or localities; wider distributions within Angola are presented as an alphabetical list of provinces abbreviated as follows: BE – Benguela; BI – Bié; CC – Cuando Cubango; CN – Cuanza-Norte; CS – Cuanza-Sul; CU – Cunene; HI – Huíla; HU – Huambo; LS – Lunda-Sul; MA – Malanje; MO – Moxíco; and NA – Namibe*

Taxon	**Family**	**Geoxyle category**	**Highland endemic**	**Close tree relative(s)**	**Distribution**
Acalypha dumetorum Müll.Arg.	Euphorbiaceae	broad	N	N	BE
Acalypha eriophylla Hutch.	Euphorbiaceae	broad	Y	N	BI high plains
Acalypha eriophylloides S.Moore	Euphorbiaceae	broad	Y	N	BI high plains
Acalypha gossweileri S.Moore	Euphorbiaceae	broad	N	N	CN, Cazengo
Acalypha huillensis Pax & K.Hoffm.	Euphorbiaceae	broad	Y	N	Humpata Plateau
Adenodolichos mendesii Torre	Fabaceae	broad	Y	N	BI high plains
Aeschynomene benguellensis Torre	Fabaceae	broad	Y	N	BE, BI, HI, HU
Aeschynomene debilis Baker	Fabaceae	broad	Y	N	Humpata Plateau
Aeschynomene dimidiata subsp. *dimidiata* Baker	Fabaceae	broad	N	N	CC, HI, HU, LS, MA
Ampelocissus dekindtiana Gilg	Vitaceae	broad	Y	N	Humpata Plateau, Tchivinguiro
Antizoma angolensis Exell & Mendonça	Menispermaceae	broad	Y	N	HU high plains
Baphia sp. nov.	Fabaceae	strict	N	Y	CC, BI, MO
Barleria antunesii Lindau	Acanthaceae	broad	Y	N	Humpata Plateau
Barleria buddleoides S.Moore	Acanthaceae	broad	N	N	CC, HI
Barleria crabbeoides I.Darbysh.	Acanthaceae	broad	Y	N	Humpata Plateau, Lubango
Barleria eburnea I.Darbysh.	Acanthaceae	broad	N	N	BI high plains and Humpata Plateau
Barleria imatensis I.Darbysh.	Acanthaceae	broad	N	N	Humpata Plateau, Tchivinguiro
Barleria kacondensis subsp. *glabrescens* I.Darbysh.	Acanthaceae	broad	Y	N	HU high plains
Barleria kacondensis subsp. *kacondensis* S.Moore	Acanthaceae	broad	Y	N	BI high plains and Humpata Plateau
Barleria polyneura S.Moore	Acanthaceae	broad	N	N	Humpata Plateau
Barleria violascens var. *humpatana* I.Darbysh.	Acanthaceae	broad	Y	N	Humpata Plateau, Monino
Basananthe nummularia Welw.	Passifloraceae	broad	Y	N	Humpata Plateau, Lopollo
Bolusia ervoides (Baker) Torre	Fabaceae	broad	Y	N	Humpata Plateau, Lopollo

Ceratoteca reniformis Abels	Pedaliaceae	broad	N	N	BE, CS, HI, HU, MA
Chamaecrista huillensis (Mendonca & Torre) Lock	Fabaceae	broad	N	N	CC, HI, NA
Chamaecrista newtonii (Mendonca & Torre) Lock	Fabaceae	broad	Y	N	BE, HI
Clutia benguelensis Müll.Arg.	Euphorbiaceae	strict	Y	Y	BE, BI, HI, HU
Combretum argyrotrichum Welw. ex M.A.Lawson	Combretaceae	strict	Y	Y	HU high plains, Humpata Plateau
Combretum viscosum Exell	Combretaceae	strict	Y	Y	BE, BI, HI, HU
Crossandra angolensis S.Moore	Acanthaceae	broad	Y	N	BE
Crotalaria bondii Torre	Fabaceae	broad	Y	N	Humpata Plateau
Crotalaria griseofusca Baker f.	Fabaceae	broad	Y	N	BI high plains
Crotalaria ivantalensis Baker	Fabaceae	broad	Y	N	HI, NA
Crotalaria mendesii Torre	Fabaceae	broad	N	N	CU, HI
Crotalaria pittardiana Torre	Fabaceae	broad	N	N	BE, CU, HI, HU
Crotalaria pseudovirgultatis Torre	Fabaceae	broad	Y	N	Humpata Plateau, Lubango
Crotalaria subsessilis Harms	Fabaceae	broad	N	N	CC
Cryptosepalum sp. nov. aff. *maraviense*	Fabaceae	strict	Y	Y	BI high plains
Dissotis benguellensis A.Fern. & R.Fern.	Melastomataceae	strict	Y	Y	HU, Serra do Môco
Dissotis carrissoi A.Fern. & R.Fern.	Melastomataceae	strict	N	Y	CS, Huambo
Dolichos dongaluta Baker	Fabaceae	broad	Y	N	BI high plains
Dolichos elatus Baker	Fabaceae	broad	N	N	BE, MA
Droogmansia dorae var. *dorae* Torre	Fabaceae	broad	Y	N	BI high plains
Droogmansia gossweileri Torre	Fabaceae	broad	Y	N	HU high plains
Droogmansia vanderystii De Wild.	Fabaceae	broad	N	N	CS, HU
Eminia benguellensis Torre	Fabaceae	broad	N	N	BE, HI, HI, LS, MA
Eriosema albo-griseum Baker f.	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala
Eriosema cyclophyllum Baker f.	Fabaceae	broad	Y	N	BI high plains and Humpata Plateau
Eriosema gossweileri Baker f.	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala
Eriosema pygmaeum Baker	Fabaceae	broad	N	N	Humpata Plateau
Eriosema speciosum Baker	Fabaceae	broad	N	N	CN, BE, HI, HU
Erythrina pygmaea Torre	Fabaceae	strict	Y	Y	Humpata Plateau
Euclea angolensis Gürke	Ebenaceae	strict	Y	Y	Humpata Plateau

Euphorbia asclepiadea Milne-Redh.	Euphorbiaceae	strict	N	Y	BI high plains
Euphorbia parifolia N.E.Br.	Euphorbiaceae	strict	Y	Y	Humpata Plateau, Tundavala
Fadogia caespitosa Robyns	Rubiaceae	strict	N	Y	Humpata Plateau
Fadogia chrysantha K.Schum.	Rubiaceae	strict	Y	Y	HU high plains
Fadogia graminea Wernham	Rubiaceae	strict	N	Y	BI high plains
Fadogia punctulata Robyns	Rubiaceae	strict	Y	Y	HU plateau
Fadogia stenophylla Welw. ex Hiern	Rubiaceae	strict	N	Y	Humpata Plateau, Lubango
Fuerstia adpressa A.J.Paton	Lamiaceae	broad	Y	N	BE, HI
Fuerstia rigida (Benth.) A.J.Paton	Lamiaceae	broad	Y	N	Humpata Plateau, Lopollo
Ganguelia gossweileri (S.Moore) Robbr.	Rubiaceae	broad	Y	N	BI high plains
Gnidia fruticulosa Gilg	Thymelaeaceae	strict	Y	Y	Humpata Plateau
Gnidia newtonii Gilg	Thymelaeaceae	strict	Y	Y	Humpata Plateau
Gnidia rendlei Hiern	Thymelaeaceae	strict	Y	Y	Humpata Plateau, Mumpulla
Gnidia welwitschii Hiern	Thymelaeaceae	strict	Y	Y	Humpata Plateau
Grewia suffruticosa K.Schum.	Malvaceae	strict	Y	Y	Humpata Plateau
Hypericum abilianum N.Robson	Hypericaceae	strict	Y	Y	Humpata Plateau
Indigofera corallinosperma Torre	Fabaceae	broad	Y	N	Humpata Plateau
Indigofera huillensis Baker f.	Fabaceae	broad	Y	N	BE, HI
Indigofera mendesii Torre	Fabaceae	broad	Y	N	Humpata Plateau
Indigofera nummularia Baker	Fabaceae	broad	Y	N	BE, HU
Indigofera paraoxalidea Torre	Fabaceae	broad	Y	N	Humpata Plateau
Jamesbrittenia angolensis Hilliard	Scrophulariaceae	broad	Y	N	Humpata Plateau, Tundavala
Julbernardia gossweileri (Baker f.) Torre & Hillc.	Fabaceae	strict	N	Y	CC, HI, HU, MA
Lannea gossweileri Exell & Mendonça	Anacardiaceae	strict	Y	Y	BI high plains
Lannea rubra Hiern (Engl.)	Anacardiaceae	strict	Y	Y	Humpata Plateau, Tundavala
Lepidagathis gossweileri S.Moore	Acanthaceae	broad	Y	N	BE, HI
Leptactina prostrata K.Schum.	Rubiaceae	strict	N	Y	BI high plains, MO
Linariopsis prostrata Welw.	Pedaliaceae	broad	Y	N	HI
Macrotyloma bieense (Torre) Verdc.	Fabaceae	broad	Y	N	Humpata Plateau, Tchivinguiro

Meineckia phyllanthoides subsp. *trichopoda* (Müll.Arg.) G.L.Webster	Euphorbiaceae	broad	N	N	northwest Angola
Oldenlandia sipaneoides K.Schum.	Rubiaceae	broad	Y	N	Humpata Plateau, Lopollo
Orthosiphon violaceus Briq.	Lamiaceae	broad	Y	N	Humpata Plateau, Lopollo
Ozoroa xylophylla (Engl. & Gilg) R.Fern. & A.Fern.	Anacardiaceae	strict	Y	Y	BI high plains and Humpata Plateau
Pavetta nana K.Schum.	Rubiaceae	strict	Y	Y	Humpata Plateau, Tchivinguiro
Pentanisia rubricaulis (K.Schum.) Kårehed & B.Bremer	Rubiaceae	broad	Y	N	BI high plains, HI, HU
Phaulopsis lankesterioides (Lindau) Lindau	Acanthaceae	broad	Y	N	BE, HI, HU
Phyllanthus microdendron Müll.Arg.	Phyllanthaceae	strict	Y	Y	BI high plains
Polygala huillensis Welw. ex Oliv.	Polygalaceae	broad	Y	N	Humpata Plateau, Lopollo
Protea dekindtiana Engl.	Proteaceae	strict	Y	Y	Humpata Plateau, Tchivinguiro
Protea ongotium Beard	Proteaceae	strict	Y	Y	BI high plains and Humpata Plateau
Protea paludosa subsp. *paludosa* Hiern (Engl.)	Proteaceae	strict	Y	Y	BI high plains and Humpata Plateau
Protea poggei subsp. *haemantha* (Engl. & Gilg) Chisumpa & Brummitt	Proteaceae	strict	N	Y	BI highlands, MO
Protea poggei subsp. *heliophila* Chisumpa & Brummitt	Proteaceae	strict	Y	Y	HU high plains
Pseudeminia benguellensis (Torre) Verdc.	Fabaceae	broad	N	N	CC, BE, HI, HU
Psychotria moninensis (Hiern) E.M.A.Petit	Rubiaceae	strict	N	Y	CC, BE, BI, HI, HU, MA
Psychotria welwitschii (Hiern) Bremek.	Rubiaceae	strict	Y	Y	HI, HU and NA escarpment
Spermacoce aprica (Hiern) Govaerts	Rubiaceae	broad	Y	N	Humpata Plateau, Ivantala
Spermacoce terminaliflora R.D.Good	Rubiaceae	broad	N	N	Humpata Plateau
Spermacoce thymoidea (Hiern) Verdc.	Rubiaceae	broad	Y	N	Humpata Plateau
Sphedamnocarpus barbosae Launert	Malpighiaceae	broad	Y	N	HU high plains
Stachys huillensis Hiern	Lamiaceae	broad	Y	N	Humpata Plateau
Stomatanthes tundavalaensis D.J.N.Hind	Asteraceae	broad	Y	N	Humpata Plateau
Tephrosia gossweileri Baker f.	Fabaceae	broad	Y	N	BE, BI, HI, HU
Tephrosia huillensis Baker	Fabaceae	broad	Y	N	HI, HU highland
Tephrosia melanocalyx Baker	Fabaceae	broad	Y	N	Humpata Plateau, Lopollo
Tephrosia newtoniana Torre	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala
Tephrosia rigidula Baker	Fabaceae	broad	N	N	BE, CU, HI, HU
Tephrosia tundavalensis Bamps	Fabaceae	broad	Y	N	Humpata Plateau, Tundavala

Thesium lycopodioides Gilg	Santalaceae	broad	Y	N	BI high plains
Thesium triste A.W.Hill	Santalaceae	broad	N	N	CC, HI, MA
Thunbergia cycnium S.Moore	Acanthaceae	broad	Y	N	BI high plains
Thunbergia huillensis S.Moore	Acanthaceae	broad	Y	N	BI high plains and Humpata Plateau
Thunbergia retefolia S.Moore	Acanthaceae	broad	Y	N	BI high plains
Tinnea benguellensis Gürke	Lamiaceae	broad	N	N	BI high plains, MO
Tinnea gossweileri Robyns & Lebrun	Lamiaceae	broad	Y	N	HU high plains
Tricalysia angolensis A.Rich. ex DC.	Rubiaceae	strict	N	Y	CC, CU, BI high plains and Humpata Plateau
Triumfetta gossweileri Exell & Mendonça	Malvaceae	broad	Y	N	BI high plains and Humpata Plateau
Triumfetta hundtii Exell & Mendonça	Malvaceae	broad	Y	N	BE, Caconda
Triumfetta macrocoma K.Schum.	Malvaceae	broad	Y	N	Humpata Plateau, Tchivinguiro
Triumfetta rhodoneura K.Schum.	Malvaceae	broad	Y	N	Humpata Plateau
Vangueria cistifolia var. *cistifolia* (Welw. ex Hiern) Lantz	Rubiaceae	strict	N	Y	BI, HI, MA
Vangueria fulva (Robyns) Lantz	Rubiaceae	strict	Y	Y	BI high plains and Humpata Plateau
Vitex caespitosa Exell	Lamiaceae	strict	Y	Y	BI, BE, HU

Diversity and endemism in the species-rich Ceropegieae (Apocynaceae) and *Euphorbia* in highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-bruyns

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ABSTRACT

We map the distribution of the species-rich groups Ceropegieae and *Euphorbia* in southwest tropical Africa (i.e., in Angola and Namibia). This shows that they are most diverse in the highland and escarpment areas of these countries, and in the coastal areas west of these highlands. Most of the endemic species occur here too. Several 'hotspots' within highlands and escarpments of Angola and Namibia (HEAN) are identified that are common to both groups. Diversity in both groups falls off rapidly in Angola north of Benguela. This diversity also tails off substantially on the Kalahari sands to the east of the escarpment (i.e., east of the HEAN), with some notable exceptions in Namibia in *Ceropegia*. In the Ceropegieae, many species occurring in these sandy regions are widespread in southern Africa. Areas covered by Kalahari sands are almost completely devoid of *Euphorbia*. Several lineages are identified in *Ceropegia* and *Euphorbia* that have diversified in and are endemic to the margins of the Namib Desert in Angola and Namibia (i.e., in and west of the HEAN). Apart from these endemic lineages, the species found in the HEAN (and more generally in Angola and Namibia) are mostly related to others occurring further east in southern Africa. Extreme examples of this are provided by closely related species pairs that occur on opposite sides of southern Africa. While the Asclepiadeae has significant numbers of geophytic herbs and few succulents, in the Ceropegieae and in *Euphorbia* succulents are particularly common. The proportion of succulents with greatly reduced leaves is also high, suggesting that this growth form is especially successful in the region of the HEAN and in the narrow coastal area west of it. These succulents are considered to have arisen within the last 8 million years.

Keywords: Angola, *Ceropegia*, Ceropegieae, distribution, diversity, endemic lineages, *Euphorbia*, growth forms, highland, Namibia, species pairs, succulents

INTRODUCTION

The Asclepiadoideae (which makes up most of the former Asclepiadaceae) is the most diverse subfamily of the Apocynaceae in southwestern tropical Africa; i.e., Angola and Namibia. The Asclepiadoideae consists of four tribes: Asclepiadeae, Ceropegieae, Fockeeae and Marsdenieae. Of these, the Asclepiadeae and Marsdenieae are cosmopolitan, although the latter is mainly tropical. The Fockeeae is restricted to sub-Saharan Africa and the southern Arabian Peninsula. The Ceropegieae is an exclusively Old World group that occurs mainly in the tropics, around the perimeter of the Indian Ocean, from South Africa to the northern parts of Australia. It is the most diverse of the four tribes in southwestern tropical Africa.

The Ceropegieae contains about 790 species, of which around 695 species are in the recently much expanded *Ceropegia* L. The genus *Ceropegia* now includes *Brachystelma* Sims with 139 species, the traditional members of *Ceropegia* with 202 species and the stem-succulents popularly known as the stapeliads with around 353 species (Bruyns *et al.* 2017). The remaining ~95 species of Ceropegieae belong to three early-divergent lineages, the Anisotominae (the most closely allied of these three lineages to *Ceropegia*), Leptadeniinae and the Heterostemminae (Rodda 2016, Meve *et al.* 2017, Bruyns *et al.* 2023). The distributions of these early-divergent lineages coincide with the rest of the tribe, except that they are absent from the temperate regions of southwestern South Africa, and northwest Africa in Morocco, Macaronesia and around the Mediterranean. Some species of Ceropegieae endemic to the highlands and escarpments of Angola and Namibia are shown in Figure 1.

Euphorbia L. (Euphorbiaceae) is another species-rich group in southwestern tropical Africa. *Euphorbia* consists of some 1,840 species (Yang *et al.* 2012, Dorsey *et al.* 2013, Peirson *et al.* 2013, Riina *et al.* 2013) and is divided into four subgenera (Bruyns *et al.* 2006). The relationships between these subgenera and their numbers of species in Angola and Namibia are shown in Figure 2. As in *Ceropegia*, *Euphorbia* is not a single radiation (i.e., a monophyletic entity, as stated by Frazão *et al.* (2020)) in either Angola or Namibia, but it is represented in each country by offshoots of many separate lineages. Taxonomy used for *Euphorbia* is that of Bruyns (2012, 2018), Bruyns and Berry (2019) and Bruyns *et al.* (2020), with some modifications as in Bruyns (2022).

In Angola and Namibia, the distributions of many species of plant are heavily influenced by the mountainous and hilly highlands and escarpments, where the broad range of altitude over a short horizontal distance gives rise to a great variety of distinct habitats and wide variation in rainfall. Another major influence is the narrow coastal belt taken up by the hyperarid Namib Desert. This desert is most arid between Port Nolloth in South Africa and Lucira in Angola and has been hyperarid for at least the last 20 million years (Pickford *et al.* 2014). On the eastern side of the region, the Kalahari sands provide a similarly strong influence on plant distributions; these sands extend from central South Africa to the basin of the Congo River, forming the largest continuous body of sand in the world, and have been present for the last 32,000 years at least (Lancaster 1989).

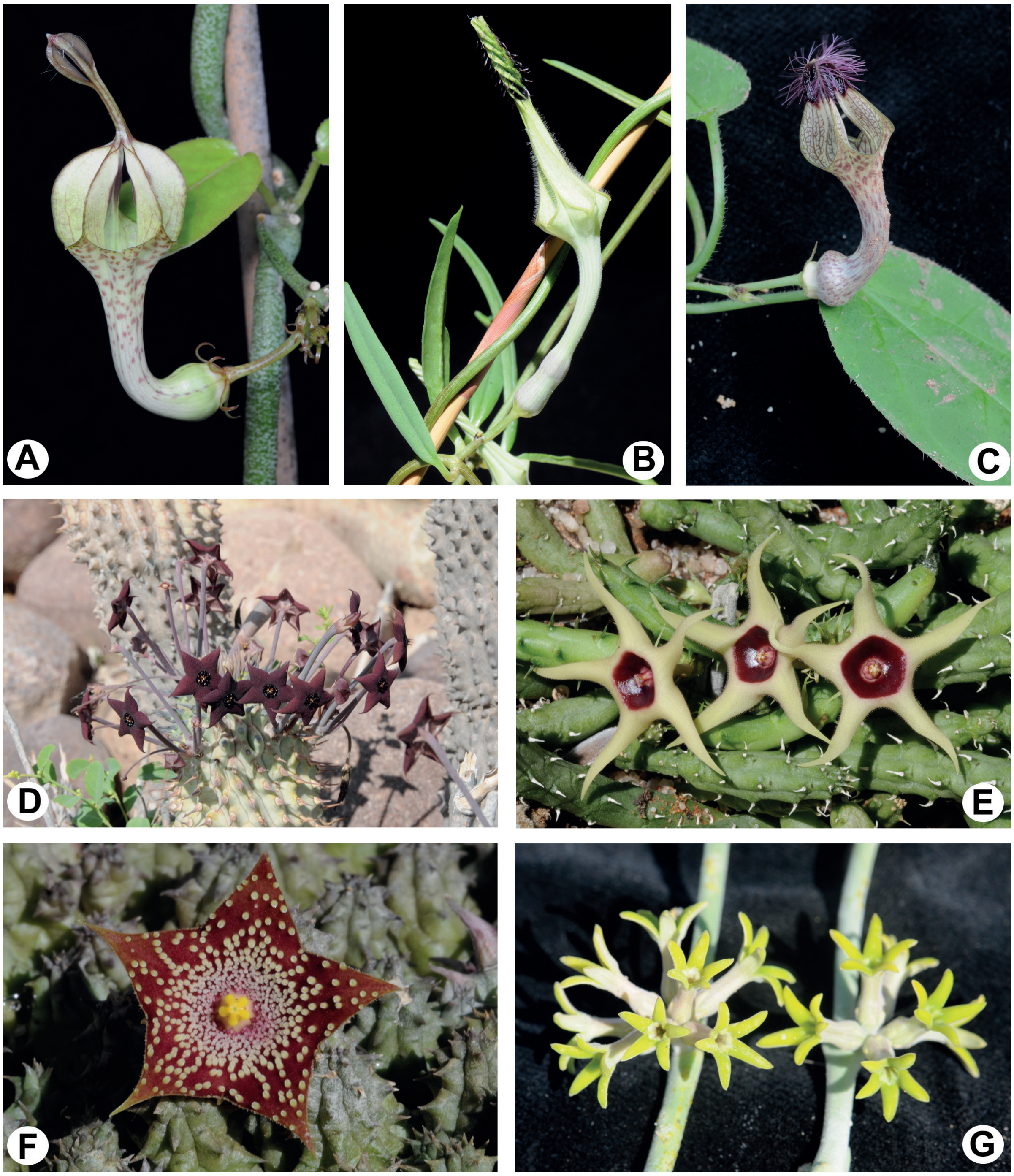

Figure 1: *Examples of species endemic to the highlands and escarpments of Angola and Namibia (HEAN) and the coastal plain west of it: A)* Ceropegia *cf.* haygarthii, *Bruyns 10444, west of Lubango, Angola; B)* Ceropegia terebriformis, *Bruyns 13289, near Caraculo, Angola; C)* Ceropegia volubilis, *Bruyns 14218, near Lucala, Angola; D)* Ceropegia mossamedensis, *near Caraculo, Angola; E)* Ceropegia angolensis, *Bruyns 10419, west of Lubango, Angola; F)* Ceropegia lopanthera, *Bruyns 10410, north of Moçâmedes, Angola; and G)* Leptadenia albida, *Bruyns 12830, near Solitaire, Namibia. Photos by P Bruyns.*

In this paper we investigate: (1) the diversity in the Ceropegieae and *Euphorbia* and the number of endemics present in Angola and Namibia; (2) how these two groups and their endemics are distributed in Angola and Namibia relative to the highlands and escarpments there; (3) how members of these two groups associated with the highlands and escarpments in Angola and Namibia (HEAN) are related to others in Africa, and whether there are any endemic lineages associated with the HEAN; and, finally, (4) which growth forms are most prevalent among these two groups and among their endemics in the HEAN.

MATERIALS AND METHODS

Data on the species of Apocynaceae occurring in Angola were extracted from Goyder (2008, 2009), supplemented by several additions to the Ceropegieae from records in the Natural History Museum Herbarium (BM), University of Cape Town Bolus Herbarium (BOL), University of Coimbra Herbarium (COI), Royal Botanic Gardens Herbarium (K), Jardim Botânico Tropical, Instituto de Investigação Científica Tropica Herbário (LISC), Instituto Superior de Ciencias da Educação (LUBA) and the South African National Biodiversity Institute (NBG) (Thiers 2020). Maps were drawn up from 334 records from these herbaria. Data on the species of Apocynaceae occurring in Namibia are from Bruyns (2014). This amounts to 1,392 specimens for the Ceropegieae. For *Euphorbia*, records from BM, BOL, COI, K, LISC, LUBA, NBG, the South African National Biodiversity Institute National Herbarium (PRE) and the National Herbarium of Namibia (WIND) were used to draw up the maps, which amounted to 439 specimens from Angola and 1,142 specimens from Namibia.

Appendices 1–5 list the species known from the respective regions. This adds to and refines those lists published in Goyder (2008) and Frazão *et al.* (2020) and provides a firm basis for the numbers given in Tables 1 and 2, Figures 2–4 and 6–7 and elsewhere in the text.

Phylogenetic trees shown are adapted and modified from previously published accounts, mainly from Bruyns *et al.* (2014, 2015) for *Ceropegia* (Figure 8) and from Bruyns *et al.* (2011) for *Euphorbia* (Figure 2). Other results are cited from as-yet unpublished data. All photographs are by P Bruyns.

An endemic is defined here as a species that only occurs in the area concerned. Near-endemics, i.e., species with small numbers of records outside the area, such as *Cryptolepis decidua* (Planch. ex Benth.) N.E.Br. and *Raphionacme inconspicua* H.Huber of the Apocynaceae and *Euphorbia virosa* Willd. in *Euphorbia*, are not considered. This account is confined to species; subspecies and varieties are not considered.

For growth forms, many of the Asclepiadeae have been characterised as 'perennial herbs' with 'annual aerial stems' (e.g., Goyder (1998a) for *Pachycarpus*; Goyder (1998b) for *Stathmostelma*; and Goyder and Nicholas (2001) for some species of *Gomphocarpus*) or 'coming up after fires from narrow, tuberous, perennial rootstocks' for *Glossostelma* (Goyder 1995). These are plants that appear to retreat into their rootstock during the dry season. In our assessment of growth forms, they are included under 'geophytic herbs'.

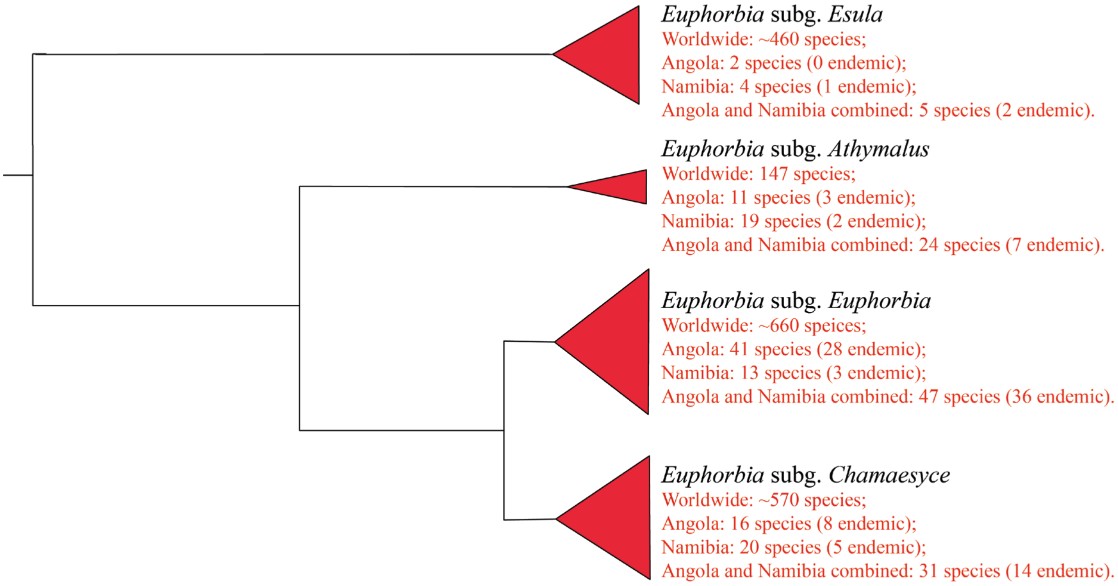

Figure 2: *Relationships between the four subgenera recognised in* Euphorbia *as derived from analysis of DNA data. The total number of species, the numbers of species in Angola and in Namibia and the number of endemics in Angola and Namibia combined are given for each subgenus. The vertical side of each triangle is proportional to the total number of species in the subgenus. Three species are not placed in this system (see Appendix 4).*

RESULTS

Our results are summarised below and in the maps (Figures 3–4 and 6–7). Table 1 provides statistics for numbers of species and endemics in the Apocynaceae and some of its subdivisions. Table 2 summarises information on several growth forms and the extent to which leaves are reduced to rudiments in these groups.

1. How diverse are these groups and how many endemics are there?

(i) Ceropegieae

The Apocynaceae *sensu stricto* (Table 1) is more than eight times as rich in species in Angola as in Namibia, but it is particularly poor in endemics. Of the subfamilies listed in Table 1, the Asclepiadoideae is by far the most diverse. In Angola the Asclepiadoideae (Table 1) makes up 50% of the family (and almost all the endemics), but in Namibia it makes up 86% of the family (and almost all the endemics). In the two countries combined, it makes up 62% of the family (and again almost all the endemics).

A comparison of the tribes that make up the Asclepiadoideae shows that the Ceropegieae is the most diverse. In Angola the Asclepiadeae comes a close second, since there the Asclepiadeae and Ceropegieae have roughly the same number of species. However, in Namibia, which is generally much drier, the Ceropegieae is nearly three times as diverse as the Asclepiadeae. The much higher number of stapeliads in Namibia (more than double that in Angola) contributes considerably to this difference (Appendices 1, 2 and 3). The number of Marsdenieae is small, underlining the generally poor representation of this tribe in Africa as a whole (most of its species occur in Australasia), and there is only one endemic species in Namibia. The Fockeeae is a small tribe altogether, with a total of nine species and no endemics in either Angola or Namibia (Bruyns & Klak 2006).

The Ceropegieae has three to four times as many endemics as any of the other tribes, even when Angola and Namibia combined is considered. That the percentage of *Ceropegia* (for example) endemic to the combined country area is significantly higher than the percentage in either country is due to the species that are endemic to the Kaokoveld, which straddles their common border.

(ii) *Euphorbia*

Euphorbia has a total of 70 species in Angola (Figure 2, Appendix 4) and 56 species in Namibia (Figure 2, Appendix 5). In total, 107 species occur in Angola and Namibia combined.

For Angola, 39 species (i.e., 56%; 61% according to Frazão *et al.* 2020) are endemic, whereas in Namibia only 11 (20%) are endemic. Of the 107 species in the two countries, 59 (55%) are endemic; i.e., more than half of them occur nowhere else.

This shows that in southwestern tropical Africa, while the diversity of *Euphorbia* and *Ceropegia* (for example) is similar, endemism is higher in *Euphorbia*.

2. Where are these groups most diverse and where do the endemics occur?

(a) Namibia

(i) Ceropegieae

The Ceropegieae is found over most of Namibia (Figure 3). However, diversity is concentrated in the highlands and escarpments, with areas of highest diversity around Grootfontein, Gobabis, Naukluft–Tiras, Rosh Pinah and the Groot Karasberge.

Table 1: *Numbers of species in the Apocynaceae and its subdivisions in Angola (adapted from Goyder 2008, 2009, Goyder* et al. *2018 and newer records in the appendices to this paper), in Namibia (data from Bruyns 2014) and in the two countries combined.*

	Angola			Namibia			Angola and Namibia		
	Total species	Endemic species	Endemic species %	Total species	Endemic species	Endemic species %	Total species	Endemic species	Endemic species %
Apocynaceae	235	24	10	153	20	12	326	58	18
Apocynaceae s.s.	88	1	1	10	0	0	92	2	2
Asclepiadoideae	119	21	18	131	17	13	202	51	25
Asclepiadeae	52	5	10	33	3	9	70	10	14
Ceropegieae	56	16	29	90	13	14	117	41	35
Ceropegia	52	15	29	88	13	15	113	39	35
‘stapeliads’	24	8	33	59	11	19	68	26	38
Fockeeae	2	0	0	4	0	0	4	0	0
Marsdenieae	9	0	0	4	1	25	11	1	9
Periplocoideae	23	2	9	11	3	27	27	5	19
Secamonoideae	5	0	0	1	0	0	5	0	0

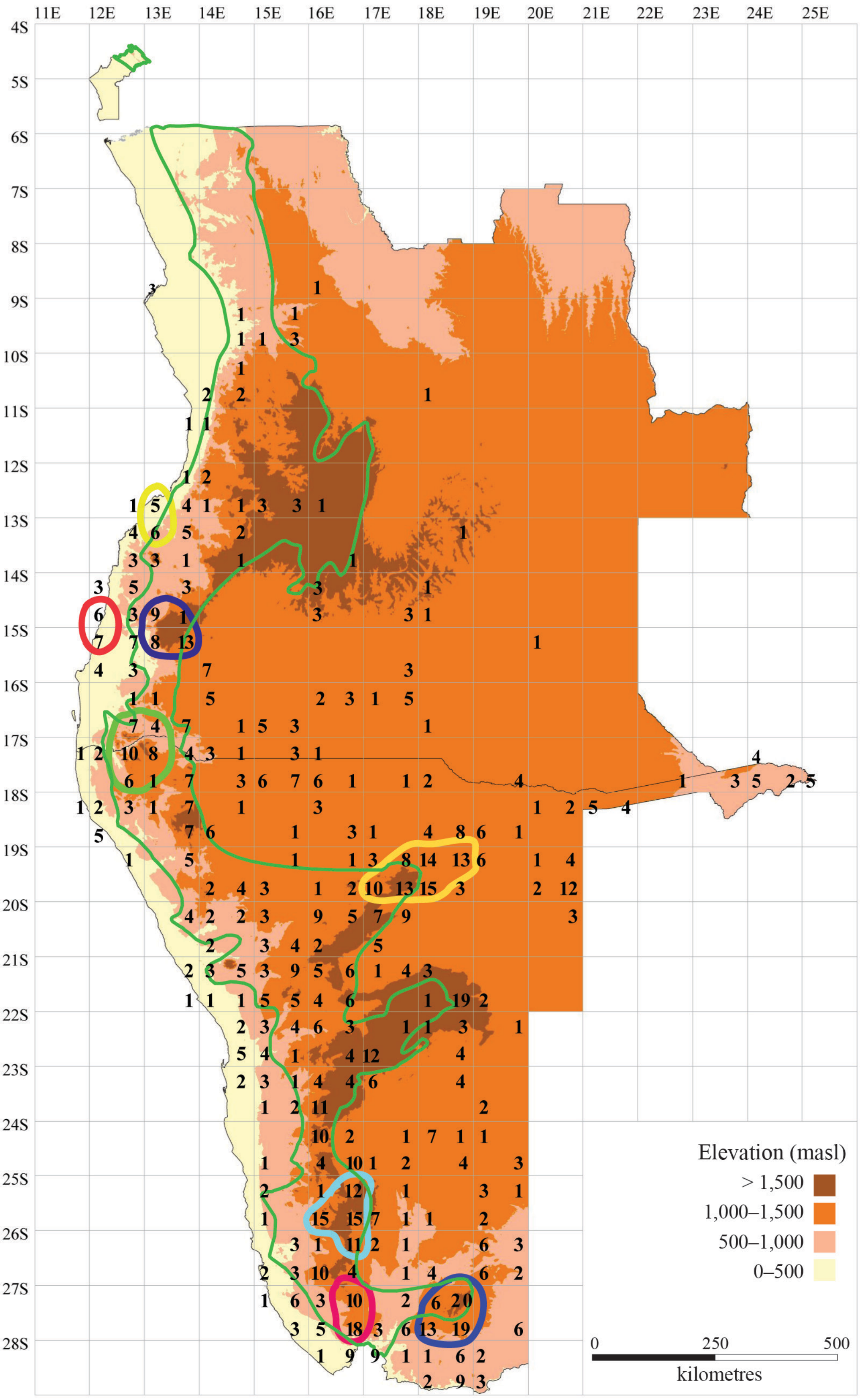

Figure 3: *Occurrence of Ceropegieae in Angola and Namibia (combined). Numbers indicate the numbers of species recorded per half-degree square. Centres of diversity are indicated, approximately, as follows: yellow = Benguela; red = Moçamedes; deep blue = Serra da Chela; thick green = Kaokoveld; orange-yellow = Otavi Mountains; turquoise = Naukluft–Tiras; pink = Namuskluft; and blue = Groot Karasberge. The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

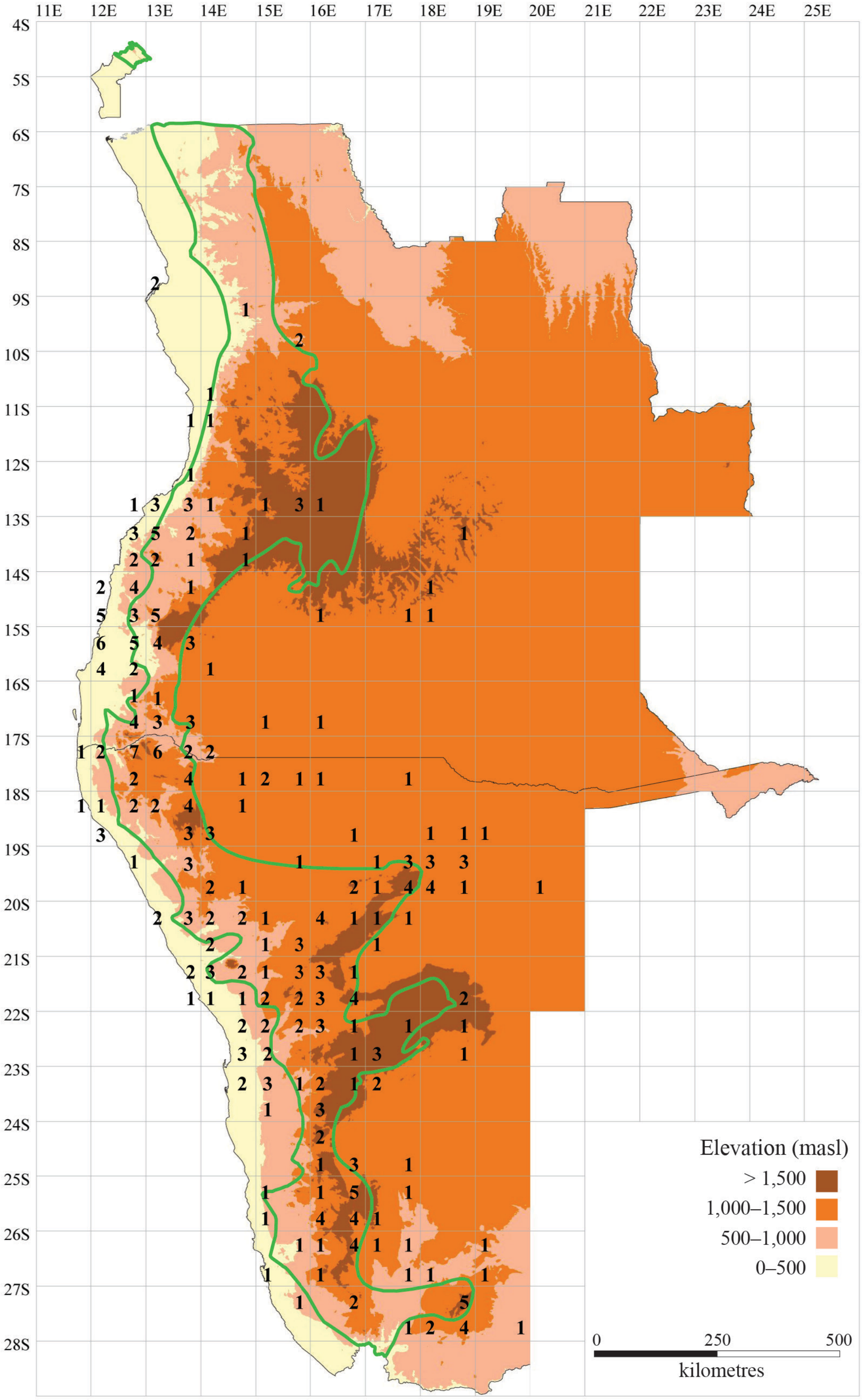

Figure 4: *Diversity of endemic Ceropegieae in Angola and Namibia (combined). Numbers of endemic species to Angola and Namibia are recorded in each half-degree square. The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

Endemic species (Figure 4) are mainly associated with the more arid parts of the country and are closely associated with the highlands and escarpment, where endemics are most numerous in the Kaokoveld, Naukluft–Tiras and in the Groot Karasberge. With respect to endemics, Rosh Pinah falls away, as most of the species here are common to the neighbouring arid winter-rainfall parts of South Africa. In Namibia there are far fewer endemics in the most arid coastal zones than in the semi-arid parts. This corresponds closely to the conclusions of Simmons *et al.* (1998: Figure 1a) for all plants in Namibia. Inselbergs (such as the Brandberg and the Groot Karasberge) are not known to harbour any endemics in the Ceropegieae (nor in the Apocynaceae, more generally, or in *Euphorbia*).

The number of endemics in the Kalahari sands east of these highlands is extremely low. Thus, for example, in the square 1920D there is fairly high diversity (12 species; Figure 3), but none of the species is endemic to Namibia (0 species; Figure 4). Species occurring in the Kalahari sands are mostly widely distributed in southern Africa, and a typical example of their wide distribution is shown in Figure 5 for *Ceropegia lugardiae*. The same holds true for southern Namibia, where most of the species are also found in neighbouring South Africa. This is particularly clear in the Groot Karasberge (2718B, 2718D), where diversity is the highest in Namibia (closely followed by the Rosh Pinah area, 2716D), but the number of endemics is lower than in the Kaokoveld (though here species endemic to Angola and Namibia combined contribute to keeping this number high).

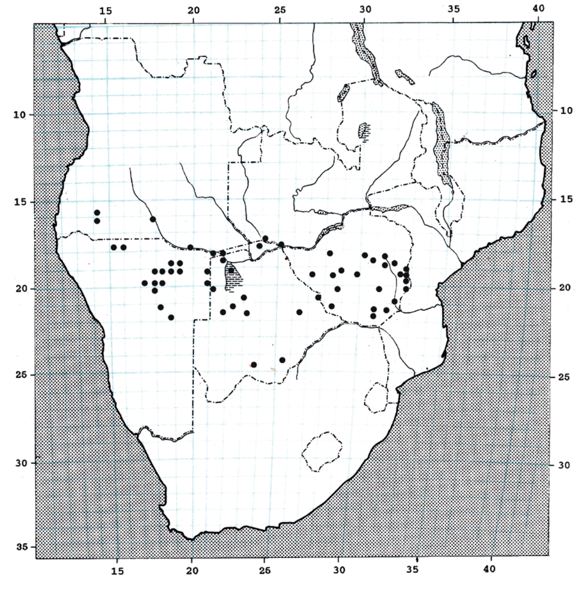

Figure 5: *The distribution of* Ceropegia lugardiae*, a typical species of the drier parts of the Kalahari sands. Here, the concept of this species does not follow Goyder* et al. *(2012), but rather of Bruyns (2014), with its distribution restricted to Angola, Botswana, Namibia and Zimbabwe.*

(ii) *Euphorbia*

Euphorbia presents a similar picture to *Ceropegia*. It is most diverse along and west of the HEAN (Figure 6) in the Kaokoveld–Orupembe area in the extreme north, and Rosh Pinah and the Groot Karasberge in the southern part of the country. Diversity in the Groot Karasberge (2718B, 2178D) is considerably exceeded by that in the Rosh Pinah area (2716D) which receives winter rainfall.

Endemics are extremely few. They are mostly concentrated in the Kaokoveld and are almost completely absent in the south (Figure 7). In particular, the very diverse areas of the Groot Karasberge (where most of the species recorded also occur further east and south in South Africa) and the Rosh Pinah area (where most occur further south in South Africa) have no endemics.

(b) Angola

(i) Ceropegieae

Records are scanty for the Ceropegieae in Angola (Figure 3) and more collecting is required to obtain a clearer picture of the distribution of many of the species. However, although there are still several species awaiting description, further collecting is unlikely to change the fact that the diversity in Ceropegieae in Angola is substantially lower than in Namibia. There is a very strong decrease in numbers northwards as the rainfall increases and the steepness of the escarpment decreases.

In Angola the concentration of the Ceropegieae along and west of the highlands and escarpments is more striking than in Namibia (Figure 3). The Ceropegieae is most diverse in the Serra da Chela (around Lubango, in the squares 1413C, 1513A, 1513B). It is also diverse around Moçamedes, around Lucira (all three on the western side of the country, within the HEAN or west of it).

Endemics (Figure 4) are mainly concentrated along the highlands and escarpments of Angola and west of it, especially in the Serra da Chela, in the Moçamedes area and around Iona. These areas are primarily semiarid, covered with scrub (often very open mopane scrub) and open savanna. Several endemic species occur in the Serra da Chela, perhaps partly reflecting higher collecting activity. The endemics are found in shallow, nutrient-poor soils overlaying sandstones and a few of them are associated with the extensive *Brachystegia* woodland that extends eastwards from here onto Kalahari sands. This is the preferred habitat of the *Ceropegia umbraticola* group (Stopp 1964; with some endemic species) and the rare endemic *Orthanthera gossweileri* (Goyder *et al.* 2018). The major, more isolated inselbergs of Angola have not been investigated in sufficient detail to know whether any endemics occur there.

(ii) *Euphorbia*

Euphorbia in Angola is mainly confined to the highland and escarpment areas and areas west of these. The Serra da Chela is diverse in *Euphorbia* (Figure 6), but it is equalled by the diversity on the northern edge of the Namib Desert around Benguela and is exceeded in the much drier area around Moçamedes (1512A, 1512C). There is also notable diversity in the mountains around Iona. Except for a few geophytic species, there are virtually no records of *Euphorbia* in the vast regions east of the highlands and escarpments in Angola covered by Kalahari sands and *Brachystegia* woodland.

Unlike in Namibia, many of these *Euphorbia* species are endemic. Most of the endemics are found in or west of the highlands and escarpments of Angola, especially in the Serra da Chela, in the Moçamedes area and around Benguela (Figure 7). There are almost no endemics east of the highlands and escarpments in Angola.

Figures 3–4 and 6–7 show that, in Angola, the patterns found in the Ceropegieae are closely followed in *Euphorbia*. One major difference is that *Euphorbia* is almost absent from all regions covered by Kalahari sands and is almost restricted to the highlands and escarpments and to the Namib Desert to the west of these.

3. Which growth forms are most common among these two groups and among the endemics?

The growth forms of the Apocynaceae and *Euphorbia* are discussed below and summarised in Table 2.

(i) Apocynaceae

In the Apocynaceae there are no annuals known in Africa south of the equator.

(a) Apocynaceae *sensu stricto*

Geophytes in the Apocynaceae *sensu stricto*, are unknown. Succulents are also uncommon and are found in *Adenium* Roem. & Schultes and *Pachypodium* Lindl. Of the two endemic species (out of the 92 species of Apocynaceae s.s. in Angola and Namibia combined, Table 1), one is the spiny succulent tree *Pachypodium lealii* (the other is the non-succulent *Landolphia gossweileri*). *Pachypodium* comprises 21 species (Burge *et al.* 2013), with 16 species in Madagascar and five in southern Africa; all are succulent. Two of the five southern African species of *Pachypodium* are spiny succulent trees and both are associated with the escarpment zone in Namibia and Angola (i.e., the HEAN), though only one is endemic to it. (The other, *P. namaquanum* Welw., occurs from southern Namibia into the extremely arid adjacent valley of the Orange River in South Africa.) So in the Apocynaceae *sensu stricto*, four out of 92 species in southwestern tropical Africa are succulent, while 50% of the endemics are succulents.

Table 2: *Numbers of the Asclepiadeae, Ceropegieae, Fockeeae, Periplocoideae and* Euphorbia *in Angola, Namibia and in the two countries combined exhibiting various growth forms.*

	Annual		**Geophytic**		**Succulent**		**Succulent with reduced leaves***	
	Total species	Endemic species	Total species	Endemic species	Total species	Endemic species	Total species	Endemic species
Asclepiadeae								
Angola	0	0	38	4	2	0	1	0
Namibia	0	0	12	0	4	0	3	0
Angola + Namibia	0	0	42	5	4	1	3	0
Ceropegieae								
Angola	0	0	24	7	31	9	24	8
Namibia	0	0	26	2	67	11	59	11
Angola + Namibia	0	0	41	12	77	28	68	27
Fockeeae								
Angola + Namibia	0	0	3	0	4	0	0	0
Periplocoideae								
Angola	0	0	11	1	0	0	0	0
Namibia	0	0	6	2	0	0	0	0
Angola + Namibia	0	0	13	3	0	0	0	0
Euphorbia								
Angola	12	5	12	8**	48	29	30	21
Namibia	10	3	1	1	41	7	34	6
Angola + Namibia	19	9	13	9**	76	43	55	34

* Leaves are rudimentary or each is reduced to a spine.

** The three unplaced endemic species (Appendix 4) are probably geophytic herbs, but this is not certain and they are omitted from these numbers.

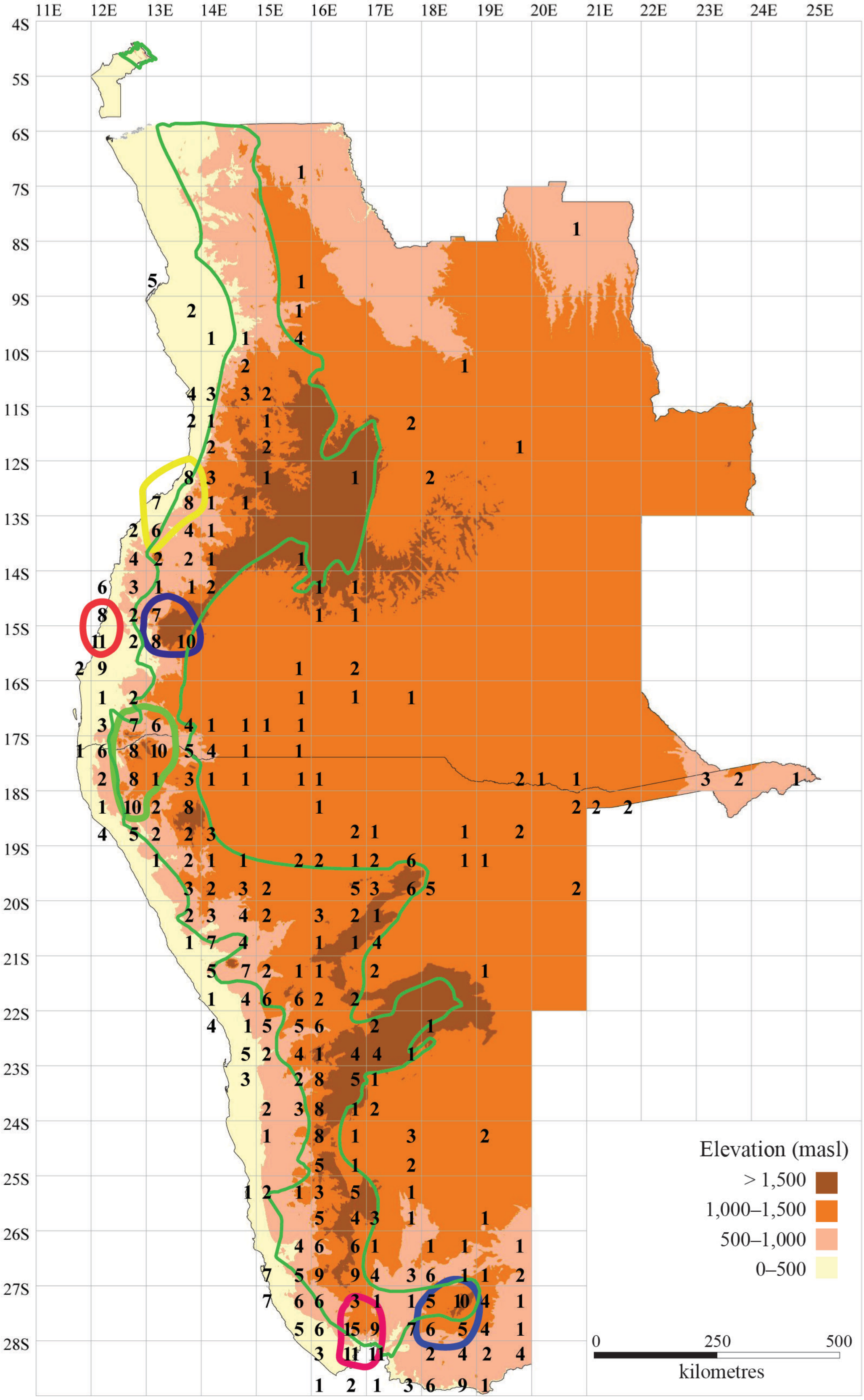

Figure 6: *Occurrence of* Euphorbia *in Angola and Namibia (combined). Numbers indicate the numbers of species recorded per half-degree square. Centres of diversity are indicated, approximately, as follows: pale yellow = Benguela; red = Moçamedes; deep blue = Serra da Chela; thick green = Kaokoveld; pink = Namuskluft; and blue = Groot Karasberge. (Here the Otavi Mountains and Naukluft–Tiras are absent.) The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

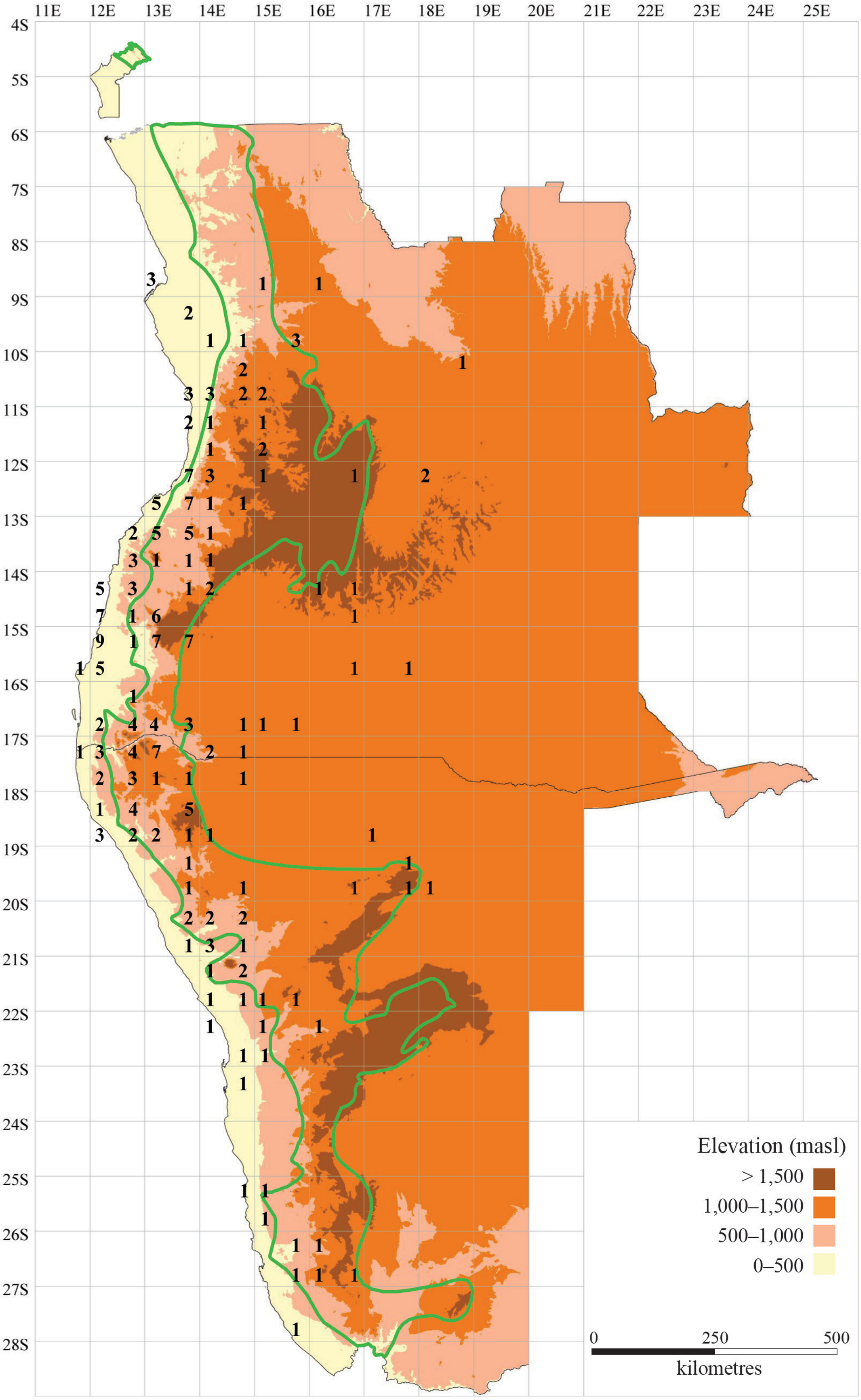

Figure 7: Diversity of endemic Euphorbia *in Angola and Namibia (combined). Numbers of endemic species to Angola and Namibia are recorded in each half-degree square. The thin green line indicates the zone of highlands and escarpments of Angola and Namibia.*

(b) Asclepiadeae

Geophytes are especially common in the Asclepiadeae (Table 2), where they make up over half (60%) of the 70 species in Angola and Namibia combined. There are very few endemic geophytes (only 6% of the total).

Succulents, on the other hand, are rare in the Asclepiadeae. Here only 6% of the 70 species found in Angola and Namibia combined are succulent and only one of them is endemic.

(c) Ceropegieae

Geophytes make up less than half (35%) of the 117 species of the Ceropegieae (Appendix 1), though they still form a significant proportion for Angola and Namibia combined. Of these 41 geophytic species, 29% are endemic.

In the Ceropegieae, the earlier diverging lineages are all non-succulent plants with well-developed leaves. An example is provided by the widespread, arid-adapted lineage of nine species of the subtribe Leptadeniineae, which is mainly found from the deserts and semi-deserts of NW India to the Sahel in West Africa (Bruyns *et al.* 2023). This lineage is represented in Angola and Namibia by the three species, *Leptadenia albida* (endemic to the Namib Desert of Angola and Namibia); *L. jasminiflora* (widespread in Kalahari sands from Zambia to South Africa) and *L. gossweileri* (an Angolan endemic from near Menongue).

A significant 66% of the 117 species of the Ceropegieae in Angola and Namibia are succulent. Succulents with reduced leaves (rudimentary or reduced to spines) are also the most common growth form, making up 58% of the 117 species of Ceropegieae in Angola and Namibia combined. Of these 77 succulent species, 35% are endemic.

(ii) *Euphorbia*

Annuals (Table 2) make up 18% of the 107 species of *Euphorbia* in Angola and Namibia combined. Geophytes make up 12% of these 107 species.

In *Euphorbia*, most of the ~1,840 species are not succulent. This is true especially of the subgenera *Chamaesyce* and *Esula* in the northern hemisphere. In the predominantly southern African subgenus *Athymalus*, most of the species are succulent, and in subgenus *Euphorbia* all the African members are succulent. However, even in subgenus *Athymalus*, the earlier-diverging lineages are non-succulent. Examples in Angola and Namibia are provided by non-succulent, deciduous tree-like species (such as *Euphorbia currorii* and *E. matabelensis* in subgenus *Athymalus*, *E. espinosa* and *E. guerichiana* in subgenus *Chamaesyce*) that are mainly associated with the edge of the Namib Desert.

In numbers of species, subgenus *Athymalus* and subgenus *Euphorbia* dominate in southern Africa generally. This is also true in Angola and Namibia (Figure 2). Consequently, most species of *Euphorbia* are succulent in Angola (where 48 out of 70 are succulent, Appendix 4) and in Namibia (where 41 out of 56 are succulent, Appendix 5). Across Angola and Namibia, of the 107 species of *Euphorbia*, 76 (or 71%) are succulent, while among the 59 endemics, 43 (or 73%) are succulent. Those with reduced leaves (55 out of 107) make up 51% of the total. Of these 55 species with reduced leaves, 62% are endemic.

DISCUSSION

1. To which species are those in and west of the HEAN related?

In the Crassulaceae, the species of *Crassula* in the Serra da Chela of SW Angola are closely allied to others in the eastern parts of South Africa. A species of *Umbilicus*, also found in the Serra da Chela, is closely related to others from further north in Africa (Bruyns *et al.* 2019), more specifically to plants from Kenya (H.Schaefer pers. comm.). In the Crassulaceae, therefore, plants have arrived in hospitable parts of SW Angola from further north in Africa (for *Umbilicus*) and from further SE in Africa (for *Crassula*). This pattern is repeated in the Ceropegieae and in *Euphorbia*.

(i) Ceropegieae

Species belonging to the traditional concept of *Ceropegia*, such as *C. haygarthii* and *C. lugardiae* or *C. stenoloba* are all members of lineages that are widespread on the eastern flank of Africa from South Africa to northeastern Africa and the Arabian Peninsula. Here the endemic members (Figure 8) are scattered among others of wider occurrence but there are no lineages endemic to the HEAN or west of it in the Namib Desert. On the other hand, all sampled members of the ‘stapeliads’ (now also included in *Ceropegia*) in Angola and Namibia have their closest relatives in southern Africa (Bruyns *et al.* 2014). However, no major radiations exist in either Angola or Namibia. The largest known endemic radiation consists of *C. oculatoides*, *C. urceolata*, *C. calosticta* and *C. similior*, a unique well-supported lineage (Figure 8) within section *Huernia* that has speciated in Angola and tropical Namibia, probably along the eastern margins of the Namib Desert. Other members of section *Huernia* that were sampled are not closely related and they belong to other southern African lineages. In section *Stapelia*, the Angolan species are nested among others from Namibia and the western side of South Africa, suggesting that they too have speciated northwards along the edges of the Namib Desert. The same is true of parts of section *Hoodia* and section *Larryleachia*.

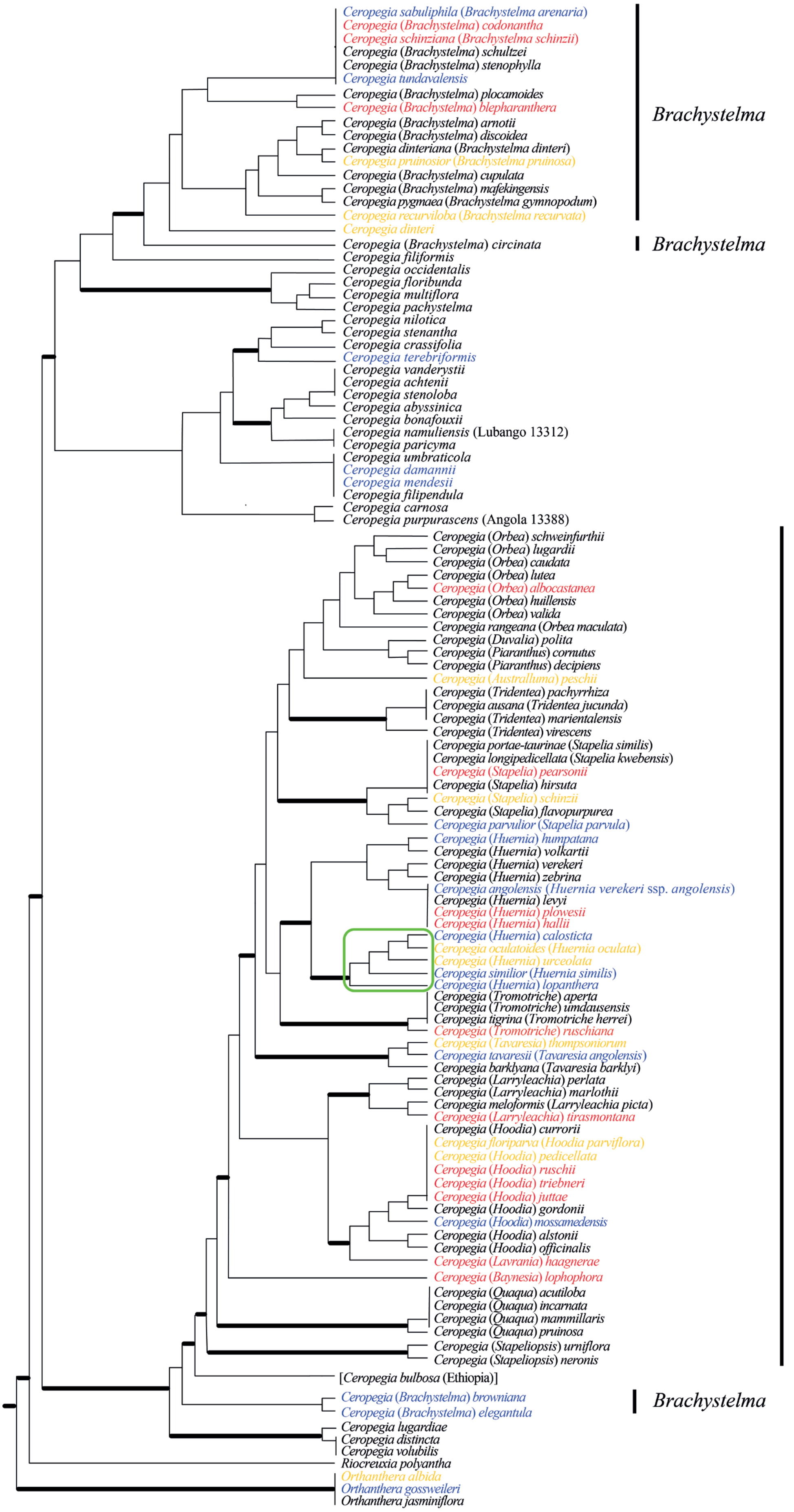

Figure 8: *Relationships among the Namibian and Angolan members of the Ceropegieae. [Caption continued on next page]*

Figure 8: *[Caption continued from previous page] Here all known species are listed from Bruyns (2014) and Goyder (2008), and also includes newer records. Angolan endemics are indicated in blue, Namibian endemics in red and species that are only endemic to Angola and Namibia, combined, in beige. The cladogram is adapted from Bruyns* et al. *(2014, 2015) and additional unpublished data. Former genera for the stapeliads and other familiar generic names (such as* Brachystelma*) are given in brackets. Important to observe here is the manner in which the stapeliads are nested deep within* Ceropegia*, where their closest relative is* Ceropegia bulbosa *(from outside our area, but nevertheless indicated here). Also important is the nesting of the erect, tuberous* Ceropegia dinteri *among the former species of* Brachystelma *and the two fusiform-rooted species of* Brachystelma *that have an entirely different position to the other species of* Brachystelma *with tubers. Species with a vertical line to their left have not been sequenced and their position is assumed from morphological features. Thickened branches are well supported (with bootstrap percentage > 80). The unique clade endemic to Angola and Namibia (combined) is ringed in green.*

(ii) *Euphorbia*

Relationships in *Euphorbia* are similar (unpublished results, not shown). *Euphorbia sapinii* De Wild. and *E. teke* Schweinf. ex Pax, both recorded only in northern Angola, are related to others from West Africa and represent the furthest south that these groups penetrate. Most of the species found in Angola have their closest relatives further southeast in southern Africa. All of the small spiny members of 'sect. *Tetracanthae*' (Leach 1976) are related to others from eastern South Africa but they do not form a lineage. The only lineage of *Euphorbia* that has diversified to any degree in Angola and Namibia (combined) is one made up of *E. atrocarmesina*, *E. cannellii*, *E. dekindtii*, *E. dispersa*, *E. ingenticapsa*, *E. otavibergensis*, *E. otjingandu*, *E. semperflorens*, *E. strangulata* and *E. virosa*. This lineage has diversified along the entire length of the HEAN, with all except *E. virosa* endemic to it. *Euphorbia virosa* occurs outside the HEAN, only in South Africa in the adjacent, extremely arid valley of the Orange River (Bruyns 2022: Figure 5.357).

2. Disjunct species pairs

Our results show unexpectedly that closely related species may be found on opposite sides of the subcontinent. This is the case with the closely related pair of species of *Ceropegia* section *Australluma* (Bruyns *et al.* 2014), namely *Ceropegia peschii* and *C. ubomboensis* (I.Verd.) Bruyns (the latter found along and east of the Lebombo Mountains in Mozambique, South Africa and Zimbabwe; Figure 9).

This case is closely mirrored In *Euphorbia* (unpublished data) by the respective distributions of the two very closely related species, *E. candelabrum* Welw., a prominent feature of the western coastal plain of Angola (west of the HEAN; Bruyns & Berry 2019) and *E. confinalis*, mainly found along the Lebombo Mountains in Mozambique, South Africa and Zimbabwe (Figures 10 and 11). Another example is provided by the spatially very isolated *E. faucicola* (from a remote rocky area along a tributary of the Cubango River in southeastern Angola) which is the closest known relative of *E. cooperi*, a species that is widespread from South Africa to Tanzania.

3. Succulence in the HEAN and succulence in the Cape Floral Kingdom

Not all lineages that have diversified in and west of the HEAN are succulent. For example, the entirely non-succulent *Euphorbia* section *Tenellae* has species in the driest parts of the west coast (*E. claytonioides*, *E. phylloclada*) and others at 2,000 m in the Serra da Chela (*E. parifolia*), so that it too has been able to exploit the niches offered by the HEAN. Nevertheless, the presence of succulents is sufficiently striking that it bears comparison with other areas where succulents are common.

The remarkable dominance of succulents in the arid and semi-arid parts of the winter-rainfall Cape Flora in southern Namibia and western South Africa is well known (Manning & Goldblatt 2012, Snijman 2013). This dominance is particularly a consequence of the high diversity of leaf-succulents in the families Aizoaceae and Crassulaceae in the Cape Flora. For

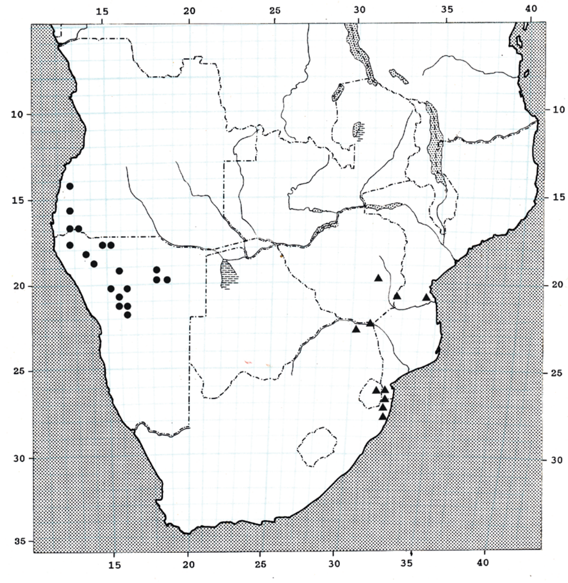

Figure 9: *An example of the distribution of a closely related species pair of* Ceropegia*,* C. peschii *(•) and* C. ubomboensis *(▲), which are found on opposite sides of southern Africa.*

example, the Aizoaceae is the largest family in the 'Succulent Karoo' (Snijman 2013) and is the fifth-largest family in the 'Core Cape Flora' (Manning & Goldblatt 2012). It is less well known that *Ceropegia* and *Euphorbia* (along with *Aloe* L.) are also diverse in this winter-rainfall region. A striking subdominance of succulents continues for the length of Namibia and extends into Angola as far as the Benguela District, after which it fades away northwards as rainfall increases and as the escarpment becomes less steep and rocky. Nevertheless, it reappears occasionally further to the north on isolated, locally dry, rocky areas, such as in the hills at Pungo Andongo. The relatively high percentage of succulent species in *Ceropegia* and *Euphorbia* in the HEAN suggests that this could be a continuation of the dominance of succulents in the arid and semi-arid parts of the winter-rainfall region in southern Namibia and western South Africa. However, here the leaf-succulent families Aizoaceae and Crassulaceae are almost absent. Furthermore, the lineages in *Ceropegia* and *Euphorbia* that provide their diversity in the Cape Flora are mostly different to those that supply the diversity in Angola and Namibia (and in the HEAN more particularly); i.e., these groups of succulents in different areas have different origins.

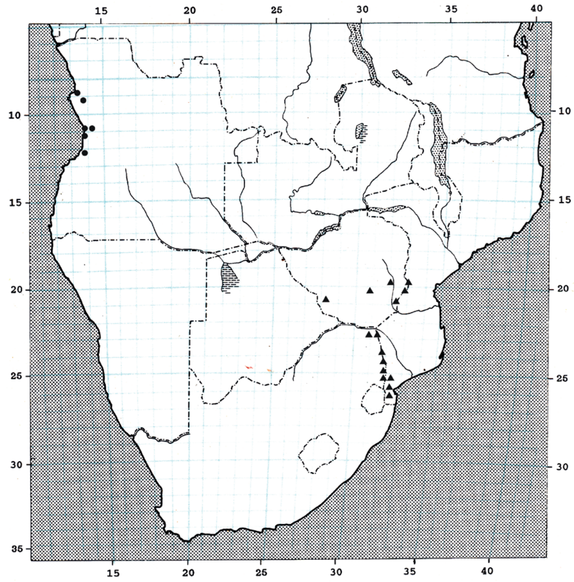

Figure 10: *An example of the distribution of a very closely related species pair of* Euphorbia, E. candelabrum *(•) and* E. confinalis *(▲), which are found on opposite sides of southern Africa.*

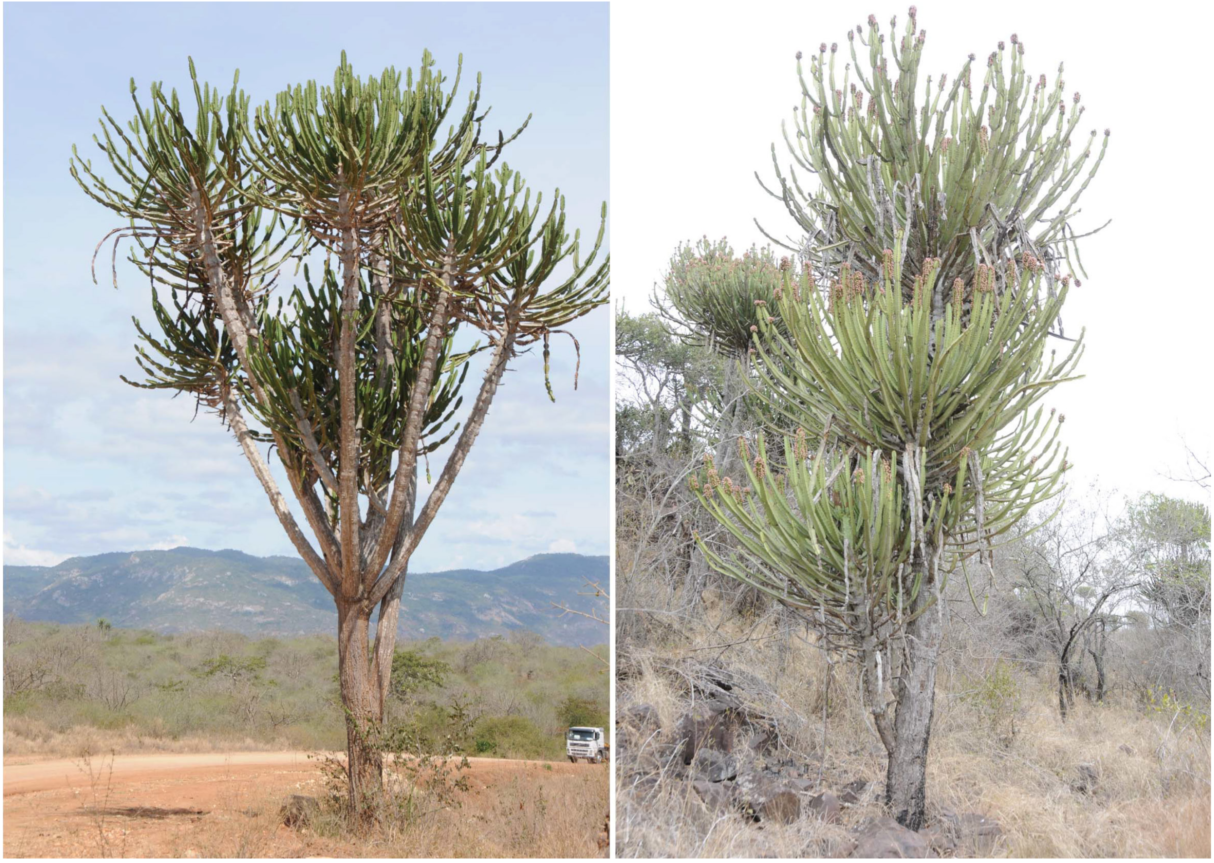

Figure 11: *Two very closely related species from opposite sides of southern Africa. Left:* Euphorbia candelabrum *east of Egito Praia, Lobito District, Angola, at the western foot of the highlands with the escarpment in the background. Right:* E. confinalis, *PVB 11764, near Komatipoort, western slopes of Lebombo Mountains, South Africa. Photos by P Bruyns.*

4. Ages of lineages

Most of the diversity and most endemics in the Ceropegieae and *Euphorbia* of Angola and Namibia are associated with their highlands and escarpments. They are mostly succulent, indicating that succulent lineages have been favoured in this region. Generally, succulents are a relatively recent development in the groups where they are found (Arakaki *et al.* 2011, Bruyns *et al.* 2011 for *Euphorbia*; Bruyns *et al.* 2015 for *Ceropegia*). This suggests that at least the succulent endemics in this region originated within the last 8 million years (Arakaki *et al.* 2011) and are unlikely to have evolved during the early aridification of the Namib which occurred 20 mya or earlier (Pickford *et al.* 2014).

ACKNOWLEDGEMENTS

We are very grateful to Fernanda Lages, who provided much-needed logistical assistance during our travels in southern Angola.

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Appendix 1: *Endemic species of Apocynaceae s.s. and all species of Asclepiadoideae, Periplocoideae and Secamonoideae that are known in Angola (partly from Goyder 2008, 2009, Goyder* et al*. 2018, Venter 2009 and other herbarium records), and their placement in sections (for* Ceropegia*). Growth form and nature of the leaves of each species are also given.*

Taxon	**Section**	**Growth form**	**Leaf**
Apocynaceae s.s.			
Landolphia gossweileri (Stapf) Pichon*		rhizomatous subshrub	with blade
Asclepiadoideae			
Asclepiadeae			
Asclepias ameliae S.Moore		geophytic herb	with blade
A. aurea (Schltr.) Schltr.		geophytic herb	with blade
A. foliosa (K.Schum.) Hiern		geophytic herb	with blade
A. minor (S.Moore) Goyder		geophytic herb	with blade
A. palustris (K.Schum.) Schltr.		geophytic herb	with blade
A. randii S.Moore		geophytic herb	with blade
A. schumanniana Hiern		geophytic herb	with blade
Aspidoglossum masaicum (N.E.Br.) Kupicha		geophytic herb	with blade
Cynanchum adalinae (K.Schum.) K.Schum.		climber	with blade
C. ethiopicum Liede & Khanum		climber	with blade
C. polyanthum K.Schum.		climber	with blade
C. schistoglossum Schltr.		climber	with blade
C. viminale (L.) Bassi ex L. (incl. *Sarcostemma welwitschii* Hiern)		succulent	rudimentary
Glossostelma angolense Schltr.*		geophytic herb	with blade
G. cabrae (De Wild.) Goyder		geophytic herb	with blade
G. carsonii (N.E.Br.) Bullock		geophytic herb	with blade
G. ceciliae (N.E.Br.) Goyder		geophytic herb	with blade
G. erectum (De Wild.) Goyder		geophytic herb	with blade
G. lisianthoides (Decne.) Bullock		geophytic herb	with blade
G. spathulatum (K.Schum.) Bullock		geophytic herb	with blade
G. xysmalobioides (S.Moore) Bullock*		geophytic herb	with blade
Gomphocarpus fruticosus (L.) W.T.Aiton		shrub	with blade
G. munonquensis (S.Moore) Goyder & Nicholas		geophytic herb	with blade
G. praticola (S.Moore) Goyder & Nicholas		geophytic herb	with blade
G. semiamplectens K.Schum.		geophytic herb	with blade
G. semilunatus A.Rich.		shrub	with blade
G. swynnertonii (S.Moore) Goyder & Nicholas		geophytic herb	with blade
G. tomentosus Burch.		shrub	with blade
Kanahia laniflora (Forssk.) R.Br.		shrub	with blade
Pachycarpus bisacculatus (Oliv.) Goyder		geophytic herb	with blade
P. firmus (N.E.Br.) Goyder		geophytic herb	with blade
P. lineolatus (Decne.) Bullock		geophytic herb	with blade
Pergularia daemia (Forssk.) Chiov.		climber	with blade
Schizoglossum angolense Schltr. & Rendle*		geophytic herb	with blade
S. graminifolium C.Norman*		geophytic herb	with blade
S. saccatum Bruyns		geophytic herb	with blade
Schizostephanus gossweileri (S.Moore) Liede		succulent scrambler	with blade
Stathmostelma fornicatum (N.E.Br.) Bullock		geophytic herb	with blade
S. incarnatum K.Schum.*		geophytic herb	with blade
S. welwitschii Britten & Rendle		geophytic herb	with blade
Xysmalobium andongense Hiern		geophytic herb	with blade
X. clavatum S.Moore		geophytic herb	with blade
X. holubii Scott-Elliot		geophytic herb	with blade
X. kaessneri S.Moore		geophytic herb	with blade
X. rhomboideum N.E.Br.		geophytic herb	with blade
X. sessile (Decne.) Decne.		geophytic herb	with blade
X. stocksii N.E.Br.		geophytic herb	with blade
X. undulatum (L.) W.T.Aiton		geophytic herb	with blade
Vincetoxicum caffrum (Meisn.) Kunze		geophytic herb	with blade
V. congolanum (Baill.) Liede & Meve		climber	with blade
V. conspicuum (N.E.Br.) Liede & Meve		climber	with blade
V. sylvaticum (Decne.) Kunze		climber	with blade

Taxon	**Section**	**Growth form**	**Leaf**
Ceropegieae			
Ceropegia abyssinica Decne.	*Laguncula*	geophytic climber	with blade
C. achtenii De Wild.	*Laguncula*	geophytic climber	with blade
C. angolensis (L.C.Leach) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. barklyana Bruyns	*Tavaresia*	dwarf succulent	spine
C. bonafouxii K.Schum.	*Laguncula*	geophytic climber	with blade
C. browniana (S.Moore) Bruyns*	*Stenatae*	geophytic herb	with blade
C. calosticta (Bruyns) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. caudata (N.E.Br.) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. currorii (N.E.Br.) Bruyns	*Hoodia*	succulent shrub	spine
C. damannii Stopp*	*Umbraticolae*	geophytic herb	with blade
C. dinteri Schltr.	*Chamaesiphon*	geophytic herb	with blade
C. dinteriana Bruyns (=*Brachystelma dinteri* Schltr.)	*Chamaesiphon*	geophytic herb	with blade
C. elegantula (S.Moore) Bruyns*	*Stenatae*	geophytic herb	with blade
C. filipendula K.Schum.	*Umbraticolae*	geophytic herb	with blade
C. floriparva Bruyns	*Hoodia*	succulent shrub	spine
C. haygarthii Schltr	*Phalaena*	slender succulent climber	with blade
C. huillensis (Hiern) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. humpatana (Bruyns) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. longipedicellata (A.Berger) Bruyns	*Stapelia*	dwarf succulent	rudimentary
C. lopanthera (Bruyns) Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. lugardiae N.E.Br.	*Phalaena*	slender succulent climber	with blade
C. lutea (N.E.Br.) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. mendesii Stopp*	*Umbraticolae*	geophytic herb	with blade
C. mossamedensis (L.C.Leach) Bruyns*	*Hoodia*	dwarf succulent	spine
C. multiflora Baker	*Ceropegiella*	geophytic succulent climber	with blade
C. namuliensis Bruyns	*Laguncula*	geophytic climber	with blade
C. nilotica Kotschy	*Calopegia*	geophytic succulent climber	with blade
C. oculatoides Bruyns	*Huernia*	dwarf succulent	rudimentary
C. parvulior Bruyns*	*Stapelia*	dwarf succulent	rudimentary
C. pedicellata (Schinz) Bruyns	*Hoodia*	dwarf succulent	spine
C. peschii (Nel) Bruyns	*Australluma*	dwarf succulent	rudimentary
C. plocamoides (Oliv.) Bruyns	*Chamaesiphon*	geophytic herb	with blade
C. polita (N.E.Br.) Bruyns	*Duvalia*	dwarf succulent	rudimentary
C. pruinosior Bruyns	*Chamaesiphon*	geophytic herb	with blade
C. purpurascens K.Schum.	*Pseudoceropegiella*	geophytic climber	with blade
C. pygmaea Schinz	*Chamaesiphon*	geophytic herb	with blade
C. racemosa N.E.Br.)**	*Carnosae*	slender climber	with blade
C. rangeana (Dinter & A.Berger) Bruyns	*Orbea*	dwarf succulent	rudimentary
C. recurviloba Bruyns	*Chamaesiphon*	geophytic herb	with blade
C. sabuliphila Bruyns*	*Chamaesiphon*	geophytic herb	with blade
C. schinzii (A.Berger & Schltr.) Bruyns	*Stapelia*	dwarf succulent	rudimentary
C. similior Bruyns*	*Huernia*	dwarf succulent	rudimentary
C. stenantha K.Schum.	*Calopegia*	geophytic succulent climber	with blade
C. tavaresii Welw. ex Bruyns*	*Tavaresia*	dwarf succulent	spine
C. terebriformis Bester*	*Callopegia*	geophytic succulent climber	with blade
C. thompsoniorum	*Tavaresia*	dwarf succulent	spine
C. tundavalensis Bruyns*	*Chamaesiphon*	geophytic herb	with blade
C. umbraticola K.Schum.	*Umbraticolae*	geophytic herb	with blade
C. urceolata (L.C.Leach) Bruyns	*Huernia*	dwarf succulent	rudimentary
C. vanderystii De Wild.	*Laguncula*	geophytic climber	with blade
C. volkartii (Peitsch. ex Werderm. & Peitsch.) Bruyns	*Huernia*	dwarf succulent	rudimentary
C. volubilis N.E.Br.	*Phalaena*	slender succulent climber	with blade
Leptadenia albida (Schinz) Bruyns		shrub	with blade
L. gossweileri (C.Norman) Bruyns*		creeping herb	with blade
L. jasminiflora (Burch. ex Decne.) Bruyns		creeping herb	with blade
Riocreuxia polyantha Schltr.		slender climber	with blade

Taxon	**Section**	**Growth form**	**Leaf**
Fockeeae			
Fockea angustifolia K.Schum.		geophytic climber	with blade
F. multiflora K.Schum.		massive climber	with blade
Marsdenieae			
Gymnema sylvestre (Retz.) R.Br. ex Schult.		climber	with blade
Marsdenia abyssinica (Hochst.) Schltr.		climber	with blade
M. angolensis N.E.Br.		climber	with blade
M. crinita		climber	with blade
M. latifolia (Benth.) K.Schum.		climber	with blade
M. macrantha (Klotzsch) Schltr.		climber	with blade
M. magniflora P.T.Li		climber	with blade
M. schimperi Decne.		climber	with blade
Telosma africana (N.E.Br.) N.E.Br.		climber	with blade
Periplocoideae			
Batesanthus parviflorus C.Norman		climber	with blade
Cryptolepis decidua (Planch. ex Benth.) N.E.Br.		shrub	with blade
C. gossweileri S.Moore*		climber	with blade
C. microphylla Baill.		climber	with blade
C. nigrescens (Wennberg) L.Joubert & Bruyns		climber	with blade
C. oblongifolia (Meisn.) Schltr.		climber	with blade
C. producta N.E.Br.		climber	with blade
C. sanguinolenta (Lindl.) Schltr.		climber	with blade
Mondia whitei (Hook.f.) Skeels		climber	with blade
Raphionacme angolensis (Baill.) N.E.Br.*		geophytic herb	with blade
R. globosa K.Schum.		geophytic herb	with blade
R. inconspicua H.Huber		geophytic herb	with blade
R. lanceolata Schinz		geophytic herb	with blade
R. linearis K.Schum.		geophytic herb	with blade
R. madiensis S.Moore		geophytic herb	with blade
R. michelii De Wild.		geophytic herb	with blade
R. monteiroae (Oliv.) N.E.Br.		geophytic herb	with blade
R. utilis N.E.Br. & Stapf		geophytic herb	with blade
R. velutina Schltr.		geophytic herb	with blade
R. welwitschii Schltr. & Rendle		geophytic herb	with blade
Tacazzea apiculata Oliv.		climber	with blade
T. pedicellata K.Schum.		climber	with blade
T. rosmarinifolia (Decne.) N.E.Br.		climber	with blade
Secamonoideae			
Secamone africana (Oliv.) Bullock		climber	with blade
S. brevipes (Benth.) Klack.		climber	with blade
S. dewevrei De Wild.		climber	with blade
S. erythradenia K.Schum.		climber	with blade
S. punctulata Decne.		climber	with blade

* Endemic to Angola.

** The NE-African *Ceropegia affinis* Vatke, included among the Angolan species by Goyder (2008), is omitted here. This follows Huber (1957), who placed the collection cited by Goyder (2008) under *C. racemosa* N.E.Br.

Appendix 2: *Species of Apocynaceae that are endemic to Namibia, and their placement in sections (for* Ceropegia*). Their growth form and the nature of their leaves are also given.*

Family and species	**Section**	**Growth form**	**Leaf**
Asclepiadoideae			
Asclepiadeae			
Microloma hereroense Wanntorp		twining herb	with blade
M. penicillatum Schltr.		shrub	with blade
Vincetoxicum fleckii (Schltr.) Meve & Liede*		shrub	with blade
Ceropegieae			
Ceropegia albocastanea (Marloth) Bruyns	sect. *Orbea*	dwarf succulent	rudimentary
C. blepharanthera (H.Huber) Bruyns**	sect. *Chamaesiphon*	geophytic herb	with blade
C. codonantha (Bruyns) Bruyns	sect. *Chamaesiphon*	geophytic herb	with blade
C. haagnerae (Plowes) Bruyns	sect. *Lavrania*	dwarf succulent	rudimentary
C. hallii (E.&B.M.Lamb) Bruyns	sect. *Huernia*	dwarf succulent	rudimentary
C. juttae (Dinter) Bruyns	sect. *Hoodia*	succulent shrub	spine
C. lophophora (Bruyns) Bruyns	sect. *Baynesia*	dwarf succulent	rudimentary
C. pearsonii (N.E.Br.) Bruyns	sect. *Stapelia*	dwarf succulent	rudimentary
C. plowesii (L.C.Leach) Bruyns	sect. *Huernia*	dwarf succulent	rudimentary
C. ruschiana (Dinter) Bruyns	sect. *Tromotriche*	dwarf succulent	rudimentary
C. ruschii (Dinter) Bruyns	sect. *Hoodia*	succulent shrub	spine
C. tirasmontana (Plowes) Bruyns	sect. *Hoodia*	succulent shrub	rudimentary
C. triebneri (Nel) Bruyns	sect. *Hoodia*	succulent shrub	spine
Marsdenieae			
Stigmatorhynchus hereroensis Schltr.***		shrub	with blade
Periplocoideae			
Ectadium rotundifolium (H.Huber) Venter & Kotze		shrub	with blade
Raphionacme haeneliae Venter & R.L.Verh.		geophytic herb	with blade
R. namibiana Venter & R.L.Verh.		geophytic herb	with blade

* Sometimes stated to occur in Somalia as well (Thulin 2006), but here this is assumed to be a parallel development.
** The citation of Angola in Bruyns (2014) referred to material subsequently described as *C. tundavalensis*.
***A species very similar to this is also known in Somalia and eastern Ethiopia (Thulin 2006), but here this is also assumed to be a parallel development.

Appendix 3: *Species of Apocynaceae that are endemic only to Angola and Namibia (combined), and their placement in sections (for* Ceropegia*). Their growth form and the nature of their leaves are also given.*

Taxon	**Section**	**Growth form**	**Leaf**
Apocynaceae s.s.			
Pachypodium lealii Welw.		tree	with blade
Asclepiadoideae			
Asclepiadeae			
Schizoglossum saccatum		geophytic herb	with blade
Schizostephanus gossweileri		trailing succulent shrub	with blade
Ceropegieae			
*Ceropegia currorii**	*Hoodia*	succulent shrub	spine
C. dinteri	*Chamaesiphon*	geophytic herb	with blade
C. floriparva	*Hoodia*	succulent shrub	spine
C. oculatoides	*Huernia*	dwarf succulent	rudimentary
C. pedicellata	*Hoodia*	succulent shrub	spine
C. peschii	*Australluma*	dwarf succulent	rudimentary
C. pruinosior	*Chamaesiphon*	geophytic herb	with blade
C. recurviloba	*Chamaesiphon*	geophytic herb	with blade
C. schinzii	*Stapelia*	dwarf succulent	rudimentary
C. thompsoniorum	*Tavaresia*	dwarf succulent	spine
C. urceolata	*Huernia*	dwarf succulent	rudimentary
Leptadenia albida		shrub	with blade

* Previously considered to consist of two subspecies, one occurring in Angola and Namibia combined and the other in Botswana, South Africa and Zimbabwe; new molecular results suggest the second is unrelated to *C. currorii*, so here we use the traditional concept of '*Hoodia currorii*'.

Appendix 4: *Species of* Euphorbia *found in Angola, and their placement in the sections and subsections of the four subgenera. Their growth form and the nature of their leaves are also given.*

Taxon	**Section or subsection*****	**Growth form**	**Leaf**
Subgenus *Athymalus*			
E. benthamii Hiern	sect. *Crotonoides*	annual herb	with blade
E. caperonioides R.A.Dyer & P.G.Mey.**	sect. *Crotonoides*	annual herb	with blade
E. sarmentosa Welw. ex Pax*	sect. *Crotonoides*	annual herb	with blade
E. trichadenia Pax	subsect. *Dactylanthes*	geophytic herb	with blade
E. currorii N.E.Br.**	sect. *Lyciopsis*	small non-succulent tree	with blade
E. acalyphoides Hochst.	sect. *Pseudacalypha*	annual herb	with blade
E. gariepina E.Mey. ex Boiss.	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. indurescens L.C.Leach*	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. lignosa Marloth	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. monteiroi Hook.f.	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. linearibracteata L.C.Leach*	sect. unknown	geophytic herb	with blade
Subgenus *Chamaesyce*[1]			
E. arabicoides N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. granulata Forssk.	sect. *Anisophyllum*	annual herb	with blade
E. loandensis N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. mossamedensis N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. subterminalis N.E.Br.*	sect. *Anisophyllum*	annual herb	with blade
E. zambesiana Benth.	sect. *Anisophyllum*	perennial herb	with blade
E. negromontana N.E.Br.**	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. espinosa Pax	sect. *Espinosae*	small non-succulent tree	with blade
E. guerichiana Pax	sect. *Espinosae*	small non-succulent tree	with blade
E. transvaalensis Schltr.	sect. *Frondosae*	succulent shrub	with blade
E. agowensis Hochst. ex Boiss. (*E. pearsonii* N.E.Br.)	sect. *Scatorhizae*	perennial herb	with blade
E. claytonioides Pax*	sect. *Tenellae*	perennial herb	with blade
E. glanduligera Pax	sect. *Tenellae*	annual herb	with blade
E. macra Hiern*	sect. *Tenellae*	geophytic herb	with blade
E. parifolia N.E.Br.*	sect. *Tenellae*	geophytic herb	with blade
E. radiifera L.C.Leach*	sect. *Tenellae*	geophytic herb	with blade
Subgenus *Esula*[2]			
E. berotica N.E.Br.**	subsect. *Africanae*	succulent shrub	rudimentary
E. cyparissioides Pax	sect. *Esula*	perennial herb	with blade
Subgenus *Euphorbia*			
E. atrocarmesina L.C.Leach*	sect. *Euphorbia*	succulent shrub to tree	rudimentary
E. brevis N.E.Br.*	sect. *Euphorbia*	geophytic succulent	with blade
E. candelabrum Welw.*	sect. *Euphorbia*	succulent tree	rudimentary
E. cannellii L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. dekindtii Pax*	sect. *Euphorbia*	succulent shrub	rudimentary
E. desmondii Keay & Milne-Redh.	sect. *Euphorbia*	succulent tree	with blade
E. dispersa L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. eduardoi L.C.Leach**	sect. *Euphorbia*	succulent tree	rudimentary
E. faucicola L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. gracilicaulis L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. hiernii Croizat*	sect. *Euphorbia*	succulent tree	with blade
E. imitata N.E.Br.*	sect. *Euphorbia*	geophytic succulent	with blade
E. ingens E.Mey. ex Boiss.	sect. *Euphorbia*	succulent tree	rudimentary
E. ingenticapsa L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. mwinilungensis L.C.Leach	sect. *Euphorbia*	geophytic succulent	with blade
E. oligoclada L.C.Leach*	sect. *Euphorbia*	geophytic succulent	with blade
E. opuntioides Welw. ex Hiern*	sect. *Euphorbia*	succulent shrub	rudimentary
E. otjipembana L.C.Leach**	sect. *Euphorbia*	succulent shrub	rudimentary
E. parviceps L.C.Leach*	sect. *Euphorbia*	succulent tree	rudimentary
E. semperflorens L.C.Leach*	sect. *Euphorbia*	succulent shrub	rudimentary
E. strangulata N.E.Br.*	sect. *Euphorbia*	succulent shrub	rudimentary
E. teixeirae L.C.Leach*	sect. *Euphorbia*	succulent tree	rudimentary
E. teke Schweinf. ex Pax	sect. *Euphorbia*	succulent tree	with blade

Taxon	**Section or subsection*****	**Growth form**	**Leaf**
E. vallaris L.C.Leach*	sect. *Euphorbia*	succulent tree	rudimentary
E. virosa Willd.	sect. *Euphorbia*	succulent shrub	rudimentary
E. coerulans Pax*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrublet	rudimentary
E. cuneneana L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. demissa L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. nubigena L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. otjipembana L.C.Leach**	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. sapinii De Wild.	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	with blade
E. scitula L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. subsalsa Hiern**	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
E. neoangolensis Bruyns*	sect. *Monadenium*	geophytic succulent	with blade
E. neocannellii Bruyns*	sect. *Monadenium*	succulent shrub	with blade
E. neogossweileri Bruyns*	sect. *Monadenium*	succulent shrub	with blade
E. orobanchoides (P.R.O.Bally) Bruyns	sect. *Monadenium*	geophytic succulent	with blade
E. pseudosimplex Bruyns	sect. *Monadenium*	geophytic succulent	with blade
E. carunculifera L.C.Leach*	sect. *Tirucalli*	succulent shrub	rudimentary
E. congestiflora L.C.Leach**	sect. *Tirucalli*	succulent shrub	rudimentary
E. damarana L.C.Leach**	sect. *Tirucalli*	succulent shrub	rudimentary
E. neochamaeclada Bruyns*	sect. *Tirucalli*	succulent shrub	rudimentary

* Endemic to Angola.

** Endemic only to Angola and Namibia combined.

*** The three Angolan endemic species *E. asclepiadea* Milne-Redh., *E. carinifolia* N.E.Br. and *E. tuberifera* N.E.Br. are unplaced in this system.

[1] *Euphorbia parva* N.E.Br belongs to *E. indica* Lam., according to a note by S. Carter on the type specimen (there referred to *E. hypericifolia* L.), but see Carter and Leach (2001: 347). Both *E. indica* and *E. hypericifolia* are introduced weeds so are not listed here.

[2] The specimen *Welwitsch 286* (LISU) was included, doubtfully, by Hiern (1900: 952) under *E. genistoides*, a species from the Western Cape Province of South Africa, but Brown (1911: 542) included this specimen under *E. cyparissioides*, which is more probable and is followed here.

Appendix 5: *Species of* Euphorbia *found in Namibia and their placement in the sections and subsections of the four subgenera. Their growth form and the nature of their leaves are also given.*

Taxon	**Section or subsection**	**Growth form**	**Leaf**
Subgenus *Athymalus*			
E. benthamii	sect. *Crotonoides*	annual herb	with blade
*E. caperonioides***	sect. *Crotonoides*	annual herb	with blade
E. crotonoides	sect. *Crotonoides*	annual herb	with blade
*E. insarmentosa**	sect. *Crotonoides*	annual herb	with blade
*E. currorii***	sect. *Lyciopsis*	small non-succulent tree	with blade
E. matabelensis Pax	sect. *Lyciopsis*	small non-succulent tree	with blade
E. braunsii N.E.Br.	subsect. *Medusea*	succulent shrub	rudimentary
E. caput-medusae L.	subsect. *Medusea*	succulent shrub	rudimentary
E. crassipes Marloth	subsect. *Medusea*	succulent shrub	rudimentary
E. duseimata R.A.Dyer	subsect. *Medusea*	succulent shrub	rudimentary
E. friedrichiae Dinter	subsect. *Medusea*	succulent shrub	rudimentary
E. melanohydrata Nel	subsect. *Medusea*	succulent shrub	rudimentary
E. namibensis Marloth*	subsect. *Medusea*	succulent shrub	rudimentary
E. celata R.A.Dyer	subsect. *Pseudeuphorbium*	dwarf succulent shrub	rudimentary
E. dregeana E.Mey. ex Boiss.	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. gariepina	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. hamata (Haw.) Sweet	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. lignosa	subsect. *Pseudeuphorbium*	succulent shrub	with blade
E. monteiroi	subsect. *Pseudeuphorbium*	succulent shrub	with blade
Subgenus *Chamaesyce*			
E. chamaesycoides B.Nord.*	sect. *Anisophyllum*	annual herb	with blade
E. inaequilatera Sond.	sect. *Anisophyllum*	annual herb	with blade
E. neopolycnemoides Pax & K.Hoffm.	sect. *Anisophyllum*	annual herb	with blade
E. pergracilis P.G.Mey.*	sect. *Anisophyllum*	annual herb	with blade
E. burmanni E.Mey. ex Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. ephedroides E.Mey. ex Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. giessii L.C.Leach*	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. herrei A.C.White *et al.*	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. juttae Dinter	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. negromontana N.E.Br.**	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. rhombifolia Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. spartaria N.E.Br.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. stapelioides Boiss.	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. verruculosa Marloth*	sect. *Articulofruticosae*	succulent shrub	rudimentary
E. espinosa	sect. *Espinosae*	small non-succulent tree	with blade
E. guerichiana	sect. *Espinosae*	small non-succulent tree	with blade
E. leistneri R.Archer*	sect. *Frondosae*	succulent shrub	with blade
E. transvaalensis	sect. *Frondosae*	succulent shrub	with blade
E. glanduligera	sect. *Tenellae*	annual herb	with blade
E. phylloclada Boiss.	sect. *Tenellae*	annual herb	with blade
Subgenus *Esula*			
*E. berotica***	subsect. *Africanae*	succulent shrub	rudimentary
E. mauritanica L.	subsect. *Africanae*	succulent shrub	rudimentary
E. stolonifera Marloth ex A.C.White *et al.*	subsect. *Africanae*	succulent shrub	rudimentary
E. corneliae Bruyns*	sect. *Esula*	geophytic herb	with blade
Subgenus *Euphorbia*			
E. avasmontana Marloth	sect. *Euphorbia*	succulent shrub	rudimentary
*E. eduardoi***	sect. *Euphorbia*	succulent tree	rudimentary
E. ingens	sect. *Euphorbia*	succulent tree	rudimentary
E. otavibergensis Bruyns*	sect. *Euphorbia*	succulent shrub	rudimentary
E. otjingandu Swanepoel*	sect. *Euphorbia*	succulent shrub	rudimentary
E. virosa	sect. *Euphorbia*	succulent shrub	rudimentary
E. kaokoensis (A.C.White *et al.*) L.C.Leach*	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
*E. otjipembana***	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary
*E. subsalsa***	sect. *Euphorbia* '*Tetracanthae*'	succulent shrub	rudimentary

Taxon	**Section or subsection**	**Growth form**	**Leaf**
*E. congestiflora***	sect. *Tirucalli*	succulent shrub	rudimentary
*E. damarana***	sect. *Tirucalli*	succulent shrub	rudimentary
E. gregaria Marloth	sect. *Tirucalli*	succulent shrub	rudimentary
E. gummifera Boiss.	sect. *Tirucalli*	succulent shrub	rudimentary

* Endemic to Namibia.

** Endemic only to Angola and Namibia combined.

High endemism of the genus *Petalidium* (Acanthaceae) in the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-dexter

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ABSTRACT

Petalidium (Acanthaceae) is a speciose genus of woody shrubs with its diversity centred in arid regions of central to northwestern Namibia and southwestern Angola. Here, we compiled distribution information for all accepted species in the genus from herbarium specimens and our own fieldwork to determine the number of endemics and near-endemic species in the highlands and escarpments of Angola and Namibia (HEAN). In the process, we provide an informal overview of all accepted species of *Petalidium*, which we hope will facilitate further research on the genus. We found that 22 of 36 species are endemic or near-endemic to the HEAN, clearly indicating the importance of this area for plant conservation. Furthermore, our results presented here, coupled with evolutionary studies that show the genus to be rapidly diversifying, suggest that the highlands and escarpments have played a significant role in plant speciation. We conclude by highlighting the advantages of studying this genus further as a model system for plant ecology and evolution in arid environments.

Keywords: Angola, deserts, endemism, escarpments, highlands, Namibia, *Petalidium*

A BRIEF INTRODUCTION TO *PETALIDIUM*

Petalidium Nees (Acanthaceae) is one of the iconic plant genera of arid regions of central and northwestern Namibia and southwestern Angola. It is the third-most diverse plant genus in the Kaokoveld Centre of Endemism, which lies at the core of the Highlands and Escarpments of Angola and Namibia (HEAN), after *Euphorbia* L. (Euphorbiaceae) and *Indigofera* L. (Fabaceae) (Craven 2009). It also has several species in the Gariep Centre of Endemism, although these species are not particularly associated with the HEAN (van Wyk & Smith 2001). *Petalidium* is one of four evolutionary radiations of Acanthaceae in western Namibia and southwestern Angola, the others being *Monechma* Hochst., *Blepharis* Juss. and *Barleria* L. (Fisher *et al.* 2015, Tripp *et al.* 2017, Darbyshire *et al.* 2020). These other genera, both within and outside of Acanthaceae, are widespread and diverse beyond the HEAN, while most species of *Petalidium* are restricted to the HEAN and neighbouring areas in Namibia and Angola. As a monophyletic radiation in and around the HEAN (Loiseau *et al.* 2023), *Petalidium* represents an ideal system for understanding the biodiversity patterns and evolutionary history of this study area.

Petalidium is not a montane genus per se; many of its species occupy areas of lower elevation within the HEAN and other species occur in flatter areas towards the Atlantic Ocean or in non-montane areas east of the HEAN (Figure 1). Nevertheless, it seems probable that the rugged topography of the HEAN has played a significant role in the diversification of *Petalidium* (Tripp *et al.* 2017, Loiseau *et al.* 2023). Many species of *Petalidium* are characterised by having small populations, and mountain barriers may have contributed to allopatric isolation (Hughes & Atchison 2015). Complex topography also interposes diverse geological and edaphic substrates which can drive plant speciation (Kruckeberg 1986).

Petalidium varies in its growth form from entirely prostrate plants in hyperarid areas, namely the Namib Desert, to upright shrubs that can reach 2 m in height (e.g., *P. bracteatum* and *P.* sp. nov. Dexter & Tripp 7296). Plants of *Petalidium* always have at least some aboveground woody tissue and often bear taproots which can exceed 80 cm in length. *Petalidium* is distinguished from other Acanthaceae in the region by its paired, leaflike bracts, two-seeded capsules with fracturing placentae, triangular pollen in polar view with 12 pseudocolpi, and four areas of raised

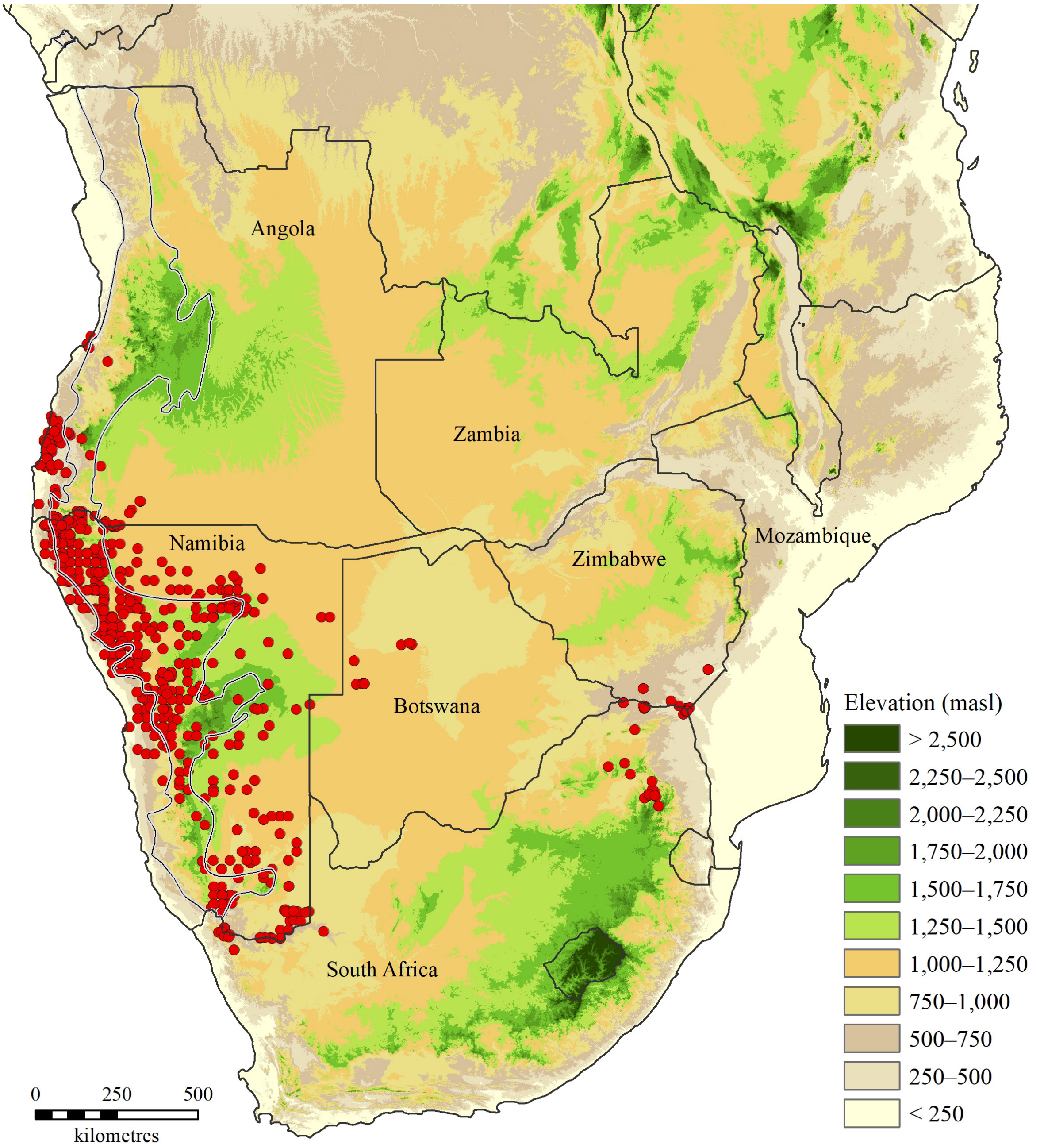

Figure 1: *Occurrences of* Petalidium *across southern Africa. Each red dot represents a georeferenced herbarium voucher, with data derived from vouchers primarily held at the Natural History Museum Herbarium (BM), University of Colorado Museum Herbarium (COLO), Royal Botanic Garden Edinburgh Herbarium (E), Royal Botanic Gardens Herbarium (K), Instituto Superior de Ciencias da Educação Herbarium (LUBA), South African National Biodiversity Institute National Herbarium (PRE) and the National Herbarium of Namibia (WIND). The background colour of the map depicts the elevation in metres above sea level. The grey lines represent country borders, while the black line with white shadowing shows the limits of the highlands and escarpments of Angola and Namibia.*

tectum on the pollen surrounding each aperture (Tripp *et al.* 2013, Manzitto-Tripp *et al.* 2021). Like some other genera of Acanthaceae (e.g., *Ruellia*; Tripp *et al.* 2021), *Petalidium* displays a remarkable diversity of floral forms, varying from large campanulate, open flowers to tubular red flowers that attract sunbirds and minute maroon flowers that are probably pollinated by long-tongued flies.

In this contribution, we give an overview of our current understanding of the genus, including a brief description of all known species. We present distribution maps for each species based on our own fieldwork and reviews of herbarium vouchers at the herbaria that house most existing specimens of *Petalidium* worldwide (BM, K, LUBA, PRE and WIND). There has been no taxonomic revision of *Petalidium* since Obermeyer (1936), and that work only included 18 species. Our contribution here represents the combined and current knowledge of several scientists that are actively working on the genus. Future systematic and taxonomic research may very well change our understanding of the morphological limits of individual species and their geographical distributions, but our contribution here represents the most up-to-date information available. Overall, we find that nearly two thirds (22 of 36) of the accepted African species of *Petalidium* represent endemics or near-endemics of the HEAN.

INFORMAL MORPHOLOGICAL GROUPS, THEIR CONSTITUENT SPECIES AND GEOGRAPHICAL DISTRIBUTIONS

The following five groups used to categorise species of *Petalidium* are based largely on the morphology of the overall inflorescence and individual flowers. In some cases, the groups appear to be 'natural', or reciprocally monophyletic, in the latest phylogenies produced for *Petalidium*. In other cases, the groups are clearly not monophyletic. Our phylogenetic understanding of the relationships of species of *Petalidium* is a work in progress, and we only give reference to the phylogenetic nature of groups where we are confident in that result based on our phylogenetic studies to date (Tripp *et al.* 2017, Loiseau *et al.* 2023).

1. Large-, open-flowered group

This group consists of ten species known to date that are characterised by their large, open campanulate flowers. The androecium and gynoecium are bilaterally symmetric, like all species in the genus, but the corolla approaches radial symmetry. Hereafter, when we refer to floral symmetry, we are referring to the form of the corolla. The species in this group represent the earliest diverging branches in the phylogeny of *Petalidium* (Loiseau *et al.* 2023), and their floral form may represent the ancestral form for the genus. The colour of the flowers varies from white to yellow to light pink and purple. The species in this group are mostly upright shrubs and tend to occur in cooler, moister areas with less water stress than most other species of *Petalidium* that occur in the HEAN and the Namib Desert.

HEAN endemics

Petalidium cymbiforme Schinz: This species (Figure 2) is distinguished from other species in this group by its combination of narrow, linear leaves and white flowers. It is restricted to the southernmost portion of the HEAN. Note that for Figures 2–36 the colours and lines shown in the distribution maps are the same as those described in Figure 1.

Petalidium luteo-album A.Meeuse: This species (Figure 3) and *P. giessii* (Figure 4) are close relatives that occur in hyperarid areas, in contrast to the other species in the group. They are similar in having large papery cordate bracts that are persistent long after the flowers fall. They can be distinguished from each other by their flower colour, with *P. luteo-album* having mostly cream to white corolla lobes (except for the lower corolla lobe, which is yellow), while *P. giessii* has all corolla lobes yellow. The bracts of *P. luteo-album* are larger, more opaque, often drying red or brown, and more strongly cordate. *Petalidium*

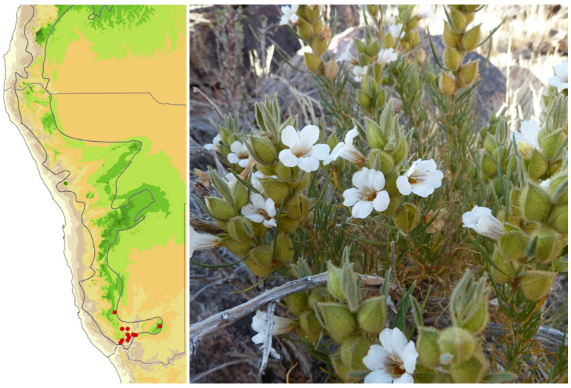

Figure 2: *Occurrences of* Petalidium cymbiforme *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2078.*

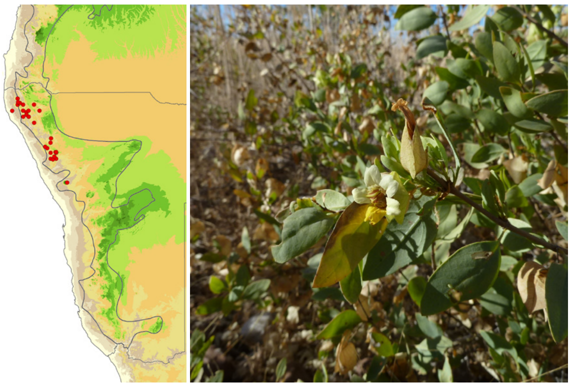

Figure 3: *Occurrences of* Petalidium luteo-album *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 830.*

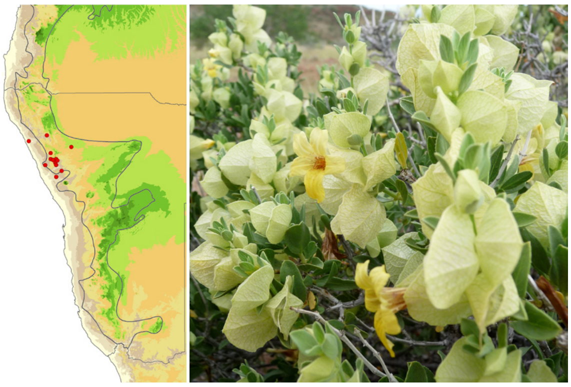

Figure 4: *Occurrences of* Petalidium giessii *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 825.*

luteo-album also has a larger range yet is more clearly restricted to the HEAN than *P. giesii*.

HEAN near-endemics

Petalidium giessii P.G.Mey.: See *P. luteo-album* (above) for morphological differences with that species. *Petalidium giessii* occurs in the HEAN, but also at lower elevations to the west of the escarpment on the Namibian coastal plain (Figure 4).

Petalidium rautanenii Schinz: This is the only species from the 'large, open-flowered group' that occurs in central northern Namibia. It is found at the northeastern extreme of the highlands in Namibia around the Otavi Mountains, but also occurs in surrounding areas just outside the designated highland area (Figure 5).

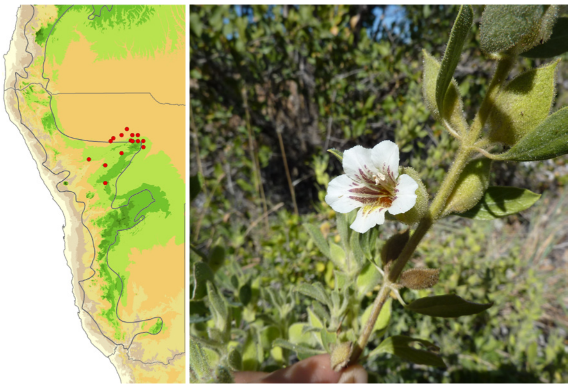

Figure 5: *Occurrences of* Petalidium rautanenii *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4796.*

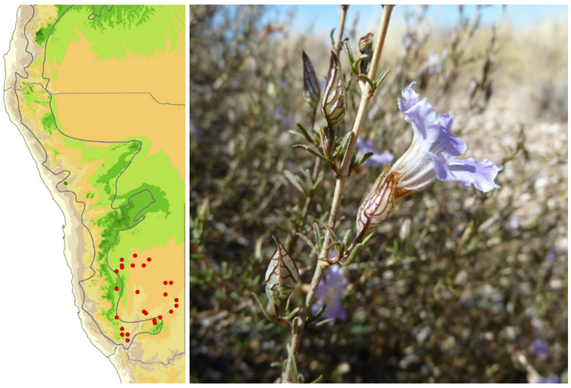

Figure 6: *Occurrences of* Petalidium linifolium *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2031.*

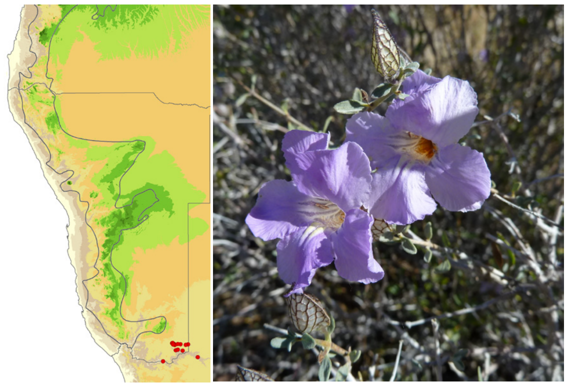

Figure 7: *Occurrences of* Petalidium lucens *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2065.*

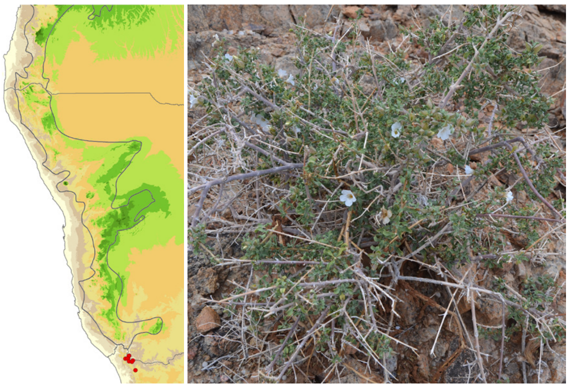

Figure 8: *Occurrences of* Petalidium mannheimerae *with photograph (by L Nanyeni) of individual vouchered as Nanyeni 936.*

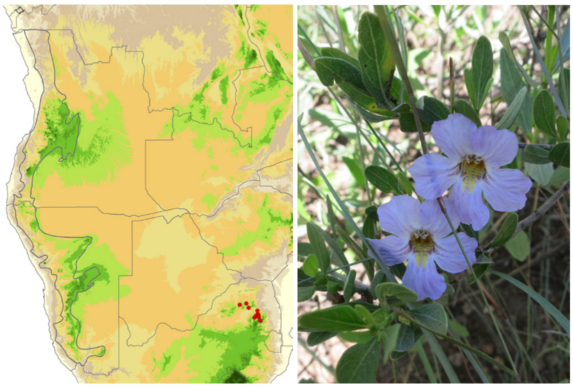

Figure 9: *Occurrences of* Petalidium oblongifolium *with photograph (by K Dexter) of individual vouchered as Dexter 6859.*

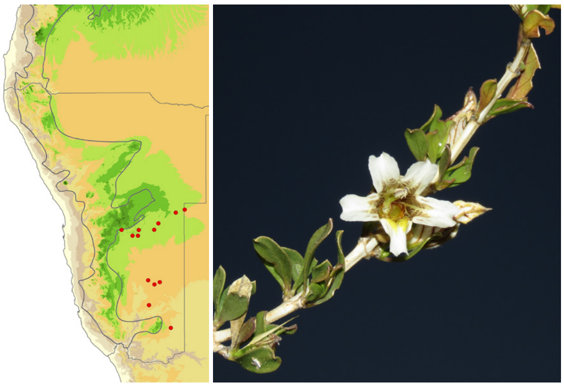

Figure 10: *Occurrences of* Petalidium parvifolium *with photograph (by W Swanepoel) of individual vouchered as Swanepoel 623.*

Other species not associated with the highlands and escarpment

Petalidium barlerioides (B.Heyne ex Roth) Nees: This is the only species of *Petalidium* whose range is outside of Africa, and it is the sister species to the rest of the genus (Tripp *et al.* 2017). It occurs in the Himalayan foothills of India and Nepal, and elsewhere in India. No map or photo shown.

Petalidium linifolium T.Anderson: This species is similar to *P. cymbiforme* (above) in its linear leaves, but has pale pink to purple flowers. It does occur in the southern portion of the HEAN, but also further eastward and does not seem particularly associated with the HEAN (Figure 6).

Petalidium lucens Oberm.: This species (Figure 7) is easily confused with *P. parvifolium* (Figure 10), and questions persist about distinctions among the two. However, they appear to be geographically segregated, with *P. lucens* occurring along the most southerly border of Namibia with South Africa. This species occurs well eastward of the HEAN.

Petalidium mannheimerae Swanepoel, Nanyeni & A.E.van Wyk: Illustrated in Figure 8, this is a recently described species that was previously lumped with *P. parvifolium* (Figure 10) and is also similar to *P. lucens* (Figure 7). It is distinguished from these species in its uniformly white flowers, semi-succulent leaves and puberulent indumentum on vegetative parts. It occurs just to the south of the southern end of the HEAN (Figure 8).

Petalidium oblongifolium C.B.Clarke: This is the earliest diverging species among African *Petalidium* and is geographically segregated from the remainder, occurring in the Mpumalanga and Limpopo provinces of South Africa (Figure 9). It occupies more mesic environments than all other African species in the genus.

Petalidium parvifolium Schinz: As with *P. lucens* (Figure 7), this species (Figure 10) has large purple to pink to white flowers, elliptic to lanceolate (rather than linear) leaves and papery, semi-transparent bracts with marked venation. It is found east of the highlands and escarpment of central and southern Namibia, as far north as Rehoboth and Gobabis, and is also found in central-western Botswana.

2. Midsized-, open-flowered group

This group of species has smaller flowers than the previous group, but with a similar overall form, approaching radial symmetry, albeit perhaps more clearly bilateral. The colour of the flowers varies from white to yellow to light or deep pink, purple and even magenta, sometimes within individual species. Many species in this group show high variability in growth form, from upright shrubs in areas with higher water availability to completely prostrate forms in the Namib Desert. Most species in this group are associated with the highlands and escarpments of Namibia and southern Angola.

HEAN endemics

Petalidium ohopohense P.G.Mey.: This species is distinguished from others in the group by its consistently prostrate growth form and flowers that have larger corolla lobes that are consistently pink. It is restricted to a small area around the town of Opuwo (Figure 11).

Petalidium rossmanianum P.G.Mey.: This species has a relatively large range across the northern highlands and escarpment within Namibia (Figure 12). Its flowers vary from white (with coloured nectar guides) to pink to purple and is superficially easy to confuse with *P. variabile* (Figure 17). They are distinguished in their pubescence (branching in *P. rossmanianum*, not so in *P. variabile*), and their ranges do not overlap.

Petalidium sesfonteinense Swanepoel & E.Tripp: This species (Figure 13) is similar to *P. rossmanianum* (Figure 12) and *P. variabile* (Figure 17), but is

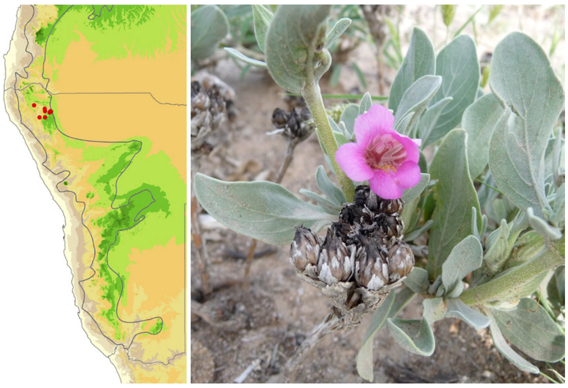

Figure 11: *Occurrences of* Petalidium ohopohense *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 849.*

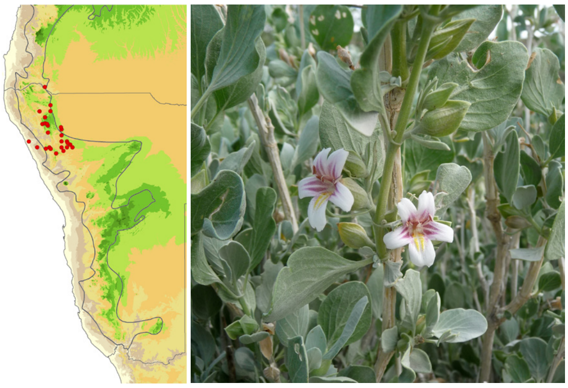

Figure 12: *Occurrences of* Petalidium rossmanianum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 832.*

distinguished by dense dentritic and glandular trichomes. The trichomes of *P. rossmanianum* are not as dense as *P. sesfonteinense* and are not generally glandular. *Petalidium sesfonteinense* shows high variability in flower colour like *P. rossmanianum* and *P. variabile*. It is restricted to a relatively small area around Sesfontein in Namibia and westwards.

Petalidium subcrispum P.G.Mey.: This species (Figure 14) is vegetatively distinct from all other species in this group, having densely pubescent and pungent leaves with an undulate margin. In fact, vegetatively it is very similar to *P. crispum* (Figure 23) including vegetative odours nearly indistinguishable to the human nose, but the flowers are completely different (open cup-shaped flowers in *P. subcrispum* versus tubular orange flowers in *P. crispum*). This species has a very narrow range in the northern Kaokoveld of Namibia.

HEAN near-endemics

Petalidium canescens (Engl.) C.B.Clarke: Of the species with the characteristic flowers of this group, this is the only one where the inflorescence consists of a clustered ‘head’ (Figure 15), which in this case is sub-woody, similar to *P. setosum* (Figure 34). The individual flowers project from this congested head-like structure. Individuals of *P. canescens* can be quite small even when flowering (10 cm x 10 cm), but they do still bear aboveground woody tissue. This species occupies the central highlands and escarpment of Namibia and occurs peripherally into the Namibian coastal plain.

Petalidium pilosi-bracteolatum Merxm. & Hainz: This species (Figure 16) is most easily confused with *P. rossmanianum* (Figure 12) and *P. variabile* (Figure 17), but its flowers are more consistently dark pink and the bracts subtending the flowers typically bear long, straight, glandular trichomes. The species appears to have two disjunct areas of distribution, a northern one restricted to the HEAN and centred around Bergsig and a southern one that occurs in the HEAN and also on the coastal plain towards Swakopmund.

Petalidium variabile (Engl.) C.B.Clarke: This species (Figure 17) resembles many others in the group and is rather variable, as the specific epithet indicates, but is consistently distinguished from others by its unbranched trichomes. Similar to *P. canescens* (Figure 15), it occurs across the central highlands and escarpment of Namibia, and extends into the Namibian coastal plain.

Figure 13: *Occurrences of* Petalidium sesfonteinense *with photograph (by K Dexter) of individual vouchered as Dexter 7559.*

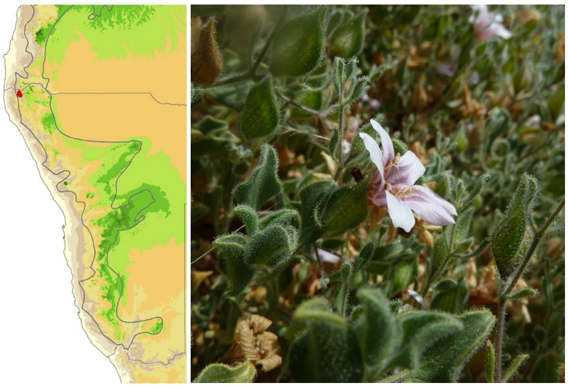

Figure 14: *Occurrences of* Petalidium subcrispum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 2013.*

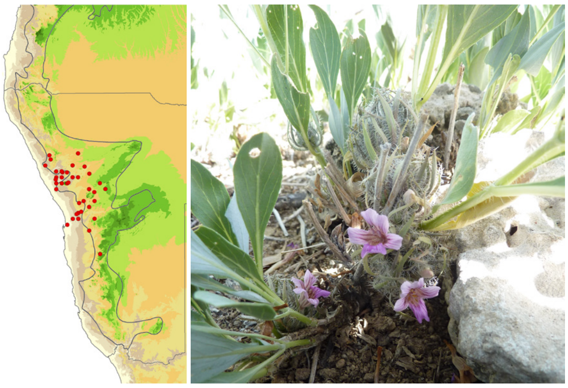

Figure 15: *Occurrences of* Petalidium canescens *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 882.*

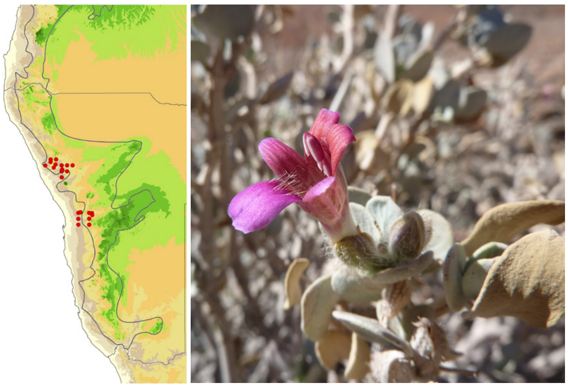

Figure 16: *Occurrences of* Petalidium pilosi-bracteolatum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4096.*

Petalidium welwitschii S.Moore: This species has long pubescence across the leaves and inflorescence, often glandular, which sets it apart from other species in the group. It is also the most northerly distributed, being common in southwest Angola (Figure 18). Within Angola, it regularly occurs on the coastal plain, but is otherwise mostly restricted to the highlands and escarpments in Namibia.

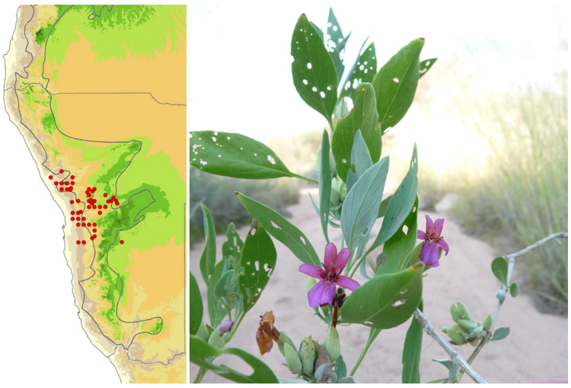

Figure 17: *Occurrences of* Petalidium variabile *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 776.*

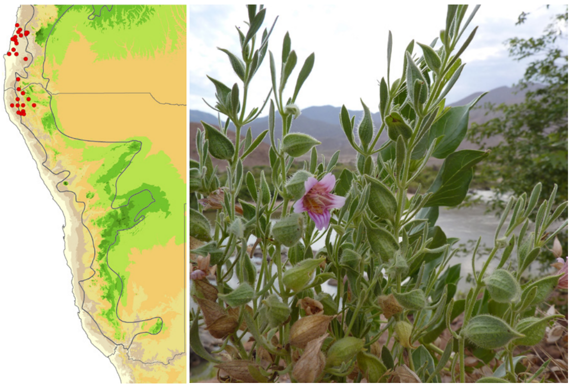

Figure 18: *Occurrences of* Petalidium welwitschii *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4085.*

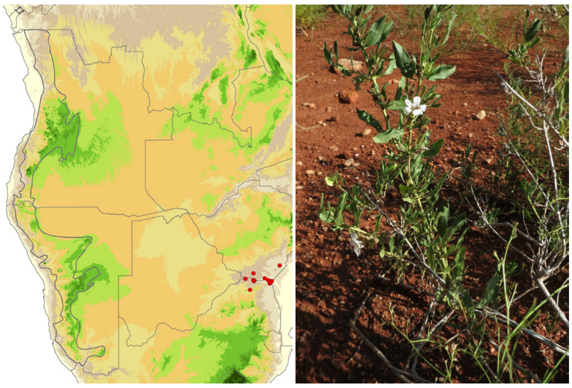

Figure 19: *Occurrences of* Petalidium aromaticum *with photograph (by K Dexter) of individual vouchered as Dexter 6862.*

Other species not associated with the HEAN

Petalidium aromaticum Oberm.: This species consistently bears white flowers, in contrast to most other species in the group. It occurs in the Limpopo Province of South Africa and across the border into Zimbabwe, well disjunct from all other species of *Petalidium* (Figure 19).

Petalidium englerianum (Schinz) C.B.Clarke: This species is distinguished from others in the uniformly glaucous appearance of the vegetation (Figure 20). In other species, some leaves on an individual may appear glaucous, but other leaves on the same individual are green. It is also distinct in having orange to brown upper petals with a yellow lower petal. It occurs in the central highlands of Namibia, but also well eastward across Kalahari sands into Botswana. There is one set of populations at the western edge of its range that has flowers resembling *P. physaloides* (Figure 31; maroon and with a more bilaterally symmetric coralla), and this may represent a novel species endemic to the HEAN.

Petalidium rupestre S.Moore: This species has white flowers but is perhaps most distinct in its incredibly sticky leaves that are flabellate to nearly reniform in shape. The species has a very narrow distribution

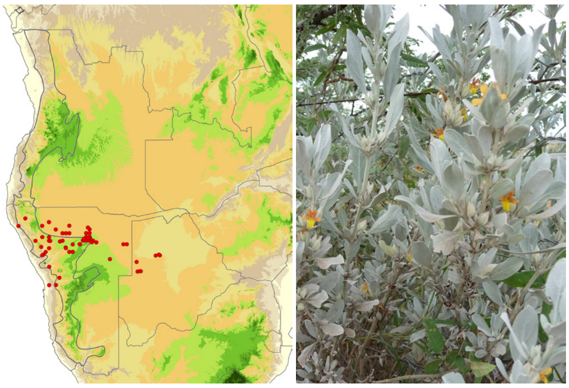

Figure 20: *Occurrences of* Petalidium englerianum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 778.*

Figure 21: *Occurrences of* Petalidium rupestre *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6964.*

along the rocky walls of the gorge of the Rio Giraul, set in the coastal plain of Angola (Figure 21).

3. Long, tubular-flowered group

All the species in this group have tubular flowers that are strongly exerted from between the two bracts. The flower colour varies from orange to red to dark pinkish purple to white. Most of these species have a floral morphology that suggests sunbird pollination, while the white flowers of *P. angustitubum* (Figure 25) rather suggest pollination by sphingid moths or other nocturnal animals.

HEAN endemics

Petalidium coccineum S.Moore: This species (Figure 22) is similar to *P. crispum* (Figure 23) in its orange to red, curving tubular inflorescence, but tends to occur in sandy washes rather than on rocky slopes. It forms a more upright shrub than *P. crispum*, albeit still with an overall sprawling growth form. Amongst the species in the group, this species has the widest distribution, ranging from across northwest Namibia into southwest Angola. Locally, however, it is typically rare, occurring as one to a few scattered individuals.

Petalidium crispum A.Meeuse ex P.G.Mey.: This species (Figure 23) is similar to *P. coccineum*, but is distinguished on several characters outlined above, additionally by its stickier leaves with an undulate margin (see also *P. subcrispum*, Figure 14). It has a fairly narrow distribution within the far northwestern highlands of Namibia.

Petalidium huillense C.B.Clarke: This species has axillary spines (Figure 24), which is unique in the genus. (Note: we consider *P. spiniferum* to be a synonym of this species.) We have limited observations of the floral morphology on living individuals, while herbarium specimens suggest partially exerted flowers, verging on tubular, which are most similar to those of *P. glandulosum* (Figure 27). *Petalidium huillense* has a restricted distribution along and near the Cunene River as it traverses the HEAN.

HEAN near-endemics

Petalidium angustitubum P.G.Mey.: This is the only species in the genus with white tubular flowers (Figure 25). It has a narrow geographic range on the western edge of the escarpment in northern Namibia, with scattered peripheral populations into the coastal plain.

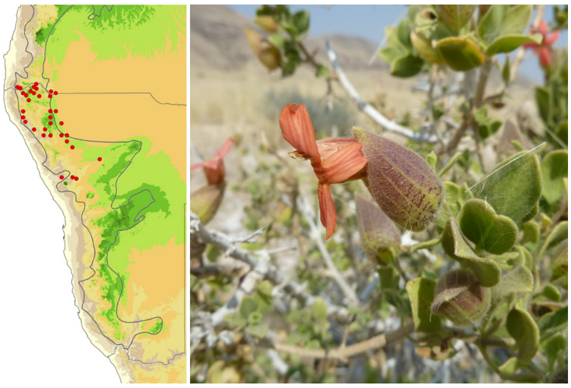

Figure 22: *Occurrences of* Petalidium coccineum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 872.*

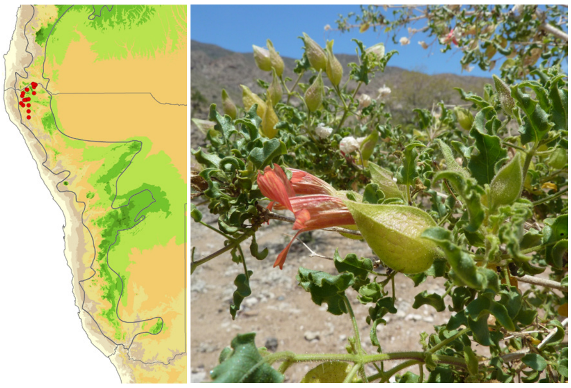

Figure 23: *Occurrences of* Petalidium crispum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4056.*

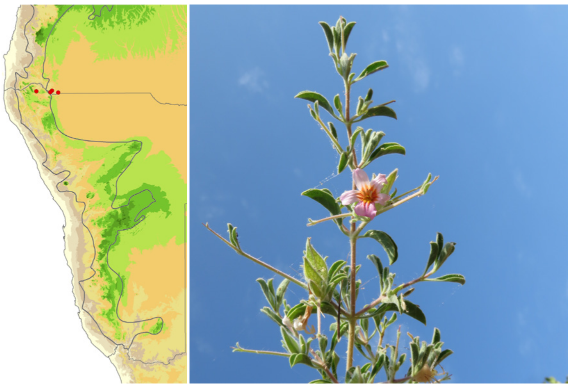

Figure 24: *Occurrences of* Petalidium huillense *with photograph (by W Swanepoel) of individual vouchered as Swanepoel 631.*

Other species not associated with the HEAN

Petalidium bracteatum Oberm.: This species (Figure 26) resembles *P. coccineum* (Figure 22) but is a taller plant overall, sometimes scandent on other shrubs or rocks, and the flowers are larger and deeper red in colour (rather than orange). It occurs primarily east of the highlands in northern Namibia and southern Angola; most records from the HEAN are likely to represent misidentifications of *P. coccineum*.

Petalidium glandulosum S.Moore: This species has flowers that are less orange or red than others in the group, tending towards dark pink to purple (Figure 27). The flowers have a characteristic bend in the tubular part of the flower. The species is primarily distributed on the coastal plain of Angola, with an outlying northern population near Benguela that may represent a new species and certainly the most northerly population of *Petalidium* in Africa.

4. Midsized-, maroon-flowered group

This group of species has a flower type that can be considered intermediate in form between the group with minute maroon flowers (see below) and that with long tubular flowers (see above). The flowers of this fourth group often have the colouration of the minute-, maroon-flowered group, yet they are larger in size. In colour, the flowers are darker than any in the previous groups, being either maroon or deep purple to pink. The species in the group often have a thick base to the trunk, sometimes over 10 cm in diameter, and can form large upright shrubs.

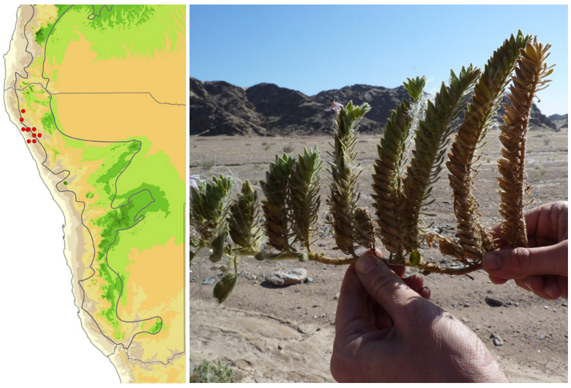

Figure 25: *Occurrences of* Petalidium angustitubum *with photograph (by L Nanyeni) of individual vouchered as Nanyeni 862.*

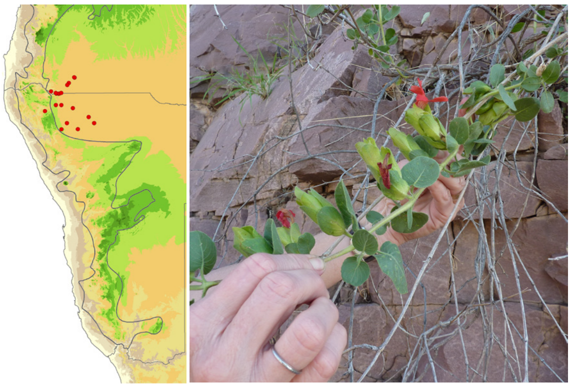

Figure 26: *Occurrences of* Petalidium bracteatum *with photograph (by L Nanyeni) of individual vouchered as Nanyeni 4054.*

HEAN endemics

Petalidium kaokoense Swanepoel: This is a recently described species that is distinguished by its stout base and white peeling bark. It has a very restricted distribution in the Hartmann Mountains and nearby areas to the east (Figure 28).

HEAN near-endemics

Petalidium cirrhiferum S.Moore: This species is distinct among *Petalidium* in having a toothed, crenulate leaf margin (Figure 29). Within this group, it is distinct in having flowers that tend towards a deep purple-pink colour rather than maroon. The species occurs near the Cunene River where the river traverses the highlands and escarpment, but also eastwards and westwards of the HEAN.

Petalidium sp. nov. Dexter & Tripp 7296: This is a recently discovered, putatively novel species that requires further study. It is similar to *P. physaloides* (Figure 31) in its flowers, but forms larger, more robust plants, with a stout base similar to *P. kaokoense* (Figure 28). It is only known from a population found near the entrance to Iona National Park in Angola, on the western edge of the HEAN (Figure 30). At present, we consider it too data deficient to determine if it is an endemic of the HEAN or not.

Other species not associated with the HEAN

Petalidium physaloides S.Moore: This species is similar to *P. kaokoense* (Figure 28) and *P.* sp. nov. Dexter & Tripp 7296 (Figure 30), but it has a more delicate growth form with spindly, ascending branches

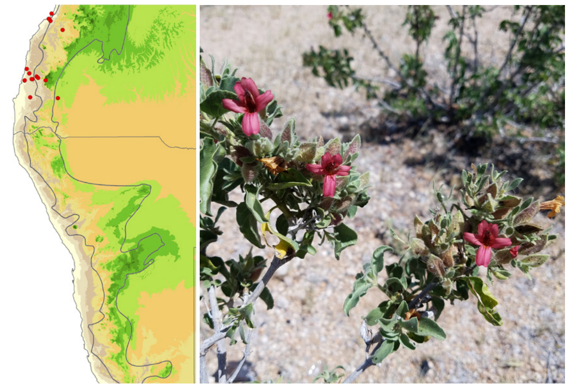

Figure 27: *Occurrences of* Petalidium glandulosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6926.*

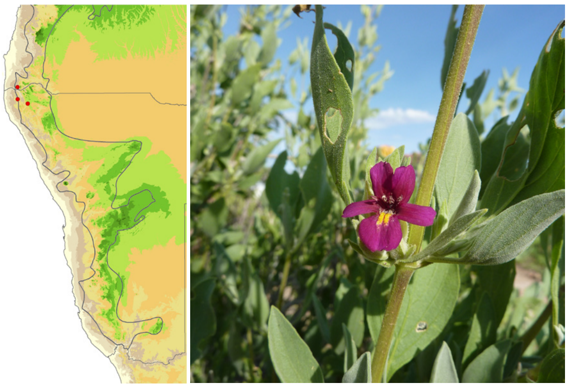

Figure 28: *Occurrences of* Petalidium kaokoense *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4075.*

(Figure 31). While there are multiple records from Namibia, we believe these are misidentifications and that the species is restricted to Angola, where it occurs primarily in the coastal plain west of the highlands and escarpment.

5. Minute-, maroon-flowered group

The species in this group are characterised by minute maroon flowers with yellow nectar guides, similar to that of *P. physaloides* (Figure 31), but smaller. Only *P. setosum* (Figure 34) has a flower that approaches the size of those in the previous group. Also, the species in this group have congested inflorescences, forming a sub-woody (*P. setosum*) or woody 'head-like' structure (*P. halimoides, P. lanatum* and *P. lepidagathis*; Figures 32, 33 and 35, respectively). Species tend to be prostrate (except *P. setosum* that can be more upright) and some grow extensively via runners (*P. ramulosum* and *P. tomentosum*; Figures 36 and 37). No species in this group is endemic to the HEAN.

HEAN near-endemics

Petalidium halimoides (Nees) S.Moore: This species (Figure 32) is very similar to *P. lanatum* (Figure 33) in its prostrate growth form with inflorescences in woody heads. It only seems distinguishable by a deltoid leaf shape with a flat base, while *P. lanatum* has more elliptic leaves with the base attenuate on the petiole. Intermediate forms have been observed. These two species have parapatric distributions across the HEAN, with *P. halimoides* occurring in northern Namibia and on the coastal plain in southern Angola.

Petalidium lanatum (Engl.) C.B.Clarke: See the previous species (*P. halimoides*) for morphological limits of this species. It occurs in the highlands, escarpment and coastal plain of central Namibia (Figure 33).

Petalidium setosum C.B.Clarke ex Schinz: This species is distinguished from others in the group in its larger, more upright growth form and its larger flowers (Figure 34). Vegetatively and in the form of the inflorescence, it is very similar to *P. canescens* (Figure 15), but the flowers are clearly distinct. It has one of the widest latitudinal distributions of any species of *Petalidium* but is largely restricted to the highlands and escarpments of Namibia and neighbouring areas to the east and west.

Other species not associated with the HEAN

Petalidium lepidagathis S.Moore: The inflorescence of this species (Figure 35) is very similar to that of *P. halimoides* and *P. lanatum* (Figures 32 and 33, respectively), but the leaves are much more lanceolate and nearly linear (Figure 35). It is primarily found on the coastal plain in southern Angola. It has a parapatric distribution with respect to *P. halimoides*, and we have observed putative hybrids, assessed on morphology, where their ranges meet.

Petalidium ramulosum Schinz: This species (Figure 36) and *P. tomentosum* (Figure 37) are characterised by long rooting runners, but they have completely non-overlapping distributions. The leaves are glaucous and covered in dense pubescence similar to

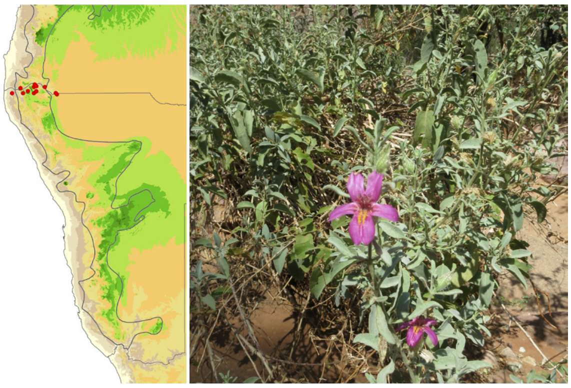

Figure 29: *Occurrences of* Petalidium cirrhiferum *with photograph (by K Dexter) of individual vouchered as Dexter 7489.*

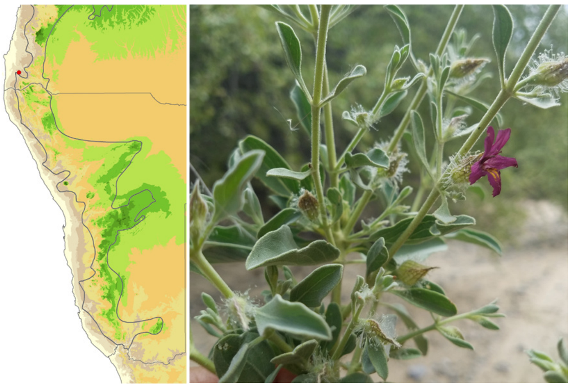

Figure 30: *Occurrences of* Petalidium *sp. nov. Dexter & Tripp 7296 with photograph (by K Dexter) of individual vouchered as Dexter 7296.*

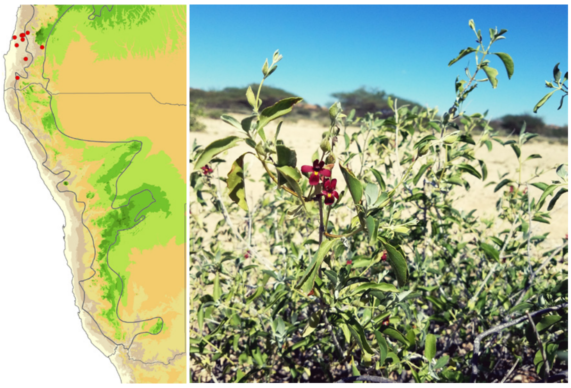

Figure 31: *Occurrences of* Petalidium physaloides *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6954.*

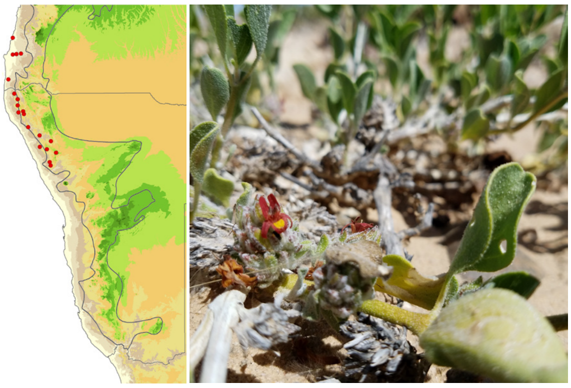

Figure 32: *Occurrences of* Petalidium halimoides *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6943.*

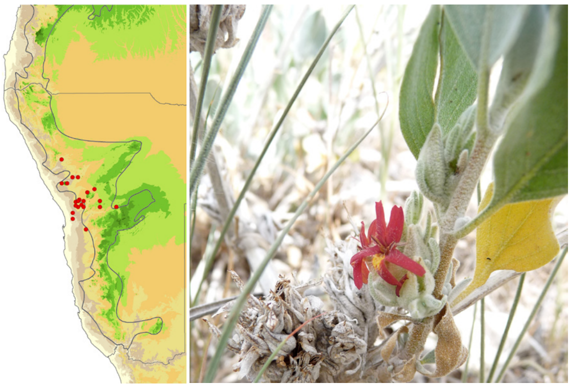

Figure 33: *Occurrences of* Petalidium lanatum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 833.*

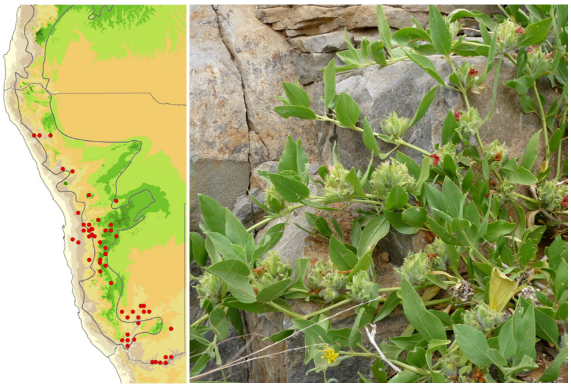

Figure 34: *Occurrences of* Petalidium setosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 887, growing upwards at base of cliff .*

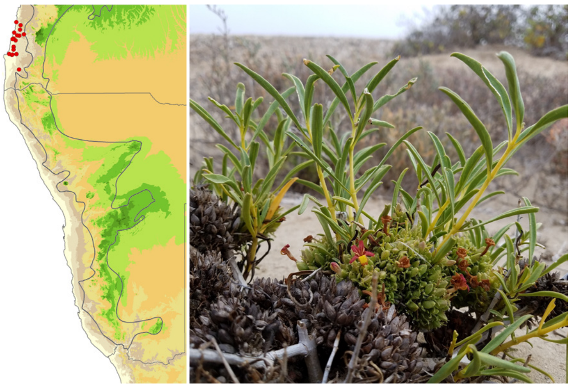

Figure 35: *Occurrences of* Petalidium lepidagathis *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6941.*

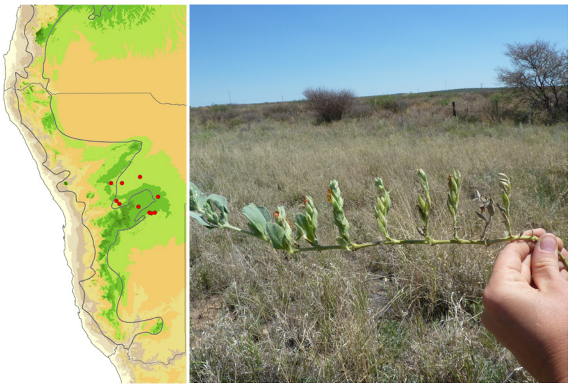

Figure 36: *Occurrences of* Petalidium ramulosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 4120.*

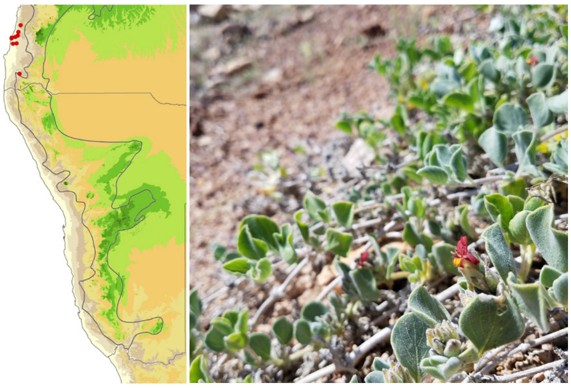

Figure 37: *Occurrences of* Petalidium tomentosum *with photograph (by E Manzitto-Tripp) of individual vouchered as Tripp 6928.*

P. englerianum (Figure 20). This species occurs primarily east of the highlands in central Namibia.

Petalidium tomentosum S.Moore: This species has the smallest leaves of any *Petalidium* and grows in a completely prostrate form under very arid conditions where few other woody plants can grow. It is largely restricted to the coastal Namib Desert in Angola (Figure 37).

DISCUSSION

Sixty-one per cent of African species of *Petalidium* (22 of 36) are endemics or near-endemics of the central and southern portions of the highlands and escarpments of Angola and Namibia (HEAN). Coupled with our knowledge that all 36 species of *Petalidium* in Africa arose in the last 1.6–4.3 million years (Tripp *et al.* 2017, Loiseau *et al.* 2023), our results here suggest that the highlands and escarpments in this area have played a key role in plant speciation and generating biodiversity. While there is certainly value to focusing conservation efforts on unique and species-poor evolutionary lineages (e.g., giant pandas, tuataras or *Amborella*), it can be considered equally imperative to focus on lineages such as *Petalidium*, which show great evolutionary lability and are undergoing evolutionary radiation. It is these radiating lineages that may present the greatest evolutionary potential in the face of environmental change (Eizaguirre & Baltazar-Soares 2014). Moving beyond academic debates on the conservation value of 'old' versus 'young' species, our contribution, which reports a high number of endemic species in the highlands and escarpments of Namibia and southern Angola, clearly shows the value of the area for plant conservation.

We may have a better understanding of species distributions for *Petalidium* than for many other plant lineages in the HEAN, but this does not mean we understand those distributions very well. Many areas of the HEAN are remote and hard to access, particularly because of challenges posed by water access when working far from roads (and thus vehicles which carry water). Nevertheless, these remote areas need to be explored. Given that many species of *Petalidium* show very restricted distributions, we are confident that more species in the genus will be documented as more botanists visit remote areas of Namibia and Angola. Collaboration with local residents, indigenous or otherwise, could aid in this effort as our personal observations have clearly shown the ability of local people to identify different species of *Petalidium*.

The recency of speciation in *Petalidium* is a double-edged sword, leading to challenging taxonomy but great opportunities for understanding plant evolution and speciation. More taxonomic work is clearly needed to understand the morphological limits of species and define conservation agendas going forward. Beyond taxonomy, we advocate for further evolutionary studies of *Petalidium*. It presents an ideal model system for plant evolutionary research, including studies of hybridisation, a process increasingly recognised as fundamental to plant evolution (Schley *et al.* 2022). In *Petalidium*, species boundaries may be incompletely formed given recent speciation, which allows for the possibility of hybridisation. We have observed multiple putative hybrids in the field, including populations that appear to represent 'mixes' of two identifiable progenitor species that are also present in the landscape. We also sometimes find populations of *Petalidium* where the vegetative morphology suggests one species and the floral morphology an entirely different species (see *P. subcrispum* (Figure 14) and *P. englerianum* (Figure 20), for example). These may be hybrid origin species and are an exciting avenue for future research.

A frequent goal of systematic and evolutionary studies is to produce a complete DNA sequence-based phylogeny of the group of species under study. This is a goal we are actively striving for with *Petalidium*, building on our previous work (Tripp *et al.* 2017, Loiseau *et al.* 2023). However, if hybridisation is common in the group, reticulate evolutionary patterns may also be common, and a single, 'correct' topology may not exist. Nevertheless, more DNA sequence data from more populations of more species will only advance our evolutionary understanding of the genus.

Petalidium is remarkable in the variety of floral forms of its species, particularly given the young age of the genus (maximum of 4.8 Ma; Tripp *et al.* 2017), and we have suggested above that this is due to adaptation to different pollinators, such as bees, sunbirds and long-tongued flies. However, we have only undertaken cursory pollinator observations in the field, and no quantitative studies of pollination biology have been carried out in the genus. Such quantitative studies, via direct observations or camera-trapping, would greatly increase our understanding of the potential role of pollinators in interspecific pollen transfer and are needed to inform on which animal species may be dependent on different species of *Petalidium*.

Petalidium offers an excellent opportunity to understand plant adaptation in arid environments. It achieves remarkably high abundance in regions that are particularly challenging for woody plants, due to low annual rainfall and high interannual rainfall variability. *Petalidium* can blanket entire valleys where it rains less than 100 mm a year on average and, in some years, it does not rain at all. How do species of *Petalidium* survive in such dry conditions? Preliminary anatomical studies of leaves suggest adaptations to arid environments (E. Manzitto-Tripp *et al.* unpubl. data), which may play a role in making photosynthesis more efficient, allowing plants to minimise the opening of stomatal pores and consequently reduce water loss. We have also observed in the field that multiple, to almost all, branches of a given *Petalidium* individual may die back but that resprouting can occur with vigour when water availability allows, demonstrating another plant strategy to deal with drought (Craine 2009, Folk *et al.* 2020). Some species of *Petalidium* may be deciduous, to allow cessation of water loss during dry periods, but further fieldwork is needed to confirm which exact species carry this trait. Ecophysiological studies are needed to study the multiple mechanisms that may allow *Petalidium* to prosper in hyperarid regions.

Lastly, species of *Petalidium* need research from a conservation perspective, beyond simple geographic studies of their distribution as done here. We recently undertook fieldwork on *Petalidium* in northwestern Namibia (April–May 2022) in areas that we visited a decade earlier during four field visits (2010–2013). In revisiting some of the same populations, we documented astounding declines in abundance. In some places, one could see numerous standing dead shrubs of *Petalidium*. In others, we could find no trace of previously collected populations. Is this due to the exceptionally dry conditions between visits, to overgrazing (particularly by goats) or a combination of the two? Interestingly, in areas where we previously documented multiple genera of Acanthaceae, *Petalidium* was greatly reduced in abundance, but *Dinteracanthus* C.B.Clarke ex Schinz, *Monechma* Hochst. and other genera seemed to be fine. Are species of *Petalidium* particularly tasty to herbivores (native or non-native)? Are human populations, and thus goat and other livestock populations, increasing in the region? Have management practices and grazing areas changed? Many of these questions could be addressed with existing data or simple field studies. Answering these questions would help us to understand the threats to species of *Petalidium* and to plant populations in general in these arid highland and escarpment areas. Such applied research is urgently needed.

ACKNOWLEDGEMENTS

We thank the governments of Namibia, Angola and South Africa for permission to do fieldwork and collect herbarium vouchers in their respective countries. We are grateful to Hendrina Hasheela, Lucinda McDade and Corné Niemandt for assistance in the field. We kindly thank Fernanda Lages for her dedicated work to improve the LUBA herbarium and for discussions on the distribution of *Petalidium* species in Angola. We are also thankful to John Mendelsohn, Pedro Vaz Pinto and Brian Huntley, the editors of this volume, for their invitation to present this work and subsequent support. We thank David Goyder and the editors, including Carole Roberts, for helpful comments and suggestions that improved the manuscript.

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Commiphora of the highlands and escarpments of Angola and Namibia

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ABSTRACT

The myrrh genus, *Commiphora* Jacq. (Burseraceae), comprises approximately 190 species of trees and shrubs worldwide that are most commonly encountered in the seasonally dry and arid biomes of sub-Saharan Africa. The diversity of *Commiphora* species in southwestern Africa is notable for its many restricted-range species, including nine that were only discovered within the last two decades. Of the 36 species native to the region, the majority (29 species) are endemic or near-endemic to Angola and/or Namibia and 22 species occur at elevations of 1,000 masl or greater. Molecular phylogenetic data reveal that early divergences within the genus probably involved exchanges between southwestern Africa and Madagascar beginning in the Miocene, and that extant species in southwestern Africa arose from several different evolutionary lineages. Some species divergences within the largest radiation of southwest African endemic species appear to be associated with elevational disjunctions or latitudinal disjunctions between the Kaokoveld and Gariep centres of endemism, some of which are hypothesised to have occurred as recently as the Quaternary. Despite *Commiphora* being renowned for its fragrant oleoresins and ethnobotany, fundamental aspects of *Commiphora*'s systematic biology, ecology and evolution remain understudied. Many species have yet to be included in molecular phylogenetic analyses. Other major avenues for investigation include characterising species' anatomical and physiological abilities to withstand the extreme heat and the water deficit of their natural environment; their reproductive ecology; and the chemical ecological interactions mediated by the diverse secondary chemistry of their oleoresins. Future research priorities include exploratory fieldwork to document the species of *Commiphora* in Angola, collaborative efforts to improve biodiversity informatic resources for the genus and integrative approaches to expand our understanding of *Commiphora*'s ecology and evolution within a comprehensive phylogenomic framework.

Keywords: Angola, *Commiphora*, escarpments, evolution, highlands, Namibia

INTRODUCTION

The myrrh genus, *Commiphora* Jacq., in the Burseraceae family is a group of conspicuous and charismatic tree species that produce fragrant oleoresins of ethnobotanical renown. The genus comprises approximately 190 species, of which around 109 species are native to Africa, with the remaining species being distributed in Madagascar, countries spanning the Arabian Peninsula and eastwards to Bangladesh, and in South America (Figure 1A). Species richness is greatest in tropical East Africa and the Horn of Africa, which contain at least 89 species as well as a biome that is characterised by the presence of the genus, the 1.6 million km^2 *Acacia-Commiphora* woodland (Olson & Dinerstein 2002). Within Africa and across their global range, *Commiphora* species are intolerant of freezing temperatures and fire and are found predominantly in seasonally dry subtropical and tropical forests, arid scrub-thickets, and deserts that are free of these disturbances. Many species are saxicolous and pachycaulescent (Figures 1B and 1C). *Commiphora* species are readily identified in the field by their typically thin bark, aromatic oleoresins, frequently spine-tipped short-shoot branches and drought-deciduous, alternate leaves that are imparipinnate, trifoliolate or unifoliolate (Daly *et al.* 2010). Species are usually dioecious, but all have paniculate or reduced (1–3-flowered) cymose inflorescences that bear small four-parted flowers. The fruits are drupes that dehisce via two or rarely four valves and produce a fleshy, lipid-rich red-to-yellow pseudaril that partially encases the endocarp.

However, the morphological and ecological diversity of *Commiphora* species results in many exceptions to the common diagnosis of the genus. For example, species have a range of habits (from upper canopy trees taller than 20 m, to small scandent trees, to multi-stemmed weeping shrubs), bark characteristics (thickly plated and brown to smooth grey, to paper-thin peels and flakes of translucent red or yellow hue revealing green underbark that is presumably photosynthetic), oleoresin traits (some species produce no apparent oleoresins whereas others produce oleoresins that vary by odour, colour, opacity and viscosity) and edaphic associations (from unconsolidated sands to exposed limestone or granitic outcrops) (Figure 2). Fruit shape and size are highly variable as are pseudarils; some species are entirely non-arillate. Many aspects of morphological and ecological diversity that are readily apparent in the field do not preserve well on herbarium sheets, or are rarely recorded in the literature. This limitation, in combination with *Commiphora*'s drought-deciduous habit and tendency to flower before leaf expansion, means that taxonomic research has been hindered by a lack of high-quality research specimens and observational data from even well-collected areas. The underlying mechanisms of other remarkable biological traits of *Commiphora*, such as its ability to withstand high temperature and extreme water deficit, and its diverse oleoresin chemistry which implicates a complex chemical ecology, remain understudied.

THE EVOLUTIONARY HISTORY AND BIOGEOGRAPHY OF *COMMIPHORA*

Multiple fossil-calibrated molecular phylogenetic studies have shown that *Commiphora* has a complex historical biogeography within Africa and beyond. *Commiphora* is hypothesised to have diverged from a common ancestor with the predominantly American genus, *Bursera*, during the Eocene; mean estimates range from 51.73 to 38.95 mya (Weeks & Simpson 2007, Weeks *et al.* 2014, Gostel *et al.* 2016a, Muellner-Riehl *et al.* 2016, Joyce *et al.* 2023). Early movement of subtribe Burserinae among continents is hypothesised to have been facilitated by boreotropical corridors within Laurasia followed by vicariance (Weeks *et al.* 2005, Weeks *et al.* 2014), based on the age of the lineage and the location in the northern hemisphere of fossils attributable to *Bursera* and *Commiphora*. Long-distance dispersal cannot be ruled out as an important force because the pseudarillate fruits of *Commiphora* are dispersed by birds (van der Walt 1975, Bleher & Böhning-Gaese 2001). Moreover, the distribution of several relatively young, continentally disjunct endemic lineages, such as the sole South American species, *Commiphora leptophloeos* (Mart.) J.B.Gillett, and multiple Madagascan clades of *Commiphora*, can only be attributed to long-distance dispersal via biotic (e.g., bird) or abiotic (e.g., oceanic currents) means because they postdate any possible subdivision of ancestral, contiguous continental populations.

The diversity of *Commiphora* species in southwestern Africa is notable for its many restricted-range species. Of the 36 species native to the region, the majority of species (n = 29) are endemic or near-endemic to Angola and/or Namibia and 22 species may be found at elevations of 1,000 masl or greater (Table 1). The most-densely sampled and fossil-calibrated *Commiphora* phylogeny to date (Gostel *et al.* 2016a) indicates that divergences of all extant species probably began 36.6 ± 9.2 mya and gave rise to six well-supported clades, four of which contain species distributed in continental Africa: the Spinescent clade, the Saxicola clade, the Gariepensis clade and the Arafy + *C. kraeuseliana* Heine clade. Southwest African species of *Commiphora* derive from each of these four clades, although not all species have been evaluated within a phylogenetic framework.

The most recent phylogenetic analysis of *Commiphora* includes 31 of the 36 species native to southwestern Africa as well as 82 other species that occur in sub-Saharan Africa, Socotra, Madagascar, the Arabian Peninsula, India and South America (Figure 3; Gostel *et al.* 2016a, Swanepoel *et al.* 2022). Phylogenetic

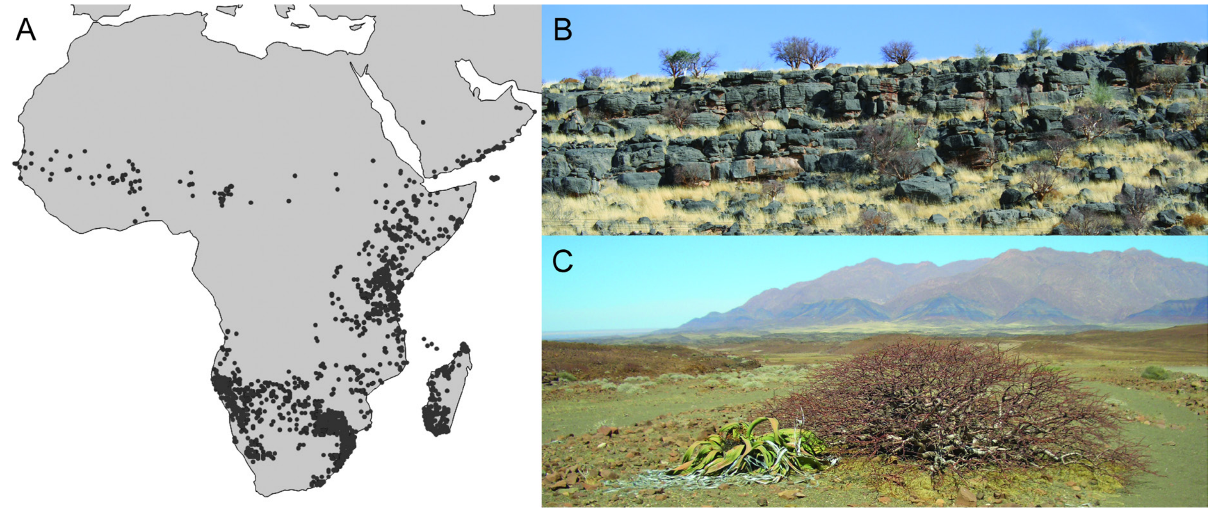

Figure 1: *A) Distribution of* Commiphora *in Africa and the Arabian Peninsula inferred from herbarium specimen records, as analysed by Ringelberg* et al. *(2020; adapted with permission). B)* Commiphora *species may be gregarious in seasonally arid, frost- and fire-free habitats; many are saxicolous. Population of the Angolan–Namibian highland endemic,* C. glaucescens*, along the Tsauchab River in the Naukluft Mountains, Namibia (c. 1,076 masl). Photo: A Weeks. C) Multiple* Commiphora *species are adapted to extremes of water-deficit and have pachycaulescent habit. Angolan–Namibian endemic* C. wildii *with* Welwitschia mirabilis *west of the Brandberg massif, Namibia (c. 429 masl). Photo: A Weeks.*

data comprise 4,379 base pairs of aligned DNA sequence from the nrDNA external transcribed spacer region and three intergenic spacers of the chloroplast genome (*trnH–psbA*, *ndhF–rpl32*, *trnD–trnT*). To preserve visual space in Figure 3, the endemic Madagascan Rhynchocarpa clade and the endemic Madagascan Arafy clade are not shown in full. Resolution of these Madagascan clades is discussed in Gostel *et al.* (2016a, 2016b).

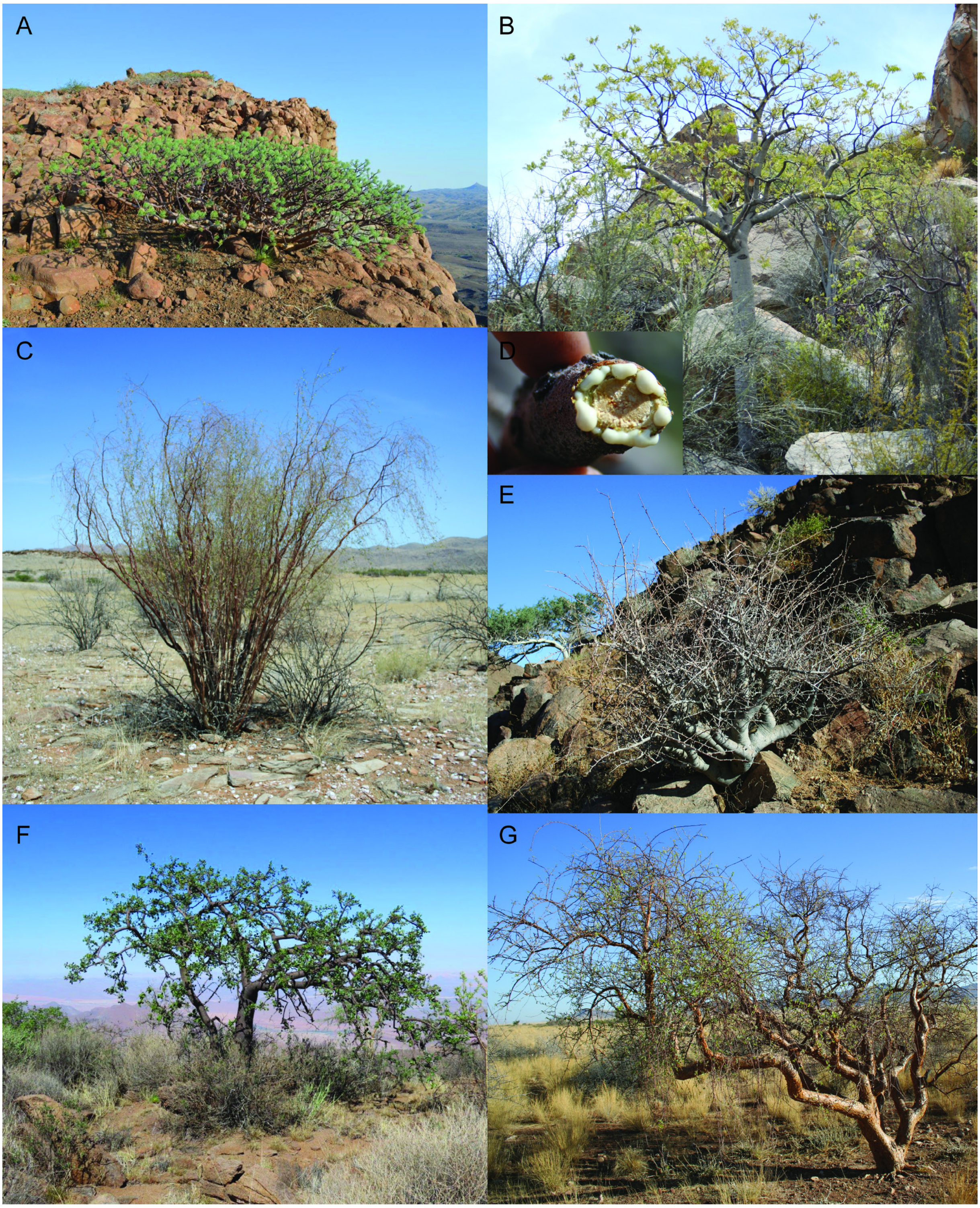

Figure 2: *Examples of* Commiphora *species endemic to the highlands and escarpments of Angola and Namibia showing diversity of substrate and habit. A)* Commiphora kraeuseliana. *Photo: W Swanepoel. B)* C. crenato-serrata. *Photo: A Weeks. C)* C. giessii. *Photo: A Weeks. D) Cut branch of* C. saxicola *showing the opaque white, viscous oleoresins characteristic of its clade. Photo: A Weeks. E)* C. capensis. *Photo: A Weeks. F)* C. otjihipana. *Photo: W Swanepoel. G)* C. glaucescens. *Photo: A Weeks.*

Most of the southwestern African species included in the phylogeny are endemic to Angola, Namibia or both countries (n = 25), of which 19 species can grow at elevations of 1,000 masl or greater. Species native to southwestern Africa but not yet sampled by any phylogeny include *C. antunesii* Engl., *C. glandulosa* Schinz, *C. mossamedensis* Mendes, *C. mulelame* (Hiern) K.Schum. and *C. otjihipana* Swanepoel, all of which are endemic to the region except *C. glandulosa*. Despite incomplete sampling, the currently understood phylogeny of the genus reveals three unanticipated features of *Commiphora*'s evolutionary history and historical biogeography in Africa which are discussed below.

Firstly, phylogenetic relationships of *Commiphora* species suggest that early diversification events within this genus happened outside the centre of its extant species diversity in eastern Africa; this assumes that widespread extinction of ancient lineages have not occurred in this area. The current locus of *Commiphora*'s greatest species richness is in eastern and northeastern Africa (Vollesen 1985, Gillett 1991, Lebrun & Stork 2011), where at least 89 species co-occur. Yet, all species that are native to these areas are members of the Spinescent clade (Figure 3), which probably radiated in the early to middle Miocene, 20.4 mya (28.8–14.0 mya, 95% confidence interval (CI); Gostel *et al.* 2016a). This clade also includes species that have more recently dispersed to South America (*C. leptophloeos*) and regions bordering the Indian Ocean basin (*C. socotrana* Engl., *C. wightii* (Arn.) Bhandari, *C. simplicifolia* H. Perrier), as well as species native

Table 1: Commiphora *species native to the highlands and escarpments of Angola and Namibia and their presence and endemism status in the two countries. X indicates presence.*

Species	Elevation range (masl)	Angola	Namibia	Endemism status
C. africana (A.Rich.) Engl.*	300–1,900	X	X	–
C. anacardiifolia Dinter & Engl.*	250–1,400	X	X	Endemic
C. angolensis Engl.*	50–1,800	X	X	–
C. angustefoliolata Mendes*	150–500	X	–	Endemic
C. antunesii Engl.	unknown	X	–	Endemic
C. benguelensis Swanepoel*	50–600	X	–	Endemic
C. buruxa Swanepoel*	200–500	–	X	Near-endemic
C. capensis (Sond.) Engl.*	50–700	–	X	Near-endemic
C. cervifolia J.J.A.van der Walt*	50–700	–	X	Near-endemic
C. crenato-serrata Engl.*	850–1,900	X	X	Endemic
C. dinteri Engl.*	450–1,850	–	X	Endemic
C. discolor Mendes*	400–1,900	X	X	Endemic
C. gariepensis Swanepoel*	300–1,000	–	X	Near-endemic
C. giessii J.J.A.van der Walt*	300–700	X	X	Endemic
C. glandulosa Schinz	500–2,050	X	X	–
C. glaucescens Engl.*	500–2,000	X	X	Endemic
C. gracilifrondosa Dinter ex J.J.A.van der Walt*	100–800	–	X	Near-endemic
C. kaokoensis Swanepoel*	200–1,100	–	X	Endemic
C. kraeuseliana Heine*	450–900	–	X	Endemic
C. kuneneana Swanepoel*	200–1,800	X	X	Endemic
C. mollis (Oliv.) Engl.*	850–1,950	X	X	–
C. mossamedensis Mendes	150–800	X	–	Endemic
C. mulelame (Hiern) K.Schum.	1,400	X	–	Endemic
C. multijuga (Hiern) K.Schum.*	450–1,850	X	X	Endemic
C. namaensis Schinz*	200–900	–	X	Near-endemic
C. namibensis Swanepoel*	20–600	X	–	Endemic
C. oblanceolata Schinz*	140–1,950	X	X	Endemic
C. omundomba Swanepoel & Weeks*	10–1,300	X	X	Endemic
C. otjihipana Swanepoel	1,200–2,050	X	X	Endemic
C. pyracanthoides Engl.*	700–950	–	X	–
C. saxicola Engl.*	300–1,200	–	X	Endemic
C. schimperi Engl.*	1,700–2,050	X	X	–
C. steynii Swanepoel*	800–1,600	X	X	Endemic
C. tenuipetiolata Engl.*	20–1,850	X	X	–
C. virgata Engl.*	200–2,000	X	X	Endemic
C. wildii Merxm.*	50–900	X	X	Endemic

** Species included within the phylogenetic analysis of Figure 3.*

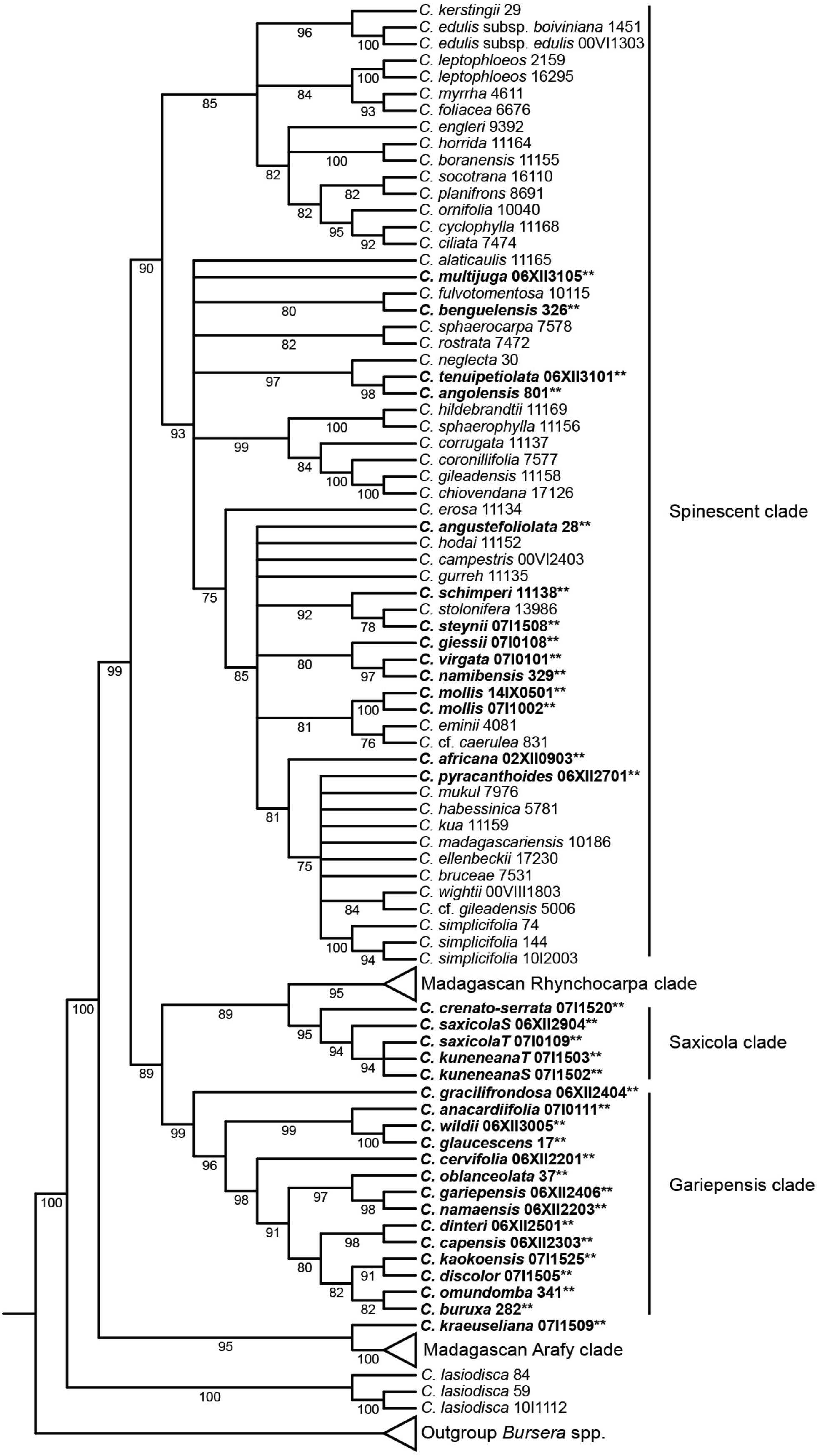

Figure 3: *Phylogeny of* Commiphora *based on the four-gene matrix of Gostel* et al. *(2016a). The topology represents the 75% consensus of 1,000 ultrafast bootstrap replicates using maximum likelihood in IQTREE; bootstrap percentages are shown below branches. To preserve space, the endemic Madagascan Rhynchocarpa clade and the endemic Madagascan Arafy clade are not shown in full but are indicated by small triangles. ** denotes species native to the highlands and escarpments of Angola and Namibia.*

to southwestern Africa (*C. africana* (A.Rich.) Engl., *C. mollis* (Oliv.) Engl., *C. pyracanthoides* Engl., *C. schimperi* Engl., *C. tenuipetiolata* Engl.) or endemic to southwestern Africa (*C. angolensis* Engl., *C. angustefoliolata* Mendes, *C. benguelensis* Swanepoel, *C. giessii* J.J.A.van der Walt, *C. multijuga* (Hiern) K.Schum., *C. namibensis* Swanepoel, *C. steynii* Swanepoel, *C. virgata* Engl.). All other clades stemming from earlier divergence events, including the sister to the Spinescent clade, comprise *Commiphora* species that are currently restricted to either southwest Africa or Madagascar.

Secondly, the close relationships of endemic southwest African and endemic Madagascan lineages reveal an unexpected and repeated biogeographical relationship between these regions during the evolution of *Commiphora*. Cross-continental disjunctions between these regions include the sister relationship of all *Commiphora* species, including early diverging lineages of southwest African species, to the Madagascan endemic, *C. lasiodisca* H. Perrier. Another includes the sister relationship between the southwest African endemic, *C. kraeuseliana,* which is restricted to the Southern Escarpment landscape of the highlands and escarpments of Angola and Namibia (HEAN) *sensu* Mendelsohn and Huntley (2023), and the lineage of 16 Madagascan endemic species of the Arafy clade, which may have diverged in the early Miocene (c. 19 mya; Gostel *et al.* 2016a). The last apparent disjunction includes the sister pair of the endemic southwest African Saxicola clade and the lineage of 26 Madagascan endemic species of the Rhynchocarpa clade, which diverged in the early to middle Miocene, 15.56 mya (23.27–8.55 mya, 95% CI) (Gostel *et al.* 2016a). The Saxicola clade contains three species native to Africa's southwestern highlands, *C. crenato-serrata* Engl. (Southern Escarpment; Central-Western Plains), *C. saxicola* Engl. (Central-Western Plains; Pro-Namib, and *C. kuneneana* Swanepoel (Southern Escarpment), and which radiated 4.03 mya (7.64–1.42 mya, 95% CI). Miocene aridification and uplift of the African continent may have caused vicariance between western and eastern limits of the continent as has been hypothesised for other woody or succulent taxa native to these areas, such as *Thamnosma* Torr. & Frém. (Rutaceae; Thiv *et al.* 2011), *Kleinia* Jacq. (Asteraceae; Pokorny *et al.* 2015) and *Euphorbia* sect. *Aphyllis* Webb & Berthel. (Euphorbiaceae; Pokorny *et al.* 2015). Multiple instances of long-distance dispersal of *Commiphora* across the Mozambique Channel between the African continent and Madagascar also occurred during this period, because this oceanic barrier predates the earliest divergences within the genus.

Lastly, the synthesis of the phylogenetic relationships, ages and extant distributions of endemic or near-endemic southwest African *Commiphora* species provides greater evolutionary context to long-recognised centres of endemism in southern Africa (van Wyk & Smith 2001). Rather than being evolutionary relicts, all extant endemics of *Commiphora* in southwestern Africa are likely to have arisen during the Miocene, Pliocene or more recently during the Quaternary period, as in the case of the sister pairs of *C. namaensis* Schinz – *C. gariepensis* Swanepoel and *C. saxicola* – *C. kuneneana*. Beyond the seven endemic species that derive from the geographically widespread Spinescent clade that began diversifying 20.4 mya (28.8–14.0 mya, 95% CI), most endemic southwest African species are restricted to the lineage containing the Saxicola, Rhynchocarpa and Gariepensis clades. This larger clade is also known as the Granulifera clade because of the granular indumentum that is present on many of its species (Gostel *et al.* 2016a). These relationships suggest that southwestern Africa is likely to have hosted a geographically restricted radiation during the Miocene beginning 19.92 mya (27.76–11.93 mya, 95% CI). The 14 endemic and near-endemic species of the Gariepensis clade, whose phylogenetic resolution is very well supported, began radiating 16.65 mya (24.62–9.73 mya, 95% CI).

Ranges of closely related *Commiphora* species appear to be stratified by elevation and latitude, which suggests that geography and abiotic factors may have been an important factor in driving species divergence, particularly within the Gariepensis clade. Nearly all endemic or near-endemic *Commiphora* species that are found at elevations above 1,000 masl are also found at much lower elevations; the sole exception is *C. mulelame* (Hiern) K.Schum. that occurs only at 1,400 masl or higher. In five of six taxon pairs within the *Commiphora* phylogeny, a high-elevation species is sister to a low-elevation species (*C. virgata* – *C. namibensis*, *C. glaucescens* Engl. – *C. wildii* Merxm., *C. gariepensis* Swanepoel – *C. namaensis* Schinz, *C. dinteri* Engl. – *C. capensis* (Sond.) Engl. and *C. omundomba* Swanepoel & Weeks – *C. buruxa* Swanepoel; Figure 3). Table 2 indicates the distributions within the HEAN of these five pairs of elevationally disjunct sister species. The species in the sixth pair, *C. kaokoensis* Swanepoel – *C. discolor* Mendes, share the ability to grow at high elevation and are both distributed in the Southern Escarpment.

Several latitudinally disjunct species pairs also suggest that allopatric speciation has been an important generative force during *Commiphora*'s evolution in southwestern Africa. Three species pairs span the Kaokoveld and Gariep Centres of endemism, whereas the fourth spans high-elevation areas in northern Namibia. *Commiphora dinteri*, which occurs along the central and southwestern escarpment of central Namibia in the Central-Western Plains and Khomas Hochland, is sister to *C. capensis*, which occurs in the extreme southwest of Namibia in the Cape and Succulent Karoo Floristic Region near the Orange River in the Pro-Namib. *Commiphora oblanceolata*, which ranges from southern Angola into the northern Namib Desert including the Southern Escarpment landscape unit, is sister to the southern Namibian pair, *C. gariepensis* – *C. namaensis*, that are distributed near the central and far eastern Orange River region including the Nama Karoo Basin (only *C. namaensis*) and Pro-Namib landscape units. *Commiphora omundomba*, which is restricted to southern Angola and northern Namibia including the Southern Escarpment landscape unit, is sister to *C. buruxa* that is known only from the central Orange River region of Namibia in the Pro-Namib landscape unit and in the mountains bordering the Orange River Valley further to the east. In the fourth disjunct pair, *C. discolor* is limited to near the Cunene River at the Namibian and Angolan border in the Southern Escarpment landscape unit but its sister, *C. kaokoensis*, is limited to areas further south in, and between, the catchment areas of the Ugab and Hoanib rivers in the same landscape unit. Statistical phylogeographic tests of these apparent geographic correlates would be required to propose probable causality, but phylogenetic data do suggest that genetic isolation imposed by the geography of southwestern Africa drove the diversification of *Commiphora*.

DEFICIENCIES IN KNOWLEDGE AND RESEARCH PRIORITIES

The multiple discoveries of new *Commiphora* species endemic or near-endemic to southwestern Africa in the last two decades highlight that much remains to be discovered about the diversity and evolution of this charismatic lineage of trees (Swanepoel 2005, 2006, 2007, 2008, 2011, 2014, 2015, Swanepoel *et al*. 2022). It is astonishing that such large and immobile terrestrial organisms remained unknown to Western science into the 21st century but is also indicative of the research barriers – both artefactual and biological, as discussed in the introduction – that are particular to the systematic study of *Commiphora*. Field observations combined with the collection of fresh plant material across the growing season and from multiple individuals are critical to capturing all morphological characters and their variation required to recognise and describe new *Commiphora* species. Expeditions to investigate the *Commiphora* of Angola are likely to yield new species, based on the results of recent fieldwork on the group in Namibia.

While herbarium material of *Commiphora* species is often missing key diagnostic features or entirely lacking from floristically underexplored areas, it has been produced in quantity from geographic areas frequented by botanists over the last c. 150 years. *Commiphora* is often one of the few woody taxa encountered by botanists in the arid environments of southwestern Africa and its specimens are relatively easy to collect and press, although they may not be identifiable to the species level if they are lacking reproductive material. Consequently, specimens of *Commiphora* – both identified and unidentified – have accumulated in herbaria around the world. If evaluated en masse these specimens would reveal a more complete picture of the morphological diversity and distribution of species than is appreciated today. However, data on most specimens are not publicly accessible in a digital form, which presents a challenge to synthesising information from all collections of *Commiphora* species. For instance, only 1,116 and 527 herbarium sheets of *Commiphora* from Namibia and Angola, respectively, are available through the Global Biodiversity Informatics Portal (GBIF.org 2022).

Table 2: *Distribution within the highlands and escarpments of Angola and Namibia (HEAN) of five pairs of sister species within the* Commiphora *phylogeny that have elevational disjunctions. The landscape units are described in Mendelsohn and Huntley (2023).*

High-elevation species	**High-elevation species distribution within HEAN**	**Low-elevation species**	**Low-elevation species distribution within HEAN**
C. virgata	Southern Escarpment; Central-Western Plains	*C. namibensis*	Southern Escarpment
C. glaucescens	Southern Escarpment; Karstveld; Central-Western Plains; Pro-Namib	*C. wildii*	Southern Escarpment
C. gariepensis	Not in HEAN but close to it in the mountains bordering the Orange River valley	*C. namaensis*	Nama Karoo Basin; Pro-Namib
C. dinteri	Central-Western Plains; Khomas Hochland	*C. capensis*	Pro-Namib
C. omundomba	Southern Escarpment	*C. buruxa*	Pro-Namib; outside the HEAN but close to it in the mountains bordering the Orange River valley

The holdings of many herbaria within the natural range of *Commiphora* and from countries of the northern hemisphere with a history of collecting in southwestern Africa do not yet serve data through the GBIF portal. Of the herbarium specimen data that are served, just over half (54%) include the latitude and longitude coordinates of the collection locality. These geospatial data are essential for generating accurate distribution maps and robust models of species' environmental niches to assess their past biogeographical movements as well as their future fate in a changing climate (Burke 2004) and in areas with increasing anthropogenic disturbance. Improving the access to herbarium material of *Commiphora* housed globally would improve our ability to conduct informed fieldwork, investigate the systematic biology of the genus and to generate and test phylogeographical and ecological hypotheses.

Uncovering the full complement of *Commiphora* species native to southwestern Africa through expanded fieldwork and herbarium-based research would also enable researchers to reconstruct the evolutionary history of the genus more completely. Current knowledge is frustratingly incomplete because phylogenies of *Commiphora* do not yet include all known extant species. Current phylogenies also lack well-supported resolution within the Spinescent clade that is essential for inferring the evolution and historical biogeography of this wide-ranging group. Several southwest African species are members of this clade, but their closest relatives remain uncertain apart from the well-supported sister pair of *C. virgata* – *C. namibensis*. Genome-scale sequence data (e.g., Khan *et al.* 2019, 2022) would be needed to produce a well-resolved phylogeny of all *Commiphora* species in the future.

As prefaced in the introduction, published research regarding the anatomical, physiological, ecological and life-history traits that may underlie the remarkable ability of *Commiphora* species to withstand extreme environmental conditions in southwestern Africa and elsewhere is lacking. This is notable because the Afrikaans common name for *Commiphora*, *kanniedood*, which translates as 'cannot die' in English, references this ecological resiliency as the most salient and recognisable feature of the genus. Yet, this feature remains largely unstudied. Listed below are three, non-exhaustive categories of key questions, whose answers would extend our understanding of how *Commiphora* managed to diversify within some of the most hostile terrestrial biomes, how it thrives there today and how *Commiphora* might respond to future global climate change.

i. Anatomical: How and where do southwest African *Commiphora* species sequester water in their tissues? To what degree does the structure of water-storing and water-conducting tissues correlate with or directly affect the habit of species (e.g., Olson *et al.* 2013)? Rather than having converged on a similar leaf phenotype in the hot, dry climate of southwestern Africa, *Commiphora* species have a range of leaf morphologies that is extraordinarily diverse compared to that of other woody genera in southern Africa. What is the possible functional and evolutionary developmental explanation of this variation (Nicotra *et al.* 2011)? What are the potential adaptive benefits of exfoliating (i.e., peeling and flaking) versus non-exfoliating bark?

ii. Physiological: What role does photosynthetic bark play in the annual carbon budget of *Commiphora* species that are leafless for much of the year (e.g., Cernusak & Cheesman 2015, Vandegehuchte *et al.* 2015)? Which species conduct photosynthesis in their phelloderm (e.g., Girma *et al.* 2013)? What other benefits might photosynthetic bark confer, such as heat balance or mineral nutrient resource efficiency, compared to non-photosynthetic bark? And if photosynthetic bark does confer any benefit to the plant, why do some species in the same environment lack this trait?

iii. Ecological: What is the annual recruitment and demographic structure of *Commiphora* populations and to what degree are they controlled by interannual precipitation (e.g., Mduma *et al.* 2007, Reddy *et al.* 2012, Tolera *et al.* 2013, Mengich *et al.* 2020)? How long do *Commiphora* species take to reach reproductive maturity and how long do they live? Given the erratic rainfall in southwestern Africa and its concomitant effect on leaf expansion and flowering in *Commiphora*, how does the associated fauna of pollinators (e.g., Farwig *et al.* 2004), herbivores (e.g., Iannella *et al.* 2021) and seed dispersers (e.g., Bleher & Böhning-Gaese 2000) vary from year to year and how does this effect reproductive output? To what extent does the harvesting of oleoresin by humans impact the longevity and reproductive output of *Commiphora* species (e.g., Cunningham *et al.* 2018)?

Finally, a long overdue frontier for research in *Commiphora* includes the integrative exploration of the ecology and evolution of the diverse secondary chemistry present in the oleoresins of its species. The oleoresins, which are best known for their ethnobotanical uses (Langenheim 2003), may be produced in any tissue and are contained within schizogenously formed ducts associated with phloem tissue. These resins comprise 30–60% water-soluble compounds such as polysaccharides and proteins, 3–8% essential oil, and 25–40% alcohol-soluble compounds including terpenes and terpenoids, steroids and sterols (Khalid 1983, Ulrich *et al.* 2022). Some chemical ecological research has focused on its sister genus, the predominantly New World copal genus *Bursera* (e.g., Becerra *et al.* 2009), but very little comparable work on *Commiphora* oleoresins has been conducted beyond the characterisation of more than 300 secondary metabolites from the c. 25 species commonly used in traditional medicine or other cultural practices (Shen *et al.* 2012, Dekebo *et al.* 2022). Reports of the biocidal properties (i.e., antimicrobial, antifungal, acaricidal, anthelminthic and insect antifeedant properties) of the oleoresins from these ethnobotanically important species suggest numerous chemical ecological interactions between the plants and their environment. But most of the research on oleoresins has focused on their pharmacologically active compounds that affect vertebrate physiology or pathogen infection and that could potentially improve human health (i.e., guggulsterones, triterpenes and furanosesquiterpenes; Waterman 1996, Ulrich *et al.* 2022). Characterising the oleoresin chemical profiles of all *Commiphora* species would help us determine the endogenous function of these chemicals within the plants and facilitate chemical ecological experiments required to understand their possible mediation of each species' interaction with its abiotic and biotic environment (e.g., Lwande *et al.* 1992, Assad *et al.* 1997, Chaboo *et al.* 2016, Sommerlatte & van Wyk 2022). Evaluating species' chemical trait data in a phylogenetic context would also reveal how *Commiphora*'s secondary chemistry has evolved over geological time and provide the framework for exploring the functional genomic architecture of these biochemical phenotypes. Interestingly, a major constraint to further advances in natural product chemistry of *Commiphora* has been the inability to obtain accurately identified and properly vouchered plant material that can support replication and expansion of prior experimental findings (Shen *et al.* 2012). Establishing collaborations between systematists, chemical ecologists, ethnobotanists and natural product chemists would be a fruitful way forward in uncovering the biology, ecology and evolution of *Commiphora*'s oleoresin chemistry as well as understanding the sustainability of utilising these oleoresins as natural resources.

CONCLUSIONS

Our knowledge of the systematic biology of *Commiphora* in southwestern Africa has improved considerably within the last two decades, as evidenced by new species descriptions and the advent of expanded molecular phylogenetic analyses that lend insight into the evolution and historical biogeography of the genus. Excellent atlases (e.g., Curtis & Mannheimer 2005) and field handbooks (e.g., Mannheimer & Curtis 2018) have also been produced as aids to further research in Namibia. But as this review has discussed, much remains to be uncovered about *Commiphora* at all levels of organisation: at the ecosystem level, at the species level and at the biochemical level. Exploratory fieldwork on *Commiphora* in Angola, comparable to that which has been conducted to document the Namibian flora, remains to be completed (Goyder & Gonçalves 2019). Readily accessible Angolan plant atlases and field handbooks for *Commiphora* species that can convey information to the non-specialist for education and conservation also remain unwritten. Thus, while the vision for the next two decades of research needs to include fundamental species discovery and integration of expertise from the fields of biodiversity informatics, genomics, anatomy, physiology and ecology to understand the evolutionary biology of *Commiphora* more fully, new partnerships and collaborations across intellectual traditions and international borders will be required to achieve it.

ACKNOWLEDGEMENTS

Data presented were collected with support from US National Science Foundation awards #0919179 and #1403150.

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Green gem of the Northern Escarpment: biodiversity and endemism of the Serra do Pingano Forest Ecosystem

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-lautenschlager

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ABSTRACT

The highlands and escarpments of Angola extend into the country's northern province, Uíge. The mountain ranges and scattered inselbergs there are characterised by small-scale geomorphological diversity that in turn supports a rich biodiversity, and together make up the Serra do Pingano Forest Ecosystem (SPFE). Drawing on previous studies, this paper briefly describes various taxonomic groups (fungi, Trachaeophyta, Bryophytes, Odonata, butterflies, moths, amphibians, reptiles, birds and mammals) of the SPFE in terms of their diversity and endemism rates. The initial results presented show the need to fill the existing data gaps and point to the importance of a conservation status for the SPFE.

Keywords: Angola, biodiversity, endemism, escarpments, highlands, Serra do Pingano Forest Ecosystem

INTRODUCTION

At its very northern edge, the Angolan escarpment opens up into an elevated plane known as the Highland of Mucaba. Its western flanks rise abruptly from the surrounding lowlands of 500–700 masl to maximum elevations of 1,300 masl, gently sloping towards the northeast. The most striking and unique geomorphological feature in this remote part of the Northern Escarpment in Angola are several chains of parallel-running, densely forested mountain ranges or cordilleras – the Serra Canacanjungo, Serra Masselele, Serra do Pingano, Serra Uíge and Serra Vamba – and a number of scattered calcareous inselbergs that together form the Serra do Pingano Forest Ecosystem (SPFE; compare Ernst *et al.* 2020). Geologically, the area is almost entirely composed of siliciclastic sedimentary rocks (largely) and minor carbonates, such as arenite and limestone of the Schisto-Gressoso Group (de Carvalho 1974, Schermerhorn 1981), which matches the Mpioka Subgroup of the West Congolian Group in the Democratic Republic of the Congo (DRC; Gärtner 2014).

The mountain ranges run in a northwest–southeast direction, forcing clouds from the Atlantic Ocean to ascend and discharge their moisture (Figure 1a). As a result, a highly branched network of watercourses dissects the area. While the northeastern part of Uíge Province and of the highlands drain northwards into the Congo watershed, the serras are located in the Cuanza River's basin area. Its most important drainage line, the Loge River, meandering between the Serra Uíge and Serra do Pingano runs northwestwards and then westwards discharging into the Atlantic Ocean. The area's hydrological features support the persistence of sizable rainforest fragments (Figure 1b) that are unique to Angola (Lautenschläger & Neinhuis 2014, Lautenschläger *et al.* 2020a). During the rainy season (October to May), in particular, the steep slopes of the serras feature impressive waterfalls that carry large volumes of water which, over the course of time, have formed deep V-shaped valleys that today exhibit extraordinary microhabitats. The small-scale geomorphological diversity – comprising rainforest fragments on steep slopes and wet savannas at lower elevations and on high plateaus, as well as peat swamps on sandy soils (Figure 1c), limestone formations with extensive cave systems and isolated inselbergs (Figure 1d) – mirrors the exceptional biodiversity of the area making the SPFE very likely to be a bio- and geodiversity hotspot.

DATA COMPILATION

Limited accessibility, particularly in the aftermath of the struggle for independence and the civil war which ended in 2002, largely prevented any scientific exploration in the region. Consequently, there is a limited number of museum specimens from Uíge Province. This situation has very recently changed, and systematic and intensified scientific assessments that aim at filling crucial knowledge gaps are now underway. In northern Angola, a working group led by Technische Universität Dresden and consisting of colleagues from the Senckenberg Natural History Collections (Dresden and Görlitz), the University of

Figure 1: *Landscapes and threats in the Angolan northwestern escarpment: a) Serra Uíge and Serra do Pingano in clouds; b) rainforest in Serra Uíge; c) swamp near Mucaba; d) inselbergs; e–g) slash-and-burn farming is one of the major threats; and h) logging of globally traded tree species (e.g.,* Entandrophragma *sp.) and subsequent transport to Luanda. Photos by authors.*

Hamburg and Purdue University has been working in cooperation with the regional university Kimpa Vita since 2012. During this period, numerous joint field trips were undertaken and material collected. The systematic assessments conducted by this association over the course of the past ten years plus have provided first basic data in support of the hypothesis that SPFE plays a pivotal role in shaping the biogeography of the entire western Central African realm. These findings have prompted the Angolan Ministry of Culture, Tourism and Environment to foster and promote the conceptualisation of a national protected area, which would make the SPFE the first and only protected rainforest area in Angola (Lautenschläger *et al.* 2020b).

The taxonomic sections that follow summarise the preliminary results and data generated by recent efforts and provide a first glimpse on the taxonomic composition, biogeographic patterns and endemism of the SPFE.

RESULTS

Fungi

As is true for most of Central, West and southern Africa, the fungi of Angola are poorly documented. Only 67 species, and two slime moulds, catalogued by Welwitsch and Currey (1868) represent the knowledge base of this group for the country. Of the species reported by Welwitsch and Currey (1868), 38 were described as new. Out of these, 21 that are considered valid species have never been collected outside Angola and may represent endemic species. Because fungi form symbioses with most known species of plants and animals, as well as acting as primary decomposers, they are essential components of ecosystem health and sustainability. Current estimates indicate that the species richness of fungi is approximately 6–30 times higher than that of plants (Hawksworth 2001, Blackwell 2011, Hawksworth & Lücking 2017). It is therefore highly likely that the actual diversity of fungi in northern Angola far exceeds current records. Between 2017 and 2019, 222 specimens of fleshy fruiting fungi were collected opportunistically in northern Angola, 202 of which have been identified to genus and/or species level. Only two of these were previously recorded in Angola (*Phallus tunicatus* Schltdl. and *Cyathus stercoreus* (Schwein.) De Toni as *Cyathus striatus* Willd.). Newly recorded genera of fleshy fungi include *Arthroxylaria*, *Bolbitius*, *Chaetocalathus*, *Clavulinopsis*, *Clitocybula*, *Crepidotus*, *Crinipellis*, *Cystolepiota*, *Datronia*, *Favolaschia*, *Galerella*, *Gerronema*, *Gleoporus*, *Hemimycena*, *Hygrocybe*, *Leocoagaricus*, *Penicilliopsis* (Figure 2e), *Pluteus*, *Podoscypha*, *Pseudofavolus*, *Pterula*, *Pterulicium*, *Ramaria*, *Russula*, *Scytinopogon*, *Simocybe*, *Tetrapyrgos* (Figure 2f), *Trogia*, *Xanthoagaricus*, *Xeromphalina* and *Xylodon*. The 202 specimens identified represent 98 different species. About half of these are potentially new species.

Limited data on fungal distribution for most of Africa impede inferences regarding endemicity of recorded species. Nonetheless, of the 202 specimens identified, 52 are probably new to science. Many of these are specialists on organic matter and debris and may represent endemics that are tightly associated with the unique flora of northern Angola. Such taxa face a high risk of coextinction with their severely threatened plant symbionts and/or the associated substrates on which they grow, as well as through direct competitive displacement by global invasives, such as *Coprinellus disseminatus* and *Schizophyllum commune* which are well adapted to anthropogenically disturbed areas and were both recently collected from the Serra Uíge, Mucaba and Serra do Pingano.

Trachaeophyta

To date, 1,063 species of Spermatophyta and Pteridophyta – about 15% of the total plant species listed for Angola (Figueiredo & Smith 2008) – have been identified in the northern Angolan provinces of Uíge and Cuanza-Norte (JACQ Consortium 2004). In recently published studies alone (Lautenschläger *et al.* 2020a, Lautenschläger *et al.* 2022), 46 species found in this northern area were added to the Angolan flora. While many species occur in many parts of Africa, the main distribution areas of those with a limited range are in the adjacent Congo Basin (Angola, DRC, Gabon and the Republic of Congo). Nevertheless, several species show a particular distribution pattern. Six species are endemic to Angola, including two species new to science: *Impatiens pinganoensis* (Figure 2a) which is only known from the Serra do Pingano in close proximity to a waterfall, at the spray zone of a creek (Abrahamczyk *et al.* 2016); and *Aloe uigensis* which was recently described from the limestone rocks east of the Serra do Pingano (Smith & Lautenschläger 2021). *Impatiens pinganoensis* was categorised as Critically Endangered by the authors of the description since it has a very limited distribution and has only been found on the cliffs of two waterfalls which have a very special microclimate; this habitat is endangered by deforestation and a proposed construction project (Abrahamczyk *et al.* 2016). Of the other Angolan endemics *Pandanus bilobatus* occurs in the rivers of the mountain ranges; *Sopubia graminicola* in the surrounding savannas; while *Crotalaria lundensis* and *Uvaria mendesii* are found further away from the escarpment but still at an elevation of 1,100 masl.

The limestone inselbergs exhibit an extraordinary flora, with species that had previously been found only in East Africa (*Begonia johnstonii*, *Rotheca wildii*), species distributed southwards (*Obetia carruthersiana*) and species protected by the

Convention on International Trade in Endangered Species (CITES) regulations (*Encephalartos* aff. *laurentianus* (Figure 2b), *Polystachya adansonia*). In addition, randomly distributed swamps host species distributed to the east (*Polygala gomesiana*), and many orchid species. Other taxa were reported as potentially new species. Overall, with these initial results and the assumption that the Northern Escarpment around the mountain ranges of the Serra do Pingano *sensu lato* probably served as a refugium for species of the tropical forests during the dry periods of glacial cycles and subsequent allopatric speciation in the wet interglacial periods (Couvreur *et al*. 2021), more plant endemics are to be expected in the area.

Bryophytes

In recent years, since 2013, our working group has started a more intensive investigation of the bryophyte flora of Uíge Province, specifically of the mountain

Figure 2: *A selection of species of the Angolan northwestern escarpment: a)* Impatiens pinganoensis*; b)* Encephalartos *aff.* laurentianus*; c)* Weissia jamaicensis*; d) foliicolous liverwort* Cololejeunea furcilobulata*; e)* Penicilliopsis *sp.; f)* Tetrapyrgos *sp.; g) large fairy hairstreak (*Hypolycaena antifaunus*); h) group of male 'forest grass yellows' (*Terias senegalensis*). Photos by authors, except 2a and 2e (Barbara Ditsch).*

ranges Serra do Pingano and Serra Uíge. This work yielded 105 bryophyte species new to the flora of Angola and additional new records for Uíge Province (Müller 2015, Müller *et al*. 2018, 2019).

Several species are characteristic for mountain rainforests and their localities in Uíge Province represent the main, or exclusive, occurrences in Angola. In addition to pantropical and palaeotropic species, the flora of the area consists of a considerable number of African endemics, e.g., the liverworts *Archilejeunea elobulata*, *Caudalejeunea dusenii*, *Caudalejeunea yangambiensis*, *Cylindrocolea abyssinica*, *Plagiochila pinniflora*, and the mosses *Fissidens usambaricus*, *Fissidens darntyi* and *Leptotrichella nitidula*.

Among the recorded species, there are many bryophytes rarely reported in sub-Saharan Africa or worldwide. Examples of species newly recorded for Angola with limited distribution and therefore of special conservation value include *Physcomitrium bukobense* (hitherto only known from Tanzania), *Pogonatum congolense* (hitherto only known from Cameroon, DRC and Gabon), *Cylindrocolea gittinsii* (hitherto only known from Cameroon, Kenya and Uganda), *Frullania letestui* (a rare West African species, hitherto only known from Cameroon, Central African Republic, DRC and Gabon) and *Isopterygium mbangae* (a species with special substrate requirements, only growing on stems of tree ferns, hitherto only known from Cameroon, DRC, Gabon, Sudan, Tanzania and Uganda). *Weissia jamaicensis*, a species hitherto unknown from Africa and previously thought to be restricted to the New World, was found at several localities in Uíge Province (Figure 2c). It not only represents a new record for the African bryoflora, but also for the palaeotropical flora in general (Müller *et al*. 2018). The species prefers rock formations and was found, for example, in crevices and on bands of calcareous rocks of the Xisto-Calcário Formation. As outlined in Müller *et al*. (2018), it appears to be a 'true' historic bryofloral element rather than a recent introduction to sub-Saharan Africa and therefore provides crucial additional evidence for the intercontinental phytogeographical relationships between Africa and the Americas.

The foliicolous liverwort flora of Angola had previously been completely uninvestigated, but during the recent investigation, 24 foliicolous liverwort taxa were encountered, all of which, with the exception of *Radula flaccida*, were new for Angola. Examples of rare species among this ecological group are *Cololejeunea diaphana* (previously known in Africa only from Bioko Island, Malawi and Uganda), *Cololejeunea apiculata* (a rare Afromontane species, previously known only from Mt Cameroon, the Uluguru Mountains in Tanzania, Bwindi Impenetrable Forest in Uganda and from Ethiopia), *Cololejeunea furcilobulata* (previously known in sub-Saharan Africa from Madagascar, Nigeria, Seychelles and Tanzania; Figure 2d), *Colura hattoriana* (previously known from Bioko Island, the Comoro Islands and Malawi) and *Colura mosenii* (previously reported, in Africa, only from Nigeria and, outside Africa, only from Java and the Caroline Islands).

As the southernmost extension of the Guineo-Congolian biogeographic region, the forest ecosystems of Uíge therefore also play a pivotal role in conserving and safeguarding an exceptional and unique bryophyte diversity.

Odonata

Angola is one of the richest countries for Odonata (dragonflies and damselflies) in Africa (Clausnitzer *et al*. 2012), with currently more than 288 recorded species and an estimation of well over 300 species based on the vast still largely unsurveyed areas (Kipping *et al*. 2019, Kipping *et al*. 2023). The expansive habitats in northern and eastern Angola, especially, have never been surveyed at all and the potentially species-rich highland catchments of the Congo, Cuanza, Cubango (Okavango) and Zambezi rivers are almost unknown.

Angola is also particularly rich in endemic Odonata species, with most of them being highland specialists found on the central plateau mainly between elevations of 1,300 m and 1,800 m and in open habitats. Angola's endemic Odonata probably originated quite recently and proximally from the forests to the north and open habitats to the east. Such a local radiation of an insect order that has otherwise diversified in the highlands to the east, and forests to the north, fits the overall affinities of Angola's endemic Odonata both geographically and ecologically (Kipping *et al*. 2023).

For the Serra do Pingano and its surroundings in the northern province of Uíge more than half of all known dragonfly species for Angola have been recorded in just two brief surveys, in 2012 and 2013 (Kipping *et al*. 2017). A total of 150 species have been recorded from the Serra do Pingano and its surroundings, including nine of Angola's endemic species, of which *Eleuthemis eogaster* (Figure 3b) has yet to be found elsewhere (so far it is known only from several large streams and rivers near Uíge (western scarp) bordered by forest).

Here, where the Lower Guinean forests open southwards to the savanna areas, the fauna of the Guineo-Congolian Region meets the fauna of the Zambezian Region resulting in an extremely species-rich dragonfly fauna with a high number of endemics. The steep topography of the Serra do Pingano adds a mosaic of streams and rivers with lush tropical gallery forests and permanent and seasonal swamps,

Figure 3: *A selection of animal species of the Angolan northwestern escarpment: a) Kimpavita longleg (*Notogomphus kimpavita*); b) sunrise firebelly (*Eleuthemis eogaster*); c) African horned toad (*Sclerophrys *cf.* superciliaris*); d) ornate African water snake (*Grayia ornata*); e) black-necked weaver (*Ploceus nigricollis*); f) female black-casqued wattled hornbill (*Ceratogymna atrata*); g) white-bellied pangolin (*Phataginus tricuspis*); and h) Angolan rousette (*Myonycteris angolensis*). Photos by authors, except 3e (Lucas Langer) and 3g (Anne Göhre).*

most of them nutrient poor on sandy soils. It is this combination of different habitats and a fauna of different origins that has resulted in the very distinct and rich fauna with many endemic species in Angola's north.

More surveys are urgently needed to complement species lists and ranges in order to understand evolutionary traits in this area. We expect more than 200 species of Odonata in the wider area around Uíge Province in northern Angola. Kipping *et al*. (2019) conclude: "… new species are most likely to be found among genera prone to narrow (highland) ranges, i.e., with known Angolan endemics like *Platycypha* and *Pseudagrion*, but also *Agriocnemis*, *Elattoneura*, *Notogomphus* (Figure 3a) and *Paragomphus*. Also possible, however, is the discovery of endemics in genera that are well represented across the country and continent, and that have highland endemics elsewhere but not in Angola, such as *Africallagma*, *Neodythemis* and *Orthetrum.* However, given the biogeographic diversity of Angola's fauna and endemics, we could expect greater surprises."

Butterflies (Papilionoidea)

There are about 4,500 species of Afrotropical butterfly species (Williams 2023), 769 of which are known from Angola (Mendes *et al*. 2019). These authors also mention 32 species as being endemic to Angola.

During eight short assessment surveys to northern Angola between 2012 and 2015, as well as in 2019, a total of 905 Papilionoidea specimens have been collected, 788 of which originate from Uíge's escarpment area. So far, 207 butterfly species have been identified. Additionally, 31 species groups were still under investigation at the time of writing this paper. The 207 identified species represent 26.9% of all Papilionoidea species known from Angola to date. This is a remarkable amount considering the limited number of surveys in an area comprising less than 0.6% of Angola's territory, and indicates the high importance of the Uíge escarpment for butterfly diversity.

Many of the recorded species are rather common (e.g., *Neptis agouale*, *Terias senegalensis*, *Haydonia pythia*, *Leptosia nupta*), widespread throughout the country (e.g., *Azanus mirza*, *Sevenia benguelae*, *Acraea atolmis*, *Libythea labdaca*) or even the Afrotropical region in general (e.g., *Anthene larydas*, *Graphium leonidas*, *Byblia anvatara*, *Hypolimnas anthedon*). Many of the recorded species are known to be associated with degraded habitats (e.g., *Euphaedra medon*, *Ypthima doleta*, *Junonia stygia*, *Telchinia acerata*). The known degree of endemism of Angolan butterflies at species level seems to be surprisingly low considering the large extent of the country and the richness of highly diverse ecoregions. However, this is probably due to limited sampling effort and a spatial/geographic bias that can only be resolved through intensified sampling across the area, including the escarpment. Moreover, unified and standardised monitoring schemes and updated taxonomies and phylogenies are urgently needed to elucidate actual diversity and endemicity patterns in Angolan butterflies.

Moths

There are 28,866 species of night-flying moths known from the Afrotropical region and 1,312 from Angola (de Prins & de Prins 2011–2020). These counts, however, are rather preliminary, as several hundreds of new species are still being described each year, and surveys regularly add species to country lists.

Identification of African moths can be challenging, as summarising works for most subgroups are either largely out of date or simply not available. The available taxonomic information is scattered over numerous scientific publications spanning a period of about 150 years. Many groups still need revision, each awaiting a large proportion of new species descriptions. For the time being, the best overview on Afrotropical moths is given by de Prins and de Prins (2011–2020) in their comprehensive database, AfroMoths.

Monitoring moths in northern Angola has been focused on snout moths (Pyraloidea). There are more than 16,400 species of snout moths in the world, 2,770 of which are known from Africa south of the Sahara (Nuss *et al*. 2003–2023). In northern Angola, snout moths were attracted using UV-lights during 40 nights. Analysis of morphological and genetic data revealed 324 species of snout moths in the Serra Uíge and Serra do Pingano. This is equivalent to 11% of all known Afrotropical snout moths. Taxonomic revisions and analyses of data from various African countries are still needed to better understand the diversity of snout moths in Angola, and to uncover possible endemics.

A case study on agricultural pest species found in fruits of *Solanum aethiopicum* (Kikongo: *mbolongwa*) at a market in Negage (Uíge Province) in 2013 (Mally *et al*. 2015) revealed the scale of yet uncovered diversity in snout moths, and probably of other moth groups in Africa. This African-wide taxonomic revision resulted in the description of seven new species, three of which had been repeatedly imported into Europe. Altogether, there are 23 species of snout moths originally described from Angola (Nuss *et al*. 2003–2023), but research is necessary to uncover their natural distributions and possible Angolan endemics.

Although local species composition shows superficial resemblance to that of the larger Congo Basin and the West African realm, identifying actual patterns of endemism and diversity requires a thorough taxonomic revision of several taxa. Particularly the so-called widespread taxa may turn out to be cryptic species complexes and a more detailed analysis will likely yield range-restricted lineages that can be considered true Angolan and/or escarpment endemics.

In addition to intensified research into insect groups that have already been addressed, systematic surveys of additional ecologically important and species-rich insect orders that have not been investigated so far (e.g., Coleoptera and Hymenoptera) are urgently needed. These will provide basic data required for addressing important issues, such as ecosystem functionality (e.g., nutrient fluxes) and ecosystem services (e.g., pollination).

Amphibians and reptiles

The history of herpetological explorations, including an updated atlas of Angolan herpetofauna has recently been summarised by Marques *et al.* (2018) and the amphibian fauna, in particular, was reviewed by Baptista *et al.* (2019). Since then, several new species of reptiles and amphibians have been described or await formal description, and new country records have been added to the lists (Bauer *et al.* 2023, Becker *et al.* 2023). Northern Angola, including the provinces of Cabinda, Lunda-Norte, Uíge and to a lesser extend Malanje and Cuanza-Norte, is unique with respect to its herpetofaunal diversity and composition because it harbours the last remaining tracts of already largely fragmented rainforest. Sizable and important patches can only be found in Cabinda and Uíge; these, particularly the SPFE, have been the sites of recent herpetological explorations.

A first comprehensive amphibian and reptile species list for this exceptional ecosystem was provided by Ernst *et al.* (2020). The herpetofauna is comparatively rich and unique for the country, consisting of species that are otherwise only known from the Central African forest systems of Cameroon and/or Gabon and have not been recorded from any other locality in Angola (e.g., *Trichobatrachus robustus*, compare Ernst *et al.* 2014; *Xenopus andrei*, compare Ernst *et al.* 2015; and *Sclerophrys superciliaris* (Figure 3c), *Cardioglossa gracilis*, *Chiromantis rufescens*, *Hyperolius* (*Alexteroon*) *hypsiphonus*, *Holaspis guentheri*, compare Ernst *et al.* 2020, 2021).

Although the number of true highland endemics appears to be limited (Becker *et al.* 2023), several phylogenetic lineages are very distinct and show signs of recent (Pliocene or even younger) species differentiation (Ernst *et al.* 2021, Jaynes *et al.* 2022), highlighting the evolutionary potential of the SPFE. Recent evidence from amphibian and reptile surveys in the region also supports an assumed late Quaternary connection with Central African forest systems and the potential role as a late Pleistocene forest refuge.

If deforestation and habitat degradation continue at the alarming rates witnessed, however, this exceptional African rainforest ecosystem including much of its herpetofaunal diversity will be lost forever. For example, a closed rainforest site connecting the Serra Uíge with the Serra do Pingano that was visited in 2016, and in which several amphibian species were recorded for the first time in Angola, had been cleared for agricultural use two years later (Figure 1f). Slash-and-burn farming is very prominent in the region and particularly harmful to the steep and still-forested slopes of the cordilleras, as chimney effects can lead to rapid and uncontrolled spread of fires that then destroy huge areas of formerly intact forest (Figure 1e). Direct consumption of amphibians (e.g., *Amietia angolensis*) has been reported by local inhabitants, but amphibians are not frequently seen on otherwise extensive bushmeat markets, nor are they important elements in local diets as is the case in West Africa.

Research including a strong focus on amphibian and reptile diversity of the Serra do Pingano *sensu lato,* including the reassessment of cryptic species complexes (Jaynes *et al.* 2022, Chaney *et al.* subm.; cf. Figure 3d) and the description of new species (Lobón-Rovira *et al.* 2021) is ongoing and provides additional support for the importance of the region both on a national and Pan-African scale. Yet, as in other parts of Africa, this is a race against time.

Birds

So far, 940 bird taxa have been confirmed to occur in Angola, 29 of which are endemic (Dean *et al.* 2019, Mills & Melo 2023). Taking bird records retrieved from the Global Biodiversity Information Facility (GBIF.org 2022) into account, the mountain ranges around Quitexe and Uíge are home to 318 species, including some endemics. This emphasises the importance of this region for bird diversity in Angola.

Mostly, endemic birds are restricted to the Afro-montane grasslands and semi-evergreen scarp forests along the escarpment in Angola (Huntley 2019). The forested mountain ranges of Uíge Province form the northern part of the escarpment, but only one bird, Braun's bushshrike (*Laniarius braunii*), is strictly endemic to the region around Quitexe. Some more taxa show narrow distribution ranges, sometimes extending into the Congolian forests further north: Angolan white-throated greenbul (*Phyllastrephus albigularis* subsp. *viridiceps*) and Hartert's camaroptera (*Camaroptera harterti*) are both strict endemics; and Angola batis (*Batis minulla*), yellow-throated nicator (*Nicator vireo*) and pale-olive greenbul (*Phyllastrephus *fulviventris*) are all quasi-endemics (Dean *et al*. 2019, Vaz Pinto & Fernandes 2020).

The rate of (bird) endemism in Uíge is not as striking as along the escarpment further south. However, according to our own survey and analysis in 2019, at least 25 Afrotropical taxa occurring in the mountain ranges around Uíge show a peculiar distribution, with main distribution ranges in West and/or Central Africa, and an isolated population in Uíge and/or the Angolan escarpment (Mills & Dean 2007, Sinclair & Ryan 2010, Dean *et al*. 2019). Examples are the black-necked weaver (*Ploceus nigricollis*) (Figure 3e) or the black-casqued wattled hornbill (*Ceratogymna atrata*) (Figure 3f). Furthermore, bird observations around Uíge and Quitexe in recent years has led to several new species records for Angola. For instance, white-collared oliveback (*Nesocharis ansorgei*) (Mills & Vaz Pinto 2015), forest swallow (*Petrochelidon fuliginosa*) (Mills & Tebb 2015) and Willcocks's honeyguide (*Indicator willcocksi*) (Mills & Boesman 2020) have recently been observed, all constituting isolated populations, disjunct from the main distribution ranges. Such findings highlight the unique setting of the Uíge mountain ranges, and their importance for endangered bird species. Braun's bushshrike for instance is a strict endemic to the region, but with only 3,500 to 7,000 remaining individuals, it is endangered (Mills *et al*. 2011).

Like tropical forests further north, the rainforest fragments around Uíge are increasingly exploited, leading to deforestation and degradation (Tegegne *et al*. 2016). This has far-reaching implications, because the species particularly threatened by forest degradation and subsequent population declines are often frugivores, like turacos, parrots, pigeons or hornbills (Whitney & Smith 1998, Menke *et al*. 2012). They avoid degraded areas where large fruiting trees have been removed by legal and illegal logging. However, frugivores are important forest tree seed dispersers and therefore crucial for forest regeneration (Chasar *et al*. 2014). Their absence in degraded areas implies that natural forest regeneration is slowed down, particularly if degradation is progressing. The mountain ranges of Uíge have the potential to remain a refuge for these iconic Afrotropical birds, but only if the rapid degradation is contained.

Mammals

The province of Uíge is a transition zone between the drier peripheral semi-evergreen Guineo-Congolian rainforest, the Zambezian dry evergreen forest and the transition woodland (White 1983) resulting in an extraordinary landscape of dense rainforest, caves, sandy swamps and savannas along the mountain ranges. This provides a diverse habitat template for very different mammal species. The proximity to the Congo Basin results in a high taxonomic overlap between the Guineo-Congolian mammal communities and those found in Uíge Province. These include numerous rodents, such as the brush-tailed porcupine (*Atherurus africanus*), the forest giant squirrel (*Protoxerus stangeri*) and the fire-footed rope squirrel (*Funisciurus pyrropus*). Preliminary opportunistic surveys conducted during independent field campaigns in 2019 yielded a total of 27 mammal species in the province (Teutloff *et al*. 2021). Although not recorded during field campaigns, charismatic megafauna, such as the African forest elephant (*Loxodonta cyclotis*), are known to occur historically but have not been reported until recently. Most recent sightings date back to the years 2018 and 2019 where elephants were seen between the Serra do Pingano and Serra Uíge.

Several primate species, some of which are heavily hunted, like the red-tailed monkey (*Cercopithecus ascanius* ssp.), have been reported. Among them are species of high conservation concern, such as the rare southern talapoin (*Miopithecus talapoin*) which is endemic to northern Angola and the coastal watersheds south of DRC (Kingdon 2019). The southern talapoin is listed as Vulnerable on the International Union for Conservation of Nature (IUCN) Red List. It is a strictly riverine species that depends on dense evergreen vegetation restricted to the banks of the rivers that criss-cross the serras (Kingdon 2019, IUCN 2021). The nominate *Colobus angolensis angolensis*, endemic to northern Angola and the Congo Basin (Kingdon 2019), is very rare in the area and was only recorded from the Mucaba area.

Among the most heavily hunted, yet strictly protected mammal species, is the white-bellied pangolin (*Phataginus tricuspis*). Although still considered one of the more abundant species among the four African pangolin species, it is listed as Endangered (EN) by IUCN Red List in Ghana, where the white-bellied pangolin represented 82% of the observed pangolins traded by the stakeholders and annually 0.4–2.7 million pangolins are hunted in Central African forests alone (Boakye *et al*. 2016, Ingram *et al*. 2018). This matches our observations from Uíge Province.

In addition to the 27 reported species, several species known from the Guineo-Congolian region are expected to occur in Uíge Province. These include Ansorge's kusimanse (*Crossarchus ansorgei*) known only from deciduous rainforest and the Lunda rope squirrel (*Funisciurus bayonii*) living in mosaics of rainforest and moist woodlands in northeastern Angola and southwestern DRC (Kingdon 2019). Furthermore, the recently discovered Angolan dwarf galago (*Galagoides kumbirensis*), observed in the adjacent province Cuanza-Norte in 2013, lives in moist, tall forest and semi-arid baobab savanna-woodland very similar to the serras of the SPFE

(Svensson *et al*. 2017). Although it has not been observed so far, the possibility of its occurrence in the serras exists.

To date, many mammal groups have not been systematically studied in the region. These groups particularly include small mammals – rodents, as well as micro- and macrochiroptera that play important roles as seed dispersers and/or pollinators and therefore also significantly contribute to forest regeneration. Moreover, they are important pathogen reservoirs and disease vectors and, as such, significantly drive socioecological developments in the country and beyond. The species which are documented so far are Egyptian rousette (*Rousettus aegypticus*), collared fruit bat (*Myonycteris angolensis*), dwarf epauletted fruit bat (*Micropteropus pusillus*), hammer-headed fruit bat (*Hypsignathus monstrosus*) and horseshoe bats (*Rhinolophus* spp.). Due to heavy and completely uncontrolled hunting, in combination with habitat degradation and loss, Uíge's mammal diversity is at risk and faces serious decline; unique species, such as the white-bellied pangolin, the endemic southern talapoin and Angola colobus are likely to disappear in the near future (Kingdon 2019, Jansen *et al*. 2020). A better understanding of the actual diversity and population status of highly threatened taxa is urgently needed.

SYNTHESIS AND CONCLUSION

The Angolan escarpment has long been recognised as an important centre of biodiversity and geodiversity (compare Huntley *et al*. 2019 and references cited therein). However, despite an increasing research interest in this landscape in recent years, the vast majority of the extensive and heterogeneous ecosystem it supports remains largely unexplored. This is particularly true for the more remote outliers, such as the SPFE in the far north of the highlands and escarpments of Angola. Yet, our preliminary surveys and the data established through these efforts highlight the fact that these edge habitats are indeed unique and very special geo- and biodiversity gems in the chain of extraordinary habitats that make up the escarpment zone. Not only several species new to science were described, but in all species groups there were new records for Angola and thus an extension of the range of several species. At the same time, many species groups have not yet been studied at all, indicating that there are still large gaps in knowledge to be filled. In the case of fungi, for example, possibly half of the samples collected are new species. For all species groups, taxonomic revisions and analyses of data from various African countries are still needed to better understand the diversity and uncover possible endemic species.

Furthermore, urgent action is required to safeguard these treasure troves that are severely threatened by human activities, such as logging, slash-and-burn farming and bushmeat trade (Figures 1e–h). Angola is at a crossroads of decisions and trade-offs around utilisation, conservation and preservation of its forests and, thus, substantial parts of the country's biodiversity. The SPFE deserves special mention in the wider context of exploring, understanding and protecting the biodiversity of the western escarpment. The establishment of a national protected area in the Serra do Pingano Forest Ecosystem is therefore a necessary and urgently needed first step towards protecting Angola's national biodiversity heritage.

ACKNOWLEDGEMENTS

Fieldwork 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, as well as a grant from the Paul-Ungerer-Stiftung. Additional surveys were supported by the Ministério do Ambiente's Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC) within the project agenda "Expansão e Fortalecimento do Sistema de Áreas Protegidas em Angola" through a grant provided by the Global Environment Facility (GEF) under the auspices of the United Nations Environment Programme (UNEP). We particularly thank J Lau and MF Branquima for support in the field. Permission to conduct biodiversity research in Angola was granted by the INBAC, Ministério do Ambiente, República de Angola and the Gabinete Provincial da Agricultura, Pecuári e Pescas do Uíge.

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The highlands and escarpments of Angola as an endemism hotspot for African dragonflies and damselflies (Insects: Odonata)

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-kipping

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ABSTRACT

The plateaus and escarpments of Angola are a major centre of Odonata endemism in Africa, rivalling and possibly surpassing the highlands of Ethiopia and South Africa. We discuss 34 likely endemic species and 8 near-endemics found in Angola's highland area. Remarkably, 20 of these endemics and near-endemics do not occur either along the western escarpment or on the high central plateau, but on the lower sandy plateaus farther east. Despite the western scarp having traditionally received much scientific attention, the first odonatological discoveries were made there only recently. Of the 42 species of interest discussed here, the taxonomy of 21 of them has yet to be fully resolved. Furthermore, many regions, particularly in northeastern Angola, are still to be explored.

Keywords: Angola, endemism hotspot, escarpments, highlands, Namibia, Odonata

INTRODUCTION

Dragonflies and damselflies (Odonata) are restricted as larvae to freshwater habitats, with range-restricted species largely confined to permanent water (Dijkstra *et al.* 2011, Clausnitzer *et al.* 2012). Odonate endemism in the highlands and escarpments of southwestern Africa is therefore limited to Angola, generally in areas with an average annual rainfall above 700 mm. While the Namibian fauna has been well studied, with 130 species recorded (Suhling & Martens 2014), serious research in Angola has only been undertaken in the last decade or so. Kipping *et al.* (2019) listed 260 species, 24 more than in the first checklist published only two years earlier (Kipping *et al.* 2017). The national fauna is predicted to include well over 300 species, making Angola one of the richest countries for Odonata in Africa. Up to the end of 2022, another 28 species were indeed added, the majority of which are new to science, and likely to be regionally endemic. While the taxonomic work is still in progress, here we discuss the ecology and distribution of all Angola's endemic and near-endemic Odonata known so far.

MATERIALS AND METHODS

The Odonata Database of Africa (ODA; see Kipping *et al.* 2009), currently holds about 142,000 records from the African continent and associated islands, with 8,700 records from Namibia and 6,840 records from Angola. Details on research history and the origin of the records are provided by Suhling and Martens (2007, 2014) for Namibia and by Kipping *et al.* (2017, 2019) for Angola. Point locality data for the plateaus, inselbergs and escarpments as delineated for this project (Mendelsohn & Huntley 2023) were selected spatially using geographic information system (GIS) software (ESRI ArcMap 10.0) and the shapefiles provided, applying a buffer of 5 km. We also consider other species known only from Angola but with localities lying outside the focal area, separating them from the western highland endemics in the tables and discussion where possible. The altitude for each point locality was inferred in GIS using an open-source global elevation model.

ENDEMIC ODONATA OF THE WESTERN HIGHLANDS

Table 1 summarises the known diversity and endemism of Odonata in Angola, Namibia and their western highlands. No endemic species are known to occur in Namibia despite potentially suitable regions such as the Erongo and Naukluft mountains and the Khomas Hochland which are all relatively well studied (Suhling & Martens 2007, 2014). Angola, on the other hand, is rich in endemic species which are clearly concentrated in the western and central plateaus, escarpments and inselbergs where average annual rainfall is higher than 700 mm.

While the proportion of endemics in Angola (12%, Table 2) is similar to that in the Ethiopian Highlands (12 endemic species; 11%) and lower than that in South Africa (30 endemics; 18%), overall species diversity is much greater in the highlands and escarpments of Angola. This ranks the region as one of Africa's foremost centres of Odonata endemism, rivalling the highlands of Cameroon (13 endemics),

Table 1: *Numbers of known and endemic Odonata species in Angola and Namibia.*

Country list of Odonata	**Total number of species**	**Number of endemic (and near-endemic) species**	**Percentage (%) of endemic species**
Angola: Kipping *et al*. (2019) and recent additions	288	34 (8)	11.8
Namibia: Suhling & Martens (2014)	130	0	0

Table 2: *Numbers of known and endemic Odonata species of the strictly delineated highlands and escarpments of Angola and Namibia (HEAN).*

Region	**Total number of species**	**Number of endemic species**	**Percentage (%) of endemic species**
HEAN	168	18	10.7
Angolan Planalto	158	18	11.4
Namibia's highlands, escarpments and plateaus	51	0	0
Escarpments	91	12	13.2
Inselbergs	142	15	10.5
Plateaus	121	11	9.1

the Albertine Rift, the Eastern Arc, and Katanga in southern Democratic Republic of the Congo (DRC).

Different levels of endemism

Table 3 lists 34 endemic species that are only known from Angola and 8 near-endemic species that extend just slightly beyond its political borders. The range and habitat, as well as the taxonomic status and relationships, of each endemic and near-endemic are briefly discussed, showing the complexity of their occurrence, ecology and affinities.

Twelve of these range-restricted species occur on Angola's western escarpment (Table 2). Three are among the longest known (Longfield 1959, Pinhey 1975, Tarboton 2009) and widest ranging endemics: *Platycypha angolensis* (Figure 1a), *Pseudagrion angolense* (Figure 1b) and *Pseudagrion estesi* (Figure 1c). Found roughly between 250 and 2,200 masl, these species range up from the escarpment to the highest parts of the central plateau (see Figure 5a). All favour streams and small rivers, usually with some forest and often with rocks (Figure 1d), and barely extend farther east onto the sandy plateaus.

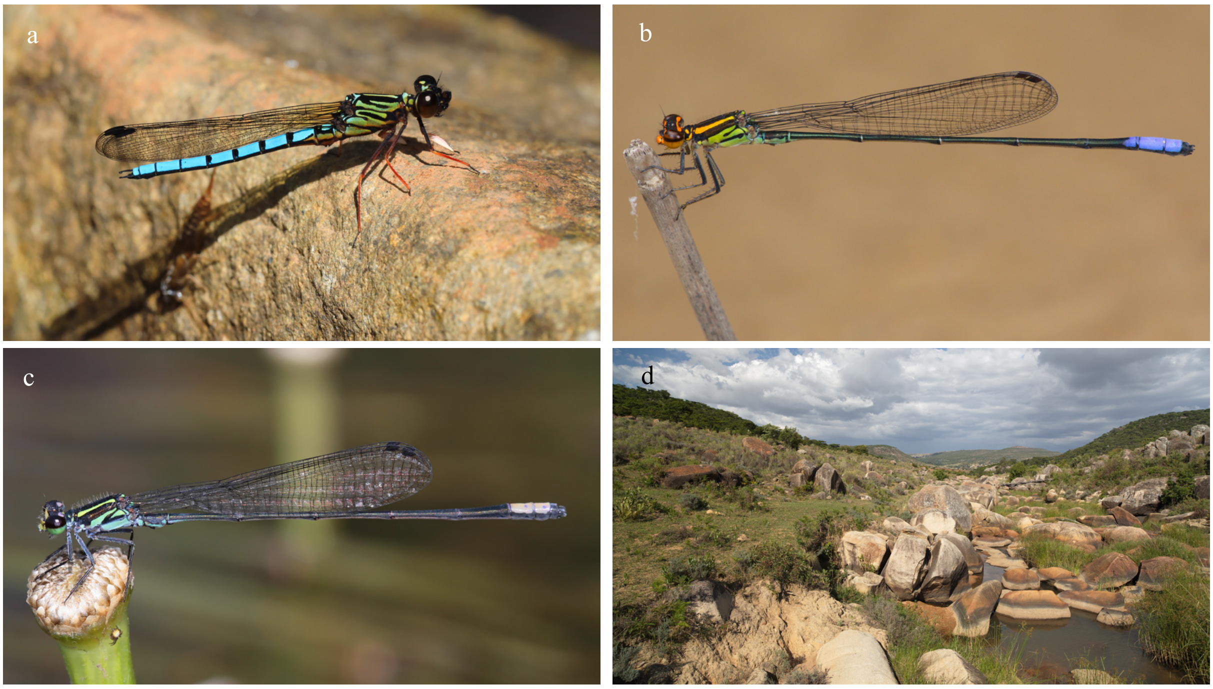

Figure 1: *a) Angola dancing jewel,* Platycypha angolensis, *male (photo by J Kipping, 13 January 2019, Ebanga, Benguela); b) Angola sprite,* Pseudagrion angolense, *male (photo by J Kipping, 2 December 2017, stream at Preciosa Mineral Water source, Lubango, Huíla); c) Estes' sprite,* Pseudagrion estesi, *male (photo by J Kipping, 15 May 2012, Cubango River source near Huambo); and d) Neve stream near Humpata, habitat of* Platycypha angolensis, Pseudagrion angolense, Pseudagrion estesi *and other endemics (photo by J Kipping, 3 December 2017, Huíla).*

Table 3: *Endemic and near-endemic Odonata species of the Angolan Planalto and surroundings.*

Species	Elevation (masl)			Occurrence and habitat	Taxonomy and biogeography
	Min.	Max.	Mean		
Calopterygidae					
Sapho sp. 'Nhime' broadwing – undescribed species	413	963	792 n = 23	Low-altitude endemic of rocky streams and small rivers in western scarp forest	Near *S. gloriosa* McLachlan, 1873 and *S. orichalcea* McLachlan, 1869 from Cabinda to Congo and Nigeria; genetics and morphology differ more from these two than they do from each other
Umma femina Longfield, 1947 Angola sparklewing (Figure 6b)	(1,345)	2,154	2,055 n = 72	High-altitude endemic of open and often rocky streams; all sites except for inaccurate (lower elevation) record "north of Cuché" (Pinhey 1975) on central plateau	Distinct, may be nearest to sympatric *U. electa* Longfield, 1933 although this has not been tested genetically
Chlorocyphidae					
Platycypha angolensis Longfield, 1959 Angola dancing jewel (Figure 1a)	261	2,127	1,189 n = 132	Wide-ranging endemic of open but often sheltered and sometimes rocky streams and small rivers; mostly along western escarpment and on Angolan Planalto	Morphologically most distinct member of Angolan radiation of genus; also genetically well defined
Platycypha bamptoni (Pinhey, 1975) highland blue jewel (Figure 7c)	1,612	2,104	1,993 n = 22	High-elevation endemic of open and often rocky streams and small rivers; largely confined to western edge of Angolan Planalto	Member of Angolan radiation of genus, but taxonomy unresolved
Platycypha sp. 'white tibiae' jewel – undescribed species	1,249	2,127	1,750 n = 33	High- and mid-elevation endemic of open streams and rivers on both Angolan Planalto and eastern plateaus	Member of Angolan radiation of genus, but taxonomy unresolved, hard to separate from *P. bamptoni* by white-coloured tibiae and abdominal pattern
Platycypha crocea (Longfield, 1947) Angola blue jewel	1,220	1,982	1,581 n = 44	High-elevation endemic largely confined to the Angolan Planalto, inhabiting smaller and softer-bottomed (e.g., muddy) streamlets than *P. bamptoni*	Fairly distinct member of Angolan radiation of genus, but taxonomy not entirely resolved
Platycypha rubriventris (Pinhey, 1975) red-bellied blue jewel	1,098	1,098	1,098 n = 1	Only type series known; two males collected in 1965 at Teixeira de Sousa, interpreted as Luau on DRC border in Lunda-Sul	Presumably also belongs to Angolan radiation of genus (Dijkstra 2007b)
Platycnemididae					
Elattoneura flavifacies (Pinhey, 1981) yellow-faced threadtail	829	1,428	1,263 n = 18	Mid-altitude near-endemic, widespread at boggy streamlets on eastern plateau, just extending into adjacent DRC and NW Zambia	Genetically and morphologically rather distinct member of genus
Elattoneura tarbotonorum Dijkstra, 2015 stout threadtail (Figure 6c)	1,238	2,215	1,788 n = 52	High- and mid-elevation endemic found at open streams and smaller rivers (often, but not always, rocky and fast flowing) around Lubango and Mt Namba on Angolan Planalto, but also lower down on eastern plateau	Distinct, probably sister species of Western Cape endemic *E. frenulata* (Hagen in Selys, 1860) (Dijkstra *et al.* 2015)

Species	**Elevation (masl)**			**Occurrence and habitat**	**Taxonomy and biogeography**
	Min.	**Max.**	**Mean**		
Elattoneura sp. threadtail – undescribed species (Figure 4)	111	1,695	1,091 n = 84	Possible mid- and low-elevation near-endemic widespread at open streams and rivers across Angola and northwards at least to western DRC, but mostly absent on Angolan Planalto	Morphologically nearest *E. glauca* (Selys, 1860) from southern and eastern Africa, but separated geographically and genetically
Coenagrionidae					
Aciagrion rarum (Longfield, 1947) tiny slim	1,171	1,171	1,171 n = 1	Only type series known, collected near Dala on Tyihumbwe River (tributary of the Kasai) in NE Angola in 1932	Distinctive, but affinities unclear
Aciagrion zambiense Pinhey, 1972 Zambia slim	1,184	1,476	1,281 n = 4	Mid-elevation near-endemic known from two sites in E Angola and one in nearby NW Zambia; habitat probably open temporary pools	Close to *A. africanum* Martin, 1908 that is widespread in West and Central Africa
Africallagma sp. ‘Hama’ bluet – undescribed species (Figure 9d)	1,421	1,421	1,421 n = 7	Mid-elevation endemic found only at reedy marsh near Alto Hama, on Angolan Planalto	Morphology distinct from other members of genus; genetic testing underway
Agriocnemis angolensis Longfield, 1947 Angola wisp	958	2,223	1,408 n = 67	Wide-ranging near-endemic found at open and often rocky streams and small rivers from high on Angolan Planalto down to rocky sections of the Okavango River in NE Namibia and NW Botswana	Genetically nearest sympatric *A.bumhilli* Kipping *et al*., 2012; former subspecies *spatulae* Pinhey, 1974; see *A. spatulae* below
Agriocnemis bumhilli Kipping *et al*., 2012 Bumhill wisp	973	1,375	1,225 n = 28	Mid-elevation near-endemic of boggy and marshy streams and rivers from eastern plateau to NE Namibia	Genetically nearest sympatric *A.angolensis* Longfield, 1947
Agriocnemis canuango Dijkstra, 2015 bog wisp (Figure 9b)	1,224	1,614	1,508 n = 28	Mid-elevation endemic of oligotrophic bogs west and east of (but not on) Angolan Planalto	Genetically and morphologically rather distinct member of genus (Dijkstra *et al*. 2015)
Agriocnemis spatulae Pinhey, 1974 finger-tipped wisp	1,349	1,445	1,438 n = 4	Mid-elevation near-endemic found at boggy and well-vegetated pools on the sandy plateaus in eastern Angola and adjacent NW Zambia	Described as a subspecies of *A. angolensis* Longfield, 1947 but morphologically and genetically distinct and probably a good species
Agriocnemis toto Dijkstra, 2015 Toto’s wisp (Figure 9c)	1,210	1,421	1,261 n = 4	Mid-elevation endemic preferring dense vegetation of reeds west of (but not east of or on) Angolan Planalto	Genetically and morphologically well-defined member of genus with unclear nearest relatives (Dijkstra *et al*. 2015)
Ceriagrion sp. ‘Cassongo’ citril – undescribed species	1,343	1,358	1,354 n = 7	Mid-elevation endemic found at temporary pools in boggy regions on sandy eastern plateau	One of many similar members of genus, but genetics and morphology distinctive; possibly sister species of widespread and sympatric *C. whellani* Longfield, 1952
Pseudagrion angolense Selys, 1876 Angola sprite (Figure 1b)	261	2,106	1,549 n = 97	Wide-ranging endemic of often rocky and (partly) forested streams and small rivers, mostly along western escarpment and on Angolan Planalto	Sister species of *P. grilloti* Legrand, 1987 from Gabon and western Congo (expected to occur in Cabinda)

Species	Elevation (masl)			Occurrence and habitat	Taxonomy and biogeography
	Min.	Max.	Mean		
Pseudagrion dundoense Longfield, 1959 Dundo sprite	660	660	660 n = 1	Only holotype known, male presumably collected near Dundo in Lunda-Norte on border with DRC in 1949	Status and affinities entirely unclear (Longfield 1959)
Pseudagrion estesi Pinhey, 1971 Estes' sprite (Figure 1c)	750	2,215	1,497 n = 88	Wide-ranging endemic of often rocky and mostly open streams and small rivers, mostly along western escarpment and on Angolan Planalto; scarce further east, e.g., isolated type locality at Quimbango, Malanje Province	Probably closest to *P. kibalense* Longfield, 1959 that is widespread in forests of Central Africa
Pseudagrion sarepi Kipping & Dijkstra, 2015 Sarep sprite	1,078	1,375	1,295 n = 40	Mid-elevation endemic found on all open sandy streams and rivers on eastern plateau almost up to border of Zambia, where likely to occur	Very close to *P. greeni* Pinhey, 1961 found higher up in Angola, northern Zambia and southern Katanga (DRC), and especially to *P. fisheri* Pinhey, 1961 from N Zambia, NE Angola, and (questionable) old records from N Botswana as *P. fisheri* in Pinhey (1976)
Gomphidae					
Notogomphus kimpavita Dijkstra & Clausnitzer, 2015 Angola longleg (Figure 3a)	612	1,777	962 n = 17	Mostly low-elevation endemic of often (partly) forested streams and small rivers along western escarpment, but extends quite high onto Angolan Planalto at Mt Namba	Genetically and morphologically well separated from sister species *N. praetorius* (Selys, 1878) from Angolan Planalto to Katanga (DRC) and South Africa
Onychogomphus rossii Pinhey, 1966 Angola claspertail (Figure 6d)	1,381	2,132	1,852 n = 7	High- and possibly mid-elevation endemic known only from rocky streams and small rivers on Angolan Planalto	Probably nearest to *O. kitchingmani* Pinhey, 1961 from NW Zambia (Dijkstra 2007a)
Paragomphus sp. 'Cuemba' hooktail – undescribed species (Figure 11c)	1,423	1,423	1,423 n = 1	Mid-elevation endemic known from single male at sandy stream near Cuemba on sandy eastern plateau (Sara Fernandes Elizalde pers. comm.)	Morphology unlike any member; no genetic data available
Paragomphus sp. 'Gabela' hooktail – undescribed species (Figure 3d)	581	953	870 n = 11	Low-elevation endemic of rather open (often disturbed) streams and small rivers with rocks or gravel along forested western escarpment	One of several superficially similar members of genus, but morphology distinct; genetic testing underway
Libellulidae					
Aethriamanta sp. 'Micongo' basker – undescribed species (Figure 23)	1,240	1,358	1,318 n = 11	Possible mid-elevation near-endemic of oligotrophic bog pools on sandy eastern plateau and in NW Zambia	Genetics and morphology rather distinct from *A. rezia* Kirby, 1889 that is widespread in Angola, tropical Africa and Madagascar
Atoconeura sp. 'Namba' highlander – undescribed species	1,705	1,705	1,705 n = 1	Possible high-elevation endemic, known only from single female from Mt Namba	Morphology inconclusive, but isolated population of mostly high-elevation genus may well be distinct (see Dijkstra 2006); genetic testing underway

Species	**Elevation (masl)**			**Occurrence and habitat**	**Taxonomy and biogeography**
	Min.	**Max.**	**Mean**		
Eleuthemis eogaster Dijkstra, 2015 sunrise firebelly (Figure 3c)	616	1,214	848 n = 12	Low- and mid-elevation endemic known only from several large streams and rivers near Uíge (western scarp) bordered by forest	Nearest relative is unnamed species near *E. buettikoferi* Ris, 1910 from NW Zambia to W Tanzania (Dijkstra *et al.* 2015)
Eleuthemis libera Dijkstra & Kipping, 2015 free firebelly (Figure 14)	1,120	1,435	1,276 n = 24	Mid-elevation near-endemic, widespread at (mostly open) streams and rivers on eastern plateau, extending to NW Angola (near Negage) and NW Zambia	Most distinctive member of genus (Dijkstra *et al.* 2015)
Micromacromia flava (Longfield, 1947) Angola micmac (Figure 7a)	1,148	1,849	1,543 n = 25	High-elevation endemic of small boggy streams and seeps on Angolan Planalto as well as near Negage	Distinct member of genus with two species in forests of West and Central Africa and another restricted to Usambara Mountains, E Tanzania (see Longfield 1947, Dijkstra & Vick 2006)
Nesciothemis sp. blacktail – undescribed species	405	2,127	1,174 n = 67	Possible wide-ranging near-endemic found at most open streams and rivers in Angola and into N Namibia and N Botswana	Genetically most distinct within complex including widespread *N. farinosa* (Förster, 1898) and *N. pujoli* Pinhey, 1971; morphology also fairly distinct
Orthetrum sp. 'Cuanavale' skimmer – undescribed species	1,275	1,390	1,369 n = 7	Mid-elevation endemic known from two bogs on sandy eastern plateau	Nearest to widespread African *O. abbotti* Calvert, 1892, but genetics and morphology distinct
Porpax sp. 'Tempue' pricklyleg – undescribed species	1,343	1,390	1,353 n = 2	Mid-elevation endemic of boggy source areas on eastern plateau	Genetics and morphology unlike any other member of genus; Africa's smallest true dragonfly
Rhyothemis sp. 'Cuito' flutterer – undescribed species	1,238	1,446	1,318 n = 11	Mid-elevation endemic that is common and widespread at open waters on eastern plateau	Genetics and morphology unlike any other member of genus
Tetrathemis sp. 'Cambondo' elf – undescribed species	412	798	666 n = 2	Low-elevation endemic found near shaded streams and rivers (probably breeds in associated pools) near Uíge and in Cambondo Forest on western escarpment	Close to *T. fraseri* Legrand, 1977 from Gabon, but genetics and morphology fairly distinct
Trithemis sp. 'Cuanavale' dropwing – undescribed species	1,209	1,358	1,261 n = 3	Mid-elevation endemic found in boggy areas along sandy rivers at three sites on eastern plateau	Only female specimens available, but these unlike any other member of genus both in genetics and morphology
Trithemis sp. 'Cumbira' scarp dropwing	831	879	855 n = 1	Possible low-elevation endemic, single males found at shaded streams on forested western scarp near Uíge and at Cumbira Forest	Near *T. integra* Dijkstra, 2007 from Albertine Rift but geographically isolated and morphology somewhat distinct; genetic comparison so far unavailable
Trithemis sp. 'Namba' dropwing – undescribed species (Figure 7b)	1,774	2,048	1,920 n = 4	High-elevation endemic found only away from water at Mt Namba; may breed in bog streams	Morphologically unlike any other species of genus; genetic testing underway
Zygonyx sp. 'Cunde' cascader – undescribed species	1,249	1,296	1,272 n = 2	Mid-elevation endemic collected only at Cunde Falls on eastern plateau	One of at least six species in complex near *Z. flavicosta* (Sjöstedt, 1900), but genetics and morphology unlike any other member

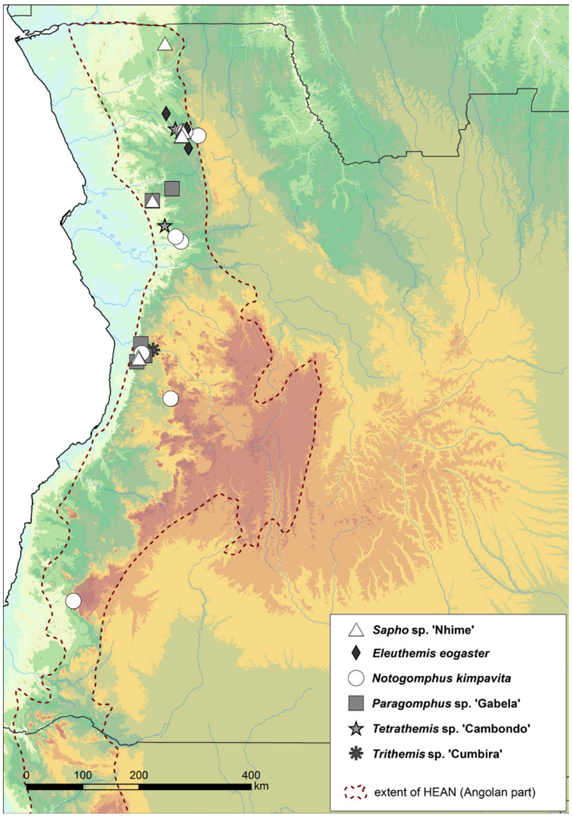

***Figure 2:** Point locality data of selected endemic species of the western scarp forests of the highlands and escarpments of Angola (HEAN):* Sapho *sp. 'Nhime',* Eleuthemis eogaster, Notogomphus kimpavita, Paragomphus *sp. 'Gabela',* Tetrathemis *sp. 'Cambondo' and* Trithemis *sp. 'Cumbira'.*

As far as known, six of the twelve species are completely restricted to flowing waters (or associated pools) on the forested Angolan escarpment (Figure 2). They have a comparatively low and narrow elevation range, found mostly between 400 and 1,000 masl, although *Notogomphus kimpavita* (Figure 3a) almost reaches 1,800 masl at a stream in Mt Namba's gallery forests (Figure 3b). Remarkably, the existence of these endemics has only just come to light: *Eleuthemis eogaster* (Figure 3c) and *N. kimpavita* were described in 2015, while new species in the genera *Paragomphus* (Figure 3d), *Sapho* and *Tetrathemis*, and possibly one in *Trithemis* remain to be described.

The final three of the twelve species appear widespread but have been confused with species found commonly elsewhere in Africa, so their exact ranges are imperfectly known. It is likely that new species of *Elattoneura* (Figure 4) and *Mesocnemis* are found at open running waters below 1,700 masl.

While being largely absent from the high plateau, they occur close to sea level, and at least the *Elattoneura* species extends into adjacent DRC. A distinct taxon of *Nesciothemis* is probably the widest ranging (near-)endemic in Angola, occurring at almost any open stream or river, while extending into northern Namibia and northern Botswana as well.

***Figure 3:** a) Angola longleg,* Notogomphus kimpavita, *male (photo by J Kipping, 5 December 2017, Bruco Pass, Tundavala, Huíla); b) stream at Mt Namba, habitat of* Notogomphus kimpavita *and* Atoconeura *sp. 'Namba' (photo by J Kipping, 20 January 2019, Cuanza-Sul); c) sunrise firebelly,* Eleuthemis eogaster, *male (photo by K-DB Dijkstra, 3 October 2013, Lumanie River, Uíge); and d)* Paragomphus *sp. 'Gabela', male (photo by J Kipping, 16 January 2019, Uiri River near Conda, Cuanza-Sul).*

Figure 4: Elattoneura *sp. near* glauca, *male (photo by J Kipping, 16 January 2019, Uiri River near Conda, Cuanza-Sul).*

Another ten species which rarely occur below 1,200 masl and frequently up to 2,200 masl are largely confined to the Angolan Planalto, although some were found in suitable habitat farther north and east (Figures 5a and 5b). All inhabit streams and rivers, generally in open grassland (Figure 6a). *Umma femina* (Figure 6b), *Elattoneura tarbotonorum* (Figure 6c), *Onychogomphus rossii* (Figure 6d) and a possible new *Atoconeura* species appear to favour faster flowing and often rocky waters. *Micromacromia flava* (Figure 7a) was found at boggy seeps and streamlets, which may also be the habitat of a new *Trithemis* species from Mt Namba with spectacularly marked wings (Figure 7b).

Aside from *Platycypha angolensis*, the endemic radiation of blue *Platycypha* species here includes the localised *P. crocea* on soft-bottomed, and the more widespread *P. bamptoni* (Figure 7c) on hard-bottomed, streams. The latter, however, has a form that is also widespread on sandy rivers farther east, and whose status as a possibly separate species is unresolved (Figure 8). Near-endemic *Agriocnemis angolensis* (Figure 7d) is unusual for the genus in being common at rocky streams on Angola's highest plateaus, as well as at fast-flowing and rocky sections of the lower Okavango in Namibia's 'Caprivi Strip'. Another taxon so far named as its subspecies *Agriocnemis angolensis spatulae* Pinhey 1974, is known from eastern Angola and northwestern Zambia. Recent collections revealed that it is most likely a distinct species favouring soft-bottomed and boggy stagnant habitats.

Notably, about half of Angola's (potential) endemics and near-endemics occur neither along the western escarpment nor on the high central Angolan Planalto. These twenty species are restricted to oligotrophic habitats on sandy soils, such as bogs and clear rivers

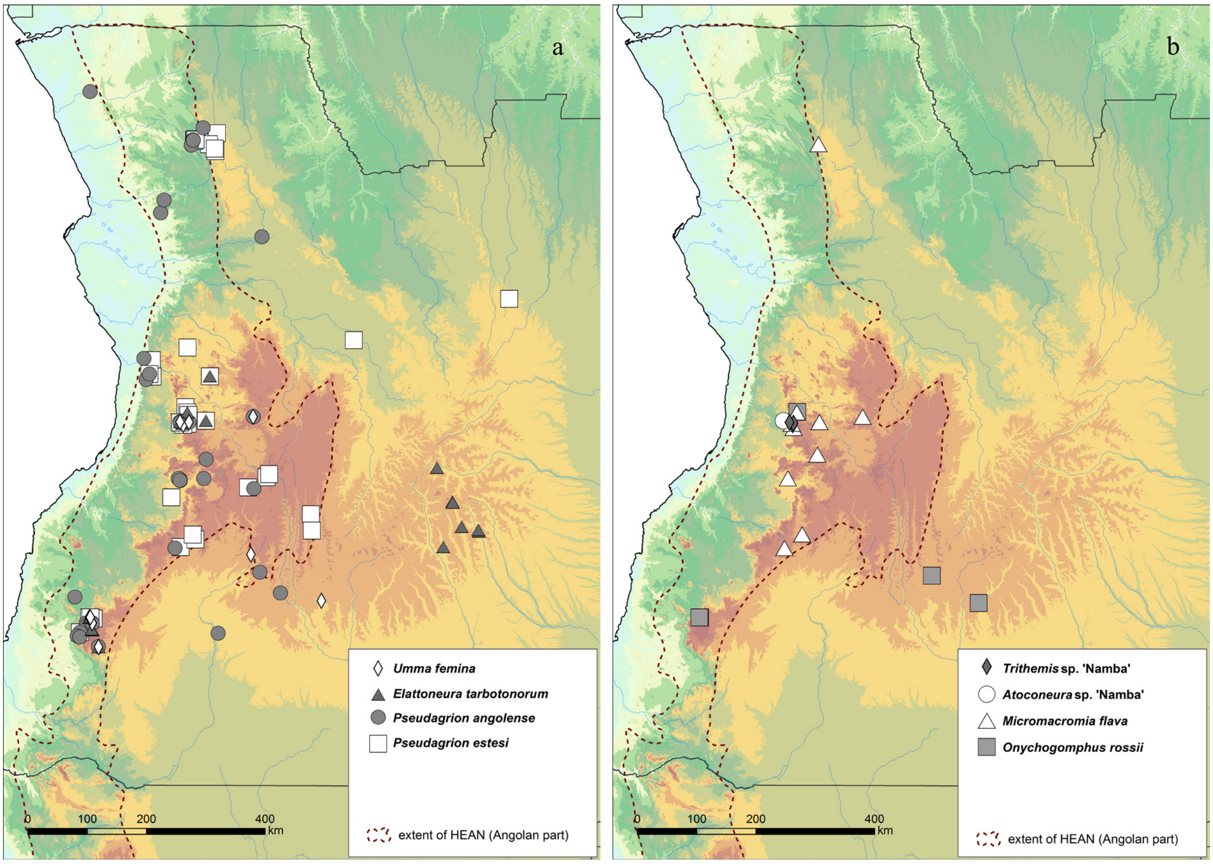

Figure 5: *Point locality data of selected endemics: a) Zygoptera species of the high Angolan Planalto* Umma femina, Elattoneura tarbotonorum, Pseudagrion angolense *and* Pseudagrion estesi*; and b)* Anisoptera species *of the Angolan Planalto* Trithemis *sp. 'Namba',* Atoconeura *sp. 'Namba',* Micromacromia flava *and* Onychogomphus rossii. *(HEAN = the highlands and escarpments of Angola and Namibia.)*

Figure 6: *a) Tchiamena stream near Tundavala, Lubango, habitat of* Elattoneura tarbotonorum, Onychogomphus rossii, Platycypha bamptoni *and* Umma femina *(photo by J Kipping, 6 December 2017, Huíla); b) Angola sparklewing,* Umma femina, *male (photo by J Kipping, 26 January 2019, Tchiamena stream near Lubango, Huíla); c) stout threadtail,* Elattoneura tarbotonorum, *male (photo by J Kipping, 6 December 2017, Tchiamena stream near Lubango, Huíla); and d) Angola claspertail,* Onychogomphus rossii, *male (photo by J Kipping, 6 December 2017, Tchiamena stream near Lubango, Huíla).*

Figure 7: *a) Angola micmac,* Micromacromia flava, *male (photo by R Ferreira, 18 November 2022, Cassongue, Cuanza-Sul); b)* Trithemis *sp. 'Namba', male (photo by R Ferreira, 29 April 2013, Mt Namba, Cuanza-Sul); c) highland blue jewel,* Platycypha bamptoni, *male (photo by J Kipping, 13 January 2019, Ebanga, Benguela); and d) Angola wisp,* Agriocnemis angolensis, *male (photo by J Kipping, 12 May 2012, Cacuchi River north of Menongue, Bié).*

(Figure 9a), mostly between 1,000 and 1,500 masl. The two endemic *Agriocnemis canuango* (Figure 9b) and *A. toto* (Figure 9c) and a recently discovered species of *Africallagma* (Figure 9d) have been found at mid-elevations north of the Angolan Planalto (Figure 10); the remainder have only been recorded on the lower sandy plateau that dominates Angola's eastern half (see Figures 12a and 12b).

Three species have not been reported for half a century or more, being known only from their type specimens and localities in northeastern Angola: *Aciagrion rarum*, *Platycypha rubriventris* and *Pseudagrion dundoense*. We owe most of the remainder of our knowledge of this sand fauna to the Okavango Wilderness Project (OWP), which focuses on the eastern plateau's importance as Angola's water tower, with sources and headwaters of many major rivers (e.g., Congo, Kasai, Cuanza, Cubango, Cunene and Zambezi) lying close to each other in the area.

Six species that were described from the eastern plateau's periphery and that (probably) just extend beyond Angola's eastern border were found to have their main occurrence here during OWP fieldwork (NGOWP 2018): *Aciagrion zambiense*, *Agriocnemis bumhilli*, *Agriocnemis spatulae* (often considered a subspecies of *Agriocnemis angolensis*; see above), *Elattoneura flavifacies*, *Eleuthemis libera* and *Pseudagrion sarepi* (Figure 11a). Moreover, distinctive new species of *Aethriamanta* (Figure 11b),

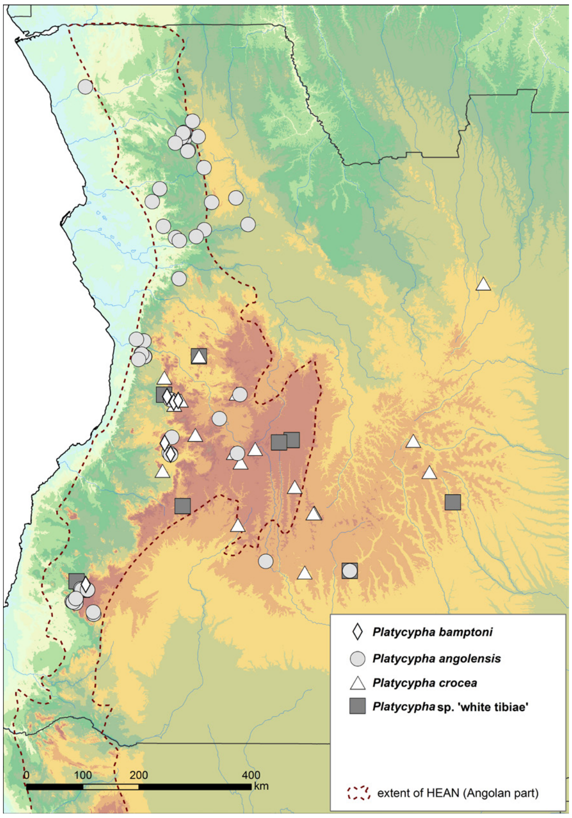

Figure 8: *Point locality data of endemic members of the blue* Platycypha *complex in Angola:* Platycypha angolensis, Platycypha bamptoni, Platycypha *sp. 'white tibiae' and* Platycypha crocea*. (HEAN = the highlands and escarpments of Angola and Namibia.)*

Figure 9: *a) The sandy Longa River, type locality of* Pseudagrion sarepi *(photo by J Kipping, 20 May 2012, Cuando-Cubango); b) bog wisp,* Agriocnemis canuango*, male (photo by J Kipping, 24 January 2019, Cassongue, Cuanza-Sul); c) Toto's wisp,* Agriocnemis toto*, male (photo by J Kipping, 24 January 2019, Cela, Cuanza-Sul); and d)* Africallagma *sp. 'Hama', male (photo by J Kipping, 1 February 2019, Hama River north of Alto Hama, Huambo).*

Ceriagrion, *Orthetrum*, *Paragomphus* (Figure 11c), *Porpax*, *Rhyothemis*, *Trithemis* and *Zygonyx* were discovered (Figures 12a, 12b and 13).

The eastern plateau is unusual because highly seasonal rainfall is held and released by very nutrient-poor sandy soils: water flows abundantly year-round, but in a largely unforested landscape. The region owes its nutrient-poor conditions to a thick layer of loose aeolian sand, deposited during episodes of Plio-Pleistocene aridity (Moore *et al*. 2009). Subsequently, aquatic habitats that are rare elsewhere in Africa dominate here. These include grassy bogs with small streams and pools, open sandy rivers with associated peaty lakes and oxbows, and extensive seasonally flooded pans.

Not only are many specialised species present, but species that are common in open habitats throughout the rest of Africa are virtually absent because of the exceptional oligotrophic and partly acidic water conditions. Population densities and the average size of individuals of most species, meanwhile, appear exceptionally low. The new *Porpax* species, for example, is the smallest true dragonfly (i.e., excluding damselflies) in Africa by far and among the smallest in the world, while the new *Aethriamanta*, *Rhyothemis* and *Trithemis* species are (among) the smallest species in their genera.

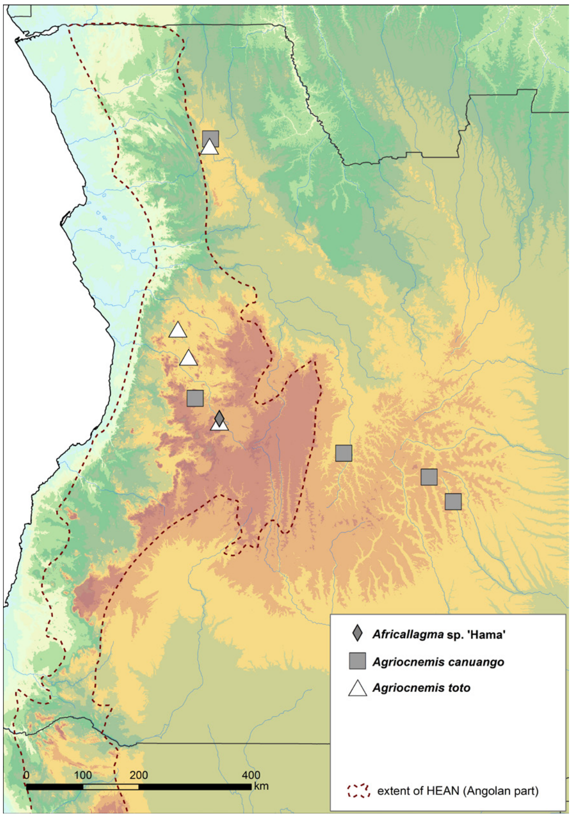

Figure 10: *Point locality data of selected endemic Zygoptera species of the lower Angolan Planalto:* Africallagma *sp. 'Hama',* Agriocnemis canuango *and* Agriocnemis toto. *(HEAN = the highlands and escarpments of Angola and Namibia.)*

Figure 11: *a) Sarep sprite,* Pseudagrion sarepi, *male (photo by J Kipping, 20 May 2012, Longa River, Cuando-Cubango); b)* Aethriamanta *sp. 'Micongo', male (photo by J Kipping, 13 December 2022, Ikelenge, Zambia); and c)* Paragomphus *sp. 'Cuemba', male (photo by D Elizalde, 19 October 2018, Cuemba, Bié).*

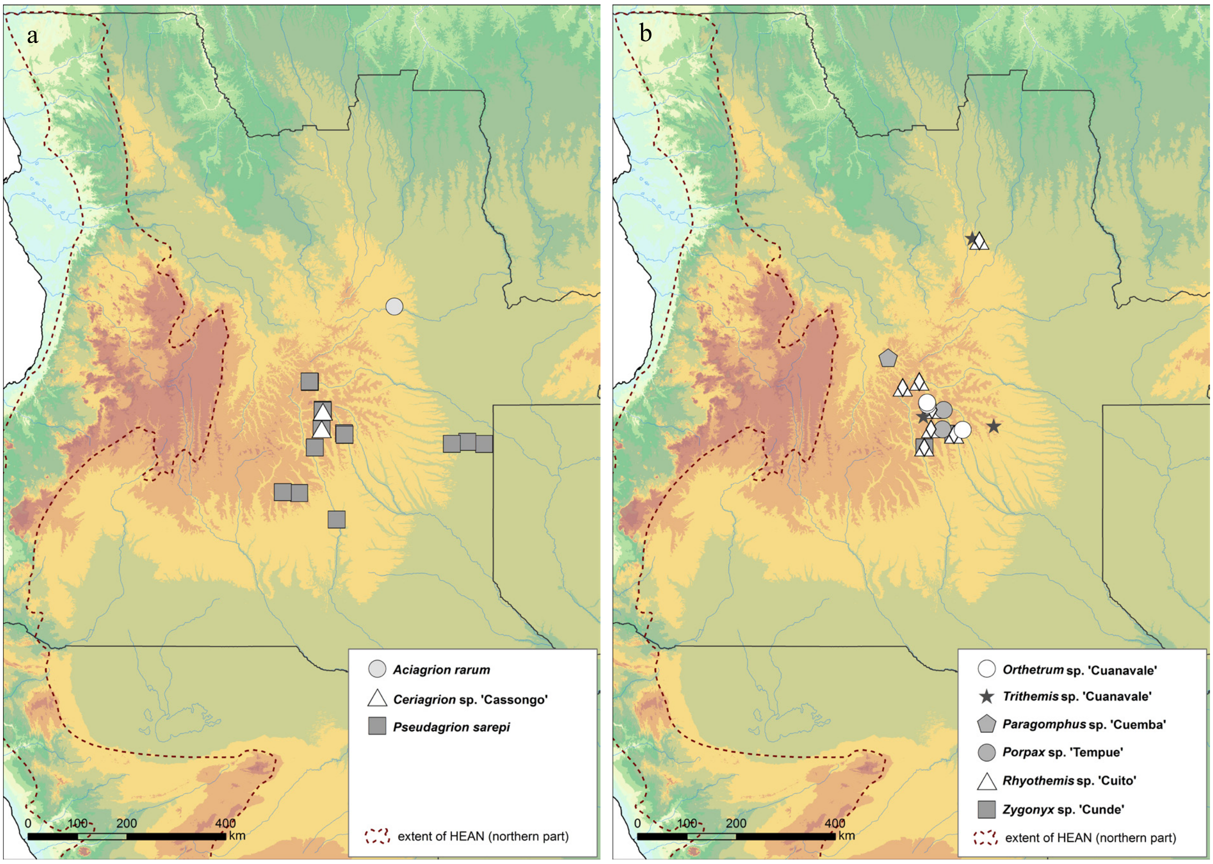

Figure 12: *Point locality data of selected endemics: a) Zygoptera species of the eastern lower plateau* Aciagrion rarum*,* Ceriagrion *sp. 'Cassongo' and* Pseudagrion sarepi*; and b) Anisoptera species of the eastern lower plateau* Orthetrum *sp. 'Cuanavale',* Trithemis *sp. 'Cuanavale',* Paragomphus *sp. 'Cuemba',* Porpax *sp. 'Tempue',* Rhyothemis *sp. 'Cuito' and* Zygonyx *sp. 'Cunde'. (HEAN = the highlands and escarpments of Angola and Namibia.)*

This, as well as our observation that more widespread species are present at sites in the region that are eutrophicated by organic pollution, indicates that the endemism is linked to the eastern plateau's exceptional ecology rather than to its relative isolation.

Origins

While some familiar patterns are apparent in the biogeographic affinities of Angola's (near-)endemic odonate species, many of them seem to be remarkably distinct phylogenetically, making their origins less clear (see Table 3).

Pseudagrion angolense, *P. estesi* and the four probably new species on the escarpment (in the genera *Paragomphus*, *Sapho*, *Tetrathemis* and *Trithemis*) have sister taxa in similar forest-stream habitats in Central Africa, with the *Trithemis* confined to the Albertine Rift. This pattern is common in escarpment birds too. Similarly, the nearest relatives of some endemics of generally more open and higher-elevation streams and rivers (*Eleuthemis eogaster*, *Notogomphus kimpavita*, *Onychogomphus rossii*, *Pseudagrion sarepi*, *Umma femina* and probably the possibly new *Atoconeura* species) are in similar habitats directly east. *Elattoneura tarbotonorum* is an exception, with the nearest relative being confined to the mountains of the Western Cape in South Africa.

The sister taxa of a majority of the (near-)endemics, however, are either very widespread in Africa, not especially obvious or are also restricted to Angola. Those with widespread relatives are *Aciagrion zambiense* and the (possible) new *Aethriamanta*, *Ceriagrion*, *Elattoneura*, *Mesocnemis*, *Nesciothemis*, and *Orthetrum* species, while those with Angolan sister taxa (but unclear affinities beyond that) are *Agriocnemis angolensis*, *A. bumhilli* and *A. spatulae*, and the four or five species of the endemic *Platycypha* radiation. *Agriocnemis canuango*, *A. toto*, *Elattoneura flavifacies*, *Eleuthemis libera* (Figure 14), *Micromacromia flava* and the new *Porpax*, *Rhyothemis* and two *Trithemis* species are among the most distinctive species in their genera, sometimes being the sister taxon to all others in the genus. We know little about the affinities of *Aciagrion rarum*, *Pseudagrion dundoense*, the new *Africallagma* species, and the new *Paragomphus* and *Zygonyx* from the eastern plateau, although each appears taxonomically unique too.

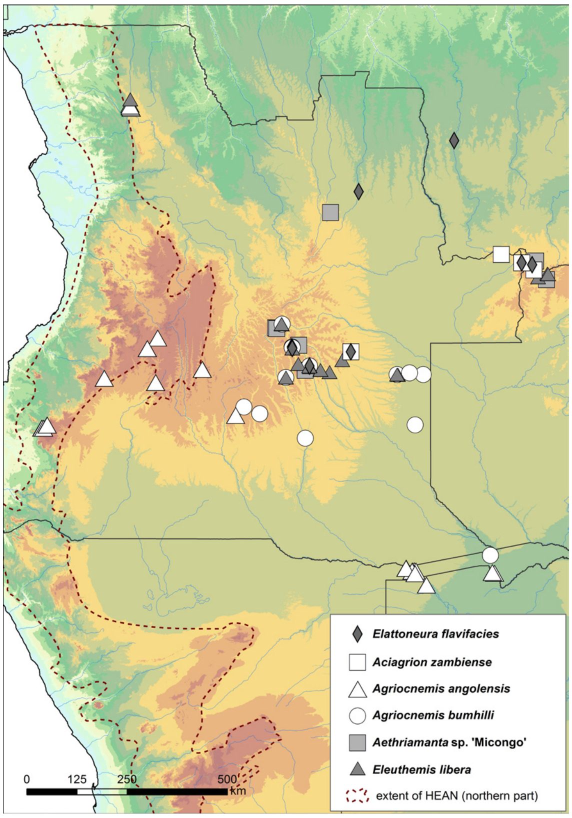

Figure 13: *Point locality data of selected near-endemic species of the Angolan plateaus and adjacent regions:* Elattoneura flavifacies, Aciagrion zambiense, Agriocnemis angolensis, Agriocnemis bumhilli, Aethriamanta *sp. 'Micongo' and* Eleuthemis libera*. (HEAN = the highlands and escarpments of Angola and Namibia.)*

These affinities suggest that, while the isolation of Angola's highlands and escarpments contributed to the evolution and survival of its (near-)endemic species, the unusual ecological conditions there may have contributed even more to localised speciation. This confirms the inferences drawn above from the species' distributions.

Figure 14: Free firebelly, *Eleuthemis libera*, male (photo by J Kipping, 3 March 2023, Mwinilunga, Zambia).

GAPS IN KNOWLEDGE AND RESEARCH PRIORITIES

Large parts of Angola have not, or only poorly, been surveyed for Odonata. One focus of this review, the western highlands, is fortunately among the better-studied regions. Many records are available from the Serra da Chela, for example, notably from around Lubango and Humpata, often over a longer period (e.g., Ris 1931, Pinhey 1975, Tarboton 2009). The recency of much of the knowledge presented for the western escarpment, however, implies that systematic surveys of the remaining forest habitats there will lead to further discoveries. So far, even well-known sites like Cumbira Forest have been visited only briefly and Serra da Neve has never been studied for Odonata yet.

However, most priorities for further research in Angola lie in the northern half of the country. Lunda-Norte Province should yield the greatest number of unrecorded species. Survey priorities for endemic species are the remaining forests north of Dondo and N'dalatando (e.g., in mountain ranges like Serra Canda and Serra Cananga), the higher-lying areas around the Cuanza Basin (notably the northern edge of the central plateau and above the escarpment between the Cuanza and Congo catchments), and the northern part of the eastern plateau (e.g., between Luena and Saurimo). Photographs taken near Saurimo, for example, show possibly unnamed species of Chlorocyphidae and Coenagrionidae (Russell Tate, pers. comm.).

In Namibia there are some mostly unexplored and hardly accessible mountain ranges in the northwest with streams flowing off to the Cunene River. Namely the Baynes and Otjihipa mountains and Ehomba Hills might hold populations of some of the highland endemics so far only known from farther north on the Angolan Planalto (F Suhling, pers. comm.).

ACKNOWLEDGEMENTS

We thank Alvaro Bruno Toto Nienguesso, the driving force behind biodiversity research in Uíge Province (Angola), and Prof. Dr Neinhuis and Dr Thea Lautenschlaeger from Technische Universität Dresden for inviting us to the field survey in Uíge Province. Part of the fieldwork in Angola was supported by a travel fund from the German Academic Exchange Service (DAAD). The published results were obtained in collaboration with the Instituto Nacional da Biodiversidade e Áreas de Conservação (INBAC) of the Ministry of Environment of Angola who also provided all necessary permits. We are grateful to Dr Paula C Francisco Coelho for making the 2012 Southern African Regional Environmental Programme (SAREP) survey in southern Angola possible, and to Dr Chris Brooks of SAREP for the preparation and organisation of this survey. We are also very grateful to Sara and David Fernandes Elizalde (Lubango) for providing their own data and expertise and for their generous support on various expeditions within

Angola. Chris Hines (now South Africa) helped with collected specimens and, together with Katy Sharpe (Windhoek), provided logistical support and company on a collecting trip. Dr André Günther (Freiberg, Germany) helped to collect specimens and provided valuable knowledge to the taxonomy of Chlorocyphidae. Further data and photographic records of Odonata were provided by Dr Manfred Haacks, Dr John Mendelsohn, Riquita Sampaio, Dr Warwick Tarboton, Russell Tate, Carel van der Merwe, Dr Pedro Vaz Pinto, and others. Prof. Dr Michael Samways of Stellenbosch University and Prof. Dr Frank Suhling (Technische Universität Braunschweig) gave valuable comments to the manuscript. This paper is dedicated to the late Rogério Ferreira (Luanda), who helped on various expeditions and provided many photographic records. He also donated some of his excellent photographs for this paper.

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Observations on the diversity of termites in Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-gunter

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ABSTRACT

Termites are widely distributed, and the highest number of genera are documented for the Afrotropical region. Nevertheless, data or species lists for southern Africa were mainly compiled by a few scientists during several field surveys between the 1950s and 1970s. However, knowledge about the diversity and endemism of termites in highland areas was not collated during these surveys and has not been assembled to date. Since then, different scientists used these datasets to measure the species richness or the endemic species richness for single countries, e.g., South Africa. Termite species lists for Angola are scarce and were compiled for only a few regions, where 10 of 93 species were found to be endemic. Our current knowledge about the termite species diversity in Namibia is substantially better, with 8 of 54 species from four families being endemic. However, recent molecular studies on single termite species show high genetic diversity. More research on the currently available material in collections as well as molecular studies on species from southern Africa is needed.

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

INTRODUCTION

Termites are eusocial insects systematically classified as roaches based on morphology, anatomy (Handlirsch 1903, 1904, Desneux 1904, Lameere 1909) and molecular studies (Lo *et al.* 2000, Inward *et al.* 2007b, Krishna *et al.* 2013). Within the roaches, termites belong to the epifamily Termitoidae; preferably, the term Isoptera is used as an unranked clade name (Krishna *et al.* 2013, Janion-Scheepers *et al.* 2016). The monogeneric family Cryptocercidae (genus *Cryptocercus*) is the sister group to the Isoptera (Eggleton 2001, Krishna *et al.* 2013). Approximately 3,000 extant termite species have been described worldwide in about 280 genera (Eggleton 2000, Kambhampati & Eggleton 2000, Uys 2002). Eggleton (2000) analysed the global termite diversity pattern and could show the highest value of genera in the Afrotropical region due to the high habitat diversity. Five termite families are represented by 54 genera in southern Africa, excluding Angola (Uys 2002). These values indicate that this region is rich in genera because the Termitidae originated in Africa (Bourguignon *et al.* 2016). The highest generic diversity of termites occurs in the Congolian rainforest (Jones & Eggleton 2010, Janion-Scheepers *et al.* 2016, Lind *et al.* 2022).

Termites alter their environment and soil properties by collecting litter, through their feeding behaviour as decomposers and due to their nest construction (Jones *et al.* 1994, Dangerfield *et al.* 1998, Sileshi *et al.* 2010, Juergens 2013, Jürgens *et al.* 2021). Additionally, they greatly impact nutrient cycling and plant species diversity (Donovan *et al.* 2001, Adams & Otárola-Castillo 2013, Erpenbach 2015, Jouquet *et al.* 2016, Wildermuth *et al.* 2021). Therefore, they are known as ecosystem engineers. Examples from southern Africa are *Macrotermes michaelseni* (Dangerfield *et al.* 1998, Wildermuth *et al.* 2021, 2022), *Psammotermes allocerus* (Juergens 2013) and *Microhodotermes viator* (McAuliffe *et al.* 2019).

TERMITE SPECIES DIVERSITY IN SOUTHERN AFRICA

The knowledge about termite families, genera and species in southern Africa, excluding Angola, was mainly gained between the 1950s and the 1970s (e.g., by Sands 1957, Coaton 1958, Williams 1966, Ruelle 1970, Coaton & Sheasby 1972, 1973). These publications were based on more than 35,000 samples from Namibia, South Africa, Zimbabwe and Eswatini (formerly Swaziland) (Uys 2002, Janion-Scheepers *et al.* 2016). The most detailed and comprehensive distribution maps, information about nest structures and biological observations were mainly collected and published by Coaton and Sheasby in national surveys of the Isoptera of southern Africa from 1973 to 1980 and published in the journal *Cimbebasia* (e.g., Coaton 1958, Coaton & Sheasby 1973, 1974, 1975, 1980). Mitchell (1980) published a survey of the termite diversity occurring in Zimbabwe. Uys (2002) compiled the documentation of 54 genera occurring in South Africa, Zimbabwe, Mozambique, Botswana, Eswatini, Lesotho and Namibia in her guide to termite genera. She identified 165 species in the 54 genera, of which 25% of the species could be endemic. The family Termitidae comprises the highest number of genera (Uys 2002).

These surveys did not collect data such as distribution maps or species diversity lists concerning termite endemics in highlands and escarpments of Angola and Namibia (the HEAN zone, Mendelsohn & Huntley 2023).

Research topics on termite phylogenies, reproductive biology, mound architecture, gut microbial communities and others were compiled by several scientists in different volumes (Krishna & Weesner 1969, 1970, Abe *et al.* 2000, Bignell *et al.* 2011). Krishna *et al.* (2013) arranged all termite species and their general distribution range in seven volumes, the 'Treatise on the Isoptera of the World'. A detailed termite literature list was published in subchapter 3.2.1 'Isoptera' by Janion-Scheepers *et al.* (2016).

Several scientists used the datasets from Coaton & Sheasby in the past. Zeidler (1997) investigated the distribution patterns of generic termite species richness from Namibia by implementing a Geographic Information System and could show that some species occur in specific annual precipitation ranges, e.g., *Psammotermes allocerus* occurs from 30 mm to 100 mm. The same dataset was recently used by Lind *et al.* (2022) to identify feeding groups of termites that consume wood, grass, detritus and soil organic material (Eggleton & Tayasu 2001) in relation to rainfall gradients in southern Africa.

From 2000 onwards, termite species richness was investigated in smaller study areas, e.g., by Zeidler *et al.* (2002). They investigated the diversity on five farms in southern Kunene Region of Namibia and could show a difference in diversity depending on the land-use intensity. Termites were also documented within the Biodiversity Monitoring Transect Analysis (BIOTA) in Africa project (Grohmann *et al.* 2010, Jürgens *et al.* 2010) on 45 sites from Namibia to South Africa. Schyra *et al.* (2018) investigated termite community structures from six sampling sites using phylogenetic analyses and revealed that species composition changes along a climate gradient. Other studies focused on single termite species regarding their spatial pattern (Grohmann *et al.* 2010, Wildermuth *et al.* 2021, 2022), nest structure (Tschinkel 2010), ecological relationships and fairy circles (Juergens 2013), physiology (Grube & Rudolph 1995), phylogenetic diversity (Gunter *et al.* 2022a, 2023, Jürgens *et al.* 2023) and morphological diversity (Gunter *et al.* 2022b).

The treatise by Krishna *et al.* (2013) and a few recently published data are the main sources for this paper.

TERMITE ENDEMISM IN ANGOLA AND NAMIBIA

Detailed biogeographical information on termite species that could be endemic in the HEAN zone is scant and can be obtained only by checking the literature by Krishna and colleagues (Krishna & Weesner 1969, 1970, Krishna *et al.* 2013) or the original maps published by Coaton and Sheasby (1972, 1973, 1974, 1975, 1980). The published maps by Coaton and Sheasby show that they are mainly focused on study sites near the main roads and do not focus on specific areas, e.g., highlands in Namibia (Coaton & Sheasby 1972). Therefore, information on the occurrence of termite species in the HEAN zone, as defined by Mendelsohn and Huntley (2023), was not mentioned.

Angola

Silvestri (1914) described the first termite observations for Angola near San Paolo de Loanda (Weidner 1956). Later, Weidner published three volumes about termite diversity in Angola (Weidner 1956, 1961, 1974). All information about species lists, morphology and nest descriptions are based on surveys by A de Barros Machado from the area of Dundo in northeast Angola. Weidner also compiled observations from other entomologists (e.g., M Burr) who stated that the most frequently encountered insects in the highlands (900–1,200 masl) are termites. Termites also occur on the highest mountains, first recorded during the Jessen survey in 1931–1932 (reported in Cosar 1934, Weidner 1956). Other authors who contributed to the study of these collections are Harris (1954), Noirot (1955), Emerson (in Weidner 1956) and de Carvalho (1971). Jürgens *et al.* (2021) recently discovered a new Hodotermitidae termite species in Angola; it is of an unknown genus, occurs mainly in the coastal region near the town of Baba and creates the largest known fairy circles (Jürgens *et al.* 2021).

In total, 93 species from three families – Hodotermitidae, Termitidae and Rhinotermitidae – are recorded and documented for Angola (Weidner 1956, 1961, 1974, Krishna *et al.* 2013, Jürgens *et al.* 2021). The family Termitidae presents the largest group and comprises 87 species from seven subfamilies. Only ten of 93 species are endemic to Angola (see Table 1). No other occurrences of these ten species are yet documented from other localities or countries. The endemics belong to the Hodotermitidae and three subfamilies of Termitidae. Molecular data have only been published for the Hodotermitidae (Jürgens *et al.* 2021), but not yet for the other nine species.

Namibia

The Namibian termite species are better documented and understood than Angola's termite diversity. The main fieldwork on species diversity in southern Africa was done by Coaton and Sheasby, as described above.

In Namibia, four termite families (Hodotermitidae, Kalotermitidae, Rhinotermitidae and Termitidae) are represented by 13 genera and at least 54 species, but only eight species were listed as endemic by Uys (2002) and Krishna *et al*. (2013). The eight species belong to three subfamilies of the Termitidae (see Table 2). The sand termite species *Psammotermes allocerus* occurs in southern Africa. However, recently published data show a high genetic diversity based on mitochondrial markers (Gunter *et al*. 2022a, 2023, Jürgens *et al.* 2023) and morphological diversity (Gunter *et al*. 2022b). The authors conclude that *P. allocerus* is a species complex. Some genetic groups occur only in Namibia (e.g., *P. allocerus* 'Northern Namib') based on the current dataset and the studied area. The other listed species occur in the western parts of Namibia and are not known to be endemic in the HEAN zone. To date, there are no molecular data available for these species.

COMPARISON OF TERMITE ENDEMISM

Detailed species lists for southern Africa exist only for Namibia and South Africa. These lists were mostly compiled over 25 years, from the 1950s to the 1970s. The species lists for Angola are based on only a few field studies, mainly around Dundo (Weidner 1956, 1961, 1974). In the following years, scientists used the datasets compiled by these individuals (e.g., Muller *et al*. 1997, Uys 2002, Lind *et al*. 2022). More information on endemics was compiled only for

Table 1: *Endemic termite species of Angola.*

Family	**Subfamily**	**Species**	**Locality in Angola**	**Reference**
Hodotermitidae		*Hodotermitidae* sp. nov.	Baba and Virei	Jürgens *et al*. (2021)
Termitidae	Cubitermitinae	*Basidentitermes trilobatus*	Luimbale	Krishna *et al*. (2013, p. 1907)
Termitidae	Cubitermitinae	*Crenetermes elongatus*	Type locality: Cameia	Krishna *et al*. (2013, p. 1910), Weidner (1974)
Termitidae	Cubitermitinae	*Crenetermes mandibulatus*	Type locality: “Vallée marécageuse de la rivière Chonga, affl. Lumege, 100 km à l’est de Vila Luso”	Krishna *et al*. (2013, p. 1910), Weidner (1974)
Termitidae	Apicotermitinae	*Hoplognathotermes angolensis*	Type locality: source of Cuílo River, 400 km SSE of Dundo, near Coemba	Krishna *et al*. (2013, p. 1394), Weidner (1974)
Termitidae	Cubitermitinae	*Noditermes angolensis*	Type locality: Alto Chicapa	Krishna *et al*. (2013, p. 1962), Weidner (1974)
Termitidae	Cubitermitinae	*Ophiotermes gracilis*	Alto Chicapa	Krishna *et al*. (2013, p. 1966), Weidner (1974)
Termitidae	Termitinae	*Pericapritermes machadoi*	Hoque	Krishna *et al*. (2013, p. 2294), Weidner (1974)
Termitidae	Cubitermitinae	*Thoracotermes grevillensis*	Type locality: Muquitixe	Krishna *et al*. (2013, p. 1982), Weidner (1974)
Termitidae	Apicotermitinae	*Trichotermes machadoi*	Type locality: Dundo	Krishna *et al*. (2013, p. 1421), Weidner (1974)

Table 2: *Endemic termite species of Namibia.*

Family	**Subfamily**	**Species**	**Locality in Namibia**	**Reference**
Termitidae	Macrotermitinae	*Microtermes dubius*	Namibia (Damaraland): Dornveld near Windhoek	Krishna *et al*. (2013, p. 1096)
Termitidae	Macrotermitinae	*Odontotermes fockianus*	Okahandja (29°59’S, 16°58’E)	Krishna *et al*. (2013, p. 1174)
Termitidae	Macrotermitinae	*Odontotermes okahandjae*	Okahandja (29°59’S, 16°58’E)	Krishna *et al*. (2013, p. 1240)
Termitidae	Macrotermitinae	*Odontotermes rehobothensis*	Rehoboth	Krishna *et al*. (2013, p. 1258)
Termitidae	Apicotermitinae	*Skatitermes psammophilus*	64.3 km ex Gobabis–Epukiro	Krishna *et al*. (2013, p. 1410)
Termitidae	Apicotermitinae	*Skatitermes watti*	96.5 km ex Rundu–Grootfontein	Krishna *et al*. (2013, p. 1411)
Termitidae	Cubitermitinae	*Lepidotermes amydrus*	64 km ex Windhoek–Göllschau crossroads	Krishna *et al*. (2013, p. 1954)
Termitidae	Cubitermitinae	*Unguitermes unidentatus*	40 km ex Rundu–Grootfontein	Krishna *et al*. (2013, p. 1987)
Rhinotermitidae	Psammotermitinae	*Psammotermes* species complex	Angola, Namibia, South Africa	Gunter *et al*. (2022a, 2023)

South Africa (Muller *et al.* 1997, Janion-Scheepers *et al.* 2016). Muller *et al.* (1997) used distribution maps of 25 species published by Coaton and Sheasby and reported that five of these 25 species are endemic to South Africa. Janion-Scheepers *et al.* (2016) analysed 39 genera and 126 species in South Africa, of which a third are said to be endemic.

The species lists and studies compiled to date indicate that further research in the field is needed to investigate the termite species diversity in Namibia and Angola. Additionally, more species from these countries should be included in molecular studies. This should be done especially for Angola, where only very few termite species have been investigated in molecular and phylogenetic studies, and further field surveys are necessary. Very few, if any, detailed distribution maps are available for the species mentioned in this study.

MOLECULAR STUDIES

Based on molecular studies, termites were grouped with roaches (Lo *et al.* 2000, Inward *et al.* 2007a, Legendre *et al.* 2008, Bourguignon *et al.* 2015). Only a few termite samples from southern Africa were used in molecular studies. Schyra *et al.* (2018) collected termites from five farms in central eastern Namibia and studied the termite community based on mitochondrial data and environmental factors. Gunter *et al.* (2022a, 2023) collected samples of sand termites, *P. allocerus*, at 113 study sites in Angola, Namibia and South Africa. The DNA (deoxyribonucleic acid) barcoding results found high genetic diversity, leading to the conclusion that *Psammotermes* is a species complex. Similar results were shown by others focusing on termite species from eastern Africa. Gunter *et al.* (2022b) could also show morphological differences within the sand termite complex that might show the sand termite to be more than one species. A new termite species for the Hodotermitidae was investigated in Angola with DNA barcoding and detailed morphological methods. These studies with these methods show that a revision of termite diversity in southern Africa, especially, is important. Janion-Scheepers *et al.* (2016) point to other termite genera, e.g., *Odontotermes* and *Microtermes*, that should be revised.

THREATS AND CONSERVATION

Currently, no termite species from southern Africa is listed on the IUCN (International Union for Conservation of Nature) Red List of threatened species. Based on the taxonomic status of the endemics, there is insufficient information and further research is essential.

CONCLUSION

As Janion-Scheepers *et al.* (2016) mentioned, future revisions of termite genera from southern Africa should first focus on current collections because there are thousands of unidentified samples. However, recent new sampling has helped with the molecular classification and determination of the genetic diversity of individual genera. A start was made by Gunter *et al.* (2022a, 2023). Additionally, modern measurement methods (geometric morphometrics, GMM) and digitisation can help to reclassify previous morphological determinations (Jürgens *et al.* 2021, Gunter *et al.* 2022a, 2022b, 2023, Jürgens *et al.* 2023). The literature review shows that Angola has the largest gap in termite sampling and knowledge of species diversity. To make additional statements about endemic occurrences of termites in southern Africa, further field studies need to be carried out.

ACKNOWLEDGEMENTS

We are very grateful to several reviewers for valuable feedback and information.

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The Neuroptera of the highlands and escarpments of Angola and Namibia

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ABSTRACT

Of the 17 families of Neuroptera (lacewings) worldwide, ten families represented by 148 species have been recorded from Namibia, and five families with 36 species from Angola. In Namibia, 17 endemic species are known, of which two are known from high-elevation escarpment localities. However, very few surveys dedicated specifically to Neuroptera have been carried out in Namibia and none in Angola, so it is therefore not possible to assess the importance of the highlands and escarpments to Neuroptera. Recommendations are made for further surveys and research.

Keywords: Angola, escarpments, highlands, lacewings, Namibia, Neuroptera

INTRODUCTION

The Neuroptera, generally referred to as 'lacewings', is one of 28 orders that comprise the animal class Insecta – the insects. The Neuroptera includes 17 families distributed worldwide, with exceptionally diverse faunas in southern Africa, especially in South Africa and Namibia which are both endowed with a rich diversity of families and species, reflecting a recent evolutionary diversification in the southern part of Africa. Ten families of Neuroptera have been recorded from Namibia and five from Angola.

GENERAL BIOLOGY OF NEUROPTERA

The name 'Neuroptera' is derived from the Greek *neuron* which means nerve or sinew and *ptera* which means wings, thus the name means 'nerve-winged insects' referring to the characteristic lace-like pattern of veins in the wings. The adults can be easily recognised by the two pairs of similar diaphanous wings that are held in a roof-like manner over the body when the insects rest with the wings folded. The antennae are also definitive, ranging from long, multi-segmented and filiform, to short and stout, to long and clubbed; features that clearly separate them from the similar-looking dragonflies and damselflies.

Adult lacewings are either predacious with biting and chewing mouthparts, or pollen and nectar feeders having mouthparts adapted for pollen and nectar collection, especially the Nemopteridae.

Lacewing larvae, by contrast, are all obligate predators, with piercing and sucking mouthparts, comprising a complementary combination between the mandibles and the lacinia of the maxillae, the latter slotting into a groove on the ventral surface of the mandibles to form a tubular canal (Figure 1) through which saliva, containing digestive enzymes can pass. The resulting liquid food can then be drawn into the alimentary canal. This feature is a highly evolved, albeit ancient, evolutionary advance which is unique to the Neuroptera, and provides the autapomorphy (i.e., specialised character or trait that is unique to a monophyletic taxonomic group) that defines the lacewings as a monophyletic evolutionary lineage. When a lacewing larva detects prey, it uses its mandibles to seize the prey, and then injects proteolytic enzymes into the prey's body. Once the internal organs are liquified, the resultant fluid is sucked into the alimentary canal of the larva, where further digestion takes place. This digestive process is highly efficient and the larvae do not excrete solid matter during the entire larval life, which can last from a few weeks to several years, depending on the species. Accumulated solid matter is voided as a single meconial pellet when the larva metamorphoses into an adult and emerges from the cocoon. This digestive system has also enabled the Malpighian tubules to depart from their normal excretory

Figure 1: *Lacewing larvae are all obligate predators with piercing and sucking mouthparts, comprising a complementary combination between the mandibles and the lacinia of the maxillae, the latter slotting into a groove on the ventral surface of the mandibles to form a tubular canal. Ventral view of head of* Palpares inclemens.

function and to evolve into silk-producing glands, another unique autapomorphic feature of the Neuroptera. All lacewing larvae spin a spherical silken cocoon in which to pupate. The cocoon protects the metamorphosing larva from parasites and predators, by affording camouflage and reducing dehydration.

While evolutionary advances such as these often lead to very limited possibilities of further biological advances, or even evolutionary cul-de-sacs, lacewings have used them to adapt to a variety of ecological niches, leading to further evolutionary adaptations and advances. They consequently provide numerous examples of habitat, biological and behavioural diversifications, which have ensured their survival by diversification through specialisation.

Habitats and life strategies

The morphological and physiological adaptations have enabled lacewings, especially the larvae, to evolve into a diversity of habitats and life strategies, including: aquatic, where larvae feed on freshwater sponges; semi-aquatic on the borders of streams; as inquilines in the nests of ants and termites; as parasites in spiders' nests; as arboreals, living on branches and foliage; and living in tree holes, caves, rock overhangs and in sand.

Significance of lacewings in ecosystems

Insects are arguably the most significant component of the biodiversity and functioning of ecosystems. They render numerous ecosystem services, ranging from pollination, nutrient recycling through biodegradation of organic matter, to population control of other invertebrates and plants. Most plants are insect-pollinated and all depend on recycled nutrients. Insects are also vital components of the food chains of other animals, especially birds, fishes and other vertebrate animals. Adults of many Neuroptera are pollinators of indigenous plants, with some having co-evolved with certain plants. The larvae are all obligate predators and limit populations of other insects and invertebrates. They are also important indicators of ecosystem health and are a significant component of the biodiversity of many ecosystems, including arid areas.

NEUROPTERA IN NAMIBIA AND ANGOLA

Namibia

Of the 17 worldwide families of Neuroptera, 10 have been recorded from Namibia, with the largest representation being the families usually known as antlions (Myrmeleontidae), thread- and ribbon-wing lacewings (Nemopteridae) and green lacewings (Chrysopidae). Other families represented in Namibia include: silky or moth lacewings (Psychopsidae; three species), owlflies (Ascalaphidae; ten species), dusty lacewings (Coniopterygidae; eight species), sponge flies (Sisyridae; one species), beaded lacewings (Berothidae; three species), raptor lacewings (Rhachiberothidae; three species) and pleasing lacewings (Dilaridae; one species). All of these families are also known from South Africa, and other southern African countries.

The ten families of Neuroptera in Namibia are represented by 148 species. Of these, 50 species – more than one third – were originally described from Namibia and 17 are endemic to Namibia. The remaining 98 taxa are more widespread and are also known from neighbouring countries, especially South Africa, with a few also occurring in Botswana and Angola.

Figure 2 illustrates some of the species which are endemic to Namibia. Of the 17 Namibian endemics, only two, *Tjederia brevicornis* (Nemopteridae, Crocinae) (Mansell 1981) and an undescribed species of *Tricholeon* (Myrmeleontidae) are specifically known from high-lying escarpment localities. *Tjederia brevicornis* occurs in the mountains around Windhoek, while the *Tricholeon* species is the only endemic lacewing known from the Brandberg (Mansell & Aspöck 1990).

Namibian surveys

Until recently, very few surveys dedicated specifically to Neuroptera were carried out in Namibia:

- The British Museum expedition of southern Africa during the 1950s included sites in Namibia. Species from this expedition were described by the great Swedish neuropterist Bo Karl Herman Tjeder, in a series of fundamental works entitled "South African Animal Life" (Tjeder 1960, 1961, 1966, 1967).

- The current author, M Mansell, did surveys during 1970–1990, that were specifically focused on the study of larvae of thread-winged lacewings (Nemopteridae, Crocinae). A wide area was covered, which included mountainous areas in and near Windhoek and the Khomas Hochland (Mansell 1981).

- In 1988, the Third International Symposium on Neuropterology was held in South Africa and included a post-symposium excursion to Namibia during which some of the world's leading exponents of Neuroptera conducted limited collections (Mansell & Aspöck 1990).

Prior to these collections, F Gaerdes and S Braine collected many species of Neuroptera that contributed to the discourse, and provided several specimens upon which new species descriptions were based. More recently, surveys have been carried out by R Becker and A Moller through their Lacewing

Monitoring Project, and by the Skeleton Coast–Iona Transfrontier Park Technology for Conservation (SCIONA) Project of the Namibia University of Science and Technology.

The survey of the Brandberg by E Marais and A Kirk-Spriggs in 1998, is the only study that has specifically inventoried any inselberg or high-lying areas in Namibia. The Neuroptera were particularly well represented in the insect samples from these collections and were comprehensively documented by Mansell (2000). It included a complete list of the Neuroptera known from Namibia at that time, and specifically listed 40 species in seven families from the Brandberg. However, all of the species recorded from the Brandberg occur elsewhere in Namibia, with the exception of a solitary adult specimen of an undescribed species of *Tricholeon*, (Myrmeleontidae) which may prove to be a Brandberg endemic (Mansell 2000).

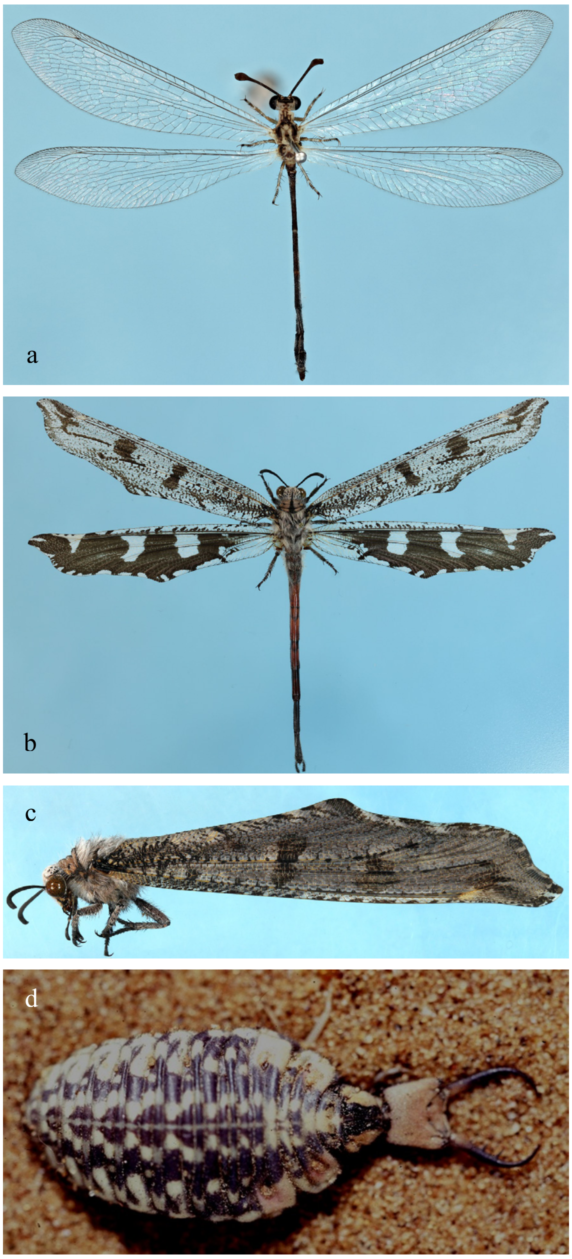

Figure 2: *A selection of Namibian Neuroptera species: a)* Isonemurus longipalpis, *a rare Namibian endemic (photo: M Mansell); b)* Crambomorphus namibicus, *a beautiful Namibian endemic, habitus (photo: M Mansell); c)* Crambomorphus namibicus, *profile, habitus (photo: M Mansell); and d)* Crambomorphus namibicus *larva, rarely encountered (photo: R Oberprieler).*

Angola

There has never been any attempt to survey Angola for Neuroptera, and all of the known species are the result of fortuitous bycatch. The neuropteran fauna of Angola is the most poorly known on the African continent and only five families have been recorded: Myrmeleontidae, Nemopteridae, Psychopsidae, Ascalaphidae and Rhachiberothidae. Most of these are known from very few records, three or fewer, in the literature. Of the 36 species known, 10 (almost one third) were originally described from specimens collected in Angola, and most are still only known by the unique type specimens. Nothing is, unfortunately, known about the Neuroptera of the escarpment areas in Angola.

DEFICIENCIES IN KNOWLEDGE, PRIORITIES FOR RESEARCH AND CONSERVATION

The main deficiency in terms of knowledge of Neuroptera in the highlands and escarpments of Angola and Namibia (HEAN) is obviously the lack of records from the highlands and escarpments of both countries. Without such records no assessment of the importance of the highlands and escarpments is possible. Thus dedicated surveys of specific areas are the first priority for research. Such surveys should target both adult specimens and larvae to gain a better understanding of their biology in particular areas. These could be conducted at the same time as surveys of other organisms, especially insects and other invertebrates. As there is essentially no knowledge of the Neuroptera in Angola in general, a wider priority should be to address this deficiency as well.

The author has expertise on the methods required to collect specimens and material for DNA analyses and could also provide taxonomic and biological information support for future surveys. Some databases are already available to provide some data, especially from Namibia. Regarding Angola, it would also be advisable to determine whether there are any specimens held in collections there, for example, in the museum in Luanda or other repositories.

For Namibian lacewings, an immediate priority would be to locate the larvae of the endemic species of *Tricholeon* in the Brandberg, and to determine through larval collections whether this species also occurs elsewhere. As we already know what the larval requirements of other species in the genus are, this would be relatively easy to achieve in the short term.

ACKNOWLEDGEMENTS

The author is grateful to Rolf Becker, Alma Moller and Vera de Cauwer for enhancing knowledge by facilitating further collections under the auspices of the SCIONA and Namibian Neuroptera projects.

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Ant endemicity in the highlands and escarpments of Angola and Namibia (Hymenoptera, Formicidae)

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-gomez

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ABSTRACT

We present the results of a spatial analysis of available ant distribution records for Angola and Namibia, identifying those species that occur within the highlands and escarpments in these countries. Within this region we document 36 described species and 78 morphospecies, including several potentially undescribed species. From the data available, *Monomorium borlei* Santschi, 1937 is recognised as the one described species endemic to these highlands. The geographic location and topographic complexity of the highlands and escarpments of Angola and Namibia form a highly interesting area, but one that has been vastly undersampled; our results therefore may not reflect the potential endemic fauna of the region. The implementation of both intensive and extensive sampling in the region could reveal a rich ant fauna with a high endemicity potential.

Keywords: Angola, ants, endemism, escarpments, Formicidae, highlands, Namibia

INTRODUCTION

The highlands and escarpments of Angola and Namibia (HEAN) fall within a narrow band running north–south through western and central Angola and Namibia, stretching some 2,700 km between the Congo River in the north and the Orange River in the south. We restrict the focus of our study on two formations within this highland band: inselbergs (isolated mountains) higher than 1,000 masl, and plateaus (flat extensions) that range from 1,600 masl to 2,500 masl (Figure 1). Although they are known to be home to large numbers of endemic plant and vertebrate species, very little is known about the endemicity of invertebrates in these highlands. Here we analyse available data on a key invertebrate group, the ants, to establish what is known and what still needs to be determined for an assessment of their endemicity in this region.

Ant diversity generally follows one of three patterns across elevational gradients: (i) most common is a mid-elevation peak in diversity, but (ii) a purely monotonic decline with increasing altitude, or (iii) constant diversity over about the first 300 m followed by a decline with further increases in altitude have also been reported (Dunn *et al.* 2010, Szewczyk & McCain 2016, Subedi & Budha 2020). In all cases, however, above about 1,500 masl there is a continuous decline with increasing altitude, often dropping to near-zero around 2,500–3,000 masl, depending on whether forest (Longino *et al.* 2019) or grassland (Bishop *et al.* 2014) sites are considered. Accompanying the decline in species richness at high altitude, there is usually also turnover in species composition, sometimes with series of congeneric cryptic species spread along altitude gradients (Delsinne *et al.* 2012). As a result, a relatively small number of species, comprising mainly high-altitude specialists, persist above about 2,000 masl. Such species do not occur at lower altitudes, so their populations are often fragmented and distributed among isolated peaks.

Isolated mountains and high plateaus therefore offer the best chance to find relict and/or endemic ant species in the Afrotropical region. In the intervening lower-lying lands, it is not uncommon for most ant species to have wide distributions, ranging across the West African forests, the Congo Basin, or the savannas of eastern and southern Africa.

Confirming the presence of endemic species in the highlands, though, is extremely difficult. The relatively poor state of taxonomy in the region, combined with the lack of intensive ant sampling over most of the Afrotropics, make it difficult to establish whether or not an apparently restricted species is truly endemic to a small area.

The first obstacle is that, despite huge advances during the past 50 years (due in large part to the extraordinary efforts of Barry Bolton), the taxonomy of many ant genera in the Afrotropical region remains in a very poor state. Of the nine most diverse genera, six (*Camponotus* Mayr, 1861, *Carebara* Westwood,

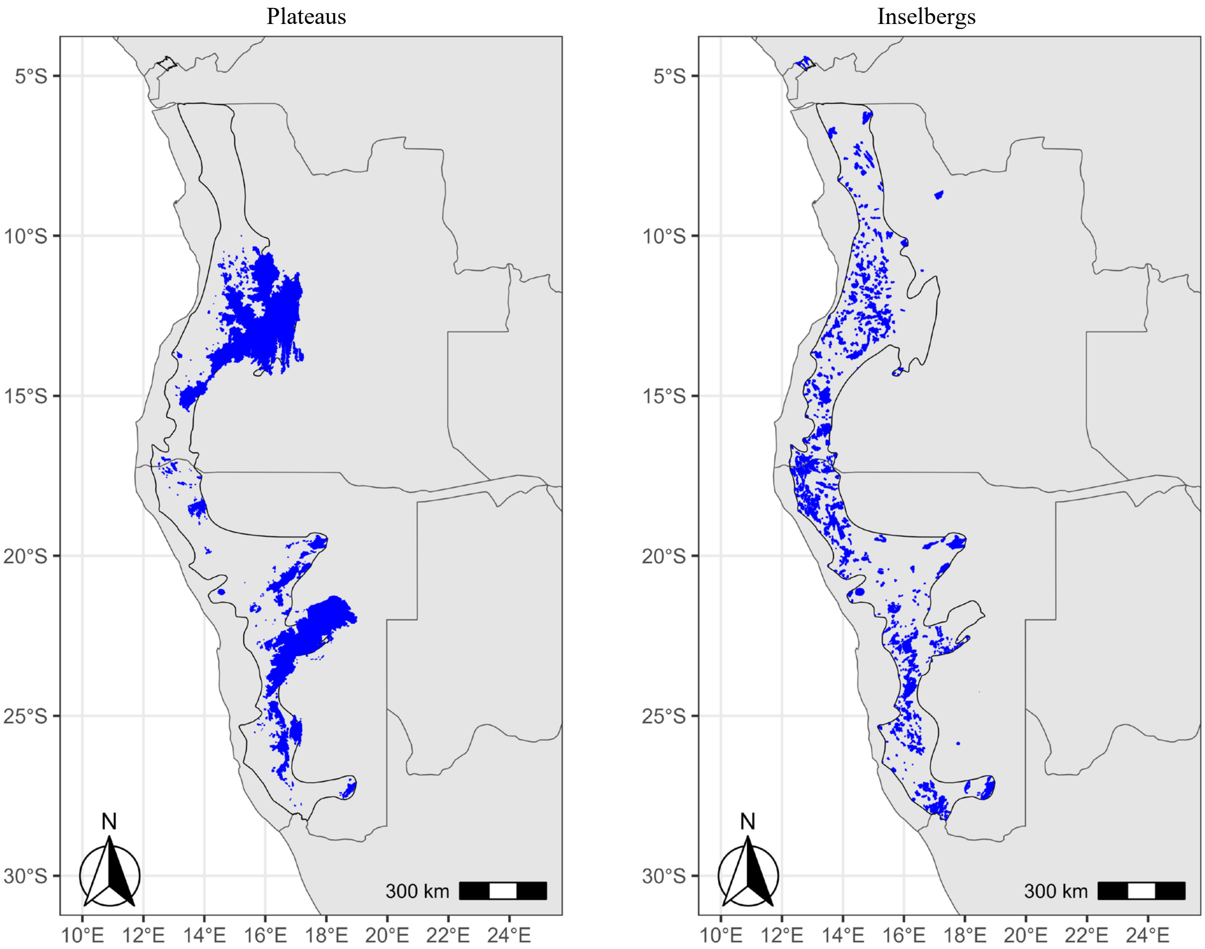

Figure 1: *Plateaus (left) and inselbergs (right), illustrated in blue, of the highlands and escarpments of Angola and Namibia (outlined in black).*

1840, *Crematogaster* Lund, 1831, *Dorylus* Fabricius, 1793, *Lepisiota* Santschi, 1926 and *Pheidole* Westwood, 1839) have never been revised except for small subgroups, and even the three that have undergone complete modern revisions (*Monomorium* Mayr, 1855, *Strumigenys* Smith, 1860 and *Tetramorium* Mayr, 1855) are each known to have several dozen newly discovered undescribed species.

This landscape has experienced some improvements, especially in the last 25 years. A major milestone was the publication by Fisher and Bolton (2016) offering a regional synopsis and keys to genus level for the Afrotropical and Malagasy ant faunas. Since 2000, other publications have provided revisions of entire genera or parts of genera and have added nine new genera: *Boloponera* (Fisher 2006), *Eburopone* (Borowiec 2016), *Erromyrma* (Fisher & Bolton 2016), *Feroponera* (Bolton & Fisher 2008), *Fisheropone* (Schmidt & Shattuck 2014), *Loboponera* (Bolton & Brown 2002), *Parvaponera* (Schmidt & Shattuck 2014), *Ravavy* (Fisher 2009) and *Vicinopone* (Bolton & Fisher 2012). From the start of 2000 to mid-2022, 250 new species have been added in 32 genera, the new species representing a 67% increase over the previously known total (373) in these genera (Bolton 2022).

Despite all these efforts, identifying Afrotropical ants to species level remains challenging, and sometimes impossible, for many genera. As a result, morphospecies are accumulating in collections, waiting to be described.

The second obstacle is a lack of information derived from both intensive and extensive sampling. A combination of both is required to properly assess levels of endemicity. A species known only from, or near its type locality might be: (i) truly restricted to a small region; (ii) widespread but not collected subsequent to its original discovery due to rarity, small size, cryptic lifestyle or a lack of (appropriate) sampling; or (iii) actually widespread and already collected elsewhere, but erroneously described several times under different names from different parts of its range (a common mistake in the late 1800s and early 1900s), and therefore might appear to represent a suite of range-restricted species. Also, the opposite has already happened: species that were thought to be the same have been split, and what once were considered widespread species have each become a series of species with far smaller distributions, potentially including localised endemics. An example is the works on *Lasius* (Linneus, 1758) (e.g., Schär *et al*. 2022), including the endemic mountain ant *Lasius balearicus* Talavera, Espadaler & Vila (Talavera *et al*. 2015), previously identified as *L. niger* (Linneus, 1758). Similar patterns can result from misidentifications.

Which of these scenarios applies to a given species can be determined only with adequate distribution data, the development of well-resolved taxonomy and the cultivation of taxonomic expertise within the region.

Although study of the Afrotropical ant fauna has a long history, survey coverage of the region is extremely patchy. As a continent, Africa has possibly the most poorly known ant fauna on Earth. Most of the historical expeditions are well known, for example, Angola (Santschi), Mt Nimba in Guinea and Côte d'Ivoire (Bernard), Imatong Mountains in South Sudan and Uganda (Weber), Ghana (Bolton), Nigeria (Bolton & Taylor) and Democratic Republic of the Congo (previously Belgian Congo; Wheeler). However, these were conducted more than 50 years ago and were quite limited in extent, duration and collecting methodology. Modern expeditions have included other interesting locations, for example, Angola (Brian L Fisher (BLF) and Peter G Hawkes (PGH)), Central African Republic (BLF), Gabon (BLF), Gambia (Kiko Gómez (KG)), Ghana (BLF, Flávia Esteves (FAE), KG and PGH), Ivory Coast (Kolo Yeo and KG), Kenya (Francisco Hita Garcia and Georg Fischer), Mozambique (BLF, FAE and PGH), Namibia (PGH), Rwanda (KG, Wouter Dekoninck and Venuste Nsengimana), Senegal (KG), South Africa (PGH), Tanzania (PGH), Zambia (BLF, PGH and John LaPolla) and Zimbabwe (PGH), but were also mostly of limited extent and covered only a small proportion of African countries. These expeditions have, however, revealed an extremely rich biodiversity, partially due to the inclusion of modern collecting techniques (e.g., mini-Winkler leaf-litter extraction and canopy fogging) as well as more intense, quantified and replicated sampling.

Even with these modern expeditions, the Congo Basin remains undersampled, as do wide expanses of southwestern Africa, including Angola and much of Namibia. The intensive regional sampling that would be required to evaluate endemicity in the HEAN is entirely lacking. Even in more intensively surveyed countries such as South Africa, where the total number of species recorded is higher than any other non-tropical area of equivalent size, many new species continue to be discovered annually and the distributions of most described species are largely unknown (PG Hawkes, unpublished data).

The main consequence of these two factors is that the actual distribution of most Afrotropical ant species is unknown. For this reason, declaring a species ‘endemic’ is often difficult to justify, even when a name can be applied to a specimen, or it can be recognised as a new species. This is particularly true in the highlands and escarpments of Angola and Namibia.

MATERIALS AND METHODS

To assess ant species richness from the HEAN, we compiled specimen records from Namibia and Angola from the online resources AntWeb (AntWeb 2021) and AntMaps (Janicki *et al*. 2016, Guénard *et al*. 2017, AntMaps 2021), our own collections and available publications (Santschi 1930, Robertson 2000). From these resources, we compiled 7,529 specimen records for both countries and georeferenced localities when needed. We then performed spatial queries against topography with the sf package in R (Pebesma 2018) to select the species present in the HEAN (Table 1, Figure 2). This list was then checked against global species distributions available at AntMaps (Janicki *et al*. 2016, Guénard *et al*. 2017, AntMaps 2021) to find rare or endemic species.

RESULTS

Data in the studied localities are extremely scarce (Table 1, Figure 2) and, based on our spatial assessment, only 36 described species were recorded from the HEAN:

Acropyga arnoldi Santschi, 1926
Anochetus levaillanti Emery, 1895
Anoplolepis steingroeveri (Forel, 1894)
Bondroitia lujae (Forel, 1909)
Camponotus vestitus (Smith, 1858)
Cardiocondyla emeryi Forel, 1881
Crematogaster melanogaster Emery, 1895
Euponera brunoi (Forel, 1913)*
Lepisiota monardi (Santschi, 1930)
Megaponera analis termitivora (Santschi, 1930)
Melissotarsus emeryi Forel, 1907
Messor denticornis Forel, 1910
Monomorium australe Emery, 1886
Monomorium borlei Santschi, 1937
Monomorium esharre Bolton, 1987
Monomorium exiguum Forel, 1894
Monomorium fugelanum Bolton, 1987
Monomorium havilandi Forel, 1910
Monomorium schultzei Forel, 1910
Monomorium vatranum Bolton, 1987
Monomorium viator Santschi, 1923
Myrmicaria irregularis Santschi, 1925

Myrmicaria natalensis obscuriceps Santschi, 1937
Ocymyrmex velox Santschi, 1932
Paratrechina zanjensis LaPolla *et al.*, 2013
Pheidole megacephala duplex Santschi, 1937
Pheidole tenuinodis Mayr, 1901
Platythyrea cribrinodis (Gerstäcker, 1859)
Plectroctena subterranea Arnold, 1915
Promyopias silvestrii (Santschi, 1914)
Tapinoma danitschi Forel, 1915
Tetramorium clunum Forel, 1913
Tetramorium khyarum Bolton, 1980
Tetramorium rufescens Stitz, 1923
Tetramorium subcoecum Forel, 1907
Trichomyrmex robustior (Forel, 1892)

* Listed as *Euponera sharpi* Forel, 1901, which is an Indomalayan species, but almost certainly represents a misidentification of the very similar and widespread Afrotropical species, *Euponera brunoi* (Forel, 1913).

Table 1: *Total numbers of ant specimen records compiled from all resources (online, authors' collections and publications), and those restricted to plateaus and inselbergs within the highlands and escarpments of Angola and Namibia.*

	Namibia	Angola	Total
All records	5,524	2,005	7,529
Plateaus	985	523	1,508
Inselbergs	810	271	1,081

In addition, 78 morphospecies, some of which may turn out to be described species, but many of which are likely to be new to science, have been recorded within the HEAN, listed by genus in Table 2.

With the limited data available, one described species is currently known from within the HEAN and nowhere else: *Monomorium borlei* (Figure 3) from Sangueve, Angola (13.89S, 15.82E). There are three good candidates to be new species in the genera *Anochetus*, *Lioponera* and *Strumigenys*. However, considering that Robertson (2000) found nine *Leptanilla* species on the Brandberg in Namibia, and in 2023 there are still only three described *Leptanilla*

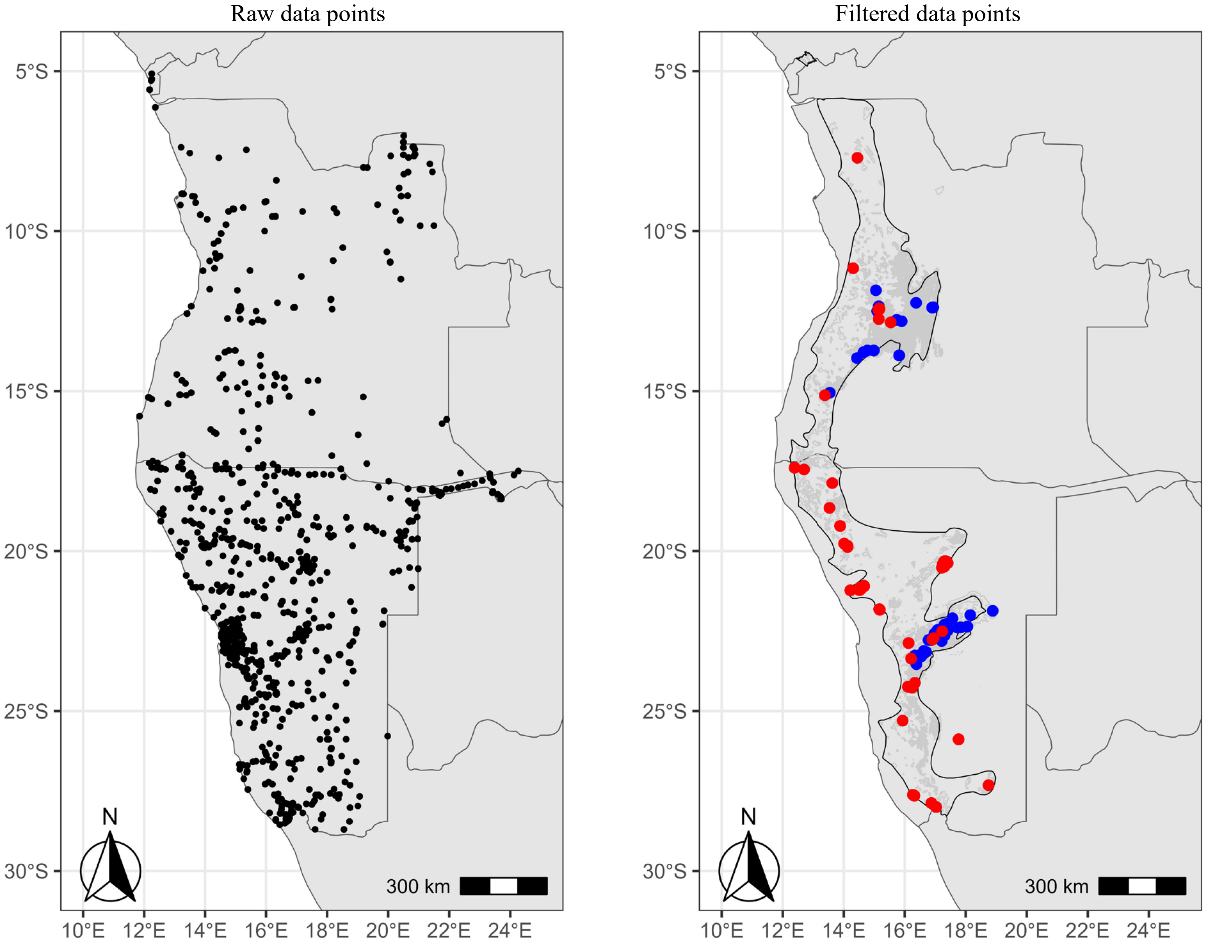

Figure 2: *Raw ant data for Angola and Namibia (left) and records filtered to the inselbergs (red dots) and plateaus (blue dots) of the highlands and escarpments of Angola and Namibia (right).*

Table 2: *Numbers of morphospecies of ants recorded in the highlands and escarpments of Angola and Namibia.*

Genus	**Number of morphospecies**
Aenictus	1
Anillomyrma	1
Anochetus	2
Baracidris	1
Bothroponera	2
Calyptomyrmex	1
Camponotus	8
Cardiocondyla	1
Carebara	2
Crematogaster	2
Dorylus	1
Euponera	1
Hypoponera	7
Leptanilla	10
Leptogenys	1
Lioponera	1
Megaponera	1
Mesoponera	1
Monomorium	11
Nylanderia	1
Paraparatrechina	1
Pheidole	4
Plagiolepis	2
Polyrhachis	1
Solenopsis	2
Stigmatomma	1
Strumigenys	1
Tetramorium	10

species in the Afrotropical region (*L. africana* Baroni Urbani, 1977, *L. australis* Baroni Urbani, 1977 and *L. boltoni* Baroni Urbani, 1977, none of which has been recorded from Angola or Namibia), clearly a minimum of six undescribed *Leptanilla* species inhabit the Brandberg alone. It is likely that there are many endemic ant species within the inselbergs and plateaus of the HEAN. At present, these are hidden within unidentified material collected to date, or have never been sampled and are awaiting discovery.

Monomorium borlei is known only from the type series collected at about 1,600 masl by Monard in 1933, and there is no information on its biology or habitat in the original description by Santschi (1937). For this, and any other species identified as being candidate endemics, studies of habitat requirements and biology would help to determine their likely sensitivity to influences such as habitat transformation and climate change.

DISCUSSION

Little is known about the ant fauna of Angola and Namibia. AntMaps (2021) listed 308 indigenous ant taxa for Angola and 194 for Namibia. Combining the lists gave a total of 440 species and subspecies for the two countries, with only 62 species common to both. In comparison, South Africa, with a land area of 1,221 million km^2, just over half the combined area

Figure 3: *Holotype of* Monomorium borlei *Santschi, to date known only from Sangueve, Angola. A) Full-face view, B) profile view, C) dorsal view and D) labels. Images of CASENT0913564 photographed by Z Lieberman, from AntWeb (2021).*

(2,071 million km^2) of Angola and Namibia, has a far higher total with 764 species and subspecies. To develop a clearer picture of both true diversity and endemicity of the ant fauna of Angola and Namibia, more intensive long-term sampling expeditions at both local and regional levels are needed. This needs to be combined with thorough taxonomic investigations of material that cannot be identified using currently available identification resources.

Southwestern Africa has been dramatically undersampled, so our knowledge of both the overall diversity and the degree of endemicity of the ant fauna of the HEAN is extremely limited. Based on the available data we think that these highlands and escarpments have the potential to house a rich endemic fauna. Indeed, despite limited sampling, several species currently await formal description. Our findings agree with those of Robertson (2000) on the Brandberg (Namibia), as he found that even in ant genera with well-developed taxonomy, 30% of the species were potentially new to science. Interestingly though, Kass *et al.* (2022) predict that the northern, but not the southern, parts of the HEAN are expected to become a centre of ant species richness under increased sampling. Additionally, apart from a small area around Windhoek in central Namibia, no area of this region is predicted to become a centre of ant rarity or endemicity, and the current very small areas of empirical ant rarity within the HEAN are mostly predicted to fall away with further sampling. Extensive and intensive sampling of the region would provide interesting tests of these predictions.

Intensive ant-sampling expeditions, especially in the least explored areas, such as the high mountains and plateaus, would also massively increase the known biodiversity. However, this research should ideally be complemented by surveys at mid and low elevations in the surrounding areas to determine which of the species present at higher altitudes also occur lower down and are likely to be widespread.

ACKNOWLEDGEMENTS

We would like to thank Wouter Dekoninck for thoughtful comments and valuable suggestions on an earlier draft of this paper.

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The endemic butterflies of Angola and Namibia and their evolutionary implications

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-gardiner

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ABSTRACT

The currently described endemic butterfly species and subspecies to Angola and Namibia are presented together with their known distributions. This butterfly fauna has been placed into the biogeographic units of Carcasson (1964) and Burgess *et al.* (2004). Aspects of the evolution and biogeography of the fauna, such as their association with other mountainous areas of Africa and their linkage to dry areas of East Africa, are discussed. The information suggests large gaps in our knowledge of the Angolan highland fauna. The importance of utilising such fauna for identifying conservation priorities in these two countries is highlighted.

Keywords: Angola, biogeography, butterfly, endemism, escarpments, evolution, highlands, Lepidoptera, Namibia

INTRODUCTION

Angola and Namibia form a geographical region of great biodiversity interest (e.g., Huntley *et al.* 2019). The unique and interesting biodiversity of Angola has been demonstrated for plants (Goyder & Gonçalves 2019) and a few animal groups, mostly the large and charismatic vertebrates: fish (Skelton 2019), amphibians (Baptista *et al.* 2019), reptiles (Branch *et al.* 2019), birds (Dean *et al.* 2019) and mammals (Beja *et al.* 2019). While the above authors all consider their group to be understudied in Angola, this is even more pronounced for the group with the most species described globally: the invertebrates.

Butterflies belong to the insect order Lepidoptera, or scale-winged insects. The butterflies have been traditionally grouped under the term Rhopalocera which is allied to the more recent superfamily name Papilionoidea. The Papilionoidea includes the following butterfly families: Hesperiidae, Papilionidae, Pieridae, Lycaenidae, Riodinidae and Nymphalidae. It should also include the moth-like butterflies – the Hedylidae – which do not occur in Africa and are not dealt with here.

The recording of butterfly species from Angola effectively began in the 1860s (Mendes *et al.* 2019) with a noticeable increase in records during the first ten years and then a constant increase over the next 70–80 years. During the period of political unrest, from about the 1960s to the 1990s, the number of species recorded decreased but then picked up once the country had stabilised (Mendes *et al.* 2019). Recording butterfly species in Namibia also began in the mid-19th century and from about this time the area was documented as part of southern Africa, for instance any species known from Namibia was documented by Ronald Trimen in his "Rhopalocera Africae Australis; a catalogue of South African butterflies" (Trimen 1862–1866). This trend continued up until the 1990s with the publication of "Pennington's butterflies of southern Africa" (Pringle *et al.* 1994). The level of invertebrate sampling in Angola remains low compared to most other African countries (e.g., Ferreira 1971, Serrano & Capela 2015) probably largely due to the fear of land mines, which are still being cleared, and poor infrastructure especially in rural areas.

In Huntley *et al.*'s (2019) "Biodiversity of Angola" the Odonata – dragonflies and damselflies – (Kipping *et al.* 2019) and the Papilionoidea – all butterflies except Hedyloidea – (Mendes *et al.* 2019) are presented as indicator groups for the invertebrates. Kipping *et al.* (2019) provided a revised checklist for the Odonata comprising 260 species and discussed the history of research and the biogeography of the fauna, indicating the rate of endemism (7%) and the potential for further discoveries. The national total for Angola has now risen to 288 species, of which 12% are endemic (Huntley *et al.* 2023), which makes Angola one of the richest countries for Odonata in Africa. The evolution and biogeography of the invertebrates, particularly the butterflies, is dealt with in less detail than the vertebrates but useful checklists with endemism were provided. Mendes *et al.* (2013a, 2013b) have provided some taxonomic and ecological information on the Angolan butterflies.

In this paper, we document the present knowledge on the geographical distribution of the endemic butterflies (Papilionoidea) of Angola and Namibia. We also provide some insights into possible factors influencing the evolution of the butterfly fauna in this region.

NUMBER OF SPECIES AND ENDEMISM

There are currently about 4,500 described species of butterflies in the Afrotropical Region (Williams 2022). Of these, 800 species (ca. 18% of the Afrotropical fauna) have been recorded from Angola (Mendes *et al*. 2019, Williams 2022) and nearly 220 species (ca. 5%) from Namibia (Table 1; Figure 1).

Fifty-seven species have been recorded from Namibia but not from Angola, giving a total of 857 species for Angola and Namibia combined. Of these, 76 species are endemic or near-endemic resulting in 6.5% endemism for the two countries (Table 1). Presently Angola has an endemism rate of 5.3% (Figures 2–4, also see Mendes *et al*. 2019 for further data on endemism in Angola) and Namibia 3.6% (Table 1).

Table 1: *The number of butterfly species and endemics for Angola, Namibia and selected African countries. Numbers in brackets indicate that the number is for the combination of species and subspecies. Also provided is endemism for a few other Angolan invertebrate taxa: Cicindelinae, Paussini and Odonata.*

Taxon	**Country**	**Number of species**	**Number of endemic species**	**% of endemic species**	**Source**
Rhopalocera (butterflies)	Angola	800	42 (64)	5.3 (8)	Mendes *et al*. 2019
	Namibia	220	8 (14)	3.6 (6.4)	Williams 2022
	Angola & Namibia	857	76	6.5	Williams 2022
	Kenya	900	63	7	Williams 2022
	Zimbabwe	527	22	4.2	African Butterfly Database 2023
	Zambia	940	28	3	Williams 2022
	Tanzania	1,583	135	8.5	Williams 2022
	South Africa	668	167	25	Woodhall 2020
Cicindelinae (tiger beetles)	Angola	(89)*	(31)	(33.3)	Serrano & Capela 2013
Paussini (ant nest beetles)	Angola	46	11	22	Serrano & Capela 2015
Odonata (dragonflies)	Angola	260	18	7	Kipping *et al*. 2019

*74 species and 15 subspecies

Figure 1: *A selection of butterflies endemic to Angola: a)* Brakefieldia ochracea, *a central highland endemic found in the grassland–woodland mosaic; b)* Mashunoides carneiromendesi, *a monobasic endemic genus occurring in wetland areas on the eastern parts of the central highland watershed; c)* Acraea bellona, *a widespread endemic from the central highlands of Angola to the eastern watershed, with one doubtful record from western Zambia; d)* Zeritis krystna, *a small, strikingly marked, widespread endemic on and east of the Angolan highlands. Photos: Alan Gardiner, except* Acraea bellona: *Jonathan Francis.*

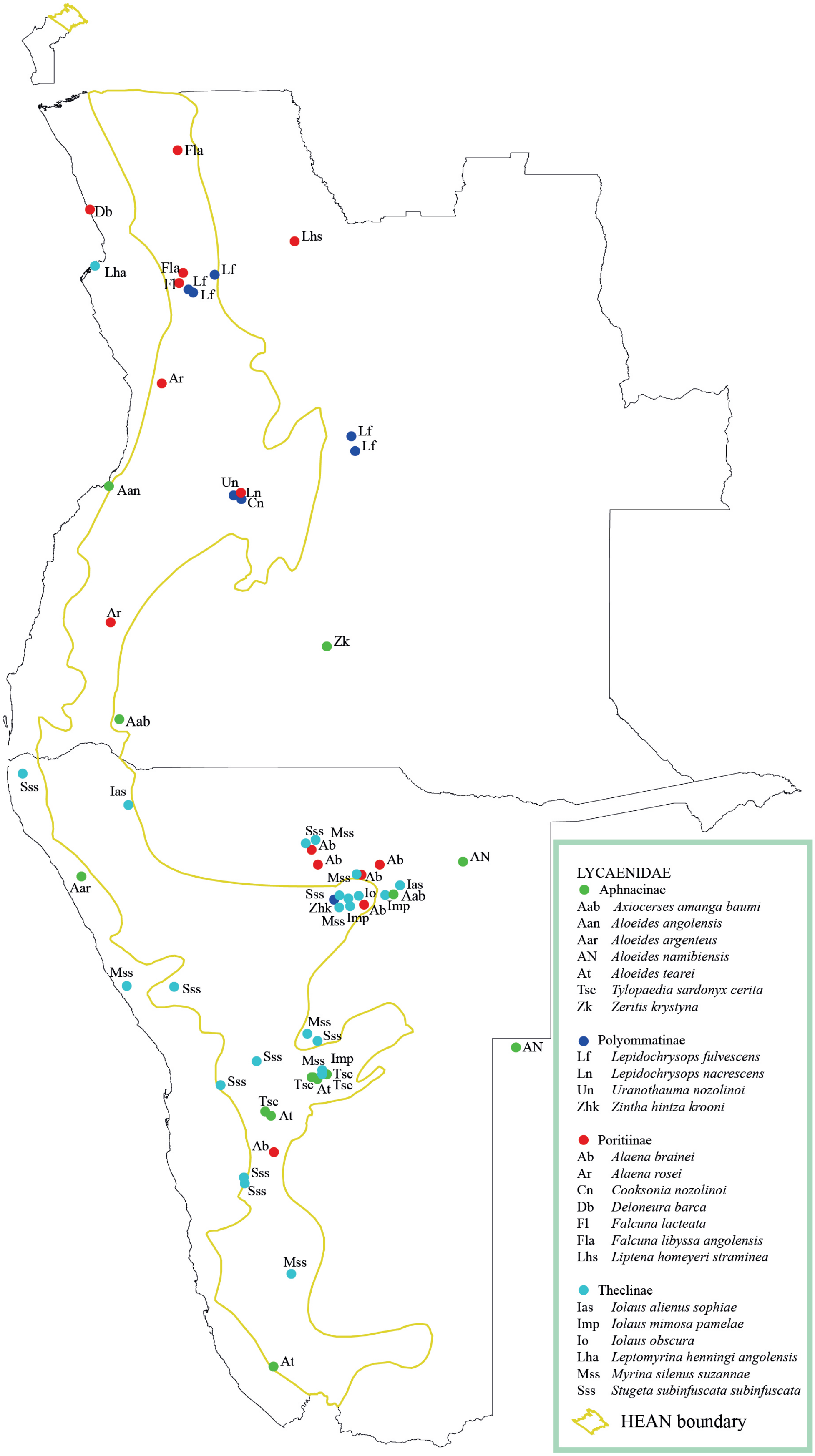

Figure 2: *Locations of endemic butterflies of the family Lycaenidae recorded in Angola and Namibia: subfamilies Aphnaeinae, Polyommatinae, Poritiinae and Theclinae. Due to the low level of sampling there is some uncertainty as to which of the endemic species are associated with highlands. There is more butterfly information for Namibia than Angola, although Namibia remains less surveyed than South Africa, Botswana and Zimbabwe. (HEAN = highlands and escarpments of Angola and Namibia.)*

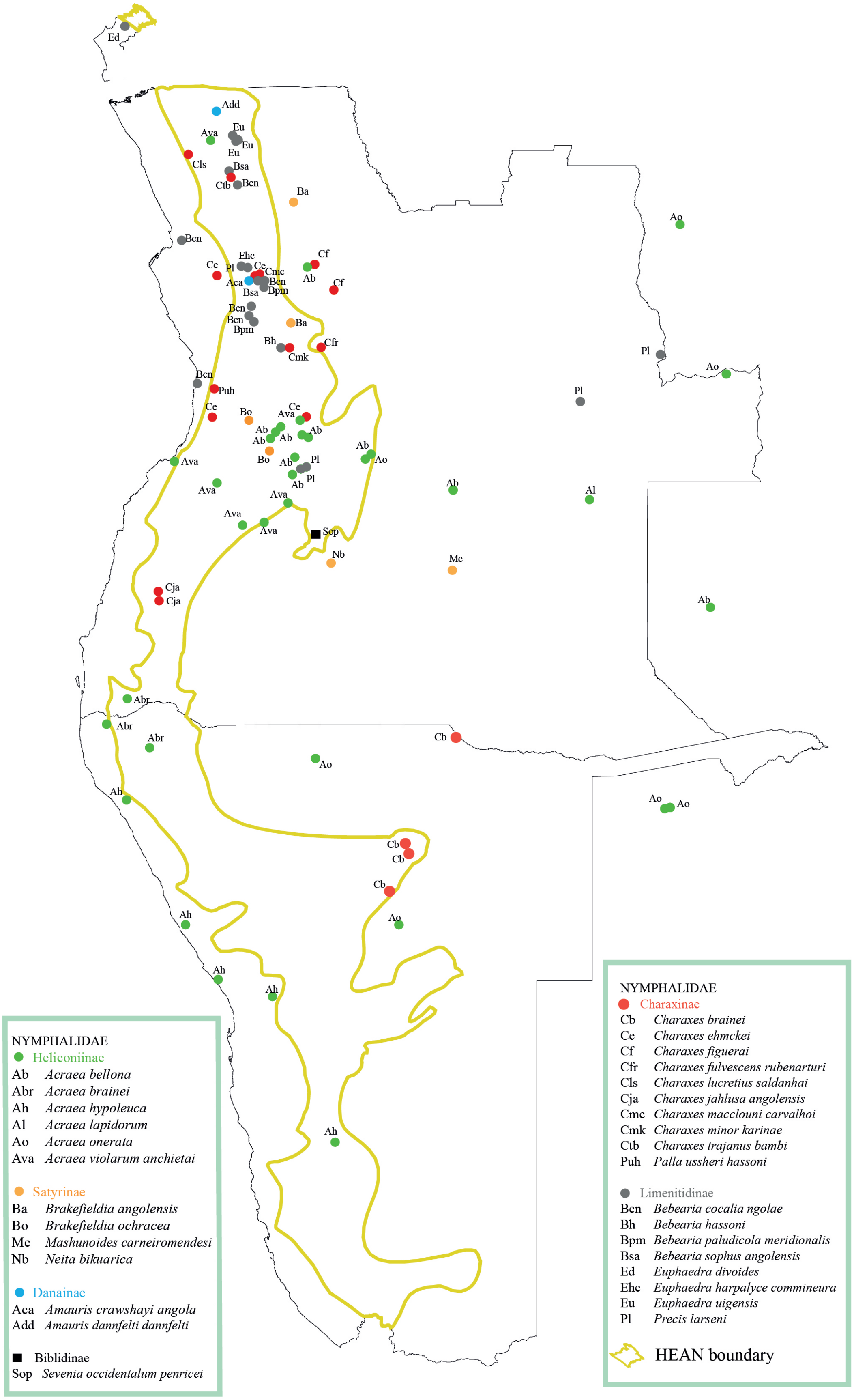

__Figure 3:__ Locations of endemic butterflies of the family Nymphalidae recorded in Angola and Namibia: subfamilies Heliconiinae, Satyrinae, Danainae, Biblidinae, Charaxinae and Limenitidinae. Due to the low level of sampling there is some uncertainty as to which of the endemic species are associated with highlands. There is more butterfly information for Namibia than Angola, although Namibia remains less surveyed than South Africa, Botswana and Zimbabwe. (HEAN = highlands and escarpments of Angola and Namibia.)

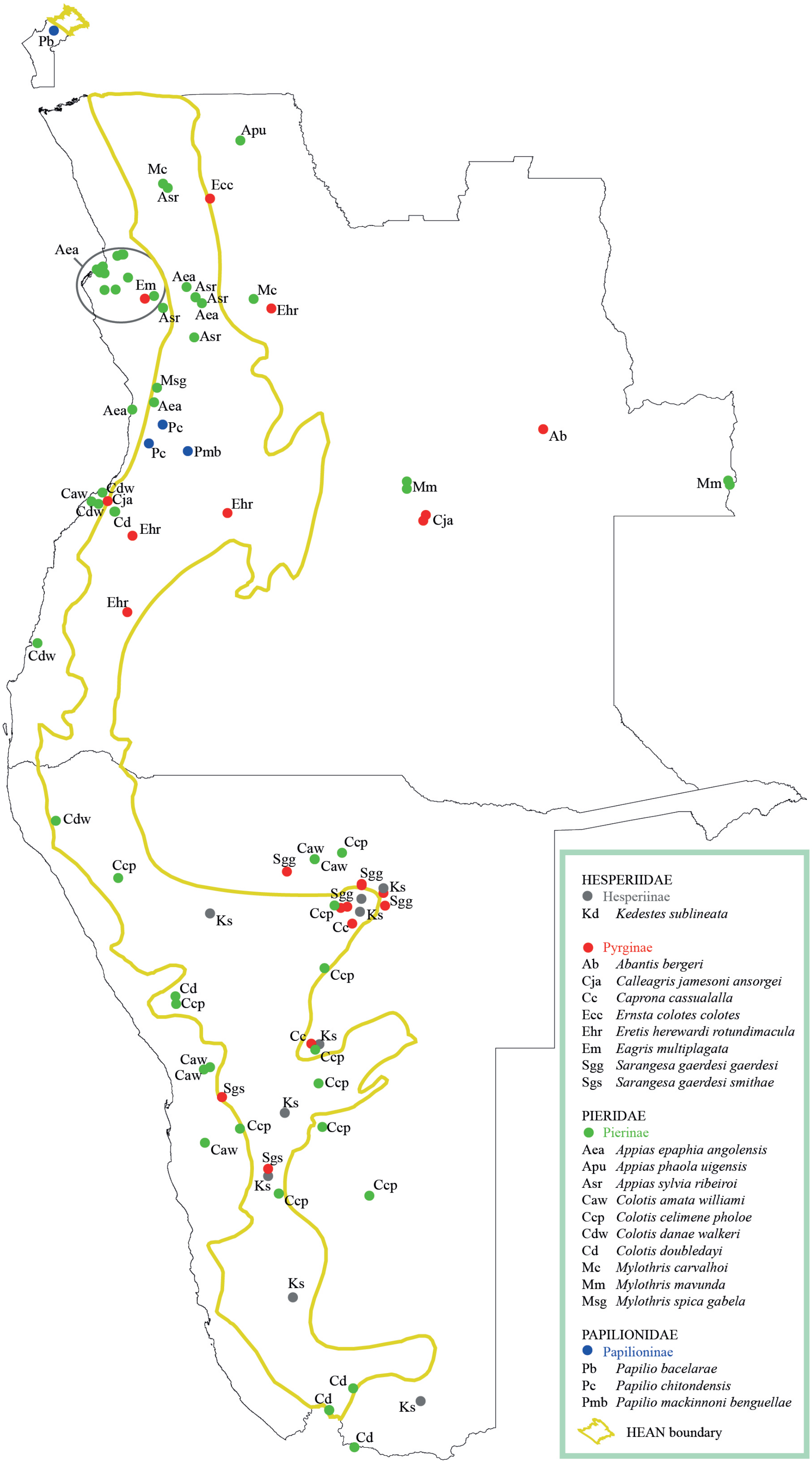

Figure 4: *Locations of endemic butterflies of the families Hesperiidae, Pieridae and Papilionidae recorded in Angola and Namibia: subfamilies Hesperiinae and Pyrginae (family Hesperiidae); subfamily Pierinae (family Pieridae); and subfamily Papilioninae (family Papilionidae). Due to the low level of sampling there is some uncertainty as to which of the endemic species are associated with highlands. There is more butterfly information for Namibia than Angola, although Namibia remains less surveyed than South Africa, Botswana and Zimbabwe. (HEAN = highlands and escarpments of Angola and Namibia.)*

High levels of endemism are typically an indication of the presence of unique habitats. Compared to the butterfly endemism of some other African countries, Angola has an endemism slightly higher than Zimbabwe (ca. 4.2%) and Namibia slightly higher than Zambia (ca. 3%). Tanzania, with its eastern arc of mountains, has an endemism of ca. 8.5% while Kenya, with a similar number of species to Angola, has an endemism of ca. 7%. South Africa has an extremely high level of endemism – about 25% – mostly due to the Western Cape's Mediterranean climate, the Cape Fold Mountains and the Drakensberg. Comparing the endemism of a few other invertebrate groups from Angola (Table 1), both the Cicindelinae (33.3%; Serrano & Capela 2013) and Paussini (22%) have very high levels of endemism while the Odonata have 12% endemism (Kipping *et al.* 2023). The lower level for the Odonata is expected, as many species are widespread and have good flying and dispersal capabilities. However, butterfly endemism is lower than might be expected from the topography, climatic conditions and vegetation types, suggesting the area is undersampled.

SUB-SAHARAN BUTTERFLY BIOGEOGRAPHY

Before we discuss the biogeography of the Angolan and Namibian butterflies we need to put it into the context of Africa. Carcasson (1964) was the first person to undertake a detailed analysis of the distribution of Africa's sub-Saharan butterfly fauna (Afrotropical Region). Carcasson dealt with 2,674 species in his publication. Even though the number of described species in sub-Saharan Africa is now about 1.7 times higher, his study remains the benchmark for the biogeography of Africa's butterfly fauna (Larsen 2005). Carcasson (1964) suggested the butterfly faunas were associated with the various vegetation types (habitats) and using the 1959 vegetation map of Africa (Aubréville *et al.* 1959) he produced his faunistic regions (Figure 5). Carcasson's divisions are briefly described below; many of the main divisions are represented in Angola and Namibia.

Carcasson's divisions

The geographic divisions of the sub-Saharan African butterflies (modified from Carcasson 1964) are shown in Figure 5.

I) Sylvan Subregion

This subregion comprises all evergreen forests on the continent and is divided into two divisions, lowland and highland forest. Angola has both Lowland and Highland Forest.

A. Lowland Forest
The separation of the Lowland and Highland Forest is around 1,500 masl at the equator, however the

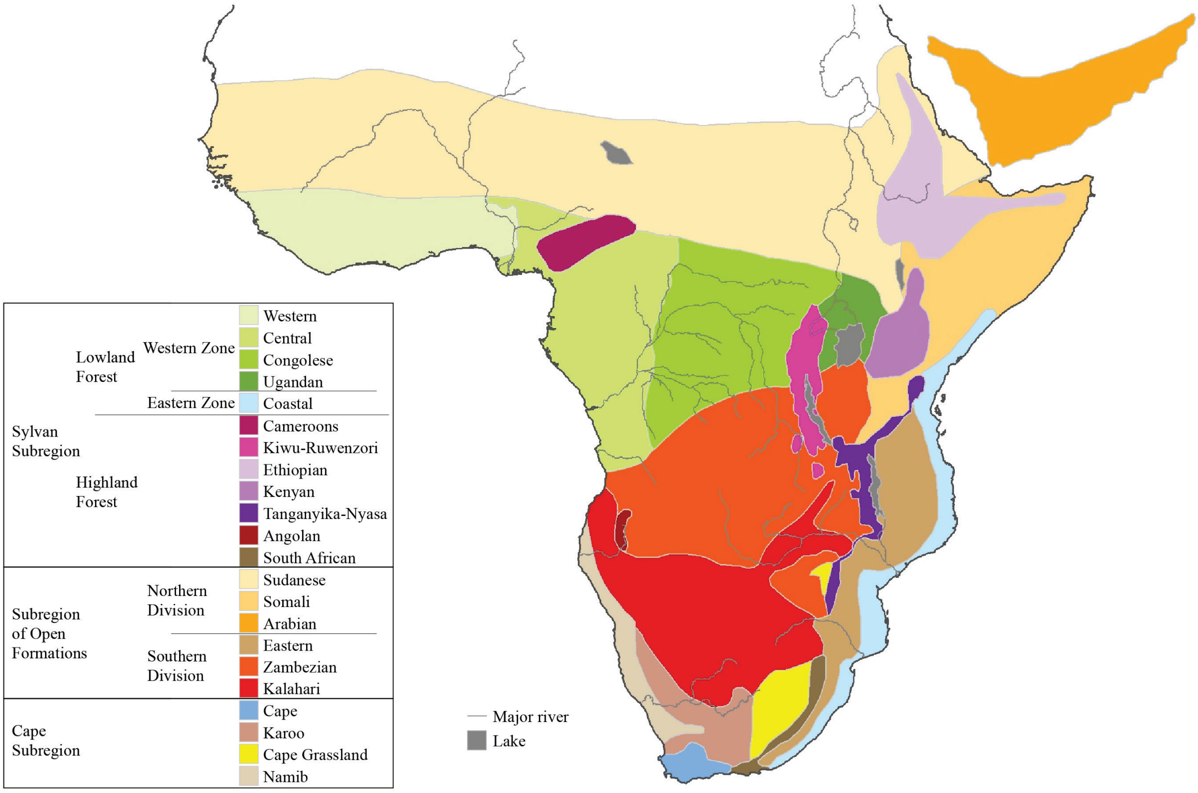

Figure 5: *Geographic divisions of the sub-Saharan African butterflies (modified from Carcasson 1964).*

Highland Forest progressively descends to sea level at 33°S (the Knysna forests of the Eastern Cape, South Africa). There is some vertical overlap of the two divisions. The greatest density of both butterfly species and individuals occurs in the Lowland Forest. The Lowland Forest was subdivided into Western and Eastern zones. The Eastern or Coastal Zone comprises all the Lowland Forest east of the African eastern highlands, from Kenya to KwaZulu-Natal. The Eastern Zone is comparatively species-poor compared to the Western Lowland Forests. The Western and Eastern Lowland Forests have a number of genera in common such as *Euphaedra*, *Cymothoe*, *Bebearia*, *Pentila* and *Ornipholidotos*, indicating a link between the two; at one or more times they were probably linked from the Democratic Republic of the Congo (DRC) and Angola through northern Zambia, Tanzania, northern Malawi and the neighbouring areas of Mozambique.

The Western Lowland Forest comprises the entire Central and West African lowland forest block from Sierra Leone (9°N) in the west to Kakamega Forest in western Kenya. This division is the most species-rich. It has four zones: i) Western, ii) Central, which includes part of Northern Angola, iii) Congolese (DRC) and iv) Ugandan (Figure 5).

B. Highland Forest

Many of the highland forest species are related to lowland species and the various patches of highland forest species have strong affinities with one another. This suggests that, at one or more times, they were more continuous with one another than they are today. Isolation periods provide ideal conditions for speciation (as is seen for other groups e.g., Roy 1997). For the East African highland forests it has also been suggested that dispersal of a species from one forest to another has resulted in minor radiations (de Jong & Congdon 1993). Both means of speciation are possible. Carcasson divided the Highland Forest into seven zones: i) Cameroons Zone; ii) Kiwu–Ruwenzori Zone; iii) Ethiopian Zone; iv) Kenyan Zone; v) Tanganyika–Nyasa (Tanzania–Malawi–Zimbabwe) Zone; vi) Angolan Zone; and vii) the South African Zone. It is worth noting that even at this time Carcasson realised the uniqueness of the Angolan highlands.

II) Subregion of Open Formations

"This subregion includes a great variety of vegetation types, in fact all formations other than closed canopy evergreen forest, montane grassland and moorland, from about 20°N to about 25°S" (Carcasson 1964). This was divided by Carcasson into a Northern and a Southern division. The Northern division contained three zones: i) Sudanese; ii) Somali; and iii) Arabian. The Southern also had three zones: iv) Eastern; v) Zambezian; and vi) Kalahari. Angola has large areas of Zambezian but also some Kalahari (Figure 5), while Namibia has some Zambezian and a significant amount of Kalahari.

The Zambezian Zone is the largest southern area of open formations and, for an open formation, the richest in species. It is mostly high plateau of an elevation between 1,100–1,500 masl. It stretches from southwest Tanzania through Zambia, Shaba Province of DRC, most of the Highveld of Zimbabwe to Angola in the west. Soils are mainly sandy and acidic, and much of the vegetation is deciduous woodland of varying density. The predominant vegetation is Miombo with dominant trees being the numerous species of *Brachystegia* and *Julbernardia*, together with *Uapaca*, *Monotes*, *Parinari* and with *Cryptosepalum pseudotaxus*, *Guibourtia coleosperma* and *Marquesia*. Annual average rainfall is up to 1,500 mm in the north, but there is a long dry season.

The Kalahari Zone is much drier than the Zambezian Zone. It stretches from the northern provinces of South Africa, southwestern Zimbabwe, Botswana, Namibia and parts of southern Angola. Most of the zone consists of Subdesert Steppe, with *Vachellia* [previously *Acacia*] spp. predominant and other genera such as *Euclea*, *Commiphora*, *Combretum*, *Terminalia*, *Boscia* and *Cadaba* being common.

III) Cape Subregion

This subregion was subdivided into four zones: i) the Namib Zone, which is the extremely arid coastal belt of western South Africa, Namibia and southern Angola; ii) the Karoo Zone, a vast area covered by low-growing, mostly succulent vegetation (Aizoaceae) which penetrates Namibia in the south; iii) the Cape Zone, the winter rainfall areas of the Western Cape Province which are home to a very characteristic vegetation, the Fynbos or Cape Maquis and which have a Mediterranean appearance; and iv) Cape Grassland Zone, the high-level grasslands which occupy much of the plateau of the Orange Free State, KwaZulu-Natal, Mpumalanga, Limpopo, as well as mountains in Lesotho and the Cape (Eastern and Western Cape provinces). The fauna of this subregion has a high level of endemism in butterflies especially in the Lycaenidae and Satyrinae (see Cottrell 1978, 1985).

BIOGEOGRAPHY OF THE ENDEMIC ANGOLAN AND NAMIBIAN BUTTERFLY FAUNA

Carcasson's butterfly ecogeographic divisions or zones, although less detailed, tie in with the ecoregions produced by Burgess *et al.* (2004); the two are compared for Angola and Namibia in Table 2. We have used the faunistic zones (ecoregions) of Burgess *et al.* (2004) in Table 2 and

Figure 6 to describe and form a guide to the biogeography of the Angolan and Namibian butterfly fauna. Ecoregion 43 Western Congolian Forest-Savanna Mosaic and ecoregion 42 Southern Congolian Forest-Savanna Mosaic penetrate, in a mixed form, into northern Angola (Figure 6; 42 & 43), this area is characterised by lowland forest species such as: *Coeliades chalybe*, *Pyrrhochalcia iphis desjongi*, *Papilio zalmoxis*, *Papilio antimachus*, *Papilio mechowi mechowi*, *Graphium tynderaeus*,

Table 2: *Biogeographic units of Burgess* et al. *(2004) and Carcasson (1964) with the known associated endemic butterfly taxa in Angola and Namibia.*

Burgess Ecoregion	**Carcasson**	**Endemic taxa**
32 Zambezian *Cryptosepalum* Dry Forests	Zambezian	**Species**: *Mylothris mavunda*
42 Southern Congolian Forest-Savanna Mosaic 43 Western Congolian Forest-Savanna Mosaic	Congolese Lowland Forest Central Lowland Forest	**Species**: *Bebearia hassoni*, *Euphaedra divoides*, *E. uigensis, Falcuna lacteata*, *Mylothris carvalhoi*, *M. gabela* **Subspecies**: *Amauris crawshayi angola*, *Appias phaola uigensis*, *A. sylvia ribeiroi*, *Bebearia cocalia ngolae*, *B. paludicola meridionalis*, *B. sophus angolensis, Charaxes fulvescens rubenarturi*, *C. lucretius saldanhai, C. macclouni carvalhoi*, *C. minor karinae*, *C. trajanus bambi*, *Euphaedra harpalyce commineura*, *Falcuna libyssa angolensis*, *Palla ussheri hassoni*, *Sevenia occidentalium penricei*
49 Angolan Miombo Woodlands	Zambezian	**Species**: *Abantis bergeri*, *Acraea bellona*, *A. lapidorum*, *Cooksonia nozolinoi*, *Deloneura barca*, *Lepidochrysops fulvescens*, *L. nacrescens, Zeritis krystyna* **Subspecies**: *Axiocerses amanga baumi*, *Calleagrius jamesoni ansorgei*, *Charaxes jahlusa angolensis*, *Cigaritis modestus modestus*, *Liptena homeyeri straminea*
43 Western Congolian Forest-Savanna Mosaic 49 Angolan Miombo Woodlands 81 Angolan Scarp Savanna and Woodlands	Central Lowland Forest Zambezian	**Species**: *Brakefieldia angolensis*, *Charaxes ehmckei*, *C. figueirai, Neita bikuarica*, *Precis larseni* **Subspecies**: *Appias sylvia ribeiroi*
82 Angolan Montane Forest-Grassland Mosaic	Angolan Highland Forest	**Species**: *Eagris multiplagata, Uranothauma nozolinoi* **Subspecies**: *Eretis herewardi rotundimacula*
58 Kalahari *Acacia-Baikiaea* Woodlands 105 Kalahari Xeric Savanna 106 Kaokoveld Desert 109 Namibian Savanna Woodlands	Kalahari Namib Karoo	**Species**: *Acraea hypoleuca* (109), *A. brainei* (109), *Alaena brainei* (58, 105), *Aloeides angolensis* (106, 109), *A. argenteus* (107, 109), *Aloeides namibiensis* (105, 109), *Aloeides tearei* (105, 109), *Caprona cassuallala* (58, 105, 106, 109), *Charaxes brainei* (58, 105), *Colotis doubledayi* (106, 108, 109), *Eretis gaerdesi* with two subspecies *E. gaerdesi gaerdesi* (105, 109) and *E. gaerdesi smithae* (106), *Iolaus obscura* (105), *Kedestes sublineata* (58, 105) **Subspecies**: *Colotis amata williami* (106, 109), *C. annae walkeri* (106, 109), *C. celimene pholoe* (58, 105), *Iolaus alienus sophiae* (58, 105, 109), *I. mimosa pamelae* (58, 105, 109), *Myrina silenus suzannae* (105, 109), *Stugeta subinfuscata subinfuscata* (105, 109), *Tylopaedia sardonyx cerita* (105), *Zintha hintza krooni* (58, 105)

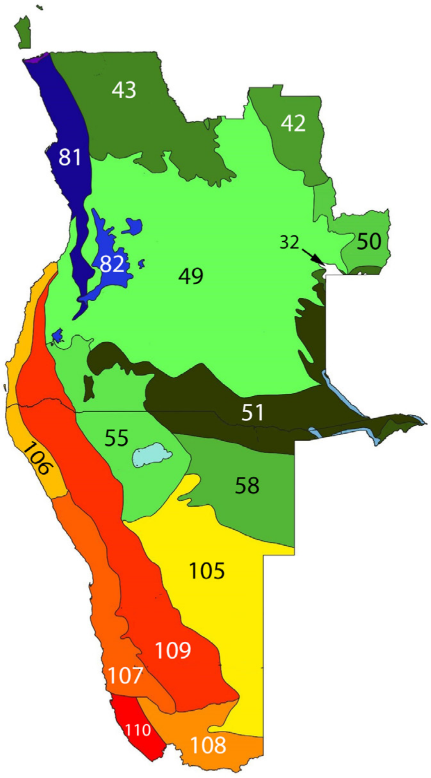

Figure 6: *The faunistic zones of Angola and Namibia (modified from Burgess* et al. *2004).*

Liptena fatima fatima, *Afriodinia tantalus*, *Charaxes zingha*, *Palla violinitens coniger*, *Cymothoe excelsa deltoides, Cymothoe beckeri beckeri*, *Cymothoe coccinata coccinata* and *Euphaedra coprates*. There are six endemic Angolan species and 15 endemic subspecies belonging to these two ecoregions (Table 2).

Little is known about the fauna of the Angolan Highland Forests (contained within ecoregion 82). Two of the recorded species are likely to be montane forest endemics: *Uranothauma nozolinoi* and *Eagris multiplagata* (Table 2). There is also one endemic subspecies *Eretis herewardi rotundimacula*. Endemics which have been recorded on, or close to, the highlands or escarpments of Angola and Namibia are mapped in Figures 2–4, but with our present knowledge it is difficult to know how strongly the species are related to these formations. There are at least two butterfly examples to suggest the former existence of a south equatorial arc: *Acraea oreas* and *Papilio mackinnoni*, both of which occur in the highlands of East Africa through higher elevations to the highland forests of Angola. It is likely this arc ran from the high plateau southwest of Lake Tanganyika (Marungu Highlands, DRC) through the Kundelungu and Mitumba mountains in Shaba (DRC) and the highlands north of Lake Nzilo (Lualaba Province, DRC) to the Angolan Highlands.

One endemic butterfly – *Mylothris mavunda* – is known from the faunistic zone Zambezian *Cryptosepalum* Dry Forest (32) and is also found just across the border in northwest Zambia. The Angolan Miombo Woodlands (49) has eight endemic species and five endemic subspecies (Table 2), however the taxonomic status of some of these needs to be examined. In addition, there are five endemic species and one subspecies associated with the following three faunistic zones: Angolan Miombo Woodlands (49), Angolan Scarp Savanna and Woodlands (81) and Western Congolian Forest-Savanna Mosaic (43) (Table 2). The Angolan and northern Namibian endemic *Acraea onerata* occurs in a number of faunistic zones: Angolan Miombo Woodlands (49), Zambezian *Baikiaea* woodlands (51) and the Angolan Mopane Woodlands (55). As a whole these wet woodlands have 21 endemic or near-endemic taxa, a surprisingly high number, and six endemic subspecies.

The drier habitats also have a surprisingly high number of endemics. There are 23 endemic or near-endemic taxa, thirteen species and 9 subspecies, associated with the following four ecoregions: Kalahari *Acacia-Baikiaea* Woodlands (58), Kalahari Xeric Savanna (105), Kaokoveld Desert (106) and Namibian Savanna and Woodlands (109). There are also two dryland endemic subspecies which are associated with the Angolan Scarp Savanna and Woodlands (81) but one, *Appias epaphia angolensis* seems to also be associated with the Namibian Savanna Woodlands (109).

SPECIAL HABITATS

In addition to ecoregions, Carcasson (1964) also associated some butterfly species with particular habitats, namely: Montane Grassland, which forms part of the Angolan Montane Forest-Grassland Mosaic (82) of Burgess *et al.* (2004); Highland Swamp Habitat and Lowland Swamp Habitat, which can be a subunit within a number of Burgess *et al.*'s (2004) ecoregions Angolan Miombo Woodlands (49), Central Zambezian Miombo Woodlands (50) and Zambezian Baikiaea woodlands (51); and Littoral Sand Dunes which similarly could be a subunit within a number of Burgess *et al.*'s coastal ecoregions. With our present knowledge, we can only briefly discuss Montane Grassland and Swamp habitats and even for these there is a lack of information.

It can be difficult to differentiate some highland species in terms of Montane Grassland, especially as grassland areas are often present within Miombo, and Miombo in a stunted form can occur at high elevations. Species such as *Zeretis* spp. occur in the Grassland Miombo ecotone and it is likely the Angolan endemic *Brakefieldia ochracea* is also present in this ecotone; it has recently been observed in grassy highland areas (Hines pers. comm.) and in Miombo woodland (Gardiner pers. obs.), and older records suggest it may also be present at lower elevations down to about 1,200 masl. There is only one endemic species which could be referred to as a Montane Grassland species; an undescribed *Erikssonia* species from Tundavala (14.82S, 13.38E) near Lubango found by S. Braine (pers. comm.).

Mashunoides carneiromendesi is not only an endemic species but the genus is monobasic and is a wetland specialist; the type specimen was caught near Longa (ca. 14.60S, 18.48E, 1,380 masl) in southeastern Angola (an area with Miombo woodland) and recently the lead author has seen it near Tempué (13.43S, 18.87E, 1,400 masl). *Mashunoides carneiromendesi* is related to the genus *Mashuna* which is also a wetland genus with two species: *Mashuna mashuna,* an endemic to wetland areas in the Highveld of Zimbabwe, and *Mashuna upemba* which has been recorded in Angola (Ackery *et al.* 1995, but exact localities are not known), DRC (Shaba Province) and southwestern Tanzania.

AN EVOLUTIONARY PERSPECTIVE ON THE BIOGEOGRAPHY OF THE BUTTERFLY FAUNA OF ANGOLA AND NAMIBIA

Geological processes, in combination with climatic factors such as temperature and rainfall, are probably the most important drivers of biological change (also implied by Lorenzen *et al.* 2012). Landscape changes promote the evolution of the flora and fauna. These have been referred to as first order controls (Turner 1989). The various factors involved are also likely to be interconnected and may take place at different times and intensities across Africa (see Knight & Grab 2016). Hence, each landscape needs to be considered in as much detail as possible in order to postulate feasible hypotheses for the origin(s) and development of the present fauna. Unfortunately, detailed geological and climatic studies are lacking for many parts of Africa including Angola and Namibia, although more information is becoming available (see references in Knight & Grab 2016 and Huntley *et al.* 2019). Here, we try to put together a brief evolutionary account for one relatively small invertebrate group, the butterflies (Papilionoidea).

African continental-scale warping took place about 85 to 42 mya which resulted in the formation of a composite, low-lying surface of continental extent that is termed the African Surface (Burke & Gunnell 2008). Analysis of only a few African genera has been completed but we know that certain African genera were formed during these turbulent times, such as the *Charaxes* about 45 mya in central Africa (Aduse-Poku *et al.* 2009). During this period, at about 60 mya, along the Okavango–Kalahari–Zimbabwe Axis (which covers part of Angola, Zambia, Namibia, Zimbabwe and Botswana) crustal flexing was occurring (Moore & Larkin 2001) and these movements must have affected the biogeography of the Angola–Namibia area. There then seems to be a period of relative geographical calm until uplifting and tilting through tectonics resulted in a change in the topography of Africa about 19 to 15 mya. Up until this time, it appears there was more connectedness amongst the fauna and it may have been a period of relative stasis. These movements resulted in the Post African I Surface (Knight & Grab 2016); this must have again disrupted the distribution patterns of many butterflies and forced a number of biological changes to take place. This is about the time when a number of African genera were established, such as *Mylothris* (17 mya), *Junonia* (20 mya), *Lepidochrysops* (22 mya), *Euchrysops* (22 mya) and *Cassionympha* (25 to 15 mya) (Monteiro & Pierce 2001, Kodandaramaiah & Wahlberg 2007, Espeland *et al.* 2023). Subsequent events or combinations of them may have resulted in the formation of other genera. For instance, the Middle Miocene climatic transition (16 to 14.8 mya) produced a drier period, and at about the same time the origin of the genus *Cymothoe* (15 mya) and major diversification within the genus *Charaxes* (Kodandaramaiah & Wahlberg 2007) occurred. Further aridification during the Miocene–Pliocene climatic transition (8 to 3 mya) may have been important for the origin of more southerly centred genera such as *Aloeides* and *Thestor* around 9.5 to 5.5 mya (Boyle *et al.* 2015). With many geological and climatic changes having taken place and the systems, working on the fauna independently or in any number of combinations, at any one period, these factors would have interacted in a complex way to form the African genera, their associated species and their present distributions.

The low level of highland endemism in Angola is likely to be due to our lack of knowledge of the Angolan highland fauna. This lack of information is also illustrated by the recent discovery of a new *Erikssonia* species near Lubango (Tundavala; Braine pers. comm.). The species of the highlands of Namibia are relatively well known, but are related, in most cases, to the dry fauna further south. The rainfall conditions and elevation, which are interconnected, have probably worked together to produce the highland endemics of Namibia. A large number of endemics are associated with the relatively dry vegetation types of this region, with many of these species having a Cape origin, or secondary Cape origin, such as the various *Aloeides* spp., while others are likely to have a dry woodland origin such as *Abantis* (*Caprona*) *cassuallala*. Some species indicate the presence of a link between the dry areas of southwestern Africa and the dry areas of East Africa. *Colotis doubledayi* in southwest Africa (Namibia–Angola) has its probable counterpart species *Colotis* *aurigineus* and possibly *C. chrysonome* in East Africa (Kenya and Tanzania). Another interesting species is *Acraea hypoleuca* which is found in dry gullies of the Namibian escarpment where its food-plant *Adenia pechuelii* is found; it has as its counterpart *Acraea chilo* which frequents riverbeds in dry savanna areas of Kenya and Tanzania. *Acraea chilo* feeds on *Adenia globosa* which, like *A. pechuelii,* is well adapted to dry conditions. These major biogeographic distribution patterns have also been shown for other taxa, for instance: i) intraspecific differences for ostrich (Miller *et al.* 2011), impala, hartebeest, wildebeest and roan (Lorenzen *et al.* 2012 and references within), and ii) interspecific connections for the Beisa oryx and gemsbok (Lorenzen *et al.* 2012) as well as connections between the various giraffe taxa (Lorenzen *et al.* 2012). This evidence suggests that populations of arid-adapted species have been isolated due to the expansion of moist conditions, stretching from the central block to the east of the continent leaving isolated populations in the southwest and northeast of Africa. This scenario is likely to have occurred on a number of occasions; for example the Pleistocene had at least five full pluvial cycles (Szabo *et al.* 1995).

This information supports the idea that on a number of occasions an arid corridor stretched from the arid parts of Kenya via the Luangwa and Zambezi valleys to southwestern Angola and western Namibia over certain periods of time. The arid parts of northern Namibia and southern Angola may have some species that have an East African origin (e.g., *Colotis doubledayi*, but DNA data is required to provide evidence for the direction of movement) while others are more likely to have a southern origin, e.g., members of the genus *Aloeides* (although *Aloeides* may have their initial origin in East Africa and then massive speciation in South Africa which resulted in their movement up the west coast from South Africa). These movements and isolating factors have resulted in the arid areas of this region being important for endemism.

From an evolutionary perspective, although not an endemic, *Metisella meninx* (marsh sylph) is of interest. This small, but striking and distinctive butterfly is restricted to the highlands of central-western Angola and to highland areas of South Africa, centred on Gauteng (Johannesburg area) but extending into the neighbouring provinces. Evans (1937) recorded three Angolan specimens but these were largely considered as some sort of error and the species began to be considered endemic to South Africa. There are now about 15 Angolan specimens in the Natural History Museum (NHM), London, with five different printed locality labels, by three different collectors (Larsen unpub. manuscript). The Angolan records are all from the central Angola mountains and plateau, except one from Zambezi (Moxico).

Metisella meninx inhabits marshy ground, usually with clean water, between 1,600 m and 1,700 m in elevation and hence is a habitat specialist. In South Africa it only oviposits on *Leersia hexandra* (Poaceae) (Henning & Roos 2001), an aquatic or semi-aquatic pantropical to subtropical grass, which often grows in fairly large, pure stands. The butterfly is considered vulnerable in South Africa (Henning *et al.* 2009), and this is likely to be the same in Angola.

The Angolan and South African populations of *Metisella meninx* appear to be disjunct by about 1,500 km and do not seem to have formed subspecies. This suggests either a connection in the comparatively recent past and/or that its habitat has remained stable in the two areas. For the similarly disjunct populations of *Erikssonia* – *E. edgei* in the Highveld of South Africa and *E. acraeina* in Angola and western Zambia – Gardiner and Terblanche (2010) suggested the following hypothesis. The crustal flexing along the Okavango–Kalahari–Zimbabwe Axis (Moore & Larkin 2001) is likely to have occurred too early to explain the disjunct distribution of *Erikssonia* from the Upper Zambezi to the Limpopo systems. However, subsequent to this flexing, a major endorheic system formed that drained into the Kalahari Basin (Moore & Larkin 2001). Erosion upstream of the Mid-Zambezi led to the capture of the Upper Zambezi in the Lower Pleistocene. This link was severed in the mid- to late Pleistocene (0.5 mya) by displacement along the Linyanti and Chobe faults, diverting the flow of the Cuando and the Zambezi headwaters into the Palaeo-Makgadikgadi, which filled to around the 945-m level (Moore & Larkin 2001). *Erikssonia* appears to be associated with rainfall of at least 600 mm per annum. It is possible that before the capture of the Upper Zambezi, the wet environment allowed a widespread distribution of *Erikssonia* from the highlands of Angola to the Waterberg in Limpopo Province, South Africa. *Erikssonia* in the north would then have been connected to the southern population via eastern Botswana and western Zimbabwe. The movement or previous widespread occurrence of *Erikssonia* may also have been influenced by cyclical climatic changes during the last 2.6 million years (Zachos *et al.* 2001, deMenocal 2004, Brown *et al.* 2007). The wetter and warmer interglacial periods are likely to have provided a more suitable and widespread habitat. It is possible that the isolation of *Erikssonia edgei* and *Metisella meninx* in South Africa is the result of more recent environmental barriers and not past climatic isolation. Without genetic studies on these species, it is impossible to tell when and if separation occurred and on how many occasions.

The monobasic and endemic *Mashunoides carneiromendesi* is of interest because it is the only butterfly species which is endemic at the genus level. This species may be associated with the headwaters and catchment area of the Lungué-Bungo [Lungwebungu], Cuando, Cuanavale and Cuito rivers. These headwaters have permanent water bodies which is unusual as they are associated with the Kalahari sand system.

It seems Miombo woodland has a relatively recent origin (4 to 3 mya) (Boom *et al.* 2021), and it has certain butterfly taxa associated with it. The origin of Miombo appears to be towards the east of Africa (oldest clade), followed by a more recent clade in southern Central Africa and the youngest in southwest Africa (Angola). The increasing aridity with periods of climatic instability and expansion of C4 savanna, due to C4 plants having a carbon fixation advantage under conditions of drought, high temperatures, and nitrogen or CO_2 limitation, experienced by the fragments of Miombo over the last million years or so would have been ideal for speciation events. Not only is the Angolan Miombo influenced by this east-to-west pattern of Miombo movement but it is also influenced by changes due to the retraction, or expansion, of forest from the north. In this regard, Angola and northwestern Zambia form a zone of "double influence". This may be the reason for the present high butterfly endemism of the Angolan Miombo and the high number of species in the Miombo–Forest intergrade. This part of Angola encompasses the following ecoregions of Burgess *et al.* (2004): Angolan Miombo Woodlands (49), Southern Congolian Forest-Savanna Mosaic (42) and the Western Congolian Forest-Savanna Mosaic (43).

GAPS IN KNOWLEDGE, AND RESEARCH AND CONSERVATION PRORITIES

It is apparent that our knowledge of the butterfly species of the Angolan highlands and Angola in general is lacking. This is also the case for many other invertebrate groups; for instance, Serrano and Capela (2013) found that some species of tiger beetles (Cicindelinae) are only represented by the holotype specimen (some without a locality), and some records are based on a single specimen or the type series. In their article, records were given for six species of Cicindelinae previously unknown from Angola which included two undescribed species, *Foveodromica* sp. n. 1 and *Foveodromica* sp. n. 2. This situation is similar for other invertebrate groups such as the longhorn beetles (Cerambycidae; Ferreira 1971), the ant nest beetles (Paussini; Serrano & Capela 2015) and the dragonflies (Odonata; Kipping *et al.* 2019), although dragonfly collecting has recently increased (Kipping *et al.* 2019).

Although butterflies can be considered charismatic, as far as invertebrates go, they receive comparatively little attention from professional taxonomists, ecologists and biologists on the African continent. We therefore rely on amateur butterfly enthusiasts to obtain knowledge on this group. The activity of amateur enthusiasts and citizen science projects means that butterflies are now our best known invertebrate taxonomic group in Africa, both in terms of identification and distribution.

It has been shown for South Africa that areas of butterfly endemism do not overlap with those of vertebrate endemism (Mecenero *et al.* 2013, Edge & Mecenero 2015) and this is likely to be the case for other invertebrates. As a result of the "Conservation Assessment of Butterflies of South Africa, Lesotho and Swaziland: Red List and Atlas" (Mecenero *et al.* 2013) it has been shown that although there is some overlap with areas of vertebrate biodiversity, most areas of butterfly interest and endemism have no form of protection (Edge & Mecenero 2015). This is undoubtedly the same for Angola and Namibia. Our present limited knowledge indicates that the Miombo woodlands and drier habitats have a high level of butterfly endemism, but it is important to locate other areas of invertebrate endemism in Angola. The Lepidoptera, in particular the butterflies, are an ideal candidate for invertebrate studies. They are more visual and charismatic than most invertebrate groups, for Africa they are relatively well known (Gardiner 1997), and they can be included in citizen science projects. Such taxonomic and ecological work is required not only in the Angolan highlands but also in the rest of Angola and parts of Namibia. We still do not know how well the ecoregions of these two countries are represented for invertebrate conservation. We also need to keep in mind that invertebrates have the highest number of species of any animal group and, although their role in driving ecosystems is not well understood, it is undoubtedly important for the health and functioning of systems (Wheeler 1990). The butterflies provide a unique opportunity to study, in more detail, biological areas of interest for Angola. They can have very short life cycles (from three months to a year), can have a very limited population distribution (sometimes only tens of metres squared), and have a wide variety of life history strategies, ranging from herbivory to predation.

For both the linkage from the dry southwest of Angola to Kenya (with *Colotis doubledayi* and *Acraea hypoleuca* in the southwest and *C. aurigineus* and *A. chilo* in the northeast) and the link between the Angola highlands and the South African Highveld (*Erikssonia* spp. and *Metisella meninx*) we do not know the origin and hence original direction of species movement. Genetic studies providing divergence times between the populations are required in order to provide evidence for the cause of the present distributions. These species provide ideal material for genetic studies and for elucidating relationships between geological events and climatic conditions with speciation and biogeography. Targeted phylogenetic studies need to be undertaken. DNA sampling would help reveal the relatedness of these species both in relation to isolated sister species as well as to other members of the group. For instance, how is *Acraea hypoleuco* related to *A. chilo*, as well as to the much more widely distributed savanna species such as *Acraea acara*? Lepidopterists need to work closely with geologists in an attempt to further unravel periods of significant evolutionary events.

In this paper, we have focused on the endemic species and a few species of interest, but a detailed analysis of the complete Angolan and Namibian butterfly fauna would be worthwhile. This would provide more information on the biogeography and origins of species as well as illustrating areas of high diversity and endemism.

It is very likely, as in most parts of Africa (Burgess *et al.* 2006), that human-induced changes are a threat to many invertebrate species in Angola. These threats are well documented (IUCN 2023) and the impacts of human activities on our systems are now obvious. These impacts are currently mainly due to land use changes and increased population pressures, especially in the highland areas, but the significance of broad climatic changes is likely to increase over the next decades (e.g., Hussain *et al.* 2020). Focusing efforts on maintaining biodiversity and minimising human impact on – and protecting – the few remaining healthy systems should be a priority. An in-depth and thorough butterfly analysis could help to inform these actions. The consideration of invertebrates in conservation planning is likely to result in improved functioning of systems.

ACKNOWLEDGEMENTS

Numerous people have assisted with this work, in particular we would like to thank Mike Wade for his major efforts in getting the figures in order and helping to locate old references. We thank John Mendelsohn, Brian Huntley, António Bivar de Sousa, Christopher Hines, Steve Braine, Peter Hamming, Clifford Nxumalo and Tabogo Malapane for inputs on reference material and discussions.

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Appendix 1: *List of endemic and near-endemic butterfly taxa of Angola and Namibia*

NYMPHALIDAE

Charaxinae

1. *Charaxes brainei* van Son, 1966 – sp. near-endemic to Namibia and Angola
Type locality: [Namibia]: "Kombat, S.W. Africa". Holotype (male) in the Transvaal Museum, Pretoria, South Africa. **Diagnosis**: The female differs from that of *Charaxes vansoni* in the marked suffusion of blue into the postdiscal spots of the forewing upperside and the discal band of the hindwing, and the slight violaceous shade on the hindwing underside (Pringle *et al.* 1994). **Distribution**: Angola (south), Botswana (northwest), Namibia (northeast). **Specific localities**: Botswana – Western Okavango (Larsen 1991l). Namibia – Kombat (TL; J Braine); between Otavifontein and Grootfontein (Pennington); western Caprivi (S Braine); Waterberg Plateau Park (Swart 2004). **Habitat**: Dry savanna. **Habits**: Similar to those of *Charaxes vansoni* but seems to be more readily attracted to fermenting fruit than *C. vansoni* (Pringle *et al.* 1994). **Flight period**: October to June; commonest in March and April (Pringle *et al.* 1994). **Early stages**: Henning (1989: 348). **Larval food**: *Peltophorum africanum* Sond. (Fabaceae) [Henning 1989: 348].

2. *Charaxes ehmckei* Homeyer & Dewitz, 1882 – sp. endemic to Angola
Type locality: Angola: "Pungo Andongo". Female first described by Bivar de Sousa 1992 (*Boletim da Sociedade Portuguesa de Entomologia* Supplement No. 3: 531 (523-541).). **Distribution**: Angola. **Specific localities**: Angola – Pungo Andongo (TL); Canhoca (Jordan 1908). **Habitat:** Evergreen, moist forest. **Habits:** Typical of the group, often flying rapidly along roads stopping to feed. **Larval food**: Probably *Senegalia schweinfurthii*.

3. *Charaxes figueirai* Bivar de Sousa & Mendes, 2014 – sp. endemic to Angola
Type locality: Type material: "MA: Duque de Bragança (today Kalandula), 5/1971, 1 holotype ♂ (BS-13287) 3 paratype ♂♂ (BS-13288/13290); 20/3/1973, 1 paratype ♂ (AF-NYM14952). Malanje, 19/3/1973, 1 paratype ♂ (AFNYM14951)". **Relevant literature**: Bivar de Sousa & Mendes (2014) on Angolan *Charaxes*.

4. *Charaxes fulvescens rubenarturi* Bivar de Sousa & Mendes, 2017 – ssp. endemic to Angola
Type locality: Angola: "Kwanza Sul: Mussende, XII-2015, AS + RC, 1 1 (BS-34880)". Place of deposition of holotype not given. **Distribution**: Angola. **Specific localities**: Angola – Mussende (TL); Quiminha (Mendes *et al.* 2017); Golungo Alto (Mendes *et al.* 2017); Salazar (Mendes *et al.* 2017); Calulo (Mendes *et al.* 2017); Inga (Mendes *et al.* 2017).

5. *Charaxes jahlusa angolensis* Mendes & Bivar de Sousa, 2017 – ssp. endemic to Angola
Type locality: Angola: Namibe: Bruco, 8-IX-1974, 1 1, PC (BS-12669). Place of deposition of holotype not given. **Distribution**: Angola. **Specific localities**: Angola – Bruco (TL).

6. *Charaxes lucretius saldanhai* Bivar de Sousa, 1983 – ssp. endemic to Angola
Type locality: Angola: "Bessa Monteiro". Type specimen in the collection of Bivar de Sousa. **Distribution**: Angola (northwest). **Specific localities**: Angola – Bessa Monteiro (TL).

7. *Charaxes macclouni carvalhoi* Bivar de Sousa, 1983 – ssp. endemic to Angola
Type locality: Angola: "Kwanza Norte: Dalatando (Salazar) 1 1 (BS-1918)". Type specimen in the collection of Bivar de Sousa. **Distribution**: Angola (northwest). **Specific localities**: Angola – Dalatando (TL); Calulo (Mendes *et al.* 2017).

8. *Charaxes minor karinae* Bouyer, 1999 – ssp. endemic to Angola
Type locality: Angola: "Cuanza Sul, I/II-1999 (T. Bouyer & M. Hasson)". Holotype (male) and allotype (female) in the Royal Museum for Central Africa (MRAC). **Distribution**: Angola. **Specific localities**: Angola – Cuanza-Sul (TL). **Larval food**: *Albizia gummifera* (J.F.Gmel.) C.A.Sm. (Fabaceae) [Bouyer 1999].

9. *Charaxes trajanus bambi* Bivar de Sousa & Mendes, 2006 – ssp. endemic to Angola
Type locality: Angola: "Uíge: Rio Bambi banks, 15-X-1964, (Bivar de Sousa – 13605)". **Diagnosis**: Differs from the nominate subspecies in the yellowish-green colour of the dorsal discal area of the hindwing (greyish-white and smaller in the nominate subspecies); much rounder shape; the clearly more individualised postdiscal white spots (dorsal and ventral surface) of the forewing; marginal brown area of hindwing in female much narrower; in the male the included white dots are much smaller and the Uíge specimens are larger (Bivar de Sousa & Mendes 2006). **Distribution**: Angola. **Specific localities**: Angola – Bambi River, Uíge Province (07°26'S, 14°27'E; 600 m) (TL). **Habits**: A scarce to rare butterfly, usually found as single specimens scattered in the forest. It keeps to

deep shade (Larsen 2005). The flight is slow and buzzing, somewhat resembling day-flying moths (Larsen 2005).

10. *Palla ussheri hassoni* Turlin & Vingerhoedt, 2013 – ssp. endemic to Angola
Type locality: Angola: Cuanza-Sul, Dinguir, 458 m, 11°19'S, 14°10'E, 13/17-III-2005. Holotype (male) in the MRAC, Tervuren, Belgium. **Distribution**: Angola. **Specific localities**: Angola – Dinguir (TL); Cassoco [11°25'S, 14°01'E] (Turlin 2013).

Danainae

11. *Amauris crawshayi angola* Bethune-Baker, 1914 – ssp. endemic to Angola
Type locality: Angola: "N'Dalla Tando, N. Angola". **Distribution**: Angola.

12. *Amauris dannfelti dannfelti* Aurivillius, 1891 – ssp. endemic to Angola
Type locality: [Angola]: "Congo-Gebiete". Holotype in the Swedish Natural History Museum (images available at www2.nrm.se/en/lep_nrm/d). **Distribution**: Angola.

Heliconiinae

13. *Acraea bellona* Weymer, 1908 – sp. endemic to Angola
Type locality: Angola: "Benguella". [Benguela, Benguela Province]. **Distribution**: Angola. **Specific localities**: Angola – Benguella (TL).

14. *Acraea brainei* Henning, 1986 – sp. endemic to Namibia and Angola
Type locality: [Namibia]: "Hartmanns Valley, 44 km S. of Cunene River". **Diagnosis**: Bears some resemblance to *Acraea nohara* but the genitalia show that it is more closely related to *Acraea neobule*. It can be distinguished from *Acraea nohara* by the following: the shape and distribution of the black spotting; the absence of heavy black spotting along the margin and outer part of the veins of the forewing; a row of spots on the marginal black border of the hindwing (Pringle *et al.* 1994). **Distribution**: Angola, Namibia (northwest). **Specific localities**: Angola – Iona Peak, Iona National Park [16°55'02.8"S, 12°36'10.6"E] (Willis 2009). Namibia – Hartmann's Valley in Kaokoland, in an area extending from about 30 km south of the Kunene River to the Engo River (TL; Pringle *et al.* 1994); Etanga, 100 km west of Opuwo (Swart 2004). **Habitat**: Dry savanna. Granite outcrops on hills and ridges (Pringle *et al.* 1994). **Habits**: Both sexes feed from the flowers of the larval host-plant (Pringle *et al.* 1994). **Flight period**: February to April (Pringle *et al.* 1994). **Early stages**: Henning (1986). **Larval food**: *Turnera oculata* Story (Turneraceae) [Braine, in Henning (1986)?]. **Relevant literature**: Schutte (2021) on evolution and host-plant relationship.

15. *Acraea hypoleuca* Trimen, 1898 – sp. endemic to Namibia
Type locality: None given in the original description (the unique holotype label data stated only 'Coll. Watson, 1871'). **General remarks**: "The first specimen of *Acraea hypoleuca* was a male collected in 1871 but with no recorded locality. Trimen did his description in 1898 from this specimen. The origin of that specimen was a point of contention for many years; Eltringham came to the conclusion that it could be from South West Africa [Namibia]. The closest relative of *Acraea hypoleuca* is *Acraea chilo* Godman, which occurs from East Africa to Arabia. The second specimen was taken by Dr Brown at Maltahöhe in South West Africa; it was a female and was described by Dr Pinhey in 1972. This specimen is illustrated in *Pennington's butterflies of southern Africa* (1978) as No. 120. In 1979 I [Stephen Braine] collected a female at Rössing and in 1982 I found a male at the Ugab River. In January 1983 I collected six males at the Ogam Hills and another male at the Ugab River. All these localities are in South West Africa [Namibia]. This butterfly is not as rare as it was originally thought to be. It has been found at several other localities by myself. … I have recorded this butterfly from the Swakop River northwards to the Sechomib River in the central section of Kaokoland." (Braine & Henning 1984). **Distribution**: Namibia. **Specific localities**: Namibia – Farm Mooirivier in the Maltahöhe district, on the edge of the Zaris mountains (H Brown); Rössing (S Braine); Ugab River (S Braine); Ogams Fountain, in Kaokoland (S Braine); Khumib Konkol (Ficq); Khan River Valley near Arandis (J Dobson, pers. comm.). **Habitat**: Arid savanna. Flies in gullies and on granite outcrops where its larval host-plant grows (Braine & Henning 1984). **Habits**: Adults fly from 10h00 to 18h00. It has been found to feed on the flowers of two *Psilocaulon* species, with a marked preference for the flowers of *Calicorema capitata* (Braine & Henning 1984). **Flight period**: December to June, with peak emergence in January and February (Braine & Henning 1984). **Early stages**: Braine & Henning (1984: 6). **Larval food**: *Adenia pechuelii* (Engl.) Harms (Passifloraceae) [Braine & Henning (1984: 6)]. **Relevant literature**: Schutte 2021 [evolution and host-plant relationship; African Butterfly News 2021 no. 2: 9].

16. *Acraea lapidorum* Pierre, 1988 – sp. endemic to Angola
Type locality: Angola: "Upper Lungwe-Bungo River, S.E. Angola". **Distribution**: Angola (southeast). Known only from the holotype. **Specific localities**: Angola – Upper Lungwe-Bungo River (TL).

17. *Acraea onerata* Trimen, 1891 – sp. endemic to Angola

Type locality: [Angola]: “Okavango River”. **Diagnosis**: Similar to *A. nohara* but the hindwing upperside marginal band in *onerata* is clearly spotted with the ground-colour of the wings (Pringle *et al.* 1994). **Distribution**: Angola. **Specific localities**: Angola – Okavango River (TL); Bihe (Eltringham 1911). **Flight period**: December appears to be the only recorded month (Pringle *et al.* 1994).

18. *Acraea violarum anchietai* Mendes & Bivar de Sousa, 2017 – ssp. endemic to Angola

Type locality: Angola: “HUAMBO, Cuíma, XII-2015, 1 1, (BS-34931”, Holotype (male) in the MUHNAC, Portugal. **Diagnosis**: Differs from the nominate subspecies in the triangular rather than round white markings on the margin of the hindwing underside (Bivar de Sousa *et al.* 2017). **Distribution**: Angola. **Specific localities**: Angola – Cuima (TL); Bihé (Eltringham 1912); Calweha (Eltringham 1912); Caconda (Eltringham 1912); Cubal R. (Eltringham 1912); Cambo (Eltringham 1912); Caquenje (Eltringham 1912); Benguella (Eltringham 1912); Baillundo [Bailundo] (le Doux 1922); Kalukembé (Monard 1956); Sangevé (Monard 1956); Tiytunda (Monard 1956); Bimbi (Monard 1956); Chimporo (Monard 1956); Chianga (Bivar de Sousa *et al.* 2017); Nova Lisboa (Bivar de Sousa *et al.* 2017); Sacaala, Nova Lisboa (Bivar de Sousa *et al.* 2017).

Limenitidinae

19. *Bebearia cocalia ngolae* Mendes, Bivar de Sousa & Lopes, 2021 – ssp. endemic to

Type locality: “Holotype, ANGOLA, Cuanza Sul, Calulo, Fazenda Klein, 1-XII-2015 (BS-35041). Paratypes: Bengo: Tentativa, 1 1, 13-III-1972 (NY6650489). Cuanza Norte, Salazar (Dalatando), 2 00, 25-V-1972 (PC-nn); Ibid, 1 1, 25-VI-1972 (PC-1000), det. as B. mardania; Ibid, 11, 25-VII-1972 (PC-nn); Ibid, 1 1, 21-XI-1972 (PC-1001); Ibid, 1 0, 31-I-1973 (PC-19824); Ibid, 1 0, 18-II-1973 (BS-14606); Ibid, 1 1, 12-VIII-1974 (PC-140); Ibid, 1 1, 18-VIII-1974 (PC-157); Ibid, 11, 23-I-1975 (PC-nn). Cuanza Sul, Cabuta, 1 1, 29-XI-2015 (n. 49) (BS-35040). Calulo, Aldeia Catembo, 1 1, 5-XI-2014 (BS-33505). Calulo, Alto Ventura, Fazenda Monte Café, (n. 49), 2 11, 1-XII-2017 (BS-36692, 36693). Calulo, Fazenda Klein, 1 1, 1 0, 1-XII-2015 (BS-35042, 35043); Ibid, 10, 8-XII-2017 (n. 44) (BS-36694) plus 1 1, 1 0 (BS-36690, 36691). Novo Redondo (Sumbe), 4 11, I-1963 (BS-15735, 15737, 15740, 15742). Uíge, Fazenda S. José, Nova Caipemba, 1 1, XII-1975 (BS-15741).” **Distribution**: Angola.

20. *Bebearia hassoni* Hecq, 1998 – sp. endemic to Angola

Type locality: Angola: Cuanza-Sul. **Distribution**: Angola. **Specific localities**: Angola – Cuanza-Sul (TL).

21. *Bebearia paludicola meridionalis* Mendes, Bivar de Sousa & Lopes, 2021 – ssp. endemic to Angola

Type locality: “Holotype, ANGOLA, Cuanza Norte: Salazar (Dalatando), 10-IV-1972 (BS-14605). Paratypes: Cuanza Norte: Salazar (Dalatando), 1 1, 14-III-1975 (PC-nn). Cuanza Sul, Calulo, Alto Ventura, Fazenda Monte Café, (n. 44), 1 0, 8-XII-2017 (BS-36695).”

22. *Bebearia sophus angolensis* Mendes, Bivar de Sousa & Lopes, 2021 – ssp. endemic to Angola

Type locality: “Holotype, ANGOLA, Cuanza Norte, Salazar, 6-I-1975 (PC-nn). Paratypes: ANGOLA, Cuanza Norte, Salazar, 1 1, III-1973 (AF-NY681001, in the NHMUP). Uíge, Inga, 1 0, IX- 1964 (BS-15791).”

23. *Euphaedra divoides* Bivar de Sousa & Mendes, 2019 – sp. endemic to Angola

Type locality: “Angola: Holotype (female): Buco Zau, Cabinda, 18-V-1952”; in the Natural History and Science National Museum, Lisbon, Portugal. **Distribution**: Angola (Cabinda). **Specific localities**: Angola – Buco Zau (TL). **Habitat**: Forest. **Habits**: Typical *Euphaedra* flies rapidly gliding above the ground, settling in patches of semi-light or to feed on the ground, often with wings open. **Note**: *Euphaedra divoides* Bivar de Sousa & Mendes (2019) is probably a synonym of *E. permixtum diva* Hecq, 1982.

24. *Euphaedra harpalyce commineura* Hecq, 1999 – ssp. endemic to Angola

Type locality: Nothing published. **Distribution**: Angola. **Specific localities**: Nothing published.

25. *Euphaedra uigensis* Bivar de Sousa & Mendes, 2017 – sp. endemic to Angola

Type locality: Angola: “Uíge, Inga, near the Vale do Loge colonial settlement, October 1964, 1 1 (BS-16154”, holotype (male) in the Museu Nacional de História Natural e da Ciência (MUHNAC), Portugal. **Distribution**: Angola. **Specific localities**: Angola – Inga, near the Vale do Loge colonial settlement (TL). **Habitat**: Gallery forest on the Loge River (Bivar de Sousa *et al.* 2017). **Flight period**: October, November, December (Bivar de Sousa *et al.* 2017).

Nymphalinae

26. *Precis larseni* Mendes, Bivar de Sousa, Vasconcelos & Lopes, 2018 – sp. endemic to Angola
Type locality: "Holotype: Moxico: Lumeje, IV-1965, 1 1 DSF (BS-17687). Paratypes: Huambo: Chianga, V-1972, 1 1 DSF (PC); VII-1975, 11 DSF (PC). Cuanza-Norte: Golungo Alto, ?-1962, MM, 2 11, 1 0 DSF (MUHNAC-17324, 17328, 17330). Moxico: As for the holotype, 1 1, 1 0 DSF (BS-17688-17689), 1 1 WSF (BS-17690); V-1965, 1 1 DSF (BS-17691); VIII-1965, 1 1 DSF (BS-17692). Teixeira de Sousa, II-1965, 1 1 WSF (BS-17693). All the types in the MUHNAC. Non-type material: Huambo: Nova Lisboa, IV-1964, 1 1, 4 00 (NA); V-1964, 1 1 (NA); VI-1964, 1 1, 1 0 (NA); VI-1965, 1 1, 1 0 (NA-); V-1970, 1 0 (NA)". **Habitat**: The studied representatives of the species were all obtained above 1,000 masl in areas with "Miombo" – mixed savanna with trees, *Brachystegia,* and open forest margin (Wild & Grandvaux-Barbosa 1967, Grandvaux-Barbosa 1970). **Habits**: The African leaf commodore, eared commodore or African leaf butterfly, *Precis tugela*, was reported by Larsen (1996) in Kenya in forest clearings and along roads but also in more open areas including agricultural fields and Kielland (1990) stressed it is common in Tanzania in forests and forest margins and that it may fly from 350–2,500 masl. (*P. tugela aurorina*) or from 800–2,000 masl. (*P. tugela piryformis*). Willis & Woodhall (2010, sub *Junonia*) reports the nominate *Precis tugela* to occur in the Afromontane forests of the South African eastern escarpment.

Biblidinae

27. *Sevenia occidentalium penricei* (Rothschild & Jordan, 1903) – ssp. endemic to Angola
Type locality: Angola: "Calweha River, Angola". **Distribution**: Angola.

Satyrinae

28. *Brakefieldia angolensis* (Kielland, 1994) – sp. endemic to Angola
Type locality: Angola: "Bango, Dr Ansorge (no date)." Holotype in NHM, London. **Distribution**: Angola.

29. *Brakefieldia ochracea* (Lathy, 1906). Aduse-Poku *et al.* 2016 comb. n.
Type locality: Angola: "Bihé District, Angola". **Distribution**: Angola (central plateau). **Specific localities**: Angola – Benguella (Weymer, 1908); Upper Cubango-Cunene Watershed (Talbot 1932). Serra de Namba; Mount Mocco.

30. *Mashunoides carneiromendesi* Mendes & Bivar de Sousa, 2009 – sp. and genus endemic to Angola
Type locality: Angola. "Cuando Cubango Province". **Distribution**: Angola (southeast – Cuando Cubango Province, Mendes & Bivar de Sousa 2009d). **Habitat**: Wetlands.

31. *Neita bikuarica* Mendes & Bivar de Sousa, 2006 – sp. endemic to Angola
Type locality: Angola: "Huila Province: Capelongo, ?/XI/1957, EAU (CZ-2964)". Described from a single male captured by the "Estudos Apicolas do Ultramar" mission (EAU) near Capelongo (14°53'S; 15°05'E, ca. 1,200 m). Holotype (male) in the Instituto de Investigação Cientifica Tropical entomological collection (CZ), Lisbon, Portugal. **Diagnosis**: Closest to *Neita victoriae*, from which it differs in the more acute forewing apex, narrower orange ring surrounding the ventral hindwing ocelli, greater width of the area delimited by the brown line enclosing the hindwing ocelli, and the presence on the posterior ventral wing of a well-defined oblique brown line that crosses the cell. On the upperside of the forewing the orange halo that surrounds the ocellus enters space two, while in *Neita victoriae* it does not pass the first cubital (Mendes & Bivar de Sousa 2006). Also resembles *Neita extensa*, which has a larger forewing ocellus but with a deep invagination on the peri-ocellar line on the hindwing underside. *Neita orbipalus* is also similar but has better developed orange/yellow in the ocelli and lacks (as do the other species in the genus), an oblique dark line across the cell on the hindwing underside (Mendes & Bivar de Sousa 2006). **Etymology**: Named for its geographical origin, close to the northern border of the Bicuar National Park. **Distribution**: Angola. **Specific localities**: Angola – Capelongo, Huíla Province (TL). Known only from the type locality (Mendes & Bivar de Sousa 2006). **Habitat**: *Brachystegia* woodland (Mendes & Bivar de Sousa 2006).

LYCAENIDAE

Poritiine

32. *Alaena brainei* Vári, 1976 – sp. endemic to Namibia
Type locality: [Nambia]: "South West Africa: Tiger Valley, Kombat". **Diagnosis**: Differs from the similar *Alaena amazoula* in that it has smaller, sharply edged ochreous-yellow spots (especially on the hindwing of males), and broader, sharply edged fuscous brown wing borders in females (Vári 1976). **Distribution**: Namibia (north-central). **Specific localities**: Namibia – Tiger Valley, Kombat (TL; Kroon); Grootfontein (J. Braine); Abachaub (Pringle *et al.* 1994); Otjiwarongo district (Pringle *et*

al. 1994); Namutoni (Pringle *et al*. 1994); Tsumeb (Pringle *et al*. 1994); Maroelaboom (Pringle *et al*. 1994); Otavi (Pringle *et al*. 1994). **Habitat**: Rocky grassland. **Habits**: Nothing published. **Flight period**: November to early May (Pringle *et al*. 1994). **Larval food**: Algae (Cyanophyta) on rocks [Pringle *et al*. 1994: 127].

33. *Alaena rosei* Vane-Wright, 1980 – sp. endemic to Angola
Type locality: Angola: "10 miles east of Gabela". **Distribution**: Angola. **Specific localities**: Angola – 16 km east of Gabela (TL); vicinity of Sadabandeira (Ackery *et al*. 1995).

34. *Cooksonia nozolinoi* Mendes & Bivar de Sousa, 2007 – sp. endemic to Angola
Type locality: Angola: "Huambo Province: Nova Lisboa [= Huambo], 12/9/1975, (NA, no number) (CZ-5265)". Holotype (female) in the CZ, Lisbon, Portugal. Known only from a single female found in the collection of the late Armando Nozolino de Azevedo, taken at Huambo (12°46'S, 15°44'E; 1,650 m). **Diagnosis**: Closest to *Cooksonia neavei* but differs from it in that the dark dot of the forewing (dorsal and ventral cell apex) is completely isolated from the costal area, the hindwing marginal area is narrower and shows small white punctuations, and the hindwing irregular blackish spots of the underside are less numerous and less extended (Mendes & Bivar de Sousa 2007). **Distribution**: Angola (Angolan Planalto). **Specific localities**: Angola – Huambo (TL). **Habitat**: Miombo woodland.

35. *Deloneura barca* (Grose-Smith, [1901]) – sp. endemic to Angola
Type locality: Angola: "Kinsombo". **Distribution**: Angola.

36. *Falcuna lacteata* Stempffer & Bennett, 1963 – sp. endemic to Angola
Type locality: Angola: "Angola". **Distribution**: Angola. **Habitat**: Primary forest.

37. *Falcuna libyssa angolensis* Stempffer & Bennett, 1963 – ssp. endemic to Angola
Type locality: Angola: "Angola". **Distribution**: Angola (north – "Uíge and Cuanza-Norte Provinces" (L Mendes pers. comm. 2018). **Habitat**: Primary and secondary forest with a canopy (Larsen 2005). **Habits**: Widely and evenly spread in forest. Males perch on the ends of twigs along forest roads and in clearings, defending their territories with vigour and a rapid flight for a poriitine. They return to their perch where they alight on the very tip with great skill. Males engage only with relatively fast-flighted congenerics, ignoring other more weakly flying poriitines (Larsen 2005). Both sexes feed at extrafloral nectaries of Marantaceae and other creepers, often in the company of other poriitines. Males of *libyssa* are aggressive at such feeding sites, pushing other individuals away with sharp flicks of their wings (Larsen 2005).

38. *Liptena homeyeri straminea* Stempffer, Bennett & May, 1974 – ssp. endemic to Angola
Type locality: Angola: "Bange Ngola". **Distribution**: Angola (except southeast). **Specific localities**: Angola – Bange Ngola (TL).

Aphnaeinae

39. *Aloeides angolensis* Tite & Dickson, 1973 – sp. endemic to Angola
Type locality: Angola: "Benguella". Holotype (male): Benguella, 26.ix.1904 (Dr Ansorge), B.M. Type No. Rh. 17228. Allotype (female); data as holotype. B.M. Type No. Rh. 17229). **Diagnosis**: Most similar to *A. damarensis*. **Distribution**: Angola. **Specific localities**: Angola – Benguella (TL). Benguela is a town and province in southwest Angola.

40. *Aloeides argenteus* Henning & Henning, 1994 – sp. endemic to Namibia
Type locality: Namibia: "riverbed near Sima Hill, Kaokoland, 30 Mar. 1986, H.C. Ficq." Holotype in Transvaal Museum, Pretoria. **Diagnosis:** Characterised by the pale orange ground-colour on the upperside of the wings, and the very pale ochreous underside with large silvery markings (Pringle *et al*. 1994). **Distribution**: Namibia. Known only from the type locality. **Specific localities**: Namibia – Ganias River, near Sima Hill, 19°15'S, 13°00'E (TL; Braine and Ficq). **Habitat**: Very arid area just inland of the coastal dunes. The type locality is in a dry riverbed (Pringle *et al*. 1994). **Habits**: Specimens settle on rocks and pebbles, many of which are white quartzitic) (Pringle *et al*. 1994). **Flight period**: March (Henning & Henning 1994).

41. *Aloeides namibiensis* Henning & Henning, 1994 – sp. near-endemic to Namibia
Type locality: Namibia: "Omatako Omuramba, 30 Dec. 49." Holotype in Windhoek Museum, Namibia. **Diagnosis**: Most closely related to *Aloeides trimeni*, from which it can be separated by the ochreous greyish brown of the upperside basal area (brown to orange in *trimeni*) and broad postdiscal markings (narrow in *trimeni*) (Pringle *et al*. 1994). **Distribution**: Botswana, Namibia. Known only from two pairs from the type locality and specimens from a single locality in Botswana. **Specific localities**: Botswana – According to G Henning (pers. comm.), I Coetzer caught this species near the tarred road between Windhoek and Ghanzi (Tsootsha) in January 1999 (Larsen 1991). Namibia – Omatako Omuramba, approximately

19°00’S, 19°30’E (TL). **Habitat**: Arid savanna. **Flight period**: The type series was collected on 30 December (Pringle *et al.* 1994).

42. *Aloeides tearei* Henning & Henning, 1982 – sp. endemic to Namibia
Type locality: [Namibia]: “13 km north of Aus”. **Diagnosis**: Differs from *Aloeides simplex* in the following respects: smaller; on the upperside of the wings the dark margins are wider. The markings on the upperside of the wings strongly resemble those of *Aloeides bamptoni*, while the hindwing underside markings are similar to those of *Aloeides nollothi*. Differs from these two taxa in the darker brown hindwing underside ground-colour and better developed submarginal lunules (Pringle *et al.* 1994). **Distribution**: Namibia (south). **Specific localities**: Namibia – 13 km north of Aus (TL; Littlewood); Kupferberg Pass, 30 km southwest of Windhoek (Stephen); Gamsberg in southwest Namibia (Swart 2004). **Habitat**: Semi-desert. **Habits**: Has the usual habits of the genus, flying rapidly for a short distance before settling abruptly, with closed wings, on rocks or on the ground. It is particularly fast-flighted and elusive for an *Aloeides* (Pringle *et al.* 1994). **Flight period**: August to October, February and May are the months so far recorded (Pringle *et al.* 1994).

43. *Tylopaedia sardonyx cerita* Henning & Henning, 1998 – ssp. endemic to Namibia
Type locality: Namibia: “Namibia: Regenstein, 4.xi.1995, F. Swart.” Described from a large series from the type locality and a single male from Kupferberg Pass, west of Windhoek. **Distribution**: Namibia (central). **Specific localities**: Namibia – Regenstein, 30 km southwest of Windhoek (TL; Swart); Kupferberg Pass, 30 km southwest of Windhoek (Stephen); Gross Herzog peak, Auas Mountains, just south of Windhoek (Swart 2004); Gamsberg in southwest Namibia (Swart 2004).

44. *Axiocerses amanga baumi* Weymer, 1901 – ssp. endemic to Namibia and Angola
Type locality: Angola: “Palmfontain und Vogelfontain”. **Distribution**: Angola, Namibia. **Specific localities**: Angola – Palmfontein and Vogelfontein (TL). **Habitat**: dry woodland (savanna).

45. *Zeritis krystna* d’Abrera, 1980 – sp. endemic to Angola
Type locality: Angola: “Muene Indala, Angola”. **Distribution**: Angola (central). **Specific localities**: Angola – Muene Indala (TL). **Habitat**: Open Miombo woodland and dambos.

Theclinae

46. *Iolaus alienus sophiae* Henning & Henning, 1991 – ssp. endemic to Namibia
Type locality: Namibia: “26 km N. of Grootfontein”. **Diagnosis**: Differs from the nominate subspecies in its more rounded wing shape, different shade of blue, restricted blue area on the forewing upperside, and more extensive white areas on the upperside of the wings in the female (Pringle *et al.* 1994). **Distribution**: Namibia (Grootfontein area). **Specific localities**: Namibia – 26 km north of Grootfontein (TL; Ficq); Opuwo in Kaokoland (Swart 2004).

47. *Iolaus mimosae pamelae* (Dickson, 1976) – ssp. endemic to Namibia and Angola
Type locality: [Namibia]: “South West Africa: Kombat”. **Diagnosis**: The blue on the upperside of the wings is much paler than in the nominate subspecies and the underside is very pale, uniform grey. In addition, the lines on the underside are much thinner and more regular. Compared to subspecies *I. m. rhodosensae* the hindwing is more elongated towards the anal angle in the male; the blue on the upperside is of a purer tone; the discal and postdiscal lines on the underside are less widely separated; and the more regular discal line (Pringle *et al.* 1994). **Distribution**: Namibia (north). **Specific localities**: Namibia – Kombat (TL Braine); Otavifontein (Pennington); Grootfontein (Pennington).

48. *Iolaus obscura* – sp. endemic to Namibia and Angola
Type locality: [Namibia]: “Windhuk in the Damaraland”. Holotype in the Swedish Natural History Museum (images available at www2.nrm.se/en/lep_nrm/o). **Diagnosis**: Similar to *Iolaus mimosae* but the underside of the wings is much darker; on the upperside forewing the blackish marking extends further basad; on the upperside of the hindwing the dark marking near the anal angle is much reduced, with only a single, well-defined, small spot in area 1B (Pringle *et al.* 1994). **Distribution**: Namibia (north), Angola (Mendes *et al.* 2018). **Specific localities**: Namibia – Windhoek (TL; two specimens); Kombat, 137 km north of Windhoek (Bampton & Braine pers. comm.; two bred specimens); eastern suburbs of Windhoek (Swart 2004). **Habitat**: Dry savanna. **Habits**: Nothing published. Despite much searching this species remained known from only four specimens (Pringle *et al.* 1994). More recently F Swart (2004) collected and bred numbers from the eastern suburbs of Windhoek. **Flight period**: December is the only month recorded (Pringle *et al.* 1994). **Early stages**: Nothing published. **Larval food**: *Plicosepalus kalachariensis* (Schinz) Danser (Loranthaceae), parasitic on *Senegalia mellifera* (Vahl) Seigler & Ebinger (Fabaceae) [Pringle *et al.* 1994: 156].

49. *Leptomyrina henningi angolensis* Dickson, 1976 – ssp. endemic to Angola
Type locality: Angola: "Luanda [08°50'S, 13°15'E". **Distribution**: Angola. **Specific localities**: Angola – Luanda (Mendes & Bivar de Sousa 2009b).

50. *Myrina silenus suzannae* Larsen & Plowes, 1991 – ssp. endemic to Namibia
Type locality: Namibia. **Diagnosis**: Characterised by the very reduced basal blue area on the upperside of the wings (Pringle *et al.* 1994). **Distribution**: Namibia (north). **Specific localities**: Namibia – Okahandja (Gaerdes); Otavifontein (Pringle *et al.* 1994); Tsumeb (Pringle *et al.* 1994); Namutoni (Pringle *et al.* 1994); Tiras Mountains (Pringle *et al.* 1994); Brandberg (Pringle *et al.* 1994).

51. *Stugeta subinfuscata subinfuscata* Grünberg, 1910 – ssp. endemic to Namibia
Type locality: [Namibia]: "Windhuk". **Diagnosis**: The main difference between *Iolaus subinfuscata* and *I. bowkeri* is the more extensive dark markings on the underside of the wings in the former (Pringle *et al.* 1994). **Distribution**: Namibia. **Specific localities**: Namibia – Windhoek (TL); Sesriem (Pringle *et al.* 1994); Namib Desert (Pringle *et al.* 1994); Namutoni (Pringle *et al.* 1994); Otavi (Pringle *et al.* 1994); Kombat (Pringle *et al.* 1994); Kaokoveld (Swart 2004); Brandberg (Swart 2004); Tsaobis Leopard Farm, Karibib district (Swart 2004); Bloedkoppie (Swart 2004). **Habitat**: Arid savanna and river courses in the Nama Karoo. **Habits**: Often flies in proximity to its larval foodplant, frequently resting on the sides of bushes (Pringle *et al.* 1994). **Flight period**: Throughout the summer months, being particularly plentiful in September and October. The nominate subspecies is possibly on the wing throughout the year (Pringle *et al.* 1994). **Early stages**: Clark & Dickson (1971: 144) [as *Stugeta bowkeri subinfuscata*; Little Namaqualand, Northern Cape Province]. Early stages unrecorded (but referred to in a comparison made with *Iolaus bowkeri* by Clark & Dickson (1971: 144)) – "The early stages have given no indication of *Stugeta bowkeri bowkeri* (Trimen) (from the eastern Cape) and *Stugeta bowkeri subinfuscata* Grünberg (from Little Namaqualand) being other than conspecific. The latter is, nevertheless, a well defined race and where it has been found by us, in Little Namaqualand, always breeds true to type." **Larval food**: *Loranthus* species (*sensu lato*) (Loranthaceae) [Pringle *et al.* 1994: 153]. *Tapinanthus oleifolius* (J.C.Wendl.) Danser (Loranthaceae) [Bampton, *vide* Pringle *et al.* 1994: 153].

Polyommatinae

52. *Lepidochrysops fulvescens* Tite, 1961 – sp. endemic to Angola
Type locality: Angola: "Samba Acenda". Holotype (male): 16.x.1903, Ansorge, B.M. Type No. Rh. 16495. Allotype (female): Cambo Caquenje, Bihe, Angola, 3.xi.1904, Ansorge, B.M. Type No. Rh. 16496. **Distribution**: Angola (highlands). **Specific localities**: Angola – Samba Acenda (TL; Ansorge); Cambo Caquenje, Bihe (Ansorge); Menjori River, Bihe (Ansorge); Ndalla Ango [Ndalatando; 9.300S, 14.910E] (Ansorge); Pedreira, Bihe (Ansorge). **Habitat**: Miombo woodland primary or degraded. **Flight period**: The type series was recorded from mid-October to the first week of November (Tite 1961).

53. *Lepidochrysops nacrescens* Tite, 1961 – sp. endemic to Angola
Type locality: Angola: "Nova Lisboa". [now Huambo -12.774°S; 15.734°E]. Holotype (male): ix.1957, J.C.[G.] Williams, B.M. Type No. Rh. 16494. **Distribution**: Angola. Known from the male holotype only. **Specific localities**: Angola – Nova Lisboa (TL). **Flight period**: The unique holotype was captured in September (Tite 1961).

54. *Uranothauma nozolinoi* Bivar de Sousa & Mendes, 2007 – sp. endemic to Angola
Type locality: Angola: "Huambo Province: Nova Lisboa, 18/IV/1965, NA, male holotype (CZ-5266)". **Diagnosis**: Most similar to *Uranothauma nubifer*. The wings are lighter but the ventral pattern is not substantially different to that of *Uranothauma nubifer*. However, the brown elements of the hindwing pattern are less distinctly individualised. The androconial patch is smaller and the shape of the valves and the development of the apical teeth of the valves are distinct from those of *Uranothauma nubifer* (Bivar de Sousa & Mendes 2007). **Distribution**: Angola. Known only from the male holotype (Bivar de Sousa & Mendes 2007). **Specific localities**: Angola – Nova Lisboa, Huambo Province (TL).

55. *Zintha hintza krooni* (Dickson, 1973) – ssp. endemic to Namibia
Type locality: [Namibia]: "Otavi". **Diagnosis**: Differs from the nominate subspecies in that it usually has more pronounced white markings on the upperside of the wings (Pringle *et al.* 1994). **Distribution**: Namibia. **Specific localities**: Namibia – Otavi (TL).

PIERIDAE

Pierinae

56. *Appias epaphia angolensis* Mendes & Bivar de Sousa, 2006 – ssp. endemic to Angola
Type locality: Angola: "Luanda: Luanda town". **Distribution**: Angola (Luanda, Bengo, Malanje, Cuanza-Norte and Cuanza-Sul Provinces). **Specific**

localities: Angola – Luanda [08°50'S, 13°15'E] (TL); Aeroporto e Estrada de Grafanil [08°50'S, 13°15'E] (Mendes & Bivar de Sousa 2006); Estrada de Catete [08°50'S, 13°15'E] (Mendes & Bivar de Sousa 2006); Caxito [08°35'S, 13°40'E] (Mendes & Bivar de Sousa 2006); Estrada da Muxima [08°50'S, 13°15'E] (Mendes & Bivar de Sousa 2006); Grafanil [08°53'S, 13°18'E (Mendes & Bivar de Sousa 2006); Quicolo [08°48'S, 13°20'E] (Mendes & Bivar de Sousa 2006); Viana [08°54'S, 13°23'E] (Mendes & Bivar de Sousa 2006); Lucala [09°24'S, 15°02'E] (Mendes & Bivar de Sousa 2006); Bom Jesus [09°10'S, 13°34'E] (Mendes & Bivar de Sousa 2006); Cacuaco [08°47'S, 13°21'E] (Mendes & Bivar de Sousa 2006); Catete [08°35'S, 13°42'E] (Mendes & Bivar de Sousa 2006); Quicama [09°11'S, 13°23'E] (Mendes & Bivar de Sousa 2006); Quiminha [08°58'S, 13°47'E] (Mendes & Bivar de Sousa 2006); Tentativa [08°36'S, 13°36'E] (Mendes & Bivar de Sousa 2006); Cassoalala [09°29'S, 14°22'E] (Mendes & Bivar de Sousa 2006); Golunga Alto [09°08'S, 14°46'E] (Mendes & Bivar de Sousa 2006); Salazar [09°18'S, 14°55'E] (Mendes & Bivar de Sousa 2006); Zenza do Itombe [09°17'S, 14°13'E] (Mendes & Bivar de Sousa 2006); Novo Redondo [11°12'S, 13°51'E] (Mendes & Bivar de Sousa 2006); Roca Rio Bimbe [11°05'S, 14°13'E] (Mendes & Bivar de Sousa 2006).

57. *Appias phaola uigensis* Mendes & Bivar de Sousa, 2006 – ssp. endemic to Angola
Type locality: Angola: "Uíge: Inga". **Distribution**: Angola. **Specific localities**: Angola – Inga, Uíge Province [07°27'S, 14°27'E] (TL).

58. *Appias sylvia ribeiroi* Mendes & Bivar de Sousa, 2006 – ssp. endemic to Angola
Type locality: Angola: "Calulo, Kuanza Sul". **Distribution**: Angola (Cuanza-Sul, Cuanza-Norte and Uíge Provinces). **Specific localities**: Angola – Calulo, Cuanza-Sul Province [09°59'S, 14°54'E] (TL); Cassoalala [09°29'S, 14°22'E] (Mendes & Bivar de Sousa 2006); Dalatando [09°18'S, 14°55'E] (Mendes & Bivar de Sousa 2006); Salazar [09°18'S, 14°55'E] (Mendes & Bivar de Sousa 2006); Inga [07°27'S, 14°27'E] (Mendes & Bivar de Sousa 2006).

59. *Colotis amata williami* Henning & Henning, 1994 – ssp. endemic to Namibia and Angola
Type locality: [Namibia]: "Namib, 7 Mar. 1976, L. Heinrich." Holotype in the Transvaal Museum, Pretoria. **Distribution**: Angola, Namibia (central and north). **Specific localities**: Angola – 10 km NNW of Namibe (Namibe) [30 m] (Willis 2009); granite inselberg 36 km NE of Namibe (Namibe) [390 m] (Willis 2009); giant *Welwitschia* site 56 km ESE of Tombua (Namibe) [177 m] (Willis 2009); floodplain of Curoca River (Namibe) (Willis 2009); Espinheira, Iona National Park [440 m] (Namibe) (Willis 2009). Namibia – Namib (TL); Brandberg [870 m] (Pringle *et al.* 1994); Etosha [1,100 m] (Pringle *et al.* 1994); Namutoni [1,098 m] (Pringle *et al.* 1994); Tsaobis Leopard Farm, Karibib district [1,006 m] (Swart 2004); Epupa Falls [614 m]; Bloedkoppie [729 m].

60. *Colotis celimene pholoe* (Wallengren, 1860)– ssp. near-endemic to Namibia and Angola
Type locality: [Botswana]: "Ad lacum N'Gami Africae". Holotype in the Swedish Natural History Museum (images available at www2.nrm.se/en /lep_nrm/p). **Distribution**: Angola, Botswana (west), Namibia, South Africa (Northern Cape Province). **Specific localities**: Botswana – Lake Ngami (TL). Namibia – Brandberg (Pringle *et al.* 1994); Kuiseb Canyon (Pringle *et al.* 1994); Okahandja (Pringle *et al.* 1994); Okosongomingo, east of Otjiwarongo (Pringle *et al.* 1994); Otavi (Pringle *et al.* 1994); Owamboland (Pringle *et al.* 1994); Rehoboth (Pringle *et al.* 1994); Sesfontein (Pringle *et al.* 1994); Windhoek (Pennington). Northern Cape Province – Tswalu Game Reserve (G. Henning and P. Roos); Richtersveld (G. Henning).

61. *Colotis danae walkeri* (Butler, 1884) – ssp. endemic to Namibia and Angola
Type locality: Angola: "Elephant Bay, south-west coast of Africa". **Distribution**: Angola (southwest), Namibia (northwest). **Specific localities**: Angola – Elephant Bay (TL). Namibia – Damaraland (Braine, Ficq & Collins); Kaokoland (Braine, Ficq & Collins); Orupembe [874 m] in Kaokoland (Brown).

62. *Colotis doubledayi* (Hopffer, 1862) – sp. near-endemic to Namibia and Angola
Type locality: [Angola]: "Congo". **Distribution**: Angola (coast), Namibia (west), South Africa (Northern Cape Province – extreme northwest). **Specific localities**: Angola – Lobito Bay (Talbot 1929); Belas Rd., 10 km S of Luanda; Luanda. Namibia – Naiam Hills, 20 miles west of Keetmanshoop (van Son 1949); Keetmanshoop (van Son 1949); Ai Ais (Pringle *et al.* 1994); Blutkuppe (Pringle *et al.* 1994); Brandberg (Pringle *et al.* 1994); Damaraland (Pringle *et al.* 1994); Fish River Canyon (Pringle *et al.* 1994); Kaokoland (Swart 2004); Kuiseb Canyon (Swart 2004); Namib Desert (Swart 2004); Orupembe (35 km east of), Spitzkoppe (Swart 2004); north of Okangwati (Swart 2004). Northern Cape Province – Vioolsdrif (Pringle *et al.* 1994); Hellskloof (Williams & Garvie pers. comm.). **Habitat**: Very arid, semi-desert. Often in dry, stony streambeds in valleys (Pringle *et al.* 1994). **Larval food**: *Maerua schinzii* Pax (Capparaceae) [Cottrell, in Dickson & Kroon 1978; Vioolsdrif, Northern Cape Province].

63. *Mylothris carvalhoi* Mendes & Bivar de Sousa, 2009 – sp. near-endemic to Angola
Type locality: [Angola]: "Uíge Province: Inga, Vale do Loge, ?/IX/1964, coll. A. Bivar de Sousa". The types are in the Instituto de Investigação Científica Tropical, in Lisbon. **Distribution**: Democratic Republic of Congo, Angola (Uíge Province, Mendes & Bivar de Sousa 2009a). **Specific localities**: Democratic Republic of Congo – Lukolela [1.07S, 17.16E] (Warren-Gash 2020); Kinshasa area (Warren-Gash 2020); mouth of the Congo River (Warren-Gash 2020). Angola – Inga, Loge River valley [07°23'S, 14°22'E] (TL); Ndalla Tando [Ndalatando] (Warren-Gash 2020). **Habitat**: Gallery forest.

64. *Mylothris mavunda* Hancock & Heath, 1985 – sp. near-endemic to Angola
Type locality: Zambia: "80 km south of Mwinilunga". Holotype (male) in NHM, London (Warren-Gash 2020). **Distribution**: Zambia (northwest), Angola (Mendes *et al.* 2018). **Specific localities**: Zambia – 80–100 km south of Mwinilunga, Chiwoma area (TL) (Heath *et al.* 2002). **Habitat**: *Cryptosepalum* forest. **Habits**: Nothing published. **Flight period**: Recorded in March, April, May, November and December.

65. *Mylothris spica gabela* Berger, 1979 – sp. endemic to Angola
Type locality: Angola: "7 mls W. de Gabela". Holotype (male) in the NHM, London (Warren-Gash 2020). Paratype in the MRAC, Tervuren, Belgium. **Distribution**: Angola (central). Known only from the type series. **Specific localities**: Angola – seven miles west of Gabela (TL).

PAPILIONIDAE

Papilioninae

66. *Papilio bacelarae* Bivar de Sousa & Mendes, 2009 – sp. endemic to Angola
Type locality: Holotype 1: "Cabinda: Buco Zau, dia, 27-VII-1952 (CZ-5639)". Paratype 1: No labels (Cabinda series) (CZ-5640). The female is unknown. **Distribution**: so far only in Cabinda, Angola. **Habitat**: Low altitude primary rainforest.

67. *Papilio chitondensis* Bivar de Sousa & Fernandes, 1966 – sp. endemic to Angola
Type locality: Angola: "Roça Chitonde-Jungo-Novo Redondo. Fevereiro de 1963". Holotype (male) in Museu Bocage. Female described by Bouyer (2005). **Distribution**: Angola. **Specific localities**: Angola – Roça Chitonde-Jungo-Novo Redondo, Cuanza-Sul Province (TL). **Early stages**: Nothing published. **Larval food**: Nothing published. **Habitat**: The species seems localised around 1,000 masl down to sea level on the western part of the Angolan Planalto. Seles in Cuanza-Sul. **Relevant literature**: Bouyer (2005) [notes and description of female].

68. *Papilio mackinnoni benguellae* Jordan, 1908 – ssp. endemic to Angola
Type locality: Angola: "Cuval River, Benguella". **Distribution**: Angola (central highlands). **Specific localities**: Angola – Cuval River (TL); Benguela Province; Huambo Province; Cuanza-Sul Province (Mendes *et al.* 2013a, 2013b). **Habitat**: Montane forest.

HESPERIIDAE

Hesperiinae

69. *Kedestes sublineata* Pennington, 1953 – sp. endemic to Namibia
Type locality: [Namibia]: "Okahandja, S.W.A.". **Diagnosis**: Distinguished from other members of the *Kedestes lepenula* group by the black scaling of the veins and the absence of black spotting on the underside of the wings (Pringle *et al.* 1994). **Distribution**: Namibia. **Specific localities**: Namibia – Okahandja [1,354 m] (TL; Gaerdes); Otjitambi [1,189 m] (Pringle *et al.* 1994); Farm Portsmut, Windhoek district [1,500 m] (Strydom and Jones, *vide* Pringle *et al.* 1994); Karasberg [1,011 m] (Pringle *et al.* 1994); Tiras Mountains [1,700 m] (Pringle *et al.* 1994); Naukluftberge [1,850 m] (Pringle *et al.* 1994); Kombat [1,609 m] (Pringle *et al.* 1994); Tsumeb [1,335 m] (Pringle *et al.* 1994); Grootfontein [1,444 m] (Pringle *et al.* 1994). **Habitat**: Dry savanna. **Flight period**: All months of the year except the winter months (Pringle *et al.* 1994).

Pyrginae

70. *Abantis bergeri* Mendes & Bivar de Sousa, 2009 – sp. endemic to Angola
Type locality: Angola: "Moxico Province, Lumeje, 20-IV-1965, (BS-14091), det. L. Berger as *Abantis b. bismarcki* (CZ-5372)". Holotype (male) in the entomological collection of the Instituto de Investigação Científica Tropical / Jardim Botânico Tropical. Described from a single male; female unknown (Mendes & Bivar de Sousa 2009c). **Diagnosis**: Similar to *A. bamptoni*. **Distribution**: Angola. **Specific localities**: Angola – Lumeje, Moxico Province [-11.561 20.782] [1,138 m] (TL). **Habitat**: Woodland (Mendes & Bivar de Sousa 2009c). **Larval food**: *Uapaca kirkiana*.

71. *Calleagris jamesoni ansorgei* Evans, 1951 – ssp. endemic to Angola
Type locality: Angola: "Elandswater, Benguella". **Distribution**: Angola. **Specific localities**: Angola – Elandswater, Benguella (TL); Benguela Province;

Bié Province; Cuando Cubango Province; Cuanza-Sul Province; Huambo Province; Lunda-Sul Province (Mendes *et al.* 2013b).

72. *Caprona cassuallala* Bethune-Baker, 1911 – sp. endemic to Namibia and Angola
Type locality: Angola: "Cassualalla, N. Angola". Type in the NHM, London. **Distribution**: Angola, Namibia (north). The distribution of this species and that of *Caprona pillaana* is discussed by Vári (1976). Recorded, erroneously, from Nigeria (Larsen 2005). **Specific localities**: Angola – Cassualalla (TL) [800 m]; Cuanza-Norte Province (Mendes *et al.* 2013b). **Habitat**: Very dry savanna. **Habits**: Similar to those of other species of the genus. Both sexes feed from the flowers of trees in spring (Pringle *et al.* 1994). **Flight period**: September to June (Pringle *et al.* 1994). Ficq, *vide* Pringle *et al.* (1994) has recorded seasonal forms of this species. **Larval food**: *Grewia* species (Tiliaceae) [G. Hobohm, in Dickson & Kroon (1978: 186)].

73. *Eagris multiplagata* Bivar de Sousa & Mendes, 2007. – sp. endemic to Angola
Type locality: Angola: "Kuanza Norte, Zenza do Itombe, 29-V-1971 (Bivar de Sousa – 14312)". **Diagnosis**: Most similar to *Eagris nottoana* but has more hyaline spots, a lighter underside, and there are genitalic differences. **Distribution**: Angola. **Specific localities**: Angola – Zenza do Itombe, Cuanza-Norte Province (09°17'S, 14°13'E; ca [82 m]) (TL). **Habitat**: Forest and dense savanna mosaic (Bivar de Sousa & Mendes 2007). **Habits**: Found flying along a forest road (Bivar de Sousa & Mendes 2007).

74. *Eretis herewardi rotundimacula* Evans, 1937 – ssp. endemic to Angola
Type locality: Angola. **Distribution**: Angola. Recorded, in error for the nominate subspecies, from Mozambique by Congdon *et al.* (2010). **Specific localities**: Angola – Benguela Province; Huambo Province; Huíla Province; Malanje Province (Mendes *et al.* 2013b).

75. *Ernsta colotes colotes* (Druce, 1875) – ssp. endemic to Angola
Type locality: Angola. **Distribution**: Angola. **Specific localities**: Angola – Loanga (Plötz 1884) [58 m]; Bengo Province; Cabinda Province; Luanda Province; Namibe Province (Mendes *et al.* 2013b). **Diagnosis**: Median band of hindwing underside composed of separate spots; forewings pointed (Pringle *et al.* 1994). **Habitat**: Dry and moist savanna (bushveld). Also in forest clearings (Cock 2016).

76. *Sarangesa gaerdesi gaerdesi* Evans, 1949 – sp. endemic to Namibia
Type locality: [Namibia]: between Abenab [1,303 m] and Grootfontein [1,445 m] (TL; Gaerdes); Otavi [1,400 m] (Gaerdes); Gaub Valley [1,542 m] (Kroon); near Tsumeb [1,335 m] (G. Henning); Halali in the Etosha National Park [1,114 m] (Ficq). **Habitat**: Dry savanna. Specimens are always found in the close vicinity of their larval host-plants. The wing coloration of each of the two subspecies is a remarkable match for the colour of the leaves of their respective host-plants. **Habits**: They fly rapidly and erratically around stands of the host-plant, usually settling on the leaves with opened wings. Both sexes feed from the small flowers of the host-plant (Pringle *et al.* 1994). **Flight period**: Possibly all year for the nominate subspecies but commonest in the midsummer months following rains (Pringle *et al.* 1994). Subspecies *smithae* has been recorded from August to October (Pringle *et al.* 1994) and in late February (Swart 2004). **Early stages**: Dickson & Kroon (1978: 185) [as *Sarangesa gaerdesi smithae*; Swakop River, Namibia]. Pringle *et al.* (1994: 314) [both subspecies]. The larva attaches several leaves together with silk to form a shelter. These shelters are normally found on the outer edge of the bush. The larva is brownish grey and pupates within the shelter. **Larval food**: *Petalidium englerianum* (Schinz) C.B.Clarke (Acanthaceae) [Dickson & Kroon (1978: 185); as *Petalidium latifolium* (Schinz.) C.B. Cl.; for the nominate subspecies].

77. *Sarangesa gaerdesi smithae* Vári, 1976. – ssp. endemic to Namibia
Type locality: [Namibia]: "South West Africa: Bloedkoppie, [about] 40 km east of Swakopmund, Namib Desert National Park". **Diagnosis**: Differs from the nominate subspecies in its ochreous coloration and the presence of a central hyaline spot on the hindwing (Pringle *et al.* 1994). **Distribution**: Namibia (south-central). **Specific localities**: Namibia – Bloedkoppie, 40 km east of Swakopmund [729 m] (TL; Bampton and Smith); Remhoogte Pass [1,600 m]. **Larval food**: *Petalidium variabile* (Engl.) C.B.Clarke (Acanthaceae) [Dickson & Kroon 1978: 185; for subspecies *smithae*].

Endemism of Arachnida (Amblypygi, Scorpiones and Solifugae) in the highlands and escarpments of Angola and Namibia: Current knowledge and future directions

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-prendini

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ABSTRACT

The arachnid fauna of Angola and Namibia is diverse and includes high levels of endemism, much of which is associated with the arid zone, especially the Namib Desert. The endemic arachnid fauna of the highlands and escarpments, including mountain ranges, plateaus and inselbergs, has received less attention. The study presented here is the first to compile existing distributional data for three arachnid orders – whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae Sundevall, 1833) – occurring in the highlands and escarpments of Angola and Namibia from published literature, online databases and natural history collections. Distribution maps were used, together with available data or expert knowledge of taxon habitat requirements, to prepare a list of described arachnid taxa considered endemic or near-endemic to the western highlands and escarpments of these two countries. In addition, arachnid endemism was assessed more broadly by scoring the presence of described and potential undescribed endemics in relevant highlands and escarpments, tallying the scores for each order, and ranking the highlands and escarpments based on the sum of all three ordinal tallies. These scores provide a rough index of the relative importance of highlands and escarpments in Angola and Namibia for prioritising decisions regarding conservation as well as further survey and inventory from the arachnid perspective. Although the highlands and escarpments of Angola and Namibia probably serve as refugia for taxa requiring cooler, more humid habitats than are available in the surrounding arid lowlands, including palaeoendemics, they appear to contain fewer endemic arachnid taxa than the lowlands. This may be because: (1) the highlands and escarpments of Angola and Namibia are relatively low, on average, providing few opportunities for insular speciation; (2) much arachnid endemism in the arid lowlands is associated with unique substrates that are absent in the highlands, including sand dunes, gravel plains and clays associated with drainage systems, all of which facilitate burrowing to escape the arid conditions and promote diversification; and (3) much of the taxonomy of the arachnids of both countries remains unresolved, and the distributions poorly understood, especially in Angola. More intensive surveys, with an emphasis on collecting genetic samples from disjunct populations across the distributions of each putative species, are needed to better understand arachnid diversity and endemism in the region.

Keywords: Amblypygi, Angola, Arachnida, endemism, escarpments, highlands, Namibia, Scorpiones, Solifugae

INTRODUCTION

Arachnids have inspired fear and fascination since antiquity, in part because they are predators and some, such as scorpions and spiders, are venomous. Few are considered medically important, however, and fewer still have been implicated in fatal or debilitating envenomation. Despite their fearsome appearance, most arachnids are harmless.

Arachnids are of particular interest to students of evolution because of the great age of their lineage. Fossil scorpions from the Silurian, 435 mya, present the first unequivocal evidence for terrestrialisation (Dunlop *et al*. 2008). The arachnid ground plan has changed little since the first scorpions colonised land: Palaeozoic arachnids closely resemble their modern descendants. Morphological conservatism, together with low vagility and stenotopic ecological requirements, make many arachnid taxa prone to vicariance and allopatric speciation (Prendini 2001b, Bryson *et al*. 2013, Loria & Prendini 2021, Schramm *et al*. 2021).

As elsewhere in southern Africa, the arachnid fauna of Angola and Namibia is diverse and includes high levels of endemism, much of which is associated with the arid zone, especially the Namib Desert (Lamoral 1979, Prendini 2005c, Prendini & Esposito 2010). The endemic arachnid fauna of the highlands and escarpments, including mountain ranges, plateaus and inselbergs, has received less attention, although the highlands probably serve as refugia for taxa requiring cooler, more humid habitats than are available in the surrounding arid lowlands, as in other parts of the world (Prendini 2003a, Bryson *et al*. 2013, Loria & Prendini 2021, Schramm *et al*. 2021). One reason is because knowledge of the taxonomy and distributions of arachnids in both countries, but especially in Angola, is limited, compared to other taxa such as vertebrates, flowering plants and even some terrestrial invertebrates.

The study presented here is the first to compile existing distributional data for three arachnid orders – whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae

Sundevall, 1833) – occurring in the highlands and escarpments of Angola and Namibia from published literature, online databases and natural history collections. Distribution maps were used, together with available data or expert knowledge of taxon habitat requirements, to prepare a list of described arachnid taxa considered endemic or near-endemic to the highlands and escarpments. In addition, arachnid endemism in the highlands and escarpments was assessed more broadly by scoring the presence of described and potential undescribed endemics in relevant highlands, tallying the scores for each order and ranking the highlands and escarpments based on the sum of all three ordinal tallies.

Although the picture may change when the taxonomy of each order is revised and the distributions are better understood, these data provide a baseline for prioritising decisions regarding conservation, as well as further survey and inventory, from the arachnid perspective. More intensive surveys, with an emphasis on collecting genetic samples from disjunct populations across the distributions of each putative species, are needed to better understand arachnid diversity and endemism in the region.

METHODS

Taxonomic and geographical constraints

The study presented here made use of the most recent published classifications for each arachnid order and relied on existing sources of distributional data (see below). Only valid, described infrageneric taxa (species and subspecies) were included in the assessment. Synonyms, *nomina dubia* and taxa, the validity of which was questioned in the most recent taxonomic treatments, were omitted. For example, *Solpugema aethiops* Lawrence, 1967 was excluded, despite having been described from the Brandberg (the only known locality for this species), as Wharton (1981) suggested that this species is almost certainly conspecific with the more widespread *Solpugista namibica* Kraus, 1956. Female solifuges are notoriously difficult to identify and, given that *S. aethiops* was described from a single female and the only known specimen, its validity must be re-evaluated.

Whereas the taxonomy of southern African whip spiders is fairly well resolved, the secretive nature and seasonal activity of these arachnids, and their need for a humid microhabitat, implies that their distributions, especially in the arid zone of Angola and Namibia, remain poorly documented.

The taxonomy of southern African scorpions has received much attention but continues to undergo active revision, and the distributions of scorpion taxa are fairly well documented due to the ease with which many (though by no means all) may be collected.

Compared to Amblypygi and Scorpiones, the knowledge of solifuges is much poorer in terms of taxonomy and distribution for the following reasons. Firstly, species-level taxonomy of Solifugae depends almost entirely on characters of adult males, which are highly seasonal and active for only a brief period annually. Secondly, the seasonality, habitat specificity and speed of most solifuges makes them difficult to collect and survey. Thirdly, there are few experts on the order, worldwide. The highland endemic status of solifuge species was therefore evaluated based on few specimens and locality records, often singletons. In addition, the precision of many historical records is unknown. This may influence whether a locality record falls on a highland or only in the vicinity thereof, which in turn affects decisions regarding whether or not a species may be endemic or near-endemic to the highland.

Given these constraints, understanding of the taxonomy, distributions, and endemism of all three arachnid orders in southern Africa lags far behind that of the vertebrates, flowering plants and even some terrestrial invertebrates, like butterflies and dragonflies. There is also a huge disparity between the knowledge of arachnids in Angola and Namibia. The fauna of Namibia has been subject to surveys, inventories and publications from the German colonial period to the present, with extensive collections deposited in natural history museums in Germany, South Africa and the National Museum of Namibia. In contrast, research on Angolan arachnids which began during the Portuguese colonial period, largely ceased during approximately three decades of war (1975–2002), a time in which no new collections were added to the Museo do Dundo. Arachnid collections from Angola represent a tiny fraction of those from Namibia and large swaths of the country have never been surveyed.

Georeferencing and mapping

A database of point locality records for mapping the distributions of arachnid taxa considered or suspected to be endemic to the highlands and escarpments of Angola and Namibia was assembled from published literature, online databases, e.g., iNaturalist (https://www.inaturalist.org), and material examined from the following natural history collections: Albany Museum, Grahamstown, South Africa; American Museum of Natural History, New York, USA; Ditsong National Museum of Natural History (former Transvaal Museum), Pretoria, South Africa; Iziko South African Museum, Cape Town, South Africa; KwaZulu-Natal Museum (former Natal Museum), Pietermaritzburg, South Africa; and National Museum of Namibia, Windhoek.

Records for which geographical coordinates were previously entered by the collector were checked for accuracy and the remaining records georeferenced using the Geographic Names Server (https://geonames.nga.mil/geonames/GNSHome), the Fuzzy Gazetteer (https://isodp.hof-university.de/fuzzyg/query) and Google Earth (https://earth.google.com). Dubious or imprecise records were omitted. The final dataset comprised 209 point localities for 22 infrageneric taxa in 16 genera and ten families. Distribution maps were produced using QGIS 3.16.10 'Hannover' Long Term Release (QGIS Development Team 2021), by superimposing point locality records on datasets representing the political boundaries, topography (inselbergs and mountain ranges, plateaus, escarpments) and major rivers of Angola and Namibia.

Assessing highland endemism

Distribution maps were used, together with available data or expert knowledge of taxon habitat requirements, to prepare a list of described arachnid taxa considered endemic or near-endemic to the highlands and escarpments of Angola and Namibia. Consistent with other treatments in the present volume, the highlands and escarpments of Angola and Namibia comprise inselbergs and mountain ranges (free-standing hills or mountains that rise at least 200 m above the surrounding land); plateaus (broad areas of flat or hilly ground, at least 1,600 masl); and escarpments (narrow areas with steep slopes on the western margins of plateaus).

Relatively few taxa were considered *bona fide* highland endemics; i.e., those exclusively restricted to highlands and escarpments. The remaining taxa were considered highland endemics or near-endemics only if most of the known locality records were situated on or adjacent to highlands and escarpments, applying the metapopulation concept (Levins 1969), whereby disjunct populations occupying highland refugia may coalesce during periods of cooler, more humid climate. Hotter, drier lowlands represent barriers to dispersal for highland taxa inhabiting disjunct refugia. In contrast, taxa with one or a few records on highlands and escarpments, but an otherwise predominantly lowland distribution, even if occurring within valleys between highlands and escarpments, were not considered highland endemics. For these taxa, highlands and escarpments represent barriers to dispersal between disjunct lowlands.

In addition, arachnid endemism was assessed more broadly by scoring the presence of described and potential but undescribed endemics in the highlands and escarpments of Namibia and Angola, tallying the scores for each order, and ranking the various highlands and escarpments based on the sum of all three ordinal tallies (a relative score of the number of endemic arachnids in each highland). Although these scores may change when the taxonomy of each order is revised and the distributions are better understood, they provide a rough index of the relative importance of highlands and escarpments for prioritising decisions regarding conservation, as well as for further survey and inventory, from the arachnid perspective.

RESULTS AND DISCUSSION

Highland endemic whip spiders

Only two species of Amblypygi may be considered endemic to the highlands and escarpments of Angola and Namibia (Table 1). Both constitute monotypic genera, palaeoendemics which diverged from other phrynichid genera before the breakup of Gondwanaland (Weygoldt 1996), and occupy refugia in the highlands, escarpments and other areas with a higher humidity (e.g., wells and watercourses) than the surrounding arid lowlands.

Phrynichodamon scullyi (Purcell, 1902), of the family Phrynichidae Simon, 1892, has been recorded from only four localities in southwestern Namibia (Figure 1), each represented by a single individual, over the course of a century (Lawrence 1967, Weygoldt 1996). These localities are situated in the Hakosberge, the Tirasberge, Naukluft Mountains and the Aus Mountains. Most of the known records of *P. scullyi* occur further south, in the Kamiesberg, Bokkeveldberge and Cederberg of South Africa (Lawrence 1949, 1955, Weygoldt 1996, 1998), where the species has been encountered slightly more often. Given the large distances between the four disjunct populations of this species in Namibia, and between them and the two disjunct populations in South Africa, it would be important to compare them genetically to assess whether more than one species is involved and to determine the timing of divergence.

Xerophrynus machadoi (Fage, 1951), considered *incertae sedis* within superfamily Phrynoidea Blanchard, 1852 by Weygoldt (1996, 2000), is known from fewer than ten localities, two (the type locality and a second record near Omahua) in southwestern Angola (Lawrence 1949, Fage 1951) and the rest in northwestern Namibia (Figure 1). Most of the known localities (and specimens) were collected from valleys on the southern slopes of the Brandberg Massif (Weygoldt 1996, 1998). The other Namibian localities are associated with the Etendeka and Otjikondavirongo mountains, the Huab outliers and the Uis Mountains of Damaraland, an area in northwestern Namibia bordered to the north by the Kaokoveld, to the west and south by the Namib Desert, and to the east by the Kalahari Desert, and encompassing a distinctive semi-desert landscape comprising vast, arid, gravel or rocky plains intersected by towering granite outcrops. As with *P. scullyi*, the large distances between the disjunct populations of *X. machadoi* in Angola, and between them and the disjunct Namibian populations in the Kaokoveld and Damaraland, emphasise the need for genetic comparison to assess whether more than one species is involved, as well as to determine the timing of divergence.

The difficulty of collecting these secretive lithophilous arachnids, which appear to retreat into deep rock crevices or exfoliations during the dry season, implies that collection efforts must be focused on the rainy season, and concentrated on areas with higher humidity, such as caves, wells and watercourses, for any possibility of success.

Damon gracilis Weygoldt, 1998, a third species of whip spider, endemic to southwestern Angola and northwestern Namibia, has been recorded from some highlands and escarpments, including the Serra da Neve in Angola and the Baynes–Otjihipa Mountains in Namibia (Weygoldt 1998, 1999, 2000). However, this species was not considered endemic or near-endemic to the highlands and escarpments as the majority of the known records are situated at low elevation, often in association with wells and watercourses. *Damon sylviae* Prendini *et al*., 2005, the fourth species of whip spider recorded in Namibia, has not been recorded from the highlands and escarpments (Prendini *et al*. 2005).

Table 1: *Described species and subspecies of whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae Sundevall, 1833) that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia, with countries and highlands of occurrence.*

Classification	Species	Country: highlands and escarpments
Amblypygi		
Phrynichidae	*Phrynichodamon scullyi* (Purcell, 1902)	Namibia: Hakosberge, Tirasberge, Naukluft Mountains and Aus Mountains; South Africa: Kamiesberg, Bokkeveldberge and Cederberg
	Xerophrynus machadoi (Fage, 1951)	Angola: lowlands; Namibia: Kaokoveld (Etendeka and Otjikondavirongo mountains), Huab outliers, and Brandberg Massif (valleys)
Scorpiones		
Bothriuridae	*Brandbergia haringtoni* Prendini, 2003	Namibia: Brandberg Massif (summit)
	Lisposoma josehermana Lamoral, 1979	Namibia: Otavi and Paresis mountains and Waterberg Plateau
Buthidae	*Uroplectes ngangelarum* Monard, 1930	Angola: southwestern highlands (e.g., Serra de Chela, Serra da Neve)
	Uroplectes tumidimanus Lamoral, 1979	Namibia: Erongo Mountains through central highlands (Khomas Hochland, Auas Mountains, Hakosberge and Gamsberg), Naukluft and Tsaris mountains, and Rooirand Plateau to Huib-Hoch Plateau and Hunsberge
Hormuridae	*Hadogenes lawrencei* Newlands, 1972	Namibia: Uri-Hauchab (inselberg, west of Awasibberge)
Scorpionidae	*Opistophthalmus scabrifrons* Hewitt, 1918	Namibia: Groot Karasberg
	Opistophthalmus schultzei Kraepelin, 1908	Namibia: Aus Mountains
	Opistophthalmus ugabensis Hewitt, 1934	Namibia: Brandberg Massif (valleys), Tafelkop and Huab outliers
Solifugae		
Ceromidae	*Ceromella focki* (Kraepelin, 1914)	Namibia: central highlands (Khomas Hochland)
Daesiidae	*Biton striatus bidentatus* Lawrence, 1955	Namibia: Kaokoveld (Etendeka Mountains) and Brandberg Massif (summit)
	Blossia angolensis (Lawrence, 1960)	Angola: highlands near Lubango
	Blossia falcifera quibensis Hewitt, 1934	Namibia: Rooirand Plateau and Huib-Hoch Plateau
	Blossia gaerdesi Lawrence, 1972	Namibia: Otavi Mountains, Waterberg Plateau, central highlands (Khomas Hochland) and Rooirand Plateau
	Hemiblossia machadoi Lawrence, 1960	Angola: Serra da Chela (highlands near Lubango)
Gylippidae	*Bdellophaga angulata* Wharton, 1981	Namibia: central highlands (Auas Mountains and Gamsberg)
	Trichotoma fusca (Roewer, 1941)	Namibia: Waterberg Plateau
Melanoblossiidae	*Melanoblossia ansie* Bird & Wharton, 2015	Namibia: Tsaukhaib (inselberg in Sperrgebiet)
Solpugidae	*Solpugista methueni* (Hewitt, 1914)	Namibia: Rooirand Plateau and Huib-Hoch Plateau
	Zeria glabricornis (Lawrence, 1928)	Namibia: Kaokoveld (Baynes–Otjihipa and Etendeka mountains) and Brandberg Massif (summit)
	Zeria schlechteri (Purcell, 1899)	Namibia: Rooirand Plateau; South Africa: Naroepberge

Highland endemic scorpions

Two genera and three species of the family Bothriuridae Simon, 1880 are endemic to Namibia. This monophyletic lineage of palaeoendemic taxa diverged from their relatives in South America and Australia when Africa separated from the rest of Gondwana ca. 140 million years ago (Prendini 2003a, 2005c). Two of the three species are highland endemics (Table 1), occupying refugia with higher humidity (e.g., wells and watercourses) than the surrounding arid lowlands.

Brandbergia haringtoni Prendini, 2003 is known from only two specimens collected at 1,650 masl in Goaseb (or Ga-Asab) gorge on the southern side of the Brandberg Massif in 1978 (Figure 1). Little is known about this species and several subsequent attempts to collect it at the type locality (including during the rainy season) were unsuccessful (Prendini 2005a). However, further attempts are considered a high priority as the male remains unknown and a genetic sample is needed for comparison with other bothriurid taxa in Namibia, South America and Australia.

Lisposoma josehermana Lamoral, 1979 is relatively common in the Otavi Mountains, where it is known from several inselbergs, and the Waterberg Plateau (Figure 1). This lapidicolous species may be found under stones and in caves on wooded, humid slopes (Lamoral 1979, Prendini 2003b, 2005a). It has also been recorded from the Paresis Mountains. Genetic comparison of the disjunct populations is needed to assess whether more than one species is involved and to test the timing of divergence from one another and from other Namibian bothriurids.

Lisposoma elegans Lawrence, 1928, the third species of endemic Namibian bothriurid, has been recorded from some highlands and escarpments (Prendini 2003b), including the Kaokoveld (Otjikondavirongo Mountains) and the Central Highlands (Khomas Hochland and Gamsberg). However, this species was not considered endemic or near-endemic to the highlands and escarpments as most of the known records are from low elevations. This lapidicolous species occurs under stones, often in humid microhabitats, such as along gulleys and episodic watercourses, in rather arid locations (Lawrence 1928, Prendini 2005a). As with *L. josehermana*, genetic comparison of the disjunct populations of *L. elegans* is needed to assess whether more than one species is involved and to determine the timing of divergence from one another and from other Namibian bothriurids. The diverse family Buthidae C.L. Koch, 1837 contains only two species considered near-endemic to the highlands and escarpments, one in southwestern Angola, and the other in central-southern Namibia (Table 1). Both are lapidicolous species of the exclusively Afrotropical genus *Uroplectes* Peters, 1861 and may be found under stones (Prendini 2001b). *Uroplectes ngangelarum* Monard, 1930 is near-endemic to the highlands and escarpments of southwestern Angola, most of the known localities having been recorded on the plateau in the vicinity of Lubango and Humpata (Figure 1). *Uroplectes tumidimanus* Lamoral, 1979 is near-endemic to the highlands and escarpments of Namibia, extending from the Erongo Mountains through the central highlands (Khomas Hochland, Auas Mountains, Hakos Mountains and Gamsberg) to the Rooirand Plateau, Huib-Hoch Plateau and Hunsberge (Figure 1). Both species appear to be closely related to the widespread *Uroplectes planimanus* (Karsch, 1879), distributed from southern Angola and northern Namibia, across Botswana and Zambia to Mozambique, Zimbabwe and the Limpopo Province of northern South Africa (Prendini 2005c), from which it appears they became isolated in the highlands and subsequently diverged. However, the timing of these events, as well as the limits of all three species, await further testing. Indeed, the taxonomy of *Uroplectes* is probably the least resolved of any group of southern African scorpions. Further collections and genetic analyses are needed to address species limits as several undescribed highland endemics are suspected.

One species of the lithophilous Afrotropical genus *Hadogenes* Kraepelin, 1894, in the family Hormuridae Laurie, 1896, is endemic to the highlands and escarpments of Namibia (Table 1). Like other species of the genus, *Hadogenes lawrencei* Newlands, 1972 inhabits the cracks and crevices of weathered rock outcrops (Prendini 2001b, 2005c). It appears to be restricted to the Uri-Hauchab, a relatively low elevation inselberg west of the Awasibberge (Figure 2), surrounded by sand dunes of the central Namib dune field, where it is presumed to have evolved in isolation since the inselberg was isolated from the escarpment in the Pliocene (Newlands 1972). This hypothesis awaits rigorous testing which will require the collection of genetic material from *H. lawrencei* and the nearest populations of *Hadogenes tityrus* (Simon, 1888) in the Awasibberge. The collection and analysis of genetic material from across the distribution of *H. tityrus* is considered an important priority for delimiting the species of this complex (Newlands & Cantrell 1985) and for better understanding distributions which suggest that some may be endemic to the highlands and escarpments of Namibia.

Another hormurid, *Hadogenes zumpti* Newlands & Cantrell, 1985, has been recorded from the Hunsberge of southern Namibia and the Richtersveld of South Africa (Newlands & Prendini 1997), but was not considered endemic or near-endemic to the highlands and escarpments of Namibia as most of the

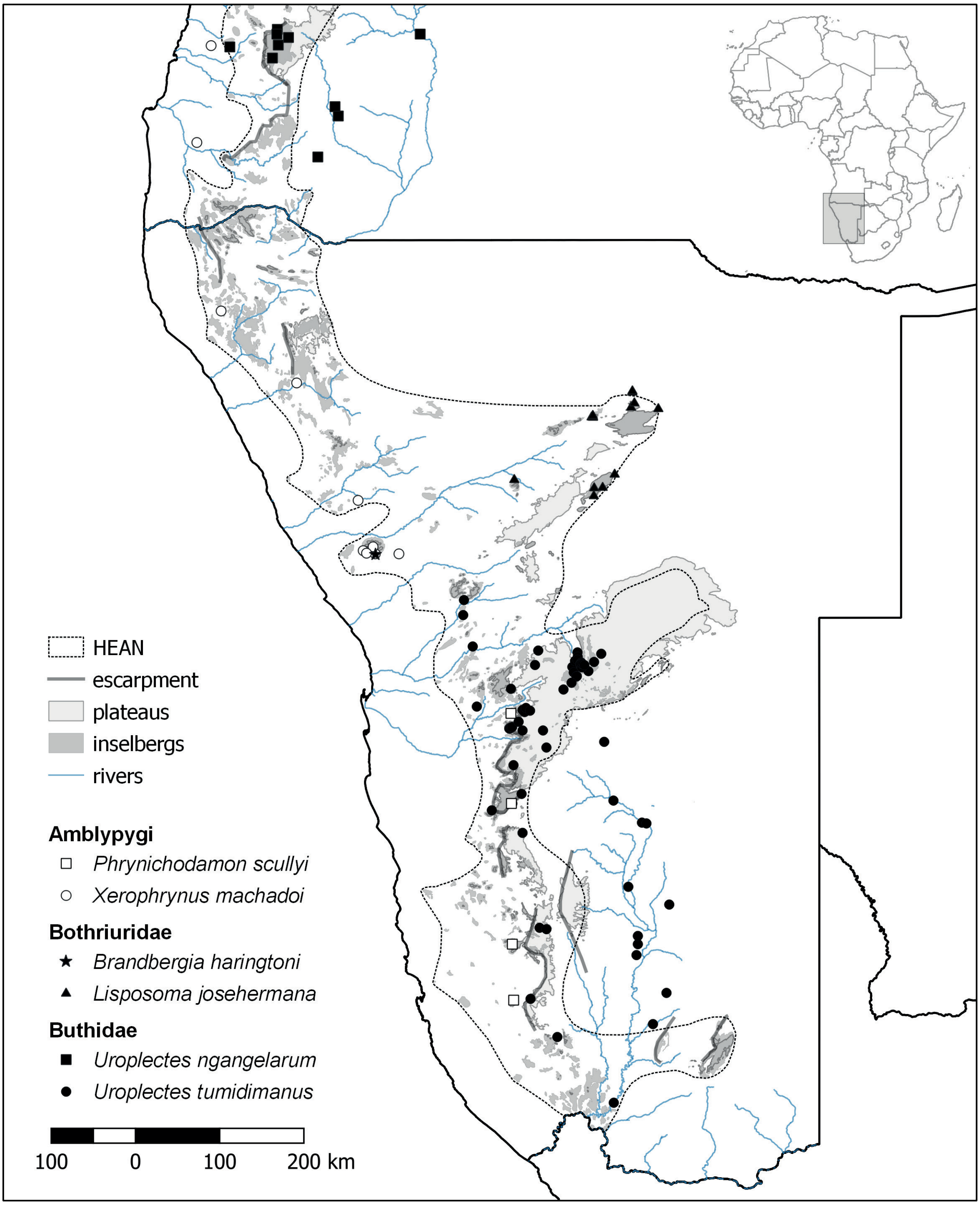

Figure 1: *Described species of whip spiders (Amblypygi Thorell, 1883) and scorpions (Scorpiones C.L. Koch, 1837) in the families Bothriuridae Simon, 1880 and Buthidae C.L. Koch, 1837 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Brandbergia haringtoni *Prendini, 2003;* Lisposoma josehermana *Lamoral, 1979;* Phrynichodamon scullyi *(Purcell, 1902);* Uroplectes ngangelarum *Monard, 1930;* Uroplectes tumidimanus *Lamoral, 1979; and* Xerophrynus machadoi *(Fage, 1951).*

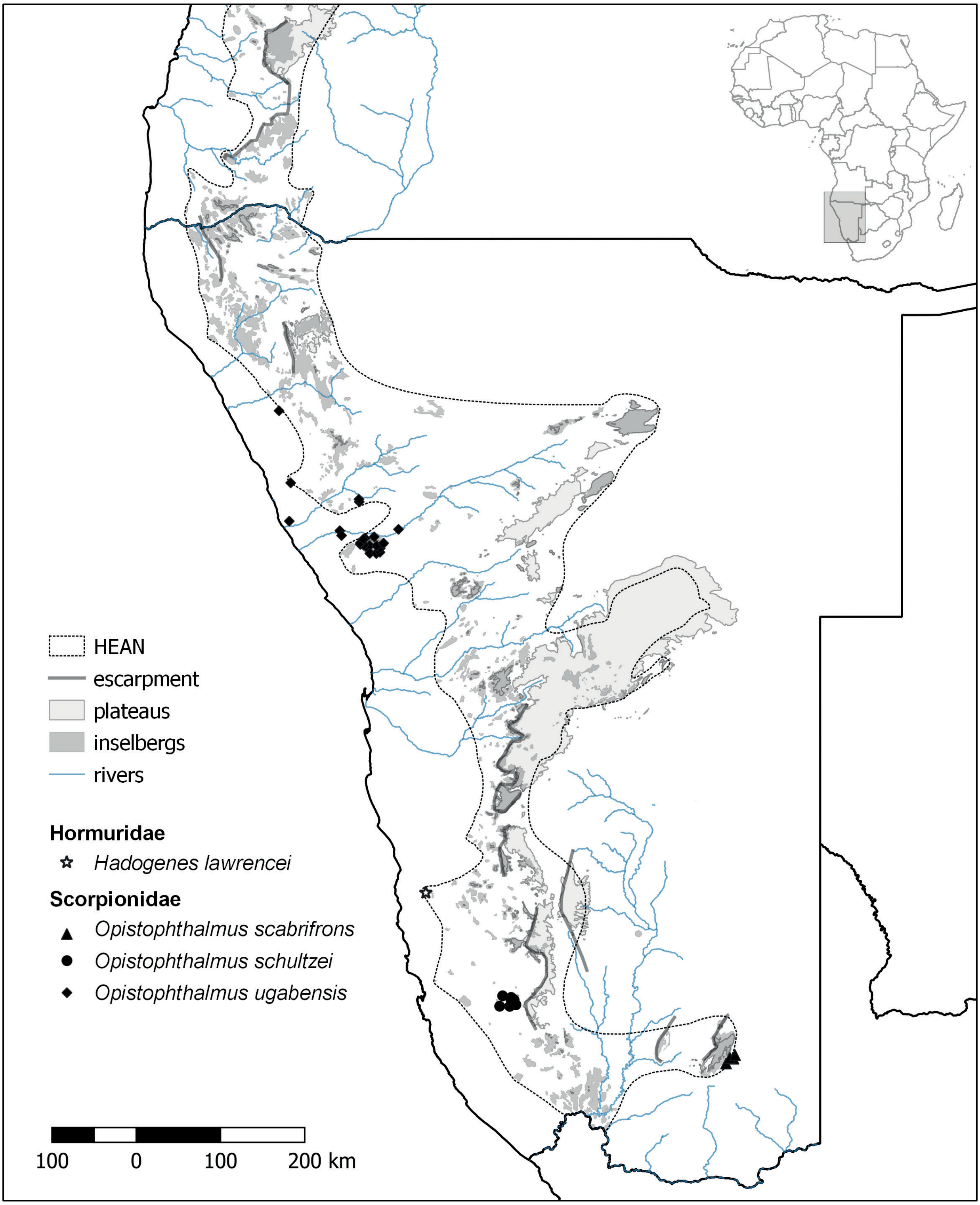

***Figure 2:** Described species of scorpions (Scorpiones C.L. Koch, 1837) in the families Hormuridae Laurie, 1896 and Scorpionidae Latreille, 1802 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Hadogenes lawrencei *Newlands, 1972;* Opistophthalmus scabrifrons *Hewit, 1918;* Opistophthalmus schultzei *Kraepelin, 1908;* Opistophthalmus ugabensis *Hewitt, 1934.*

known records are at low elevations. The same proved true for two other hormurids recorded in Angola and Namibia, *Hadogenes hahni* (Peters, 1862) and *Hadogenes phyllodes* Thorell, 1876 (Prendini 2005b).

Three species of the fossorial Afrotropical genus *Opistophthalmus* C.L. Koch, 1837 in the family Scorpionidae Latreille, 1802 (Lamoral 1979, Prendini 2001a, 2005c, Prendini *et al.* 2003) were considered endemic or near-endemic to the highlands of Namibia (Table 1). *Opistophthalmus scabrifrons* Hewit, 1918, a pelophilous species that constructs burrows under stones in shaley clay, is restricted to valleys on the eastern side of the Groot Karasberg (Figure 2). *Opistophthalmus schultzei* Kraepelin, 1908, another pelophilous species which constructs burrows in open ground and under stones in granitic sandy loam, is restricted to the Aus Mountains (Figure 2). Finally, *Opistophthalmus ugabensis* Hewitt, 1934, a semi-lithophilous species that constructs shallow scrapes under stones in sandy loam, occurs in the valleys and lower slopes of the Brandberg Massif, as well as other inselbergs in Damaraland, including the Gobobosebberge (e.g., Tafelkop) and the Huab outliers (Figure 2). Although these three species are well characterised morphologically and genetically, many other widespread Namibian species of *Opistophthalmus* represent species complexes that are the subject of ongoing revision which, once completed, will increase the number of highland endemics and near-endemics in the country (Prendini & Loria 2020).

Highland endemic solifuges

Southern Africa has the world's highest diversity of Solifugae, much of which is concentrated in the arid west of the subcontinent. This diversity is almost certainly underestimated, however, particularly for Angola (Lawrence 1960). The distributions of many solifuge species appear to be highly restricted (Wharton 1981), especially in the fossorial, psammophilous Hexisopodidae Pocock, 1897 and the small, diurnal Melanoblossiidae Roewer, 1933. In addition, many highlands and escarpments are undersampled for solifuges. More extensive sampling with more precise locality data is expected to increase the list of highland endemic solifuges presented here.

The small family Ceromidae Roewer, 1933 contains a single highland endemic, *Ceromella focki* (Kraepelin, 1914), restricted to the central highlands (Khomas Hochland) of Namibia (Table 1). It is known from only two male specimens collected in Windhoek in 1911 (Kraepelin 1914) and 2009, respectively (Figure 3).

Five species of the diverse, probably paraphyletic (Bird *et al.* 2015), family Daesiidae Kraepelin, 1899 are endemic or near-endemic to the highlands and escarpments: two to southwestern Angola, one to northwestern Namibia, one to southwestern Namibia and one to central Namibia (Table 1). *Biton* (*Biton*) *striatus bidentatus* Lawrence, 1955 is known from four records in Namibia, mostly from the Kaokoveld, including the vicinity of the Etendeka Mountains, and one from the summit of the Brandberg Massif (Figure 3). It is uncertain whether this species is strictly endemic to the highlands and escarpments, as all known localities of this species were georeferenced *a posteriori*, and the precise coordinates of the original collection localities are unknown.

Blossia angolensis (Lawrence, 1960) is known from a single female collected at an altitude of 1,500 masl in the highlands near Lubango, southwestern Angola (Figure 3). Unfortunately, the male has never been collected, and little is known about this species. *Blossia falcifera quibensis* Hewitt, 1934, recorded from only two localities on plateaus in southwestern Namibia, appears to be a *bona fide* highland endemic (Figure 3). Its congener, *Blossia gaerdesi* Lawrence, 1972, is relatively widespread in the highlands and escarpments of Namibia, from the Otavi Mountains and the Waterberg Plateau, through the central highlands, to the Rooirand Plateau (Figure 3). Many locality records of *B. gaerdesi* are not actually situated in highlands, but in the near proximity, suggesting that highlands may serve as refugia. More material is needed for morphological and genetic analysis to determine whether these populations are conspecific.

Hemiblossia machadoi Lawrence, 1960 is known from a single female collected at 2,300 masl in the Serra da Chela near Lubango, southwestern Angola, in 1949 (Figure 3), and a juvenile female collected approximately 100 km to the southeast (Lawrence 1960). More collections are needed to verify whether this species is endemic or near-endemic to the highlands and escarpments. Its congener, *Hemiblossia lawrencei* Roewer, 1933, described from a single female collected in Windhoek, Namibia, was excluded from the list of highland endemics as it was inadequately characterised (Wharton 1981). Further comparison with females of different species in the *australis* group of *Hemiblossia* Kraepelin, 1899 are needed to assess the validity of this species.

The southern African species of the small family Gylippidae Roewer, 1933 are assigned to three genera in subfamily Liphophaginae Wharton, 1981. Two of the four lipophagine species occurring in Namibia are endemic or near-endemic to the highlands and escarpments (Table 1). Available data suggest that the monotypic *Bdellophaga angulata* Wharton, 1981 is restricted to the central highlands of Namibia (Figure 4). *Trichotoma fusca* (Roewer, 1941) is known only from the type locality, the Waterberg Plateau (Figure 4). Wharton (1981) suggested that the latter may be conspecific with *Trichotoma brunnea* Lawrence, 1968, from which it is almost indistinguishable morphologically. As *T. brunnea* appears to be restricted to the Namib coast, however, *T. fusca* was assumed to be a valid species for the present assessment. A genetic comparison between material from the Namib and the Waterberg Plateau is needed to resolve this question.

The nominotypical subfamily Melanoblossinae Roewer, 1933, of the small family Melanoblossiidae, is also restricted to southern Africa. *Melanoblossia ansie* Bird and Wharton, 2015, a *bona fide* endemic, restricted to the Tsaukhaib Mountain of the Tsau ǁKhaeb (Sperrgebiet) National Park in southwestern Namibia (Bird & Wharton 2015; Figure 4), is the only highland endemic currently recognised in this family (Table 1). The melanoblossiid diversity of Namibia is probably vastly underestimated (Wharton 1981), however, due to the small size and cryptic morphology and behaviour of these solifuges. Many undescribed species are expected to be narrow endemics (Wharton 1981).

The family Solpugidae Leach, 1815 is probably the most conspicuous group of solifuges in southern Africa, on account of their size and the spectacular colour of some of the diurnal species. Based on current knowledge, three solpugid species appear to be endemic or near-endemic to the highlands and escarpments of Namibia (Table 1). *Solpugista methueni* (Hewitt, 1914) and *Zeria schlechteri* (Purcell, 1899) were both recorded from southwestern Namibia, and occur in sympatry on the Rooirand Plateau. Whereas *S. methueni* was recorded from a second locality in Namibia, the Huib-Hoch Plateau, *Z. schlechteri* is known from only a single locality in Namibia (Figure 4), but a record from the Naroep Mountains, south of the Orange River in South Africa, supports its recognition as a highland endemic.

Most of the known locality records of *Zeria glabricornis* (Lawrence, 1928) are situated in northwestern Namibia, extending across the Kaokoveld and Damaraland to the Brandberg Massif and vicinity (Figure 4). The southernmost outlier record of this species requires verification. Although many records of *Z. glabricornis* are not located on the highlands and escarpments per se, their occurrence in the foothills and lowlands associated with these highlands, suggests that this species may be near-endemic to the highlands, a hypothesis that merits further testing based on the collection of material for genetic analysis.

Relative importance of highlands

Whereas highland endemic or near-endemic arachnid taxa are distributed across the length of Namibia, within Angola they appear to be restricted to the southwest (Figures 1–4). Although this may be partly explained by the paucity of data for Angola, the pattern of endemism in Angola appears to match that of Namibia. As with Namibia, in which most of the highland endemics or near-endemics are associated with escarpments, plateaus and inselbergs in the arid west (the Namib and pro-Namib), the highland endemics and near-endemics of southwestern Angola occur in the most arid part of the country, containing the northern limit of the Namib.

Scoring the presence of described and potential undescribed endemics in relevant highlands and escarpments and tallying the scores for each order, revealed that some highlands and escarpments are more important areas of endemism for some arachnid taxa than others. The central highlands (especially the Gamsberg and to a lesser extent, the Khomas Hochland), the Hunsberge and the Brandberg Massif and Huab outliers, each contain four or more endemic scorpions. The central highlands (especially the Khomas Hochland) and the Rooirand Plateau each contain three or more endemic solifuges.

When considering the sum of all three ordinal tallies, the following areas stand out as priorities for conservation and for further survey and inventory: the central highlands (especially the Khomas Hochland, the Gamsberg and the Auas Mountains); the Brandberg Massif and Huab outliers; the Hunsberge; the mountains of the Kaokoveld (especially the Etendeka Mountains, the Baynes–Otjihipa Mountains and, to a lesser extent, the Otjikondavirongo Mountains); the Rooirand and the Huib-Hoch plateaus; the mountains of southwestern Angola (including the Serra de Chela and the Serra da Neve); the Naukluft Mountains; the Otavi Mountains; and the Waterberg Plateau. A complete ranking of the highlands according to the number of endemic arachnids in each, is provided in Table 2. Six of these highlands (i.e., the Auas Mountains, the Baynes–Otjihipa Mountains, the Brandberg Massif, the Gamsberg, the Khomas Hochland, the Naukluft Mountains and the Otavi Mountains) were among the 12 highest ranked mountains identified by Irish (2002) who used abiotic information (altitude, elevation, surface area and isolation) to infer and rank the 39 most prominent mountains or mountain ranges in Namibia for biodiversity potential.

CONCLUSIONS AND FUTURE DIRECTIONS

The arachnid fauna of Angola and Namibia is diverse and includes high levels of endemism, much of which is associated with the arid zone, especially the Namib Desert. Although highlands and escarpments may serve as refugia for taxa requiring cooler, more humid habitats than are available in the surrounding arid lowlands, fewer endemic arachnid taxa are present in the highlands than in the lowlands. This may be explained by several factors.

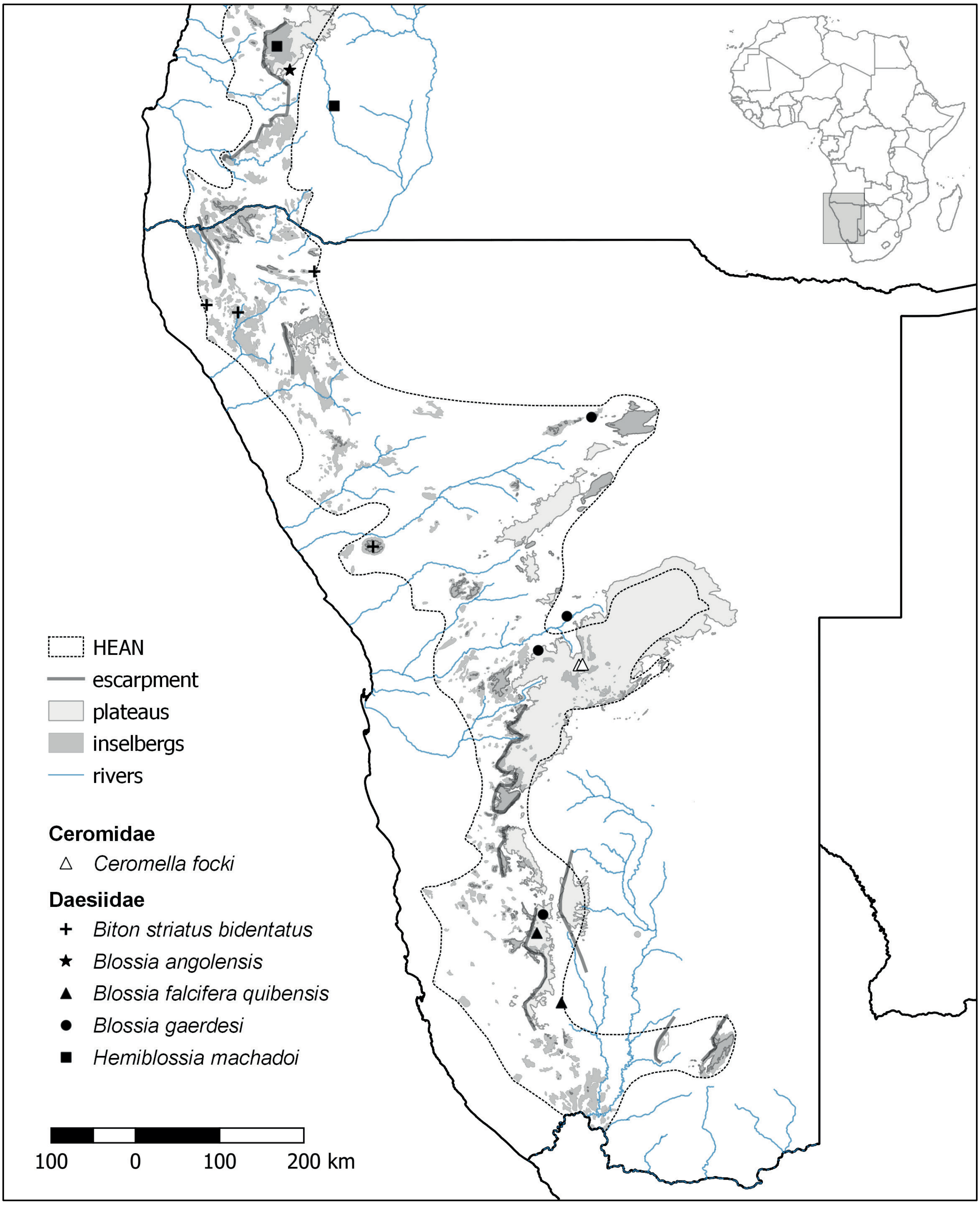

Figure 3: *Described species and subspecies of solifuges (Solifugae Sundevall, 1833) in the families Ceromidae Roewer, 1933 and Daesiidae Kraepelin, 1899 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Biton striatus bidentatus *Lawrence, 1955;* Blossia angolensis *(Lawrence, 1960);* Blossia falcifera quibensis *Hewitt, 1934;* Blossia gaerdesi *Lawrence, 1972;* Ceromella focki *(Kraepelin, 1914);* Hemiblossia machadoi *Lawrence, 1960.*

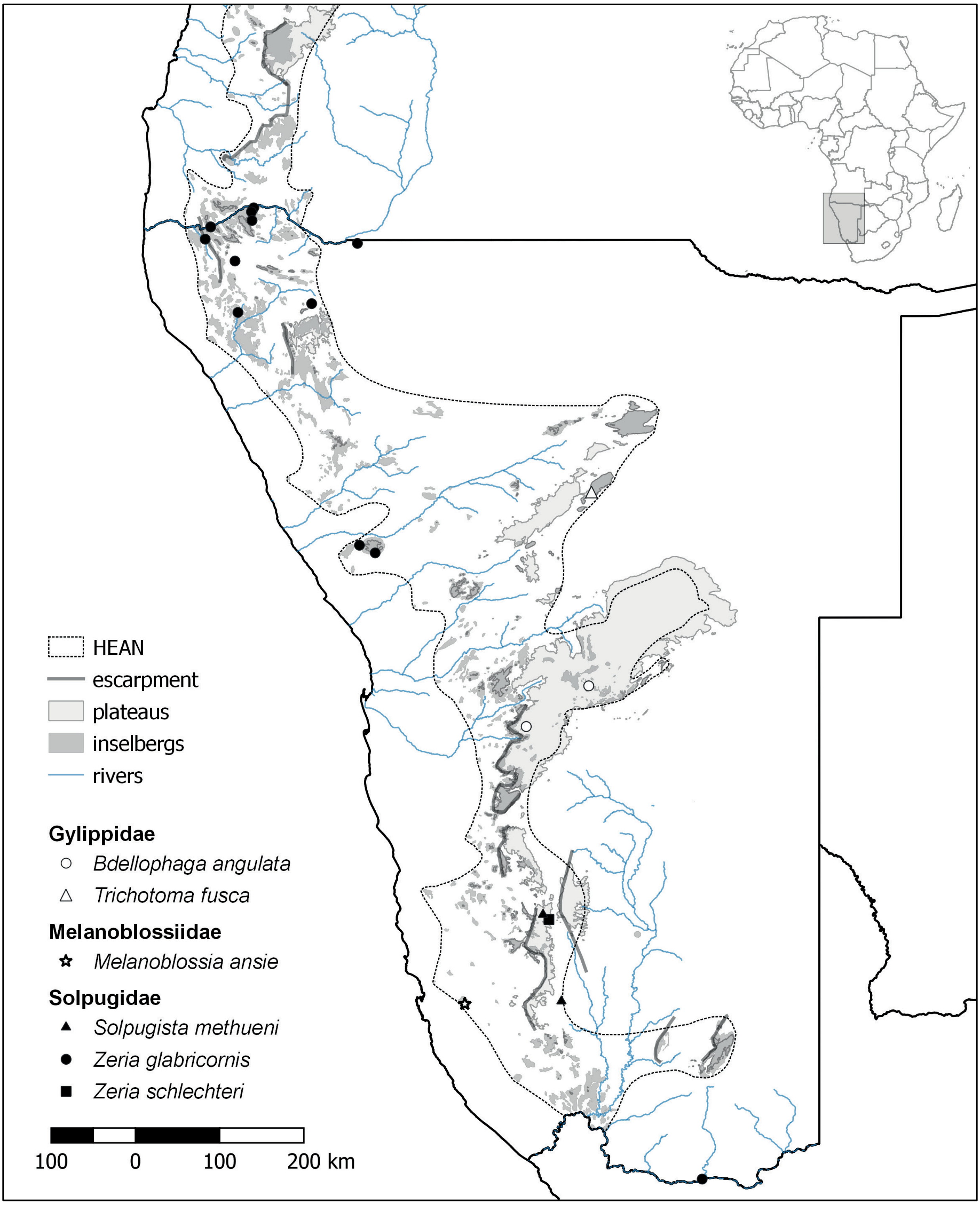

Figure 4: *Described species of solifuges (Solifugae Sundevall, 1833) in the families Gylippidae Roewer, 1933, Melanoblossiidae Roewer, 1933 and Solpugidae Leach, 1815 that are endemic or near-endemic to the highlands and escarpments, including plateaus, mountain ranges and inselbergs, of Angola and Namibia (HEAN):* Bdellophaga angulata *Wharton, 1981;* Melanoblossia ansie *Bird and Wharton, 2015;* Solpugista methueni *(Hewit, 1914);* Trichotoma fusca *(Roewer, 1941);* Zeria glabricornis *(Lawrence, 1928);* Zeria schlechteri *(Purcell, 1899).*

Firstly, the highlands and escarpments of Angola and Namibia are relatively low, on average, compared to the highlands and escarpments of other African countries, such as Ethiopia, Kenya and South Africa, providing fewer opportunities for insular speciation and/or a higher probability of extinction during unfavourable periods of increased aridity, e.g., during the Miocene and Pliocene. At 2,500 masl, the Brandberg Massif is the highest mountain in Namibia and, as might be expected, it contains several endemic or near-endemic arachnids. On the other hand, even small differences in elevation, e.g., low inselbergs 200 m above the surrounding plains, may have a profound effect on attracting precipitation in the hyperarid Namib, facilitating survival and diversification that might be impossible on the surrounding plains, as suggested by at least one endemic arachnid, the hormurid scorpion, *Hadogenes lawrencei*.

Secondly, much arachnid endemism in the arid lowlands is associated with unique substrates that are absent in the highlands and escarpments, including sand dunes, gravel plains, and clays associated with drainage systems, all of which facilitate burrowing to escape the arid conditions, and promote diversification (Prendini 2001b, 2005c).

Table 2: *Highlands and escarpments (including plateaus, mountain ranges and inselbergs) of Angola and Namibia with high levels of described and potential undescribed endemic whip spiders (Amblypygi Thorell, 1883), scorpions (Scorpiones C.L. Koch, 1837) and solifuges (Solifugae Sundevall, 1833), ranked in decreasing order of priority for conservation as well as further survey and inventory.*

Highland	**Amblypygi**	**Scorpiones**	**Solifugae**	**Total**
Khomas Hochland		4	4	8
Brandberg Massif	1	4	2	7
Gamsberg		6	1	7
Huab outliers	1	4	1	6
Hunsberge		6		6
Kaokoveld (Etendeka Mountains)	1	2	2	5
Rooirand Plateau		1	4	5
Angolan southwestern highlands (e.g., Serra de Chela, Serra da Neve)	1	1	2	4
Auas Mountains		2	2	4
Huib-Hoch Plateau		2	2	4
Kaokoveld (Baynes–Otjihipa Mountains)	1	1	1	3
Naukluft Mountains	1	2		3
Otavi Mountains		1	2	3
Waterberg Plateau		1	2	3
Aus Mountains		2		2
Awasibberge		2		2
Groot Karasberg		2		2
Hakosberge	1	1		2
Kaokoveld (Otjikondavirongo Mountains)	1	1		2
Sperrgebiet (Tshaukhaib Mountain)		1	1	2
Swakop–Khan (Scheifferberge)		2		2
Tirasberge	1	1		2
Erongo Mountains		1		1
Kaokoveld (Steilrand)			1	1
Klein Karasberg		1		1
Otjihaveraberge		1		1
Paresis Mountains		1		1
Sperrgebiet (Höhlenberg, Kirchberg, Sturmhaube)		1		1
Sperrgebiet (inselbergs between Teuffelkuppe and Agub Mountains)		1		1
Swakop–Khan (Bloedkoppie, Chuosberge, Langer-Heinrichberg and Rössing Mountain)		1		1
Tafelkop		1		1
Tsaris Mountains		1		1

Thirdly, the relatively low endemism of arachnids in the highlands and escarpments of Angola and Namibia is to some extent artefactual because much remains unknown. The arachnid fauna of Namibia has been far better surveyed and studied than that of Angola, yet, even in Namibia, much work remains to be done. Large areas have never been systematically surveyed in the optimal seasons or using techniques appropriate for collecting these secretive, seasonal taxa (e.g., pitfall trapping, ultraviolet-light detection). The use of genetic data has been sporadically applied to the systematics of arachnids in the region but is expected to reveal much cryptic diversity. More intensive surveys of the highlands and escarpments of Angola and Namibia, with an emphasis on collecting genetic samples from disjunct populations across the distributions of each putative species, are needed to better understand arachnid diversity and endemism in the region.

ACKNOWLEDGEMENTS

Authors L Prendini and T Bird acknowledge funding from the JRS Biodiversity Foundation which assisted with visits to identify arachnid collections in the natural history museums of Namibia and South Africa, and permits from the Government of Namibia's Ministry of Environment, Forestry and Tourism to survey the arachnid fauna of Namibia over several decades. Fieldwork in Namibia was supported by grants to L Prendini from the US National Science Foundation (EAR 0228699, DEB 0640219, DEB 1655050 and DEB 2003382), the Richard Lounsbery Foundation and the Stavros Niarchos Foundation. Helpful comments from Ansie Dippenaar-Schoeman, Stefan Foord, John Irish and John Mendelsohn improved earlier drafts of the manuscript.

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The amphibians of the highlands and escarpments of Angola and Namibia

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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, Ceríaco *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, Ceríaco *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).

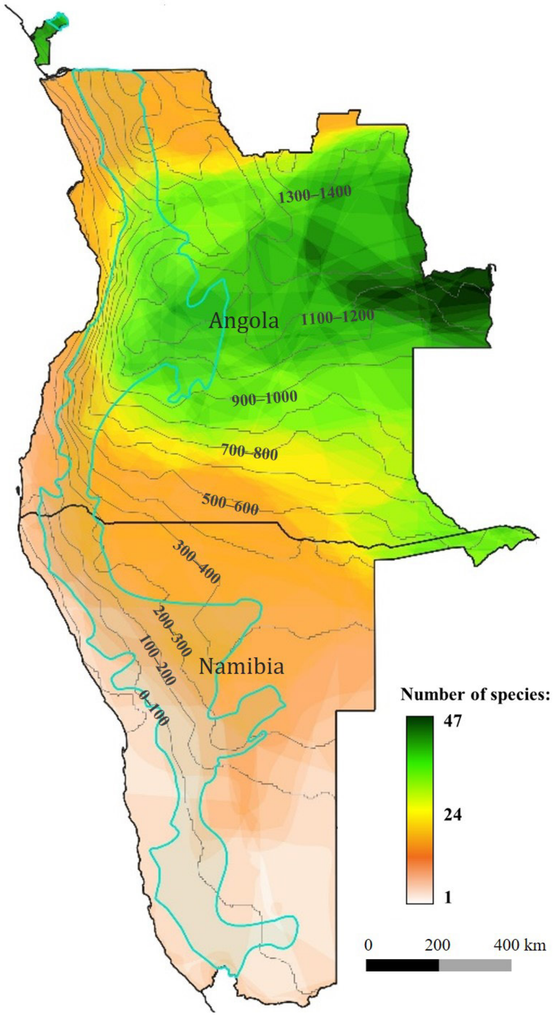

Figure 1: *Amphibian species richness throughout Namibia and Angola based on IUCN distributions, showing an overall positive relationship with annual rainfall. Average annual rainfall (mm) is indicated by labelled isohyets; the outline of the highlands and escarpments of Angola and Namibia (HEAN) is 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.*

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

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

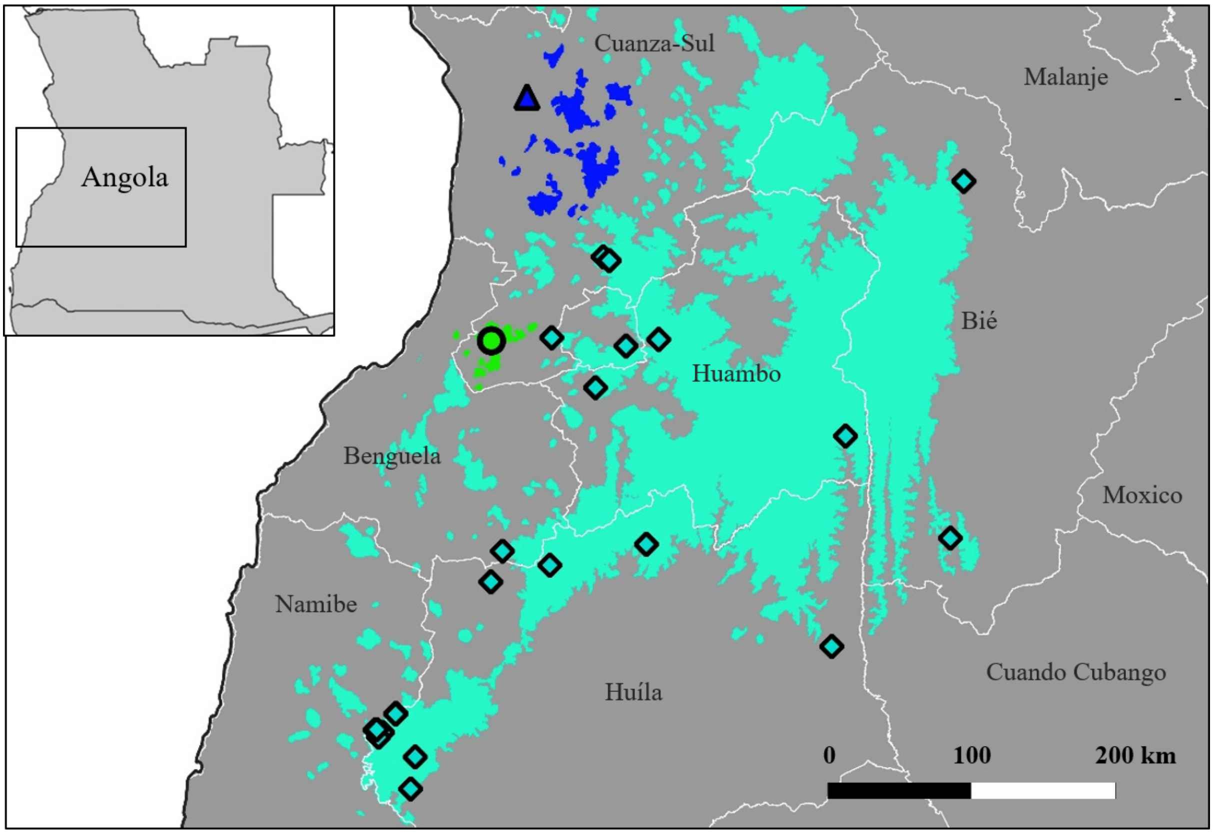

Figure 2: *Occurrence records (symbols) and possible highlands occupied (cyan area) by three highland endemic* Leptopelis *species in Angola:* L. anchietae*: cyan and diamonds;* L. jordani*: dark blue and triangle;* L. marginatus*: green and circle.*

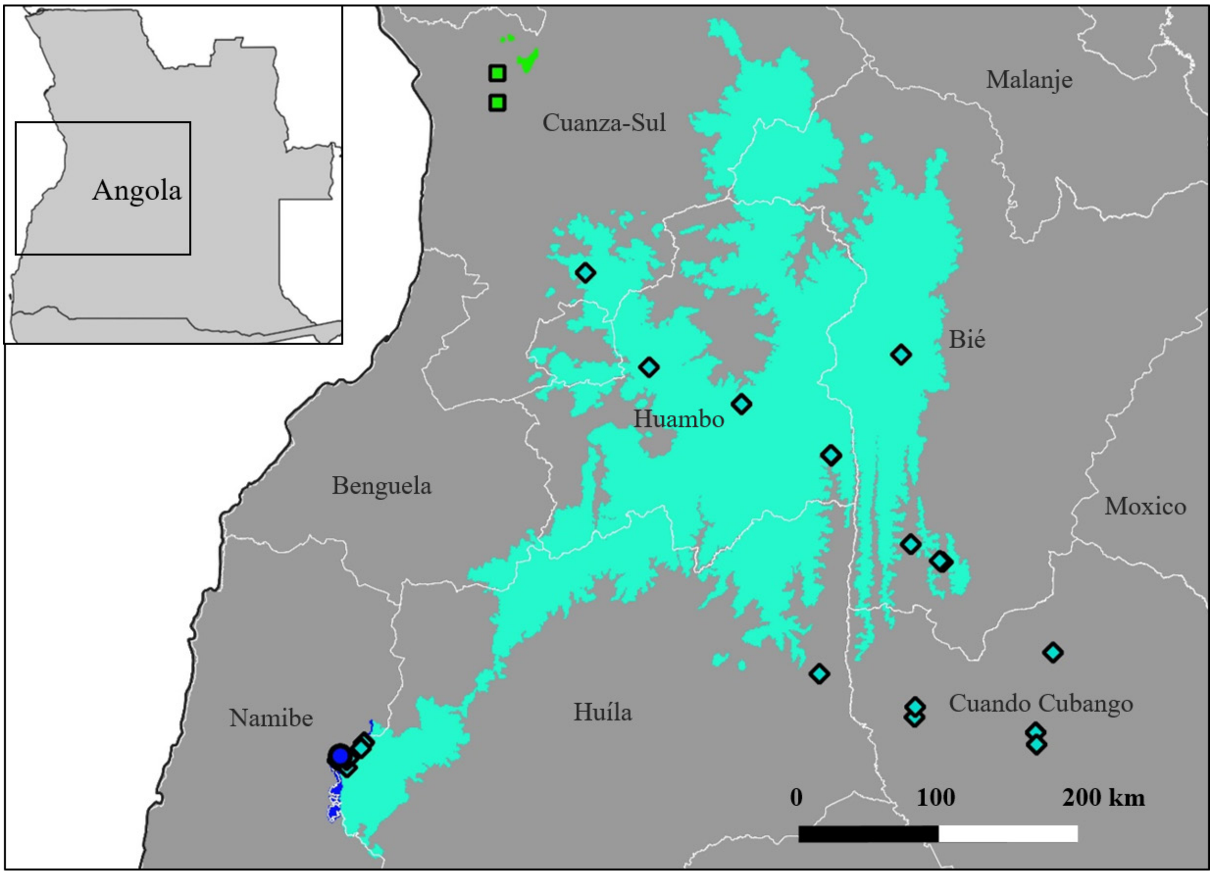

Figure 3: *Occurrence records (symbols) and possible highlands occupied (cyan area) by highland endemic amphibian species in Angola:* Hyperolius cinereus*: cyan and diamonds;* H. chelaensis*: dark blue and circle;* Amnirana parkerina*: green and squares.*

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 (Congulo 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 (Ceríaco *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 (Ceríaco *et al.* 2018). Although the species was thought to be closely related to *P. fenoulheti* (*fide* Ceríaco *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., Ceríaco *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

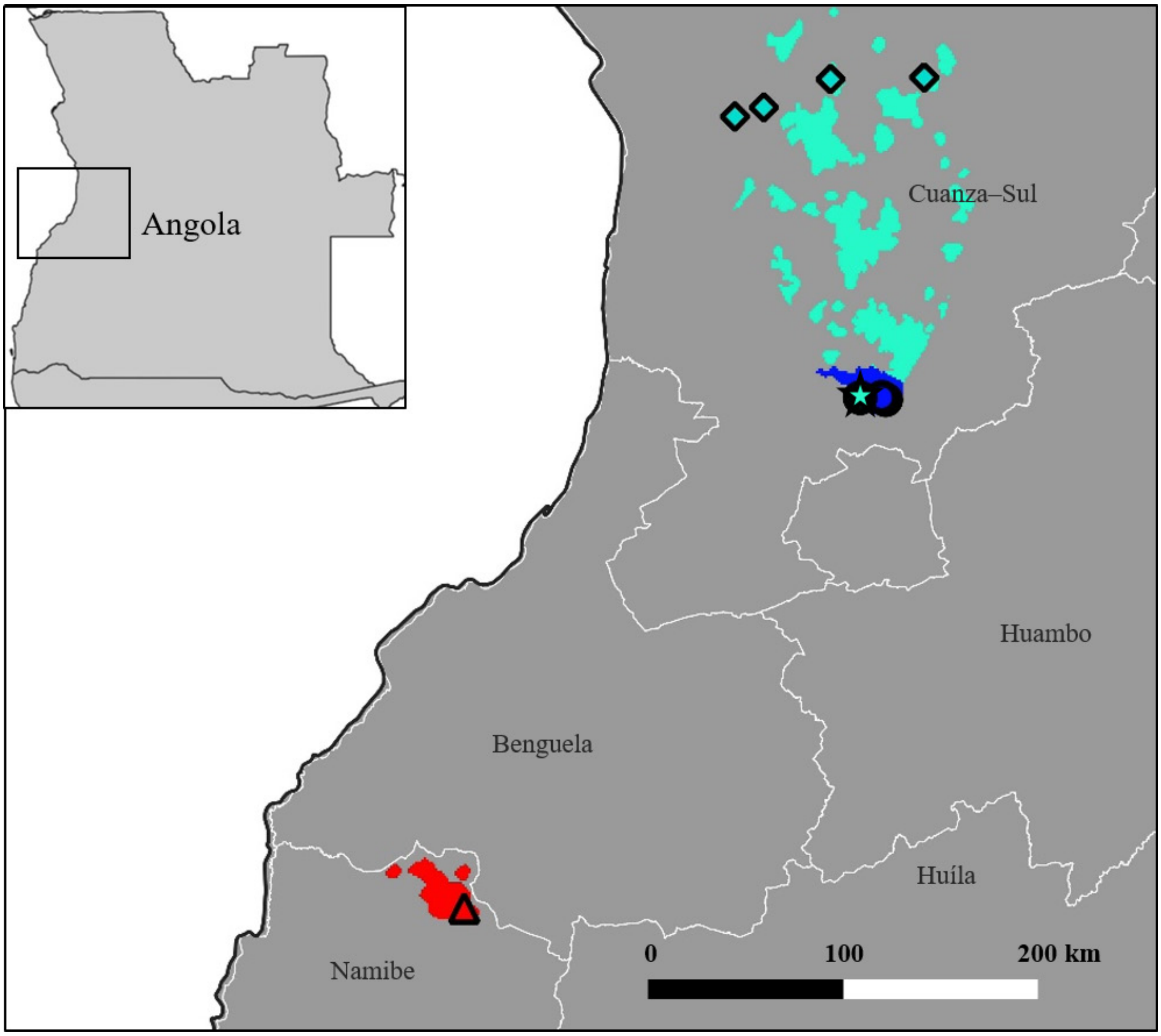

Figure 4: *Occurrence records (symbols) and possible highlands occupied (shaded area) by highland endemic* Poyntonophrynus *species in Angola.* Poyntonophrynus fernandae *s.s.: cyan and diamonds; cyan star =* P. *cf.* fernandae*;* P. nambensis*: dark blue and circle (note syntopic occurrence with* P.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

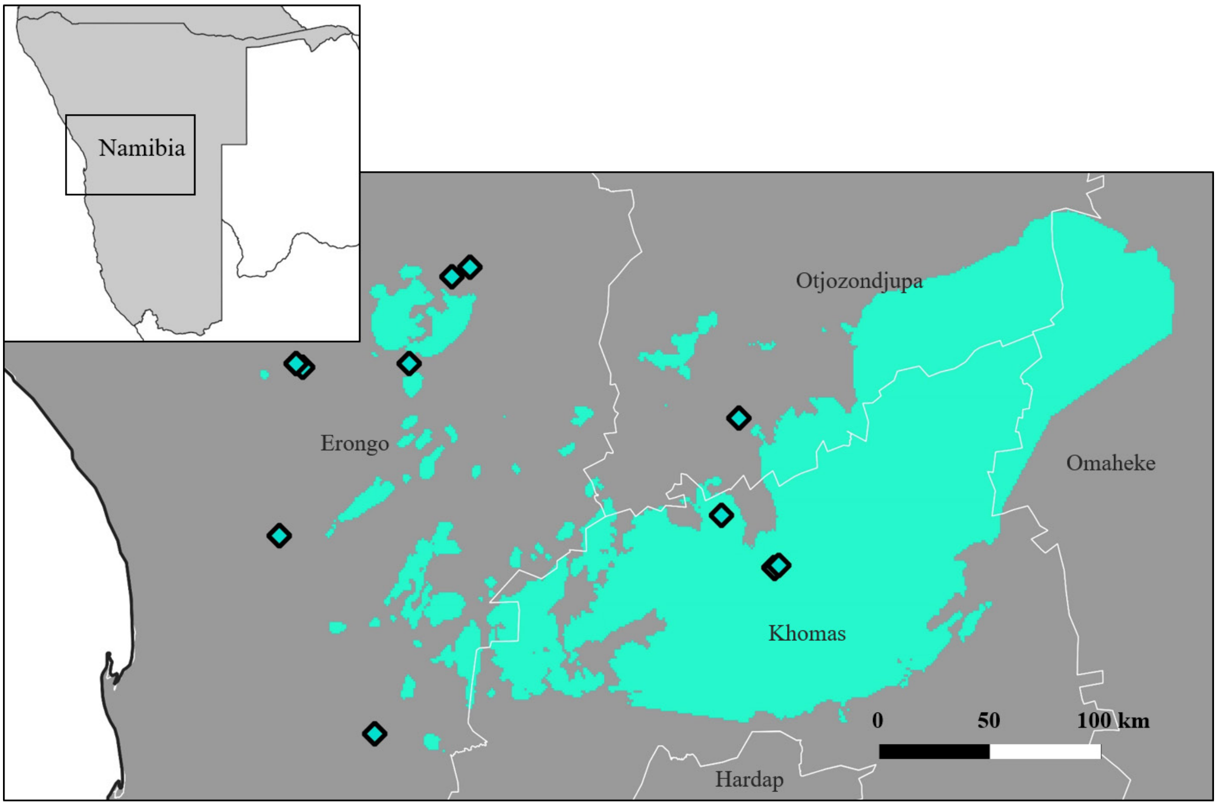

Figure 5: *Occurrence records (diamonds) and possible highlands occupied (cyan-shaded area) by the highland endemic amphibian* Poyntonophrynus hoeschi *in Namibia.*

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 (Ceríaco *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 (Ceríaco *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.

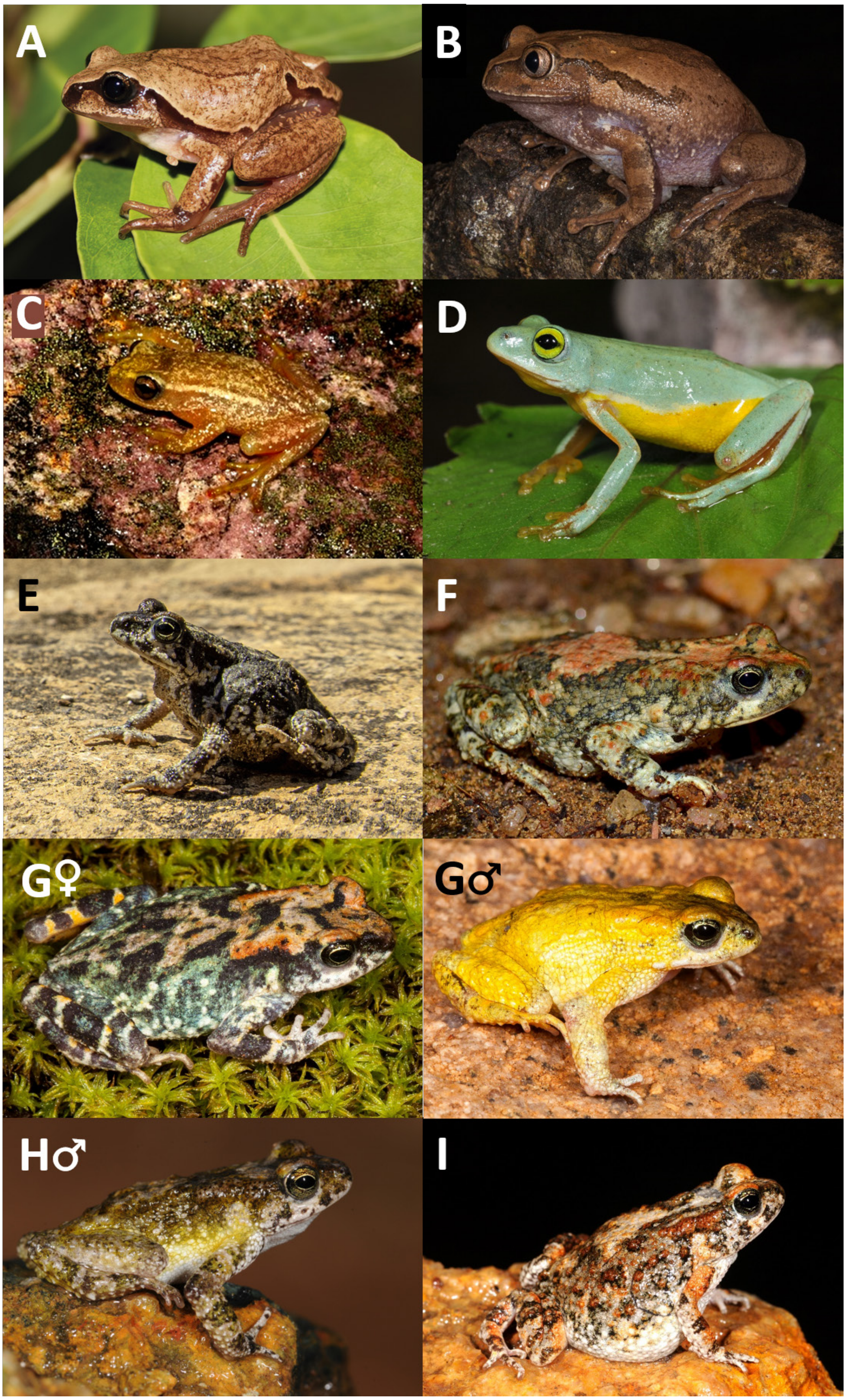

Figure 6: *Highland endemic amphibians from Angola and Namibia. A)* Leptopelis anchietae. *Photo: NL Baptista. B)* L. jordani. *Photo: P Vaz Pinto. C)* Hyperolius chelaensis. *Photo: W Conradie. D)* H. cinereus. *Photo: B Branch. E)* Poyntonophrynus pachnodes. *Photo: J Lobón-Rovira. F)* P. hoeschi. *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 hotpots 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 Universitat 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/PD/BD/140810/2018, and BIOPOLIS 2022-19.

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Highland reptiles of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-bauer

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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

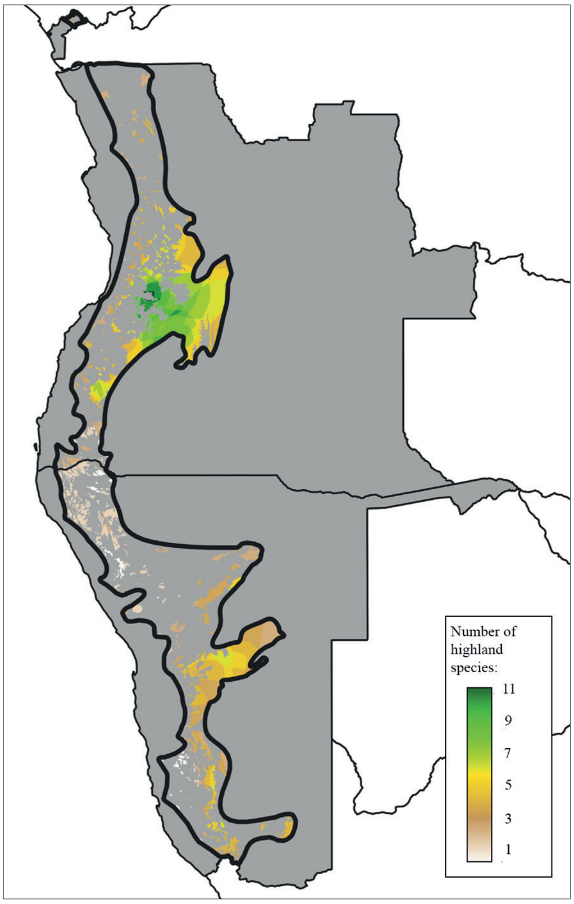

Figure 1: *Map of Angola and Namibia showing highland areas and inselbergs colour coded by the number of highland endemics and near-endemics (Table 1) co-occurring in these regions. See text for sources of data.*

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 a*l., 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).

ACKNOWLEDGEMENTS

We thank John Mendelsohn, Pedro Vaz Pinto, Brian Huntley, Alice Jarvis and Carole Roberts for their suggestions and improvements of the manuscript. Our work in Angola and Namibia has been facilitated by the Instituto Nacional de Biodiversidade e Áreas de Conservação (INBAC) and Angola's Ministry of Environment and by the National Commission on Research, Science and Technology, Namibia, and the National Museum of Namibia. Our work in the highlands and escarpments of Angola and Namibia has been supported by the JRS Biodiversity Foundation, the National Science Foundation of the United States (DEB 2146654 and earlier grants to AMB), National Geographic Society (NGS-73084R-20 to LMPC), and Fundação para a Ciência e Tecnologia (FCT) (SFRH/BD/129924/2017, COVID/BD/152155/2022 to MPM), among other sources. We are grateful to friends and colleagues in Angola and Namibia for all of their contributions to our field and museum research.

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Flat gecko (*Afroedura*) diversity, endemism and speciation in the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-conradie

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ABSTRACT

Nine species of African flat geckos (*Afroedura*) are known to be associated with the highlands and escarpments of Angola and Namibia (HEAN). Among these, the *Afroedura bogerti* group is the most speciose (with seven species) and endemic to the HEAN. Phylogenetically, it constitutes a young species group that speciated during the early Pleistocene (~1.91 mya). Although currently none of these species is regarded as threatened, their distribution falls largely outside protected areas which could compromise their future.

Keywords: *Afroedura,* Angola, diversity, endemism, flat gecko, Namibia, speciation

INTRODUCTION

African flat geckos of the genus *Afroedura* Loveridge, 1944 are medium to large (maximum snout–vent length is 83 mm) dorsoventrally flattened geckos with rupicolous (rock-living) habits. They occur from western Angola southwards to South Africa and along the eastern escarpment northwards to central Mozambique (Branch 1998, Jacobsen *et al.* 2014, Branch *et al.* 2021). They are typical highland species, found along the rocky mountainous areas of the escarpments, but apparently absent from most of the sandy lowlands in the interior of the continent.

Currently the genus comprises 34 species (Jacobsen *et al.* 2014, Branch *et al.* 2021, Conradie *et al.* 2022), many of them described in the last decade, from the northern provinces of South Africa (Jacobsen *et al.* 2014), central Mozambique (Branch *et al.* 2017) and northern Namibia and Angola (Branch *et al.* 2021, Conradie *et al.* 2022), and this number is expected to increase even further with the description of additional novel species (Makhubo *et al.* 2015, Busschau *et al.* 2019, Nicolau *et al.* 2023).

Most of the *Afroedura* species are restricted to South Africa and the eastern escarpment (Jacobsen *et al.* 2014), with only *A. africana*, *A. tirasenesis* and the *A. bogerti* species group associated with the arid highlands and escarpments of Angola and Namibia (HEAN). *Afroedura africana* and *A. tirasenesis* are restricted to the arid western and central Namibian highlands. *Afroedura africana* shows a closer phylogenetic relationship to another arid-adapted South African species, *A. karrocia,* than to other species associated with the HEAN. High genetic divergence exists among material from the Erongo Mountains and may include undescribed cryptic taxa (Jacobsen *et al.* 2014, Bauer *et al.* 2023). *Afroedura tirasensis* has not been tested in a phylogenetic framework but is expected to be closely related to the *A. africana* group. For the remainder of this paper we will focus on the *A. bogerti* group, which has received more attention in the last few years.

THE *AFROEDURA BOGERTI* GROUP

Until recently *Afroedura bogerti* was the only species of *Afroedura* known to occur in Angola and adjacent northern Namibia (Marques *et al.* 2018), but a slew of new species descriptions (Branch *et al.* 2021, Conradie *et al.* 2022) has increased this number to six endemic species (*A. bogerti*, *A. donveae*, *A. praedicta, A. pundomontana, A. vazpintorum* and *A. wulfhaackei*) from Angola (Figure 1) and one from neighbouring Namibia (*A.* o*tjihipa*; Figure 2).

These seven endemic species can be divided into two distinct groups based on morphological and molecular data: a northern group comprising three

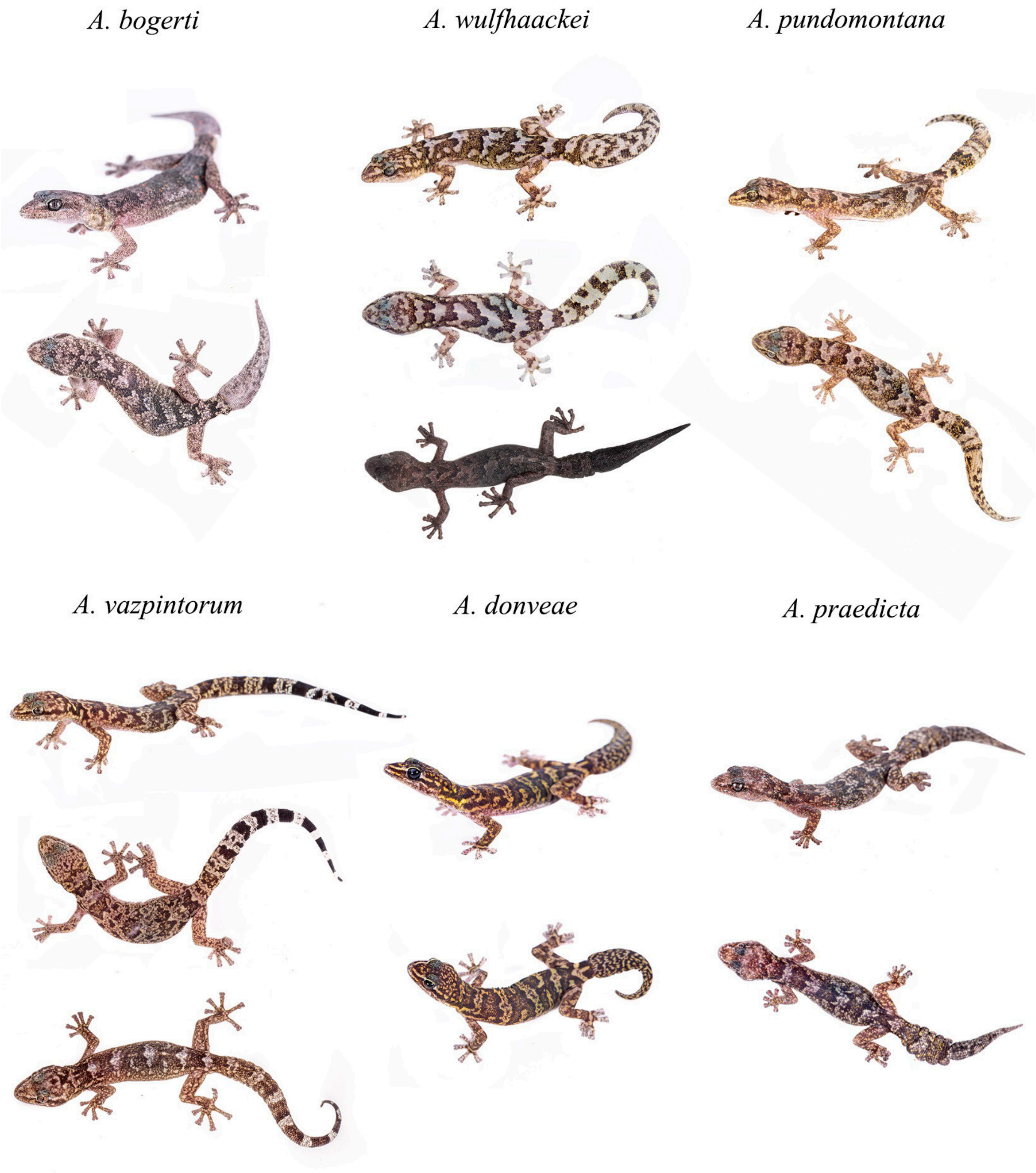

Figure 1: *Collage of the different species of African flat geckos in the* Afroedura bogerti *group from Angola:* A. bogerti *from Namba, Cuanza-Sul Province; two specimens of* A. wulfhaackei *from Lépi (top) and one from Serra do Môco (bottom), Huambo Province;* A. pundomontana *from Bocoio, Benguela Province; two specimens of* A. vazpintorum *from Kapembawé, Benguela Province (top) and one from Tundavala, Huíla Province (bottom);* A. donveae *from Omahua, Namibe Province;* A. praedicta *from Serra da Neve, Namibe Province. Photos: J Lobón-Rovira and P Vaz Pinto.*

species which are found on the Angolan Planalto and associated escarpment (*A. bogerti*, *A. pundomontana* and *A. wulfhaackei*) and a southern group comprising four species present in the southwestern highlands and coastal plain (*A. donveae*, *A. otjihipa*, *A. praedicta* and *A. vazpintorum*). Predicted distributions and known localities are shown in Figure 3.

Northern group

Afroedura bogerti Loveridge, 1994 – Namba or Bogert's flat gecko

This species is known only from the vicinity of Mt Namba in the southern part of Cuanza-Sul Province of Angola and is regarded as a strict highland-associated species. It is a nocturnal, rupicolous species typically found sheltering in crevices and under exfoliating rock on larger granite outcrops in montane grasslands and associated scattered miombo and Afromontane forests at an elevation of 1,750–1,850 masl. Its International Union for Conservation of Nature (IUCN) assessment of Least Concern (Baptista *et al.* 2020) was made before the split of the species group and consequently its status needs reassessment. Although the species has a very restricted distribution, it is relatively common in suitable habitat and known to occur in degraded habitat (Branch *et al.* 2021). The removal of rock flakes for the construction of houses or other buildings may be a threat to this species.

Afroedura pundomontana Conradie *et al.*, 2022 – Bocoio flat gecko

This species occurs at lower elevations than the other highland-associated species. It is restricted to elevations of 600–1,000 masl in Angola's Central Escarpment in central Benguela Province where it is found in low numbers on large granite rocky outcrops scattered among mixed escarpment woodlands. It has not been assessed for its threat status but could potentially trigger a threat category due to its limited distribution and the removal of rock flakes for the construction of houses and other buildings (Conradie *et al.* 2022).

Afroedura wulfhaackei Branch *et al.*, 2021 – Huambo or Mombolo flat gecko

This species occurs widely in the Angolan Planalto of Huambo Province, Angola, extending marginally into the Central Escarpment in the provinces of Benguela and Cuanza-Sul. It is mostly found sheltering in crevices and under exfoliating rock on larger granite outcrops at elevations of 1,750–2,055 masl. At least four genetically distinct, isolated populations have been identified (Branch *et al.* 2021, Conradie *et al.* 2022). This species has not been assessed for its threat status, but its habitat might be threatened by the removal of rock flakes for building construction (Branch *et al.* 2021).

Southern group

Afroedura donveae Branch *et al.*, 2021 – Iona flat gecko

Currently this species is only known from the arid coastal region of southwestern Namibe Province, Angola. It is typically found sheltering in crevices and under exfoliating rock on large granite outcrops scattered in the semidesert scrubland environment at low elevations of 340–355 masl. It is not regarded as a highland-associated species. Its threat status has not been assessed. Although it seems to have very restricted distribution, the population is probably stable and its habitat is not under threat.

Afroedura otjihipa Conradie *et al.*, 2022 – Otjihipa flat gecko

Currently this species is only known from the Otjihipa Mountains in the Southern Escarpment, Namibia, where it occurs in small sandstone outcrops in arid woodland at elevations of 1,800–1,900 masl. While it is expected to occur more widely in suitable habitat, it has not been recovered from the dolomite ridges surrounding the type locality. Its threat status has not been assessed by the IUCN, but based on the remoteness and undisturbed habitat it occurs in, it is unlikely to trigger any threat status.

Afroedura praedicta Branch *et al.*, 2021 – Serra da Neve flat gecko

This species is restricted to areas of higher elevation (1,900–2,000 masl) of the isolated Serra da Neve inselberg in northern Namibe Province. It is sympatric with another highland endemic, *Cordylus*

Figure 2: *Otjihipa flat gecko (*Afroedura otjihipa*) from the Otjihipa Mountains in northern Namibia. Photo: F Becker.*

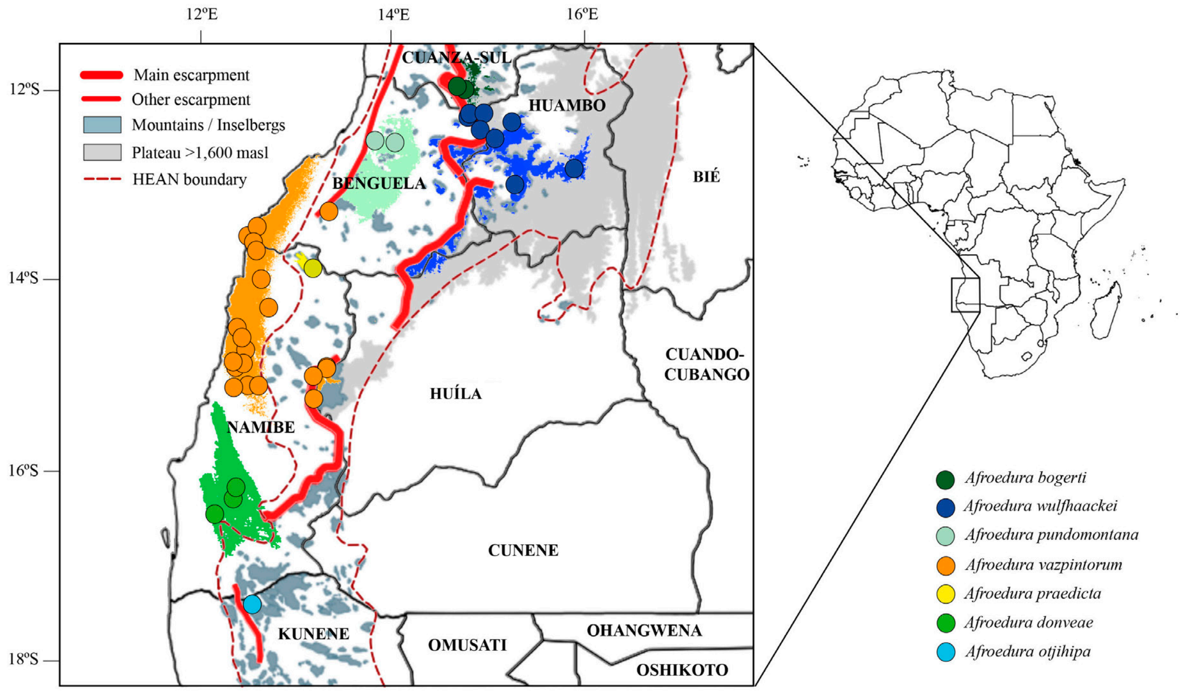

Figure 3: *Predicted distributions and known localities of species of African flat geckos in the highlands and escarpments of Angola and Namibia (HEAN). Shaded areas indicate distributions (90% confidence interval based on Maxent predictive mapping, see Conradie* et al. *2022) and points indicate known localities.*

phonolithos. The conservation status of this species has not been assessed. Although it has a very restricted distribution, no plausible threats are known thus it might not trigger any threat status.

Afroedura vazpintorum **Branch *et al.*, 2021 – coastal flat gecko**

This species is mostly associated with the low-lying (less than 500 masl) coastal semiarid environment of the Angolan Kaokoveld in Namibe and Benguela provinces. However, a possibly isolated highland population occurs on the Humpata Plateau, at elevations of 1,630–2,270 masl. This species has not been assessed for its threat status. It seems common and widely distributed and is probably not threatened.

DISCUSSION

Recent work by Conradie *et al.* (unpublished data) estimated the diversification between the northern and southern groups to have occurred somewhere between the late Pliocene and early Pleistocene (3.57–0.96 mya) based on a coalescent speciation model (stochastic models). Of particular interest is the diversification within the northern group, with *Afroedura bogerti* and *A. wulfhaackei* currently represented by scattered populations on isolated mountains at high elevation across the Angolan Planalto, and *A. pundomontana* a bit further west on the escarpment. Although the strict Mt Namba endemic *A. bogerti* occurs in similar habitat and geographical proximity to some populations of *A. wulfhaackei*, it was found to be genetically closer to the escarpment species present at comparatively lower elevation, *A. pundomontana*. Morphological conservatism between sister taxa, together with habitat and ecological overlap found in this group, support the hypothesis that Angolan *Afroedura* have undergone allopatric speciation (vicariance) in the Angolan Planalto that could be associated with a non-adaptive radiation similar to those reported for other reptile radiations (e.g., Reaney *et al.* 2018). This speciation process could be driven by the substrate-specific character of this genus, leading to isolation during periods of climatological constraints.

On the other hand, the southern group seems to have followed a more complex pattern of speciation, with various populations isolated and specialised in different habitats and one widespread taxon. This is especially true in the case of *A. vazpintorum*, a species which is widespread across the coastal semiarid lowlands but is also present on top of the southern escarpment above 2,000 masl in typical montane environment. Genetic analysis revealed two deeply divergent mitochondrial lineages in *A. vazpintorum*, one exclusive to the southern highlands but the other present both above and below the escarpment (Branch *et al.* 2021, Conradie *et al.* 2022). These findings are consistent with a southern highland origin, followed by subsequent lowland colonisation and a more recent expansion on the coastal plain and secondary contact in the highlands. Although the ecological conditions are very different on the southern highlands and semiarid coastal plain, various reptiles do occur in both regions including two representatives of the Gekkonidae, *Chondrodactylus fitzsimonsi* (Marques *et al.* 2018) and *Hemidactylus benguellensis* (Lobón-Rovira *et al.* 2021). The origin of remaining southern taxa, namely *A. donveae*, *A. otjihipa* and *A. praedicta*, is best explained by vicariance events but these are challenging to interpret with the available data. It is possible that Pleistocene climatic oscillations periodically promoted the expansion of *Afroedura* populations across the southern lowlands, followed by local extinctions when the climate became too dry, thus conferring a higher resilience on populations isolated on southern highlands and inselbergs; such dynamics may explain the origin and current distribution of southern taxa.

Overall, the speciation patterns found in Angolan *Afroedura* reveal an early split between central and southern highlands, with the former maintaining a close link with the western escarpment and the latter with the semiarid lowlands and various coastal inselbergs such as Serra da Neve or the Otjihipa Mountains. These patterns are likely to be of biogeographic significance, as they are remarkably similar to those observed for other lizards, such as *Cordylus* (Bates *et al.* 2023) and *Hemidactylus* (Lobón-Rovira *et al.* 2021), and for a rupicolous amphibian genus, *Poyntonophrynus* (Baptista *et al.* in review). These results establish the Angolan–Namibian highlands as an important biogeographic feature driving diversification processes in the HEAN, while underlining the Angolan Planalto, the western escarpment and various inselbergs as centres of endemism.

Further research is needed in this poorly known region of Africa. It is noteworthy that although the highlands and escarpments of Angola and Namibia are important for rupicolous species, they fall largely outside the currently designated protected areas and are therefore susceptible to the impacts of ongoing mining operations, human encroachment and related activities. The lack of a conservation strategy for these highlands could compromise the future of relict species and the still unknown diversity they support.

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Fishes of the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-skelton

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ABSTRACT

The fishes of the highlands and escarpments of Angola and Namibia (HEAN) are described broadly and a brief biogeographical explanation sketched. The fishes of this region are poorly documented in the literature and few records are available. Species of the families Kneriidae, Mormyridae, Cyprinidae, Danionidae, Amphiliidae, Clariidae, Mochokidae, Cichlidae and Mastacembelidae are highlighted and noted. An extraordinary radiation of *Labeobarbus* in the Cuanza River is a distinct feature. Two river systems in western Angola and Namibia, the Cuanza and the Cunene, extend from the interior down the escarpment to the coast and their fish faunas are considerably enriched. Affinities of the various taxa are pointed out including signature links with the southern Congo River basin, and East Africa. West African connections via the coast or the Congo Basin are sparse. West Zambezian faunal links are strongest but generally restricted to elements that favour rocky environments. The fishes of typical Kalahari sand systems, such as floodplains and swamps, are absent. Isolated and fragmented distributions of certain elements attest to relict situations indicative of early, more favourable, widespread distributions.

Keywords: Angola, escarpment, fishes, highlands, Namibia

INTRODUCTION

Some of the first descriptions of freshwater fishes of Angola are from the rivers originating in the highlands and escarpments of Angola and Namibia (HEAN) as these were accessible from the Atlantic ports used by early explorers. The lack of precise localities in these early descriptions hampers the understanding of the link between fish presence and elevation and it was not until several expeditions in the 1920s and 1930s from European and western countries (Nichols & Boulton 1927, Fowler 1930, 1935, Pellegrin 1936, Trewavas 1936) that more precision was introduced. There were two subsequent sources of records for freshwater fishes from the highlands, firstly, pioneering ecologically orientated studies conducted by scientists from Hamburg, Germany (Ladiges & Voelker 1961) and, secondly, collections made by individuals associated with the Dundo Museum and described by Poll (1967). More recently, surveys made in both Namibia and Angola by a post-independence generation of individuals and institutions have added to the available data.

Skelton (2019) provided a checklist of freshwater fishes from the Angolan coastal drainages. These drainages generally extend from a divide that includes the western highlands, or beyond in a few instances, to the Atlantic and consequently not all the species occur exclusively in the highland reaches. Other specific accounts that contribute data include Hay *et al*. (1997) for the Cunene and a few unpublished surveys such as Tate and Kindler (2019) for Longonjo in Huambo Province. In this account I have compiled a list of fish species (Table 1) expected to occur in the highland reaches of Atlantic coastal rivers south of the Cuanza, based on personal experience in the highlands and the Kalahari sands regions to the east.

FISHES

The fishes of the HEAN are, in general, not well known. The rivers of the highlands have not been comprehensively surveyed and the list in Table 1 is preliminary, based on current knowledge. However, there is clear evidence of an endemic HEAN fauna; in many cases species are restricted to a narrow range or even just a single river system. Figures 1a and 1b illustrate some representative fish from the HEAN. Brief summaries of the families follow.

Kneriidae

The kneriids are small specialised stream fishes, placed in two genera, *Kneria* and *Parakneria*. They belong to an ancient clade of gonorhynchiform fishes estimated by Lavouè (2019) to have been present in Africa since the Cretaceous (145–66 mya). They favour rocky habitats and are primarily distributed around the elevated rim of the Congo Basin with an extension into West Africa and outliers in East and southeastern Africa. At least five species have been recorded from the HEAN including three *Kneria* and two *Parakneria* species. *Parakneria fortuita* is known from the Cubango–Upper Zambezi systems and *P. marmorata* from the Cuanza (Table 1). *Kneria* species include *K. maydelli* which is known from streams in the mountains along the southern edge of

Table 1: *A selection of fishes associated with the highlands and escarpments in Angola and Namibia (HEAN).*

Family and species	**Species author and original record reference**	**HEAN river system**	**Comments**
Kneriidae			
Kneria ansorgii	(Boulenger, 1910)	Cuanza	
Kneria maydelli	Ladiges & Voelker, 1961	Cunene	
Kneria polli	Trewavas, 1936	Queve, Cubal–Catumbela	
Parakneria fortuita	Penrith, 1973	Cubango–Okavango	Upland western tributaries of the Cunene and Okavango are considered here as part of the highlands
Parakneria marmorata	(Norman, 1923)	Cuanza	
Mormyridae			
Cyphomyrus cubangoensis	(Pellegrin, 1936)	Cubango–Okavango	
Heteromormyrus ansorgii	(Boulenger, 1905)	Cuanza	
Heteromormyrus longilateralis	Kramer & Swartz, 2010	Cunene	
Heteromormyrus pappenheimi	(Boulenger, 1910)	Cuanza	
Heteromormyrus pauciradiatus	(Steindachner, 1866)	Cuanza	
Marcusenius multisquamatus	Kramer & Wink, 2013	Cunene	
Petrocephalus cunganus	Boulenger, 1910	Cuanza	
Danionidae			
Engraulicypris howesi	Ridden *et al.*, 2016	Cunene	
Raiamas ansorgii	Boulenger, 1910	Cuanza	
Cyprinidae			
Enteromius argenteus	(Gunther, 1868)	Cuanza	
Enteromius breviceps	(Trewavas, 1936)	Cunene, Cubango–Okavango	
Enteromius dorsolineatus	(Trewavas, 1936)	Queve	
Enteromius eutaenia	(Boulenger, 1904)	Cunene	Related species in Limpopo and SE Africa coastal rivers
Enteromius evansi	(Fowler, 1930)	Cuanza, Cubango–Okavango	
Enteromius greenwoodi	(Poll, 1967)	Cuanza	
Enteromius kessleri	(Steindachner, 1866)	Cuanza	
Enteromius lineomaculatus	(Boulenger, 1903)	Cunene, Upper Zambezi	
Enteromius mattozi	(Guimaraes, 1884)	Cunene, Cuanza, Upper Zambezi	Extended clade species in Inkisi, Upper Congo, Ruvuvu, Lake Malawi, Limpopo
Enteromius mocoensis	(Trewavas, 1936)	Queve, Cubango–Okavango	
Enteromius paludinosus	(Peters, 1852)	Cunene, Cubango–Okavango, Upper Zambezi, Lower Zambezi, Lower Orange	Related species complex in East Africa, Ethiopia, and Lower Zambezi south to KwaZulu-Natal in South Africa
Enteromius trimaculatus	(Peters, 1852)	Cunene, Cubango–Okavango, Lower Orange, Lower Zambezi south to KwaZulu-Natal in South Africa	Related species *E. poechii* in Okavango–Upper Zambezi–Kafue; *E. jacksoni* in East Africa
Enteromius wellmani	(Boulenger, 1911)	Queve	
Labeo ansorgii	Boulenger, 1907	Cunene	
Labeo rocadasi	Boulenger, 1907	Cuanza	
Labeobarbus ansorgii	(Boulenger, 1906)	Cuanza	
Labeobarbus boulengeri	Vreven, Musschoot, Snoeks & Schliewen, 2016	Cuanza, Inkisi, Lower Congo	
Labeobarbus codringtonii	(Boulenger, 1908)	Cubango–Okavango, Upper Zambezi, Kafue	Rocky habitats preferred
Labeobarbus ensifer	(Boulenger, 1910)	Cuanza	
Labeobarbus ensis	(Boulenger, 1910)	Cuanza	
Labeobarbus girardi	(Boulenger, 1910)	Cuanza	
Labeobarbus gulielmi	(Boulenger, 1910)	Cuanza	

Family and species	Species author and original record reference	HEAN river system	Comments
Labeobarbus lucius	(Boulenger, 1910)	Cuanza	
Labeobarbus rhinophorus	(Boulenger, 1910)	Cuanza	
Labeobarbus rocadasi	(Boulenger, 1910)	Cuanza	
Labeobarbus rosae	(Boulenger, 1910)	Cuanza	
Labeobarbus steindachneri	(Boulenger, 1910)	Cuanza	
Labeobarbus stenostomata	(Boulenger, 1910)	Cuanza	
Labeobarbus varicostoma	(Boulenger, 1910)	Cuanza	
Amphiliidae			
Amphilius cubangoensis	Pellegrin, 1936	Okavango	
Amphilius lentiginosus	Trewavas, 1936	Queve	
Amphilius pagei	Thomson & Swartz, 2018	Cuanza	
Doumea angolensis	Boulenger, 1906	Cuanza	
Doumea sp.		Cuanza	SAIAB records
Zaireichthys kunenensis	Eccles, Tweddle & Skelton, 2011	Cunene	
Clariidae			
Clarias cavernicola	Trewavas, 1936	Aigamas Cave	A karstveld outlier to the highlands
Clarias dumerilii	Steindachner, 1866	Queve	As identified by Trewavas (1936)
Clarias liocephalus	Boulenger, 1898	Cunene, Cubango–Okavango	
Clariallabes sp.		Cunene	SAIAB records; possible links with Queve (*C. dumerilii*); Cuanza and Okavango–Upper Zambezi (*Clariallabes* sp.)
Platyclarias machadoi	Poll, 1977	Cuanza	SAIAB records; *Platyclarias machadoi* in Cuango; Bernt *et al.* (2023)
Mochokidae			
Chiloglanis angolensis	Poll, 1967	Cunene	
Chiloglanis fasciatus	Pellegrin, 1936	Cubango, Zambezi	
Chiloglanis sardinhai	Ladiges & Voelker, 1961	Longa	
Cichlidae			
Chetia gracilis	(Greenwood, 1984)	Cutato Nganguela (Cubango-Okavango)	
Chetia welwitschi	(Boulenger, 1898)	Cunene, Longa	*Chetia welwitschi* in Longa, see Tate & Kindler (2019)
Orthochromis machadoi	(Poll, 1967)	Cunene	
Thoracochromis albolabris	(Trewavas & Thys van den Audenaerde, 1969)	Cunene	
Thoracochromis buysi	(Penrith, 1970)	Cunene	
Thoracochromis lucullae	(Boulenger, 1913)	Cuanza	
Tilapia guinasana	Trewavas, 1936	Guinas lake	A karstveld species of the highlands
Mastacembelidae			
Mastacembelus ansorgii	Boulenger, 1905	Cuanza, Queve	Queve records SAIAB
Mastacembelus frenatus	(Boulenger, 1901)	Cubango–Okavango	

the Cunene River gorge below Ruacana. This is the southernmost distribution of *Kneria* in the HEAN.

Mormyridae

The family Mormyridae is also an ancient lineage in Africa dating from Cretaceous times. These fishes are essentially nocturnal and have electrogenic and electroreceptive properties. Various species are present in the rivers of the HEAN, especially the middle-order and main streams in both rocky and floodplain environs. There is a fair degree of catchment endemism in the family with at least two endemic *Heteromormyrus* species in the Cunene and at least four endemic species generally associated with highland streams in the Cuanza. The genus *Heteromormyrus* was recently reviewed by Sullivan

***Figure 1a:** Representative fish from the highlands and escarpments of Angola and Namibia (HEAN). Top to bottom:* Heteromormyrus longilateralis, *Cunene River (photo: R Bills);* Parakneria marmorata, *Cuanza River (photo: E Swartz);* Enteromius breviceps, *Queve River (photo: P Skelton);* Enteromius evansi, *Queve River (photo: P Skelton);* Enteromius eutaenia, *Cunene River (photo: R Bills);* Labeo ansorgii, *Cuanza River (photo: E Swartz);* Labeobarbus *sp., Cuanza River (photo: E Swartz);* Labeobarbus *sp., Cuanza River (photo: E Swartz);* Labeobarbus *sp., Cuanza River (photo: E Swartz).*

Figure 1b: *Representative fish from the highlands and escarpments of Angola and Namibia (HEAN). Top to bottom:* Micralestes argyrotaenia, *Queve River (photo: P Skelton);* Clarias *sp. (cf.* liocephalus*), Queve River (photo: P Skelton);* Platyclarias machadoi, *Cuanza River (photo: E Swartz);* Amphilius pagei, *Cuanza River (photo: E Swartz);* Doumea angolensis, *Cuanza River (photo: E Swartz);* Chiloglanis *sp., Queve River (photo: P Skelton);* Mastacembelus *sp. (cf.* frenatus*), Queve River (photo: P Skelton);* Chetia *sp., Queve River (photo: P Skelton);* Pharyngochromis *sp., Queve River (photo: P Skelton); Austrotilapiine cichlid, Cuanza River (photo: R Bills).*

et al. (2022) and recognised as the valid genus for the cluster of 'slender stonebashers' from southern Africa, which were previously classified within the genus *Hippopotamyrus*. Species of *Cyphomyrus, Heteromormyrus, Marcusenius* and *Petrocephalus* make for a diverse representation of the family, especially in the larger river systems like the Cunene and the Cuanza.

Danionidae

The presence of the Family Danionidae, (subfamily Chedrinae) genus *Engraulicypris* (*E. howesi* in the Cunene, *E. brevianalis* in the Limpopo) (Ridden *et al*. 2016) is notable. The chedrins in the highlands are also represented by *Raiamas ansorgii* from the Cuanza, and *Opsaridium zambezense* in the headwaters of the Okavango (the Cubango River). The latter species is widespread in the Zambezi.

Cyprinidae

The Cyprinidae (*sensu stricto*, after Tan & Armbruster 2018) is, by far, the largest fish family occurring in the HEAN rivers. In Africa south of the Sahara the family includes the subfamilies Labeinae (labeos), Torinae (hexaploid yellowfishes) and the Smiliogastrinae (minnows). Although the systematic status of many species is not yet settled and distributions are not fully mapped in the highlands, endemicity is clearly indicated for some species or species groups. An outstanding feature is the high number of species (n = 14, Skelton 2019) of large hexaploid yellowfish in the genus *Labeobarbus* found in the Cuanza River system. Recent collections in the Longa River to the south of the Cuanza include a possible conspecific *Labeobarbus* that might indicate drainage linkage between these systems (Tate & Kindler 2019). Another species of uncertain identity has been recorded in the Queve (pers. obs.), the headwaters of which share the divide with the upper reaches of the Cuanza. A single species, *Labeobarbus codringtonii,* occurs in the headwaters of the Cubango-Okavango and Zambezi. However, this widespread Afrotropical genus has not been recorded from the Cunene. There are several minnow species (Smiliogastrini) that also connect across the drainages in the highlands such as *Enteromius mattozi, E. argenteus* and *E. evansi* in the Cunene–Cuanza; and *E. breviceps, E. evansi, E. mocoensis, E. paludinosus* and *E. trimaculatus* in the Cunene–Okavango–Upper Zambezi. Few *Labeo* species have been recorded from the HEAN. Tate and Kindler (2019) found an extremely slender *Labeo* in the Catumbela that may be an undescribed species or an eco-phenotype of *L. ansorgii*. It is possible that *L. ansorgii* (with *L. rocadasi*) reflects a Cunene–Cuanza linkage. The trans-Kalahari Cunene–Limpopo presence of *L. ruddi* is echoed by *Enteromius eutaenia* in both systems and the distribution of a related pair of minnows, *Enteromius mattozi* (Cunene) and *E. rapax* (Limpopo).

Amphiliidae

Amphiliid catfishes are significant markers of many African highland systems but they are few and relatively restricted in the HEAN. Three genera are recorded, two in the Cuanza – *Doumea* and *Amphilius*. *Doumea* is largely a Congo and Central West African genus. There are two species in the Cuanza including *Doumea angolensis* and a second, possibly undescribed, species. *Amphilius* is an Afrotropical genus with two sublineages, an east and southeastern lineage (High Africa) with 9+10 primary caudal fin rays, and a Low Africa (Congo–West Africa) lineage with a reduced number of caudal fin rays (6+7). Three species of *Amphilius* are found in the HEAN, two related species from the Low-African lineage in the Cuanza and the Queve as well as the Cuango–Congo (*A. lentiginosus*, *A. pagei*), and a representative of the 'High Africa' clade, *A. cubangoensis,* from the Cubango–Okavango–Upper Zambezi (Trewavas 1936, Thomson & Swartz 2018, Skelton 2019). In the Cunene the family is represented by the diminutive sand-dwelling *Zaireichthys cunenensis*, indicating a Cunene–Okavango linkage.

Clariidae

Clariid airbreathing catfishes are common and widespread in Afrotropical rivers and lakes. Characteristic of swamps and lakes they are not typically 'highland' fishes and it is a measure of the relatively low elevation from the interior of the HEAN that several clariid species do occur in low-order tributaries of the rivers. Few species with broad depressed heads and reduced post-orbital bones characteristic of the genera *Clariallabes* and *Platyclarias* occur in rocky reaches of certain rivers in the HEAN. *Platyclarias* is presently only known from the Cuango–Congo (Poll 1977) but a species (*P. machadoi*) from the Cuanza is attributed to this genus (Bernt *et al*. 2023). *Clariallabes* is present in rocky habitats of the Upper Zambezi–Okavango and the Cuanza and an unidentified broad-headed rock-dwelling species in the Cunene is possibly of this genus. *Clarias dumerilii* collected by Karl Jordan from the Queve (Serra do Môco) in the 1930s and identified by Trewavas (1936) is an unconfirmed, broad-headed species. These observations indicate that rivers in the HEAN host several rock-dwelling clariids that require further investigation before their significance is realised. A unique cave-dwelling clariid (*Clarias cavernicola*) inhabits a karst cave-lake system (Aigamas, Namibia) on the southern rim of the highlands (Trewavas 1936, Jacobs *et al*. 2021). This troglobitic species appears to be of the *Clarias* (*Anguilloclarias*) lineage, which are small, slender-headed clariids that inhabit floodplains, swamps and bogs. It is therefore probably a stranded relict from a former pluvial period and is not typical of other highland clariid species.

Mochokidae

Mochokid catfishes of the genus *Synodontis* are uncommon and not characteristic of the HEAN. The genus is known from the Cuanza (Skelton 2019) and the Cunene (Hay *et al*. 1997), where five recorded species occur and all are also reported from the Cubango–Okavango (Skelton 2001). Several suckermouth catlets (*Chiloglanis*) are distinctly associated with the highlands. *Chiloglanis angolensis* was described from the Cubal system in the Catumbela at 1,500 masl where it was collected together with *Kneria polli*. This species is likely to occur in the Cunene that shares a watershed with the Cubal. *Chiloglanis sardinhai* has been recorded from the Longa, south of the Cuanza (Ladiges & Voelker 1961). *Chiloglanis fasciatus* from the Cubango–Okavango is possibly also in the Catumbela system (Tate & Kindler 2019).

Cichlidae

Several species of cichlid fishes are associated with the HEAN. In particular the haplotilapiine cichlid fishes of the Cunene (Greenwood 1984) and those of the Cuanza (Schwarzer *et al*. 2012) are singled out for their endemicity and interest. The Cunene River has four endemic cichlids – *Thoracochromis albolabris, T. buysi, Orthochromis machadoi* and the downstream species *Sargochromis coulteri*. *Thoracochromis lucullae*, and downstream species *Serranochromis cuanza* and *S. swartzi* are endemic to the Cuanza and there are several species detected by the molecular analysis of Schwarzer *et al*. (2012) that have not yet been dealt with taxonomically. The precise type locality for *Chetia welwitschi*, given by Boulenger (1898) as 'Fluilla, Angola', is uncertain (Greenwood 1984) and the species is poorly known from the Angolan coastal systems. A specimen photographed by R Tate from the Longa River in 2018 (Tate & Kindler pers. comm.) appears to be of this species. Specimens from the upper reaches of the Cunene have also been tentatively identified (pers. obs.). *Chetia gracilis* described by Greenwood (1984) from the upper reaches of the Cutato Nganguela in the Cubango–Okavango system is a second species of the genus that might be characteristic of the HEAN. *Orthochromis machadoi* from the Cunene below Ruacana is another HEAN endemic. *Tilapia sparrmanii* and *Coptodon rendalli* are present

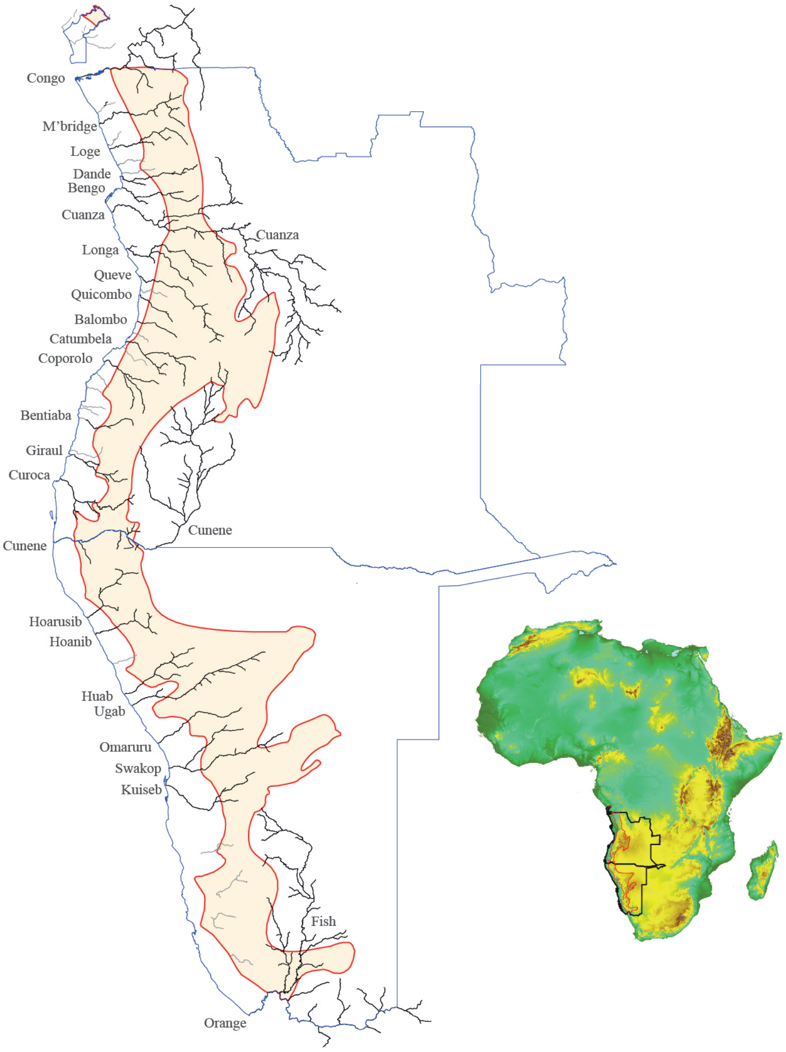

Figure 2: *Major rivers of the highlands and escarpments of Angola and Namibia (HEAN, orange outline).*

in the Cuanza and the Cunene but are not characteristic of the highland streams. Likewise *Oreochromis angolensis* is present in the coastal reaches of the Angolan coastal rivers but is not characteristic of the scarp or highland streams. *Tilapia guinasana,* closely related to *T. sparrmanii*, is an aberrant polychromatic species narrowly endemic to the Guinas sinkhole lake in the southern karst belt (Namibia). As with the cave catfish, the presence of this species is likely a relict of former pluvial conditions that prevailed from time to time over the region and is not characteristically a ‘highland’ species. The general conclusion is that the cichlids of the HEAN are poorly known and, based on work such as Schedel *et al*. (2019) and Schwarzer *et al*. (2009, 2012), could represent early radiations of the ‘Haplotilapiines’ in Africa.

Mastacembelidae

Spiny-eels (Mastacembelidae) are uncommon and known from only three rivers along the HEAN – the Cuanza *(Mastacembelus ansorgii*), the Okavango (*M. frenatus*) and the Queve (*M.* sp.). This distribution reinforces the observation of interconnection between these systems that was noted previously. Furthermore, the shared presence of the genus in both the Congo and the Upper Zambezi–Okavango indicates connection eastward into the Kalahari Basin. The rarity of such records also highlights the need for further, more comprehensive surveys of the streams and rivers in the HEAN.

Order Characiformes: Hepsetidae, Alestidae

Characiform fishes are not considered here as ‘highland’ representatives as they are more generally associated with downstream riverine and floodplain habitats. However, it is noted that representatives, such as the southern pike (*Hepsetus cuvieri*), are present in the Cuanza and the Cunene; several alestids including *Brycinus lateralis* are in the Cuanza; the silver robber, *Micralestes argyrotaenia,* possibly conspecific with the widespread *M. acutidens*, is in the Cunene. The tigerfish (*Hydrocynus vittatus*) is in the Okavango but is generally absent from the HEAN.

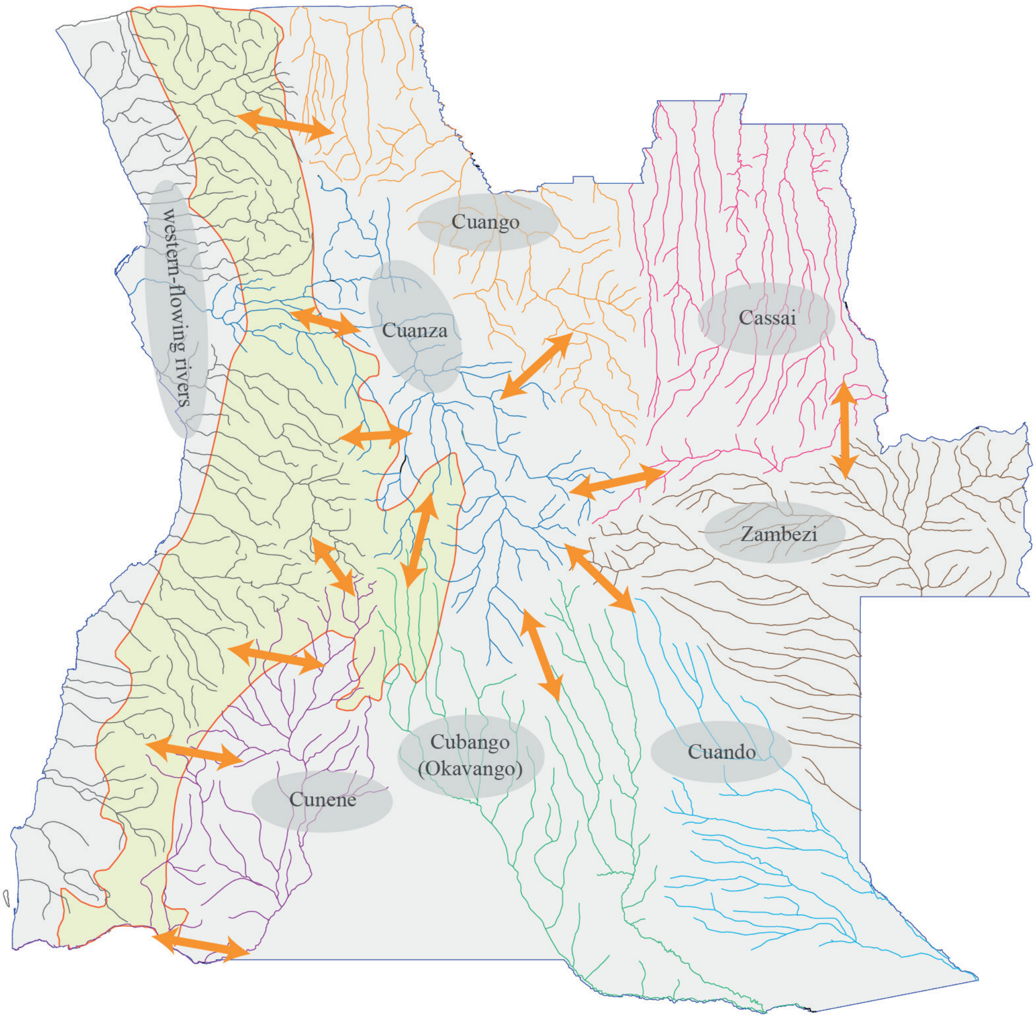

Figure 3: *Western escarpments and highlands of Angola, showing rivers and the dynamic divide between the interior basins of the Cunene and the Cuanza systems and adjacent catchments. The outline of the highlands and escarpments is shown in orange. Orange bidirectional arrows indicate the interactive zones across the divides between the interior basins and rivers.*

BIOGEOGRAPHY

Freshwater fishes are excellent biogeographic indicators as they are firmly tied to hydrographic evolution. While the hydrographic evolution of the highlands is not yet comprehensively understood, certain features have been exposed that begin to explain the history of the fauna. The HEAN represent the elevated eastern scarp of the rift between Africa and South America. Since rifting, the escarpment has been retreating eastward under the erosional force of coastal river systems, with a few notable breaches of the divide, namely, the Cuanza and the Cunene (Figure 2). Each of these two systems has tapped into major Kalahari sedimentary sub-basins (Cuanza–Luando and Cunene–proto-Etosha, respectively) and is actively expanding the respective basin rim by captures across the divide (Leturmy *et al.* 2003, Miller *et al.* 2010). Other rivers have penetrated deeply into the scarp and breached the coastal–interior watershed in less spectacular fashion, e.g., the Longa, the Queve and the Catumbela (Figure 2).

The northwestern drainages of the elevated 'Kalahari plateaus' are generally north–south in alignment along the base of the highlands and there are clear instances of drainage capture between systems along the interior (east) of the highlands (Figure 3). These captures have played a major role in faunal mixing and transfer and have imparted a clear 'West Zambezian' character to the faunal composition of these systems (e.g., Trewavas 1936, Schwarzer *et al.* 2012, Musilova *et al.* 2013). Typical West Zambezian indicator species in this respect include the southern pike (*Hepsetus cuvieri*) and the Zambezi grunter (*Parauchenoglanis ngamensis*), both of which also have Congo Basin associations. Other groups such as the serranochromine cichlids, the *Synodontis* catfishes and mastacembelid spiny eels have East African 'Rift'–Lake Tanganyika affinities (Schwarzer *et al.* 2009, 2012, Schedel *et al.* 2019). In addition, strong East African affinities are indicated by the presence of widespread species like the three-spot minnow (*Enteromius trimaculatus*) and the straightfin minnow (*E. paludinosus*). The north–south alignment of interior eastern adjacent drainages (see Figure 3, Cubango (Okavango) catchment) is a key element in the deposition of the deepest sediments of the Kalahari Basin within the Etosha Basin (Thomas & Shaw 1991). This alignment extends into the south–north drainage of the Upper Cuanza. A possibly earlier linkage from west to east across the Kalahari Basin to Central (Congo and Rift) and East Africa is still evident in the drainage lines of the Upper Cassai and the Lungwe–Bungwe–Upper Zambezi. The ichthyofaunal elements derived from this earlier west–east linkage (e.g., *Enteromius mattozi, E. paludinosus, E. trimaculatus*, kneriid species, rock-dwelling clariids, *Orthochromis machadoi*) are characteristic components of the ichthyofauna of the HEAN. This drainage connection probably existed prior to the Miocene desertification of the Kalahari Basin (Senut *et al.* 2009). Freshwater connections downstream along the coastal reaches have also contributed to the fauna of the Atlantic coastal rivers (Skelton 2019), but these involve species not generally encountered in the upland escarpment streams and rivers and are thus excluded from consideration here.

The affinities of fishes in the HEAN strongly reflect the north–south alignment of the interior drainage connections from the Cunene through to the Cuanza, as well as reflecting links across the Cuanza–Cuango–Cassai–southern Congo belt of rivers. In the north this west–east link reaches across the East African Rift System and its associated highlands to the rivers of East Africa. The postulated palaeo-drainage lines from the Okavango–Cuando–Upper Zambezi south and east to the Limpopo and southeastern coastal systems (Moore & Larkin 2001) is also reflected in the circum-Kalahari distributions of several lineages (such as *Enteromius mattozi* and *E. breviceps* chubby-head minnow lineage; *Engraulicypris* and *Kneria*). It is evident that the highlands and escarpments of Angola and Namibia have served as a geo-climate sanctuary or refuge for fishes (and likely other aquatic groups) since at least the Miocene.

ACKNOWLEDGEMENTS

I am grateful to many colleagues who facilitated opportunities and assisted me in the field over the years. The South African Institute for Aquatic Biodiversity (SAIAB) and its staff have provided support to me over the years. Maditaba Meltaf (SAIAB) located literature for this study. John Mendelsohn provided the final version of map figures. Roger Bills and Ernst Swartz provided images of fishes as acknowledged in the captions. Robert Heffer kindly prepared the fish images and composed the plates as presented in Figure 1. The article was improved by referee comments.

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Birds of the highlands and escarpments of Angola and Namibia: ornithological significance, avifaunal patterns and questions requiring further study

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-mills

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ABSTRACT

The highlands and escarpments of Angola and Namibia are recognised as an important region for the evolution and conservation of birds. However, no comprehensive study of the avifauna, and its potential evolutionary origins and links, has been made. As a basis for further study, we compiled a comprehensive list of birds largely confined to the region, together with details of links to nearest relatives, including birds from all relevant levels of the evolutionary process and taxonomic hierarchy (isolated populations to genera). A total of 233 Evolutionarily Significant Units (ESUs) were identified, comprised of four genera, 37 species, 71 subspecies and 121 taxa with isolated populations. The escarpment holds a richer diversity of ESUs than the Afromontane region, although most escarpment ESUs are separated from relatives by a break in the forest zone of about 320 km. Hence few Northern Escarpment ESUs are differentiated even subspecifically (15 of 111; 14%), and most (n = 92; 83%) involve isolated but undifferentiated populations. However, further south along the escarpment distinctiveness increases; 15 of 64 (23%) forest ESUs on the Central Escarpment are differentiated subspecifically. In contrast, the ESUs of the highlands are typically isolated from their nearest vicariants by a much larger gap. Although only 44 ESUs are found here, 26 of them have differentiated to the subspecies level and seven to species level. In the highlands, lower diversity is paired with a greater degree of differentiation, both of which are known to be the result of extreme isolation. Preliminary research has shown that the Angolan Afromontane forests are located in an area of high climatic stability, and that they constitute an important historical link between the montane bird communities of East Africa and the mountains of Cameroon. Our simple analysis reveals some potentially interesting patterns but relies on largely untested assumptions regarding the closest relatives of the region's significant bird taxa (ESUs). More detailed and extensive studies of the origins and relationships of key bird taxa are needed to explore whether counterintuitive patterns exist that are currently being masked.

Keywords: Angola, avifauna, endemism, escarpments, highlands, Namibia

INTRODUCTION

Congruent distribution patterns of restricted-range (< 50,000 km^2) terrestrial bird species have been used to identify key regions of bird endemism (Endemic Bird Areas (EBAs)), globally, as priorities for conservation (Stattersfield *et al.* 1998). Within Angola and Namibia there is one EBA (Western Angola; Figure 1), defined more than 20 years ago based on 14 restricted-range bird species; the updated taxonomy of BirdLife International (HBW & BirdLife International 2022) recognises seven additional relevant species. This EBA corresponds closely to the escarpment and highland zones in Angola, but also includes some areas adjacent to the escarpment along the coastal plain (Dean *et al.* 2019). There is also one 'Secondary Area' (defined as covering the range of a single restricted-range species), the 'Namibian Escarpment', based on the range of Herero chat *Namibornis herero*, which covers parts of both southern Angola and northern Namibia.

The EBA approach, however, is of limited use for understanding the evolutionary significance of regions such as the highlands and escarpments of Angola and Namibia (HEAN), as it was devised as a conservation prioritisation exercise, based on species as the only taxonomic entity considered and on the assumption that species with smaller ranges are more likely to be threatened. Although this is generally true, the method applies an arbitrary cutoff for range size that excludes several species which are endemic or near-endemic to the HEAN. The question of identifying evolutionary hotspots – regions where large numbers of distinctive taxa have evolved and are likely to evolve in the future – requires an approach that considers a region within the context of a wider area, links to other areas, evolutionary distinctiveness of taxa, and includes groups from all levels of the evolutionary process and taxonomic hierarchy (from isolated populations to genera, in this case). This was done at the species level for forest-dependent birds, globally (Buchanan *et al.* 2011); in that analysis the forests of western Angola ranked in the highest category of impact score for their contribution to global forest bird species richness. Previous assessments (Collar & Stuart 1988, Burgess *et al*. 2004, de Klerk *et al*. 2004) all recognise the importance of the western Angolan forests to forest birds. Yet the full contribution of the Angolan–Namibian escarpment and highlands to the evolution of the African avifauna has not yet been evaluated based on current taxonomic understanding.

Allopatric speciation is regarded as the major mode of speciation in birds (Price 2008), and typically requires the condition of disjunct patches of similar habitat. Due to their topography, the HEAN have moister and cooler conditions than their lower and more arid surrounds (Fjeldså & Lovett 1997). Most bird taxa which are endemic or near-endemic to the region occur in moister habitats than found in surrounding areas; namely, forests where there are adjacent woodlands and savannas, and savannas bordered by deserts. A second important factor that may have contributed to the high levels of endemism observed in this area is long-term habitat stability (Vaz da Silva 2015); the escarpment has trapped moisture-laden coastal air against it for millennia, bringing long-term climatic stability to the area (Hall 1960, Mills 2010).

The physical structure of the escarpment varies across its length, from north to south, which impacts habitats and, consequently, birds. Eleven broad landscape units have been defined within the HEAN based on their topographical, geomorphological, ecological and climatic characteristics (Mendelsohn & Huntley 2023); we are using these landscape units in this paper. However, even within the Central

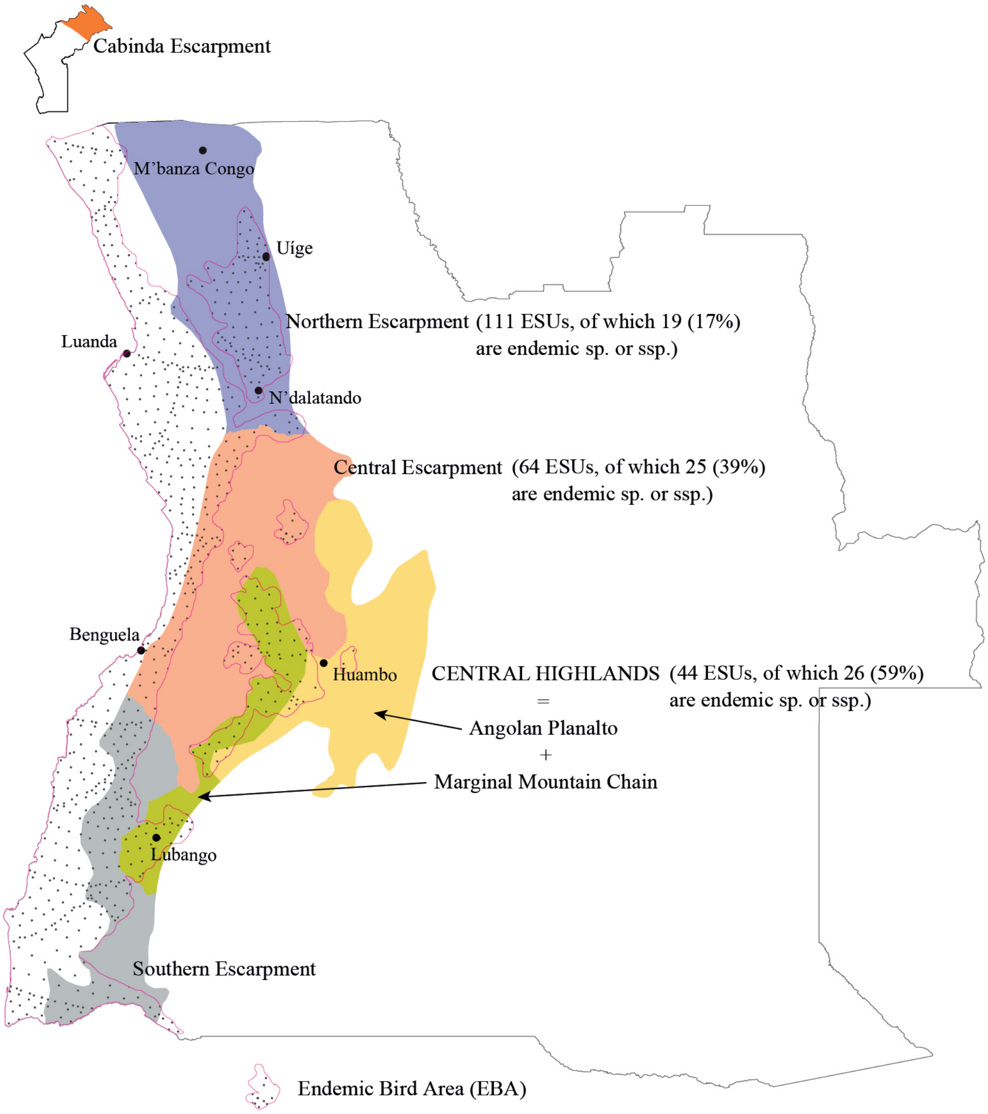

Figure 1: *Key avifaunal areas in Angola that fall within the highlands and escarpments of Angola and Namibia that are mentioned in the text. The escarpment, in its broadest sense, is divided into three main zones: Northern (purple), Central (pink) and Southern (grey). Notice the proximity of the escarpment to the Central Highlands along the Central and Southern escarpment. Also notice the decrease in the number of Evolutionarily Significant Units (ESUs) from north to south, along the escarpment, but the concurrent increase, especially in relative terms, in ESUs that are endemic species or subspecies.*

Escarpment landscape there are three distinctive forest bird communities linked to different types of forest habitats (Mills 2010).

The significance of the Angolan escarpment for the evolution of birds was studied by Hall (1960), who identified three groups of closely related birds that display different patterns of distribution relative to the escarpment. She identified three biological zones, namely the Escarpment Zone (a wedge of richer habitats on the escarpment), the *Acacia* Zone (arid savanna, including grasslands and mopane woodlands, along the coastal plain) and the *Brachystegia* Zone (miombo woodland on the plateau). The groups of birds identified were: (i) birds with a representative form in the Escarpment Zone and in either, or both, of the other zones; (ii) birds with representative forms in the *Brachystegia* and *Acacia* zones partly isolated from each other by the Escarpment Zone; and (iii) species endemic or nearly endemic to the Escarpment Zone. These groups demonstrate that the escarpment is both a centre of evolution, with taxa at different stages of evolutionary separation (groups i and iii), and a biological barrier between the more arid habitats of the coast and plateau (group ii). However, Hall (1960) did not address the distinctiveness of the escarpment in the wider context of lowland tropical forests, of which they are an outlier, and how the avifauna of the escarpment relates to that of other similar forests of the Congo Basin. Nor did she look at variation in the avifaunal composition along the escarpment, from north to south.

In this review, we assess the contribution of the HEAN to the evolution of the avifauna of the region.

METHODS

To identify potentially significant components of the avifauna for evolutionary study (here called Evolutionarily Significant Units or ESUs; Moritz 1994), we drew up a comprehensive list of birds confined or largely confined to the HEAN, using a cutoff of two-thirds of the global range or population size overlapping with the study area. This recognises that birds which currently have wider ranges, but whose distributions are centred on the study area, may be useful in understanding the biogeography of the region; they are likely to have evolved here and expanded their ranges more recently. We applied the aforementioned definition generously and without mapping in detail the ranges of the relevant birds (many of which are poorly known for Angola), and we included species which come close to matching the criteria using any dataset. While we recognise that the two-thirds cut-off is arbitrary, we believe that it is the most useful starting point for elucidating the contribution of the region (which also has arbitrarily defined borders) to the evolution of birds, and its links to other regions. Contra the general definition used in this work, we excluded Cabinda from our assessment of escarpment birds, largely because the forests and birds of Cabinda form a contiguous part of the main block of Congo Basin forests and bird populations. Consequently, there are no endemic taxa or isolated populations of birds known in Cabinda.

Each taxon that met these criteria was considered to be an ESU. For each one, we roughly estimated its degree of confinement to the study area, list whether it is an escarpment and/or montane species, list its closest relative based on best knowledge and give its distance of isolation to its sister taxon. Although the gap between the main Congo Basin forest block (immediately north of the Congo River) and the Northern Escarpment forest is rather small, at about 320 km, it constitutes a significant barrier to forest-restricted species, which tend to be highly sedentary. As such, many Congo Basin forest birds fail to cross it (based on our best knowledge) and, likewise, several Northern Escarpment forest species are not found in the nearby Congo Basin block (e.g., white-collared oliveback *Nesocharis ansorgei* and scaly-breasted illadopsis *Illadopsis albipectus*).

From this assessment flows a summary of biogeographic links to other bird communities, and priorities for further study. Although birds are one of the best-known taxonomic groups of Angola, there are still large gaps in knowledge in basics, such as the distribution and status of many species (Dean *et al.* 2019), which could impact the overall assessment.

RESULTS

Overview of avifauna

Among the bird communities of the region, we identified 233 ESUs that are associated with the HEAN (Appendix 1). We defined the escarpment in its broadest sense here, to include moister habitats at the base and top of the escarpment that would not exist without the topography of the escarpment, and similar habitats that extend into the more arid adjacent areas along rivers where the occurrence of bird populations would be unlikely without the influence of the escarpment. We also included moister montane habitats; the isolated Afromontane forests, grasslands and shrublands.

Most significant among these ESUs are four monospecific genera which are endemic to the region, namely *Achaetops* (rockrunner), *Lanioturdus* (white-tailed shrike), *Namibornis* (Herero chat) and *Xenocopsychus* (Angola cave chat) (Appendix 1). These endemic genera are a consequence of divergence events predating the Plio-Pleistocene, the period typically associated with most bird speciation events that have led to much of the current African avifauna (Beresford *et al.* 2005). Interestingly, although Namibia and southern Angola contribute little to the total number of ESUs of the study region, these four genera are all endemic to the Southern Escarpment. Thus, despite its relative lack of importance in terms of numbers of ESUs, this section of the escarpment contributes significantly to the overall evolutionary distinctiveness of the escarpment region. Additionally, Hartlaub's spurfowl *Pternistis hartlaubi* is basal to all other members of that genus, and Swierstra's francolin *P. swierstrai*, together with the other, extralimital, montane species, is part of an ancient radiation within the genus (Mandiwana-Neudani *et al.* 2019).

Next in significance are 37 taxa regarded as full species, none of which occurs exclusively in Namibia, although nine are found in Namibia and Angola. A few of these species also indicate links to the north (Gabon and Congo), and some species have distributions which extend onto the plateau of Angola, although these are generally confined to the higher-lying areas on its western margin.

The remainder of the ESUs can be divided into 71 recognised subspecies and 121 taxa with isolated populations which are not regarded as differentiated subspecifically. Together, these two groups are the most informative for understanding links to other regions, not only because of their larger sample size but also because close relatives can generally be assumed as the geographically nearest vicariant.

Of the subspecies, several have parapatric sister taxa whose differences are questionable and may, on reassessment, be found not to constitute ESUs. Similarly, other subspecies may be found to meet specific status in future assessments.

Among the ESUs represented by isolated populations, the vast majority are escarpment species with modest gaps in their range to their nearest vicariant; usually c. 320 km between the Northern Escarpment and the main Congo Basin. Given the small gaps in distribution, some gene flow is likely to persist between these populations and their vicariants, reducing the probability of them evolving along their own evolutionary trajectories. A few ESUs, however, mostly montane taxa, are isolated from closest relatives by more than 1,000 km. One can reasonably assume that gene flow is likely to be inversely proportional to gap size and so a significant proportion of these highly isolated populations may be reassessed to be independent subspecies or species in future or will evolve along independent trajectories and become genetically and phenotypically more isolated from their vicariants with time (Fjeldså & Bowie 2008).

Links to other avifaunas

First, when considering the escarpment and highlands as separate entities, it is apparent that the two areas have independent bird faunas with independent origins, although there are complicating factors. Foremost of these is the proximity between montane habitats and the escarpment in certain parts of Angola, especially within the Marginal Mountain Chain at Lubango and the Central Escarpment at Cumbira. This meeting of the two ecoregions at the top of the escarpment blurs their separation. Significantly, at Cumbira, typical lowland forest birds with links to the Congo Basin, such as buff-throated apalis *Apalis rufogularis,* and montane specialists, such as grey apalis *A. cinerea*, with links to distant montane areas, live within earshot of one another. Just above the treeline, at the same site, one also finds arid zone escarpment representatives with links to the south, such as rockrunner *Achaetops pycnopygius* and mountain wheatear *Myrmecocichla monticola*. The Central Escarpment is a particularly heterogenous area where montane habitats, lowland forest, arid escarpment and plateau miombo woodlands come together in a small area to form a region of great biological complexity.

To clarify the distinction between escarpment and highlands from an ornithological perspective, we defined any species which is absent from the main highlands (Serra do Môco and Serra da Namba region) as being an escarpment species, and any species that occurs in the main highlands but is absent from the main escarpment (generally around 700 masl) as a highland species. Only 13 of the ESUs occur in both the escarpment and highlands zones, including Angola cave chat *Xenocopsychus ansorgei* (Mount Soque and on isolated hills away from the escarpment such as around Serra da Neve), red-faced crimsonwing *Cryptospiza reichenovii* and Angola naked-faced barbet *Gymnobucco vernayi* (Serra da Namba and Cumbira). The remaining 220 taxa can be attributed to either the escarpment (n = 170) or highlands (n = 50).

The escarpment, as a whole, holds a much richer diversity of ESUs than the Afromontane region (see also Mills 2010, Mills *et al.* 2011, 2013). The vast majority of escarpment ESUs are separated from relatives by a break in the forest zone of about 320 km, between the northern tip of Pingano (the northernmost ridge of the Northern Escarpment) and the main Congo Basin forest block just north of the Congo River mouth (Figure 2). However, within this gap there are several patches of forest along rivers and in small pockets that almost certainly facilitate the movement of individuals between the two areas, and thus enhance gene flow. As a consequence, there are very few Northern Escarpment ESUs that are differentiated specifically or subspecifically from their nearest vicariants in the Congo Basin. Of a total of 111 ESUs, just 15 are endemic subspecies (14%), of which only one is confined to the Northern Escarpment, and four are endemic species (4%), of which only one is confined to the Northern Escarpment (Braun's bushshrike *Laniarius brauni*). By contrast, the majority of ESUs (n = 92; 83%) involve isolated populations along the northern scarp. The proportion of the ESUs that have differentiated specifically or subspecifically – indicative of an absence or restriction of gene flow – is thus relatively small.

From north to south along the escarpment, however, specific and subspecific distinctiveness increases (Figure 1). Of the 64 forest ESUs that occur on the Central Escarpment (south of the Cuanza River), 15 are differentiated at the subspecies level (23%), including two which are endemic to the Central Escarpment, and 10 at the species level (16%), including three species endemic to the Central Escarpment. The remaining ESUs (n = 39; 61%) are of taxa with isolated populations. In Angola's Southern Escarpment, forest bird species are largely absent and the avifaunal connection to the Congo Basin is lost almost entirely.

In contrast to the escarpment zone, the ESUs of the Central Highlands (Figure 1, and equivalent to the combined Angolan Planalto and Marginal Mountain Chain of Mendelsohn and Huntley (2023)) are typically isolated from their nearest vicariants by a much larger distributional gap (typically more than 1,500 km). Although only 44 ESUs are found here, 26 (59%) of them have differentiated to the subspecies level and seven to species level. Thus, only a quarter of ESUs in the Central Highlands remain undifferentiated (n = 11; i.e., representing an

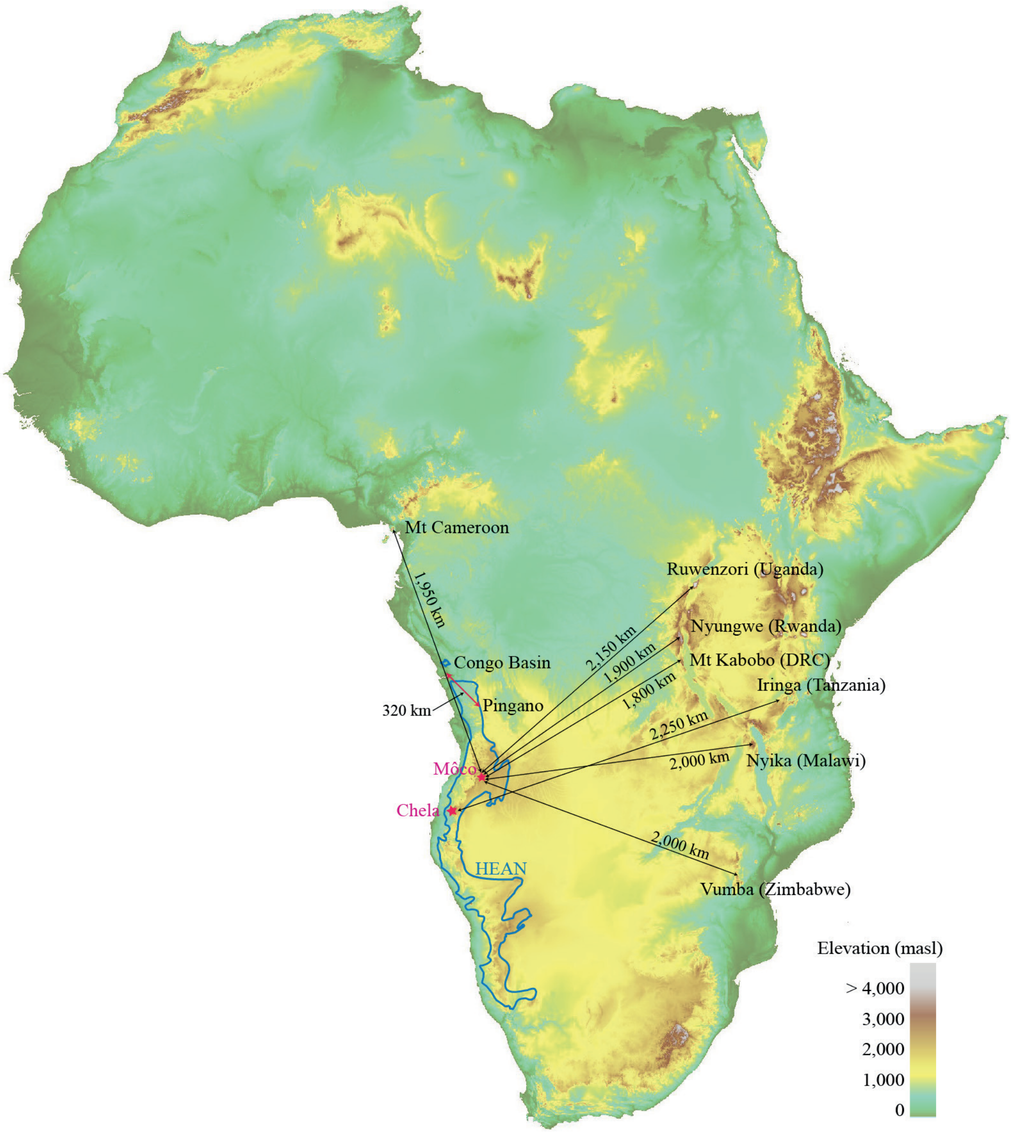

Figure 2: *Key links of the avifauna of the highlands and escarpments of Angola and Namibia (HEAN) region to other regions within Africa. The highlands (of which Serra do Môco is the highest point) lie at least 1,800 km from other Afromontane centres, whereas the gap between the Northern Escarpment and Congo Basin forests is much smaller.*

isolated population). Here the lower diversity is paired with a greater degree of differentiation, both of which are known to be the result of extreme isolation. The Afromontane forests of west-central Angola comprise the most isolated centre of the Afromontane archipelago biome (see White 1978), separated by more than 1,700 km from other similar habitats (Vaz da Silva 2015). Because of the mixed botanical composition of the Afromontane forests of Angola, they were not included in White's (1978) original definition of this phytochorion (or biome) based on plant communities. Nevertheless, their bird communities clearly identify them as belonging to the Afromontane biome (Dowsett 1986, Dowsett-Lemaire & Dowsett 1998). The number of endemics species entirely confined to these forests is small, but many subspecies, and ESUs more generally, are present (Appendix 1; Mills *et al.* 2011, 2013). Preliminary research – combining molecular data, ecological niche modelling, and the reconstruction of past climates and associated habitats – has shown that the small Angolan Afromontane forests are located in an area which has experienced high climatic stability across several glacial cycles (Vaz da Silva 2015). They also constitute an important historical link between the montane bird communities of East Africa and the mountains of Cameroon. White (1981), using plants as a model and Afromontane isolates as signals of historical connectedness (stepping stones), found evidence for a stronger link between the Ethiopian and Cameroonian highlands via a route south of the Congo Basin, via Angola, (named the Southern Migratory Track) rather than the more direct route that lies north of the Congo Basin. Dowsett-Lemaire and Dowsett (1998) found similar evidence for some birds, including two Angolan species, evergreen forest warbler *Bradypterus lopezi* and grey apalis *Apalis cinerea*. For species such as African hill babbler *Pseudoalcippe abyssinica* and Bocage's akalat *Sheppardia bocagei*, populations were isolated in the Angola mountains from very early on and are likely to constitute distinct species (Vaz da Silva 2015).

GAPS IN KNOWLEDGE

The simple analysis presented here reveals some potentially interesting patterns but relies on largely untested assumptions regarding the closest relatives of the region's significant bird taxa (ESUs). Even for taxa with published phylogenies, many are based on small sample sizes or incomplete taxon sampling. For example, rockrunner was found to be sister to Cape grassbird *Sphenoeacus afer* in one study (Beresford *et al.* 2005), whereas a second study found Cape grassbird to be sister to African moustached warbler *Melocichla mentalis* (Fregin *et al.* 2012); neither study sampled all three taxa, and so the actual relationships among the three species remains unresolved. More detailed and extensive studies of the origins and relationships of key bird taxa are needed to explore whether counterintuitive patterns exist that are currently being masked. Of special interest would be seemingly similar taxa that are assumed to be, but are not, most closely related to their geographically nearest vicariants (such as is the case with northern fiscal *Lanius humeralis* and southern fiscal *L. collaris*; Fuchs *et al.* 2011), and morphologically well-differentiated taxa that appear unrelated to nearby taxa but which actually share a common ancestor (for example, the montane white-eyes *Zosterops* spp. of East Africa; Cox *et al.* 2014).

Although bird endemism in Angola and Namibia is mostly concentrated in their highlands (escarpment and Afromontane forests), we know very little about the factors that have driven bird speciation here. Molecular data, sampled across most or all ESUs at the population level, should be obtained to elucidate the biogeography of the bird communities associated with this region (Kahindo *et al.* 2007). This alone would allow a comprehensive understanding of the diversification history of the avifauna of the highlands of Africa, highlight the dynamics of the interactions between different montane regions and between different parts of the Angolan escarpment and the Congo Basin, as well as the role of the cyclical climatic changes associated with the Plio-Pleistocene glaciations of the northern hemisphere (e.g., Voelker *et al.* 2010).

A preliminary study using five Afromontane forest bird species occurring in Angola has demonstrated the potential of genetic data to shed light on past evolutionary history (Vaz da Silva 2015). For the avifauna of the Angola escarpment, an obvious starting point would be to test the diversification hypotheses clearly put forward by Hall (1960). Ideally, this would be achieved as an 'umbrella project', built up from MSc and PhD projects carried out by Angolan and Namibian students.

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Appendix 1: *Significant bird taxa (Evolutionarily Significant Units) of the greater escarpment and highlands regions of Angola and Namibia, ranked in order of evolutionary/taxonomic significance. Taxonomy follows the International Ornithological Congress (IOC) World Bird List (Gill* et al. *2023) and all species listed by IOC are included. Additional species recognised by Handbook of the Birds of the World (HBW) and BirdLife International (HBW & BirdLife International 2022) are added, plus a few species based on recently published taxonomies that have not yet been assessed by world lists. None of our own taxonomic assessments affect the taxon list, although we do make comments where appropriate. Column heading abbreviations as follows: Ass = Percentage range association with the escarpment and highlands (67% minimum), M = Montane species, E = Escarpment species and D = Distance (km) to nearest extant relative, followed by the location of the relative (DRC = Democratic Republic of the Congo).*

Species	**Ass**	**M**	**E**	**Closest relative**	**D**	**Location of relative**
GENERA						
White-tailed shrike *Lanioturdus torquatus*	100	–	E	Western black-headed batis *Batis erlangeri* (Jonsson *et al*. 2016)	500	N Angola
Rockrunner *Achaetops pycnopygius*	100	–	E	African moustached warbler *Melocichla mentalis* (Fregin *et al*. 2012) or Cape grassbird *Sphenoeacus afer* (Beresford *et al*. 2005)	0 or 1,000	Parapatric/SW South Africa
Angola cave chat *Xenocopsychus ansorgei*	100	M	E	White-throated robin-chat *Dessonornis humeralis* (Zhao *et al*. 2023)	1,650	S Botswana
Herero chat *Namibornis herero*	100	–	E	Clade of fiscal flycatcher *Melaenornis silens* and silverbird *Empidornis semipartitus* (Zhao *et al*. 2023)	500	NW South Africa
SPECIES						
Finsch's francolin *Scleroptila finschi*	70	M	–	Possibly Whyte's francolin *Scleroptila whytei* (Mandiwana-Neudani *et al*. 2019)	500	NW Zambia
Hartlaub's spurfowl *Pternistis hartlaubi*	90	–	E	Clade of all other *Pternistis* francolins (Mandiwana-Neudani *et al*. 2019)	0	Sympatric
Swierstra's francolin *Pternistis swierstrai*	100	M	–	Clade of most other *Pternistes* francolins (Mandiwana-Neudani *et al*. 2019)	0	Sympatric
Grey-striped francolin *Pternistis griseostriatus*	100	–	E	Scaly francolin *P. squamatus* (Mandiwana-Neudani *et al*. 2019)	320	Cabinda
Red-crested turaco *Tauraco erythrolophus*	100	–	E	White-crested turaco *Tauraco leucolophus* (Perktas *et al*. 2020)	2,000	Cameroon
Red-backed mousebird *Colius castanotus*	100	M	E	Assumed speckled mousebird *C. striatus* or white-backed mousebird *C. colius*	0 or 100	Parapatric/far N Namibia
Violet wood hoopoe *Phoeniculus damarensis*	75	–	E	Green wood hoopoe *P. purpureus* (Cooper *et al*. 2001)	0	Sympatric
Monteiro's hornbill *Tockus monteiri*	75	–	E	Clade of several other *Tockus* spp. (Gonzalez *et al*. 2013)	0	Sympatric
Angola naked-faced barbet *Gymnobucco vernayi*	100	M	E	Assumed naked-faced barbet *G. calvus angolensis*	100	N Scarp of Angola
White-bellied barbet *Lybius leucogaster*	100	–	E	Assumed white-headed barbet *L. leucocephalus*	2,500	C Tanzania
Western black-backed barbet *Lybius minor*	75	M	E	Assumed eastern black-backed barbet *L. macclounii*	0	Parapatric
Rüppell's parrot *Poicephalus rueppellii*	75	–	E	Clade of all other *Poicephalus* parrots (Coetzer *et al*. 2015)	0	Sympatric
Angola batis *Batis minulla*	70	–	E	Assumed other central African forest *Batis* spp., e.g., West African batis *B. occulta*	250	C Gabon
White-fronted wattle-eye *Platysteira albifrons*	100	–	E	Brown-throated wattle-eye *P. cyanea* (Jonsson *et al*. 2016)	0	Parapatric
Monteiro's bushshrike *Malaconotus monteiri*	100	–	E	Assumed grey-headed bushshrike *M. blanchotii*	0	Parapatric
Braun's bushshrike *Laniarius [luehderi] brauni*	100	–	E	Assumed Luhder's bushshrike *L. luehderi*	320	Cabinda
Gabela bushshrike *Laniarius [luehderi] amboimensis*	100	–	E	Assumed Braun's bushshrike and/or Luehder's bushshrike	100	N Scarp of Angola
Gabela helmetshrike *Prionops gabela*	100	–	E	Assumed Retz's helmetshrike *P. retzii*	200	Plateau of Angola

Species	**Ass**	**M**	**E**	**Closest relative**	**D**	**Location of relative**
Carp's tit *Melaniparus carpi*	75	–	E	Assumed southern black tit *M. niger*	0	Parapatric
Pale-olive greenbul *Phyllastrephus fulviventris*	90	–	E	Assumed other relatives members of Genus *Phyllastrephus*	0	Sympatric
Angola white-throated greenbul *Phyllastrephus [albigularis] viridiceps*	100	–	E	Assumed white-throated greenbul. *P. albigularis*	320	Congo Basin
Pulitzer's longbill *Macrosphenus pulitzeri*	100	–	E	Assumed Kretschmer's longbill *M. kretschmeri*	2,100	SW Tanzania
Bubbling cisticola *Cisticola bulliens*	90	–	E	Assumed chattering cisticola *C. anonymus*, with which most likely conspecific	0	Parapatric
Huambo cisticola *Cisticola bailunduensis*	100	M	–	Short-winged cisticola *C. brachypterus* (Mills *et al*. in prep.)	0	Sympatric
Hartert's camaroptera *Camaroptera harterti*	100	–	E	Assumed grey-backed camaroptera *C. brevicaudata*	0	Parapatric
Bare-cheeked babbler *Turdoides gymnogenys*	100	–	E	Assumed other members of genus *Turdoides*	0	Sympatric
Angola yellow white-eye *Zosterops quanzae*	75	M	E	Clade including southern yellow white-eye *Zosterops anderssoni* (Martins *et al*. 2020)	0	Parapatric
Benguela long-tailed starling *Lamprotornis benguelensis*	100	–	E	Cunene long-tailed starling *L. violacior* and Meves's long-tailed starling *L. mevesii*	200	SW Plateau of Angola/SE Angola
Cunene long-tailed starling *Lamprotornis violacior*	100	–	E	Benguela long-tailed starling *L. benguelensis* and Meves's long-tailed starling *L. mevesii*	100	Base of S Scarp/SE Angola
Angola slaty flycatcher *Melaenornis brunneus*	100	M	–	Clade of other slaty flycatchers (Voelker *et al*. 2016)	2,000	NE Zambia/Albertine Rift
Gabela akalat *Sheppardia gabela*	100	–	E	Assumed Tanzanian montane *Sheppardia*	2,500	Probably C Tanzania
Rufous-tailed palm thrush *Cichladusa ruficauda*	70	–	E	Assumed collared palm thrush *C. arquata*	1,000	SW Zambia
Bocage's sunbird *Nectarinia bocagii*	75	M	–	Assumed Tacazze sunbird *N. tacazze*	2,100	N Tanzania
Ludwig's double-collared sunbird *Cinnyris ludovicensis*	100	M	–	Clade of other double-collared sunbirds, excluding Whyte's double-collared sunbird *C. whytei* (Bowie *et al*. 2016)	0	Sympatric
Golden-backed bishop *Euplectes aureus*	100	–	E	Yellow-crowned bishop *E. afer* (Prager *et al*. 2008)	0	Sympatric
Angola swee waxbill *Coccopygia bocagei*	100	M	–	Assumed swee waxbill *C. melanotis*	2,000	NE South Africa
Cinderella waxbill *Estrilda thomensis*	100	–	E	Assumed grey waxbill *E. perreini*	200	Parapatric
SUBSPECIES						
Orange River francolin *Scleroptila levalliantoides jugularis*	75	–	E	Conspecifics (Mandiwana-Neudani *et al*. 2019)	0	Parapatric
Red-necked spurfowl *Pternistis a. afer*	100	–	E	Red-necked spurfowl excluding *P. a. cranchii* (Mandiwana-Neudani *et al*. 2019)	2,000	E Zimbabwe/E Zambia
Rwenzori nightjar *Caprimulgus ruwenzorii koesteri*	100	M	–	Conspecifics	2,000	NE Zambia/Albertine Rift
Horus swift *Apus horus fuscobrunneus*	100	–	E	Conspecifics	300	CW Angola
African green pigeon *Treron calvus ansorgei*	100	–	E	Conspecifics	0	Parapatric

Species	Ass	M	E	Closest relative	D	Location of relative
Southern yellow-billed hornbill *Tockus leucomelas elegans*	100	–	E	Conspecifics	0	Parapatric
Crowned hornbill *Lophoceros a. alboterminatus*	100	–	E	Conspecifics	0	Parapatric
Olive bee-eater *Merops superciliosus alternans*	100	–	E	Conspecifics	1,000	SW Zambia
Naked-faced barbet *Gymnobucco calvus congicus*	75	–	E	Conspecifics	320	Cabinda
Anchieta's barbet *Stactolaema anchietae rex*	75	M	–	Conspecifics	0	Parapatric
Western green tinkerbird *Pogoniulus coryphaea angolensis*	100	M	–	Conspecifics	1,900	Albertine Rift/Cameroon
Green-backed honeybird *Prodotiscus zambesiae lathburyi*	100	M	–	Conspecifics	0	Parapatric
Elliot's woodpecker *Dendropicos elliotii gabela*	100	–	E	Conspecifics	320	Congo Basin
Rosy-faced lovebird *Agapornis roseicollis catumbella*	100	–	E	Conspecifics	0	Parapatric
Margaret's batis *Batis m. margaritae*	100	M	–	Conspecifics	500	NW Zambia
Eastern yellow-bellied wattle-eye *Platysteira a. ansorgei*	100	–	E	Conspecifics	800	S Gabon
Grey-headed bushshrike *Malaconotus blanchoti citrinipectus*	100	–	E	Conspecifics	0	Parapatric
Pink-footed puffback *Dryoscopus a. angolensis*	70	–	E	Conspecifics	800	S Gabon
Swamp boubou *Laniarius bicolor guttatus*	90	–	E	Conspecifics	200	Plateau of Angola and coast of Gabon
Dusky tit *Melaniparus funereus gabela*	100	–	E	Conspecifics	600	S DRC
Sabota lark *Calendulauda sabota ansorgei*	100	–	E	Conspecifics	0	Parapatric
Rufous-naped lark *Mirafra africana occidentalis*	100	–	E	Conspecifics	0	Parapatric
Angola lark *Mirafra a. angolensis*	100	M	–	Conspecifics	0	Parapatric
Long-billed crombec *Sylvietta rufescens ansorgei*	100	–	E	Conspecifics	0	Parapatric
Green crombec *Sylvietta virens tando*	90	–	E	Conspecifics	320	Congo Basin
Laura's woodland warbler *Phylloscopus l. laurae*	100	M	–	Conspecifics	500	NW Zambia
Evergreen forest warbler *Bradypterus lopezi boultoni*	100	M	–	Conspecifics	1,200	NC Zambia
Little rush warbler *Bradypterus baboecala benguellensis*	100	M	–	Conspecifics	0	Parapatric
Wailing cisticola *Cisticola lais namba*	100	M	–	Conspecifics	2,000	E Zambia/SW Tanzania

Species	Ass	M	E	Closest relative	D	Location of relative
Chirping cisticola *Cisticola p. pipiens*	100	M	–	Conspecifics	0	Parapatric
Croaking cisticola *Cisticola natalensis huambo*	90	M	–	Conspecifics	0	Parapatric
Desert cisticola *Cisticola aridulus lobito*	80	–	E	Conspecifics	0	Parapatric
Cloud cisticola *Cisticola textrix bulubulu*	75	M	–	Conspecifics	500	W Zambia
Banded prinia *Prinia bairdii heinrichi*	100	–	E	Conspecifics	320	W DRC
Buff-throated apalis *Apalis rufogularis brauni*	100	–	E	Conspecifics	100	N Scarp, but outside Angola in S DRC
Buff-throated apalis *Apalis rufogularis angolensis*	100	–	E	Conspecifics	250	C Scarp, but outside Angola in S DRC
Grey apalis *Apalis cinerea grandis*	100	M	–	Conspecifics, but could be brown-headed apalis *A. alticola*	2,000	If former, Cameroon/Albertine Rift, if latter, parapatric
Miombo wren-warbler *Calamonastes undosus huilae*	75	M	–	Conspecifics	0	Parapatric
Barred wren-warbler *Calamonastes fasciolatus pallidior*	100	–	E	Conspecifics	0	Parapatric
Brown illadopsis *Illadopsis fulvescens dilutior*	100	–	E	Conspecifics	320	Congo Basin
Black-faced babbler *Turdoides melanops angolensis*	100	–	E	Conspecifics	0	Parapatric
African thrush *Turdus pelios bocagei*	90	–	E	Conspecifics	0	Parapatric
Forest scrub robin *Cercotrichas leucosticta reichenowi*	100	–	E	Conspecifics	2,000	E DRC
Kalahari scrub robin *Cercotrichas paena benguellensis*	100	–	E	Conspecifics	0	Parapatric
Brown-chested alethe *Chamaetylas poliocephala hallae*	100	–	E	Conspecifics	320	W DRC
White-browed robin-chat *Cossypha heuglini subrufescens*	70	M	E	Conspecifics	0	Parapatric
Bocage's akalat *Sheppardia b. bocagei*	100	M	–	Conspecifics	500	NW Zambia
Mountain wheatear *Myrmecocichla monticola nigricauda*	100	M	–	Conspecifics	200	SW Angola
Familiar chat *Oenanthe familiaris angolensis*	100	–	E	Conspecifics	0	Parapatric
Carmelite sunbird *Chalcomitra f. fuliginosa*	95	–	E	Conspecifics	0	Parapatric
Bronzy sunbird *Nectarinia kilimensis gadowi*	100	M	–	Conspecifics	2,000	NE Zambia/E Zimbabwe/Albertine Rift
Purple-banded sunbird *Cinnyris b. bifasciatus*	75	–	E	Conspecifics	800	NE Namibia
Oustalet's sunbird *Cinnyris o. oustaleti*	100	M	–	Conspecifics	2,000	NE Zambia

Species	**Ass**	**M**	**E**	**Closest relative**	**D**	**Location of relative**
Thick-billed weaver *Amblyospiza albifrons tandae*	90	–	E	Conspecifics	800	W Zambia/Cameroon
Dark-backed weaver *Ploceus bicolor amaurocephalus*	100	–	E	Conspecifics	800	NE Angola
Red-headed malimbe *Malimbus rubricollis praedi*	100	–	E	Conspecifics	320	W DRC
Black bishop *Euplectes gierowii gierowii*	90	–	E	Conspecifics	1,900	Albertine Rift
Yellow bishop *Euplectes capensis angolensis*	70	M	–	Conspecifics	0	Parapatric
Fan-tailed widowbird *Euplectes axillaris quanzae*	100	–	E	Conspecifics	500	E Angola
White-winged widowbird *Euplectes albonotatus asymmetrurus*	80	–	E	Conspecifics	800	W Zambia
Grey-headed nigrita *Nigrita canicapillus angolensis*	100	–	E	Conspecifics	320	Cabinda
Dusky twinspot *Euschistospiza c. cinereovinacea*	100	M	–	Conspecifics	1,900	Albertine Rift
Jameson's firefinch *Lagonosticta rhodopareia ansorgei*	100	–	E	Conspecifics	800	NE Namibia
Common waxbill *Estrilda astrild angolensis*	100	M	–	Conspecifics	0	Parapatric
Nicholson's pipit *Anthus nicholsoni palliditinctus*	100	M	–	Conspecifics	0	Parapatric
Nicholson's pipit *Anthus nicholsoni moco*	100	M	–	Conspecifics	200	SW Angola
Black-faced canary *Crithagra capistrata hildegardae*	100	M	E	Conspecifics	0	Parapatric
Yellow-crowned canary *Serinus flavivertex huillensis*	100	M	–	Conspecifics	2,000	NE Zambia
Cape bunting *Emberiza capensis bradfieldi*	75	–	E	Conspecifics	0	Parapatric
Cape bunting *Emberiza capensis nebularum*	100	–	E	Conspecifics	0	Parapatric
ISOLATED POPULATIONS						
Western crested guineafowl *Guttera v. verreauxi*	100	–	E	Conspecifics	300	C Angola
Hartlaub's duck *Pteronetta hartlaubii*	100	–	E	Conspecifics	320	Cabinda
Freckled nightjar *Caprimulgus tristigma lentiginosus*	75	M	E	Conspecifics	500	W South Africa
Scarce swift *Schoutedenapus m. myoptilus*	100	M	–	Conspecifics	2,000	NE Zambia/E Zimbabwe/ Albertine Rift
Böhm's spinetail *Neafrapus b. boehmi*	100	–	E	Conspecifics	500	NW Zambia
Mottled swift *Tachymarptis a. aequatorialis*	100	M	–	Conspecifics	800	Zimbabwe/E Zambia
Fernando Po swift *Apus [barbatus] sladeniae*	100	M	–	Conspecifics	2,000	Cameroon
Great blue turaco *Corythaeola cristata*	100	–	E	Conspecifics	320	Cabinda
Green turaco *Tauraco persa persa*	100	–	E	Conspecifics	320	Cabinda
Gabon coucal *Centropus anselli*	100	–	E	Conspecifics	320	Cabinda
Blue yellowbill *Ceuthmochares aereus*	100	–	E	Conspecifics	320	Cabinda

Species	**Ass**	**M**	**E**	**Closest relative**	**D**	**Location of relative**
Dusky long-tailed cuckoo *Cercococcyx mechowi*	100	–	E	Conspecifics	320	Cabinda
Olive long-tailed cuckoo *Cercococcyx olivinus*	100	–	E	Conspecifics	320	Cabinda
Double-banded sandgrouse *Pterocles bicinctus ansorgei*	100	–	E	Conspecifics	0	Parapatric
Afep pigeon *Columba unicincta*	100	–	E	Conspecifics	320	Cabinda
African olive pigeon *Columba arquatrix*	100	M	–	Conspecifics	500	NW Zambia
Western bronze-naped pigeon *Columba iriditorques*	100	–	E	Conspecifics	320	Cabinda
Lemon dove *Columba larvata*	100	–	E	Conspecifics	500	NW Zambia
Congo serpent eagle *Circaetus spectabilis*	100	–	E	Conspecifics	320	Cabinda
Crowned eagle *Stephanoaetus coronatus*	100	–	E	Conspecifics	320	Cabinda
Rufous-breasted sparrowhawk *Accipiter r. rufiventris*	100	M	–	Conspecifics	2,000	NE Zambia
Augur buzzard *Buteo augur*	75	M	E	Conspecifics	800	NW Zimbabwe
Bar-tailed trogon *Apaloderma vittatum*	100	M	–	Conspecifics	2,000	NE Zambia/Albertine Rift
Eastern piping hornbill *Bycanistes sharpii*	100	–	E	Conspecifics	320	Cabinda
Black-casqued hornbill *Ceratogymna atrata*	100	–	E	Conspecifics	320	Cabinda
Blue-throated roller *Eurystomus gularis*	100	–	E	Conspecifics	320	Cabinda
Chocolate-backed kingfisher *Halcyon badia*	100	–	E	Conspecifics	320	Cabinda
Blue-breasted kingfisher *Halcyon malimbica*	100	–	E	Conspecifics	320	Cabinda
African dwarf kingfisher *Ispidina lecontei*	100	–	E	Conspecifics	320	Cabinda
White-bellied kingfisher *Corythornis leucogaster*	100	–	E	Conspecifics	320	Cabinda
Black bee-eater *Merops gularis*	100	–	E	Conspecifics	320	Cabinda
Speckled tinkerbird *Pogoniulus scolopaceus*	100	–	E	Conspecifics	320	Cabinda
Red-rumped tinkerbird *Pogoniulus atroflavus*	100	–	E	Conspecifics	320	Cabinda
Yellow-throated tinkerbird *Pogoniulus subsulphureus*	100	–	E	Conspecifics	320	Cabinda
Hairy-breasted barbet *Tricholaema hirsuta angolensis*	75	–	E	Conspecifics	320	Cabinda
Eastern yellow-billed barbet *Trachyphonus purpuratus*	100	–	E	Conspecifics	320	Cabinda
Cassin's honeybird *Prodotiscus insignis*	100	–	E	Conspecifics	320	Cabinda
Willcocks's honeyguide *Indicator willcocksi*	100	–	E	Conspecifics	320	Congo Basin
Least honeyguide *Indicator exilis*	100	–	E	Conspecifics	320	Cabinda
African piculet *Sasia africana*	100	–	E	Conspecifics	320	Cabinda
Buff-spotted woodpecker *Campethera nivosa*	100	–	E	Conspecifics	320	Cabinda

Species	**Ass**	**M**	**E**	**Closest relative**	**D**	**Location of relative**
Brown-eared woodpecker *Campethera caroli*	100	–	E	Conspecifics	320	Cabinda
Yellow-crested woodpecker *Chloropicus xantholophus*	100	–	E	Conspecifics	320	Cabinda
Olive woodpecker *Dendropicos griseocephalus ruwenzori*	100	M	–	Conspecifics	800	NE Angola
Red-fronted parrot *Poicephalus gulielmi*	100	–	E	Conspecifics	320	Cabinda
African pitta *Pitta a. angolensis*	100	–	E	Conspecifics	320	Cabinda
Chestnut wattle-eye *Platysteira castanea*	100	–	E	Conspecifics	320	Cabinda
Black-necked wattle-eye *Platysteira chalybea*	100	–	E	Conspecifics	500	C Gabon
Many-coloured bushshrike *Chlorophoneus multicolor batesi*	100	–	E	Conspecifics	500	Gabon
Bocage's bushshrike *Chlorophoneus bocagei*	100	–	E	Conspecifics	320	W DRC
Gorgeous bushshrike *Telophorus v. viridis*	100	M	E	Conspecifics	800	W Zambia
Petit's cuckooshrike *Campephaga petiti*	100	–	E	Conspecifics	320	Cabinda
Purple-throated cuckooshrike *Campephaga quiscalina*	100	–	E	Conspecifics	320	Cabinda
Mackinnon's shrike *Lanius mackinnoni*	100	–	E	Conspecifics	320	W DRC
Black-winged oriole *Oriolus nigripennis*	100	–	E	Conspecifics	320	W DRC
Blue-headed crested flycatcher *Trochocercus nitens*	100	–	E	Conspecifics	320	Cabinda
Bates's paradise flycatcher *Terpsiphone batesi bannermani*	100	–	E	Conspecifics	320	Congo Basin
African blue flycatcher *Elminia longicauda*	100	–	E	Conspecifics	320	Congo Basin
Ashy tit *Melaniparus cinerascens benguelae*	100	–	E	Conspecifics	0	Parapatric
Yellow-throated nicator *Nicator vireo*	100	–	E	Conspecifics	320	Congo Basin
Slender-billed greenbul *Stelgidillas gracilirostris*	100	–	E	Conspecifics	320	Congo Basin
Plain greenbul *Eurillas curvirostris*	100	–	E	Conspecifics	320	Congo Basin
Yellow-whiskered greenbul *Eurillas latirostris*	100	–	E	Conspecifics	320	Congo Basin
Swamp palm bulbul *Thescelocichla leucopleura*	100	–	E	Conspecifics	320	Congo Basin
Red-tailed bristlebill *Bleda syndactylus*	100	–	E	Conspecifics	320	Congo Basin
Brazza's martin *Phedina brazzae*	90	M	–	Conspecifics	0	Sympatric
White-throated blue swallow *Hirundo nigrita*	100	–	E	Conspecifics	320	Congo Basin
Forest swallow *Petrochelidon fuliginosa*	100	–	E	Conspecifics	800	S Gabon
Yellow longbill *Macrosphenus flavicans*	100	–	E	Conspecifics	320	Congo Basin

Species	**Ass**	**M**	**E**	**Closest relative**	**D**	**Location of relative**
Green hylia *Hylia prasina*	100	–	E	Conspecifics	320	Congo Basin
Tit hylia *Pholidornis rushiae*	100	–	E	Conspecifics	320	Congo Basin
Red-faced cisticola *Cisticola erythrops lepe*	75	M	–	Conspecifics	0	Parapatric
Pale-crowned cisticola *Cisticola c. cinnamomeus*	75	M	–	Conspecifics	1,000	NW Zambia
Wing-snapping cisticola *Cisticola a. ayresii*	100	M	–	Conspecifics	1,000	NW Zambia
Lowland masked apalis *Apalis binotata*	100	–	E	Conspecifics	1,500	NE Gabon
Black-throated apalis *Apalis j. jacksoni*	100	–	E	Conspecifics	1,900	Albertine Rift
Yellow-browed camaroptera *Camaroptera superciliaris*	100	–	E	Conspecifics	320	Congo Basin
Rufous-crowned eremomela *Eremomela badiceps*	100	–	E	Conspecifics	320	Congo Basin
Scaly-breasted illadopsis *Illadopsis albipectus*	100	–	E	Conspecifics	500	C DRC
African hill babbler *Pseudoalcippe abyssinica ansorgei*	100	M	–	Conspecifics	2,000	NE Zambia/Albertine Rift/ Cameroon
Southern hyliota *Hyliota australis slatini*	100	–	E	Conspecifics	0	Central Angola
Forest chestnut-winged starling *Onychognathus fulgidus*	100	–	E	Conspecifics	320	Congo Basin
Narrow-tailed starling *Poeoptera lugubris*	100	–	E	Conspecifics	320	W DRC
White-tailed ant thrush *Neocossyphus poensis*	100	–	E	Conspecifics	320	Congo Basin
Rufous flycatcher thrush *Stizorhina fraseri*	100	–	E	Conspecifics	320	Congo Basin
Orange ground thrush *Geokichla gurneyi otomitra*	100	M	–	Conspecifics	1,800	SE DRC
Fire-crested alethe *Alethe castanea*	100	–	E	Conspecifics	320	Congo Basin
Brown-backed scrub robin *Cercotrichas hartlaubi*	100	–	E	Conspecifics	2,000	E DRC/Cameroon
Grey-throated tit-flycatcher *Myioparus griseigularis*	100	–	E	Conspecifics	320	Congo Basin
Cassin’s flycatcher *Muscicapa cassini*	100	–	E	Conspecifics	320	Congo Basin
Dusky-blue flycatcher *Muscicapa comitata*	100	–	E	Conspecifics	320	Congo Basin
Sooty flycatcher *Muscicapa infuscata*	100	–	E	Conspecifics	320	Congo Basin
Little green sunbird *Anthreptes seimundi*	100	–	E	Conspecifics	320	Congo Basin
Grey-chinned sunbird *Anthreptes tephrolaemus*	100	–	E	Conspecifics	320	Congo Basin
Green-headed sunbird *Cyanomitra verticalis*	100	–	E	Conspecifics	320	Congo Basin
Blue-throated brown sunbird *Cyanomitra cyanolaema*	100	–	E	Conspecifics	320	Congo Basin
Olive sunbird *Cyanomitra olivacea*	100	–	E	Conspecifics	320	Congo Basin
Green-throated sunbird *Chalcomitra rubescens*	100	–	E	Conspecifics	320	Congo Basin

Species	**Ass**	**M**	**E**	**Closest relative**	**D**	**Location of relative**
Olive-bellied sunbird *Cinnyris chloropygius*	100	–	E	Conspecifics	320	Congo Basin
Superb sunbird *Cinnyris superbus*	100	–	E	Conspecifics	320	Congo Basin
Black-chinned weaver *Ploceus nigrimentus*	100	M	–	Conspecifics	800	NE Angola
Black-necked weaver *Ploceus nigricollis*	100	–	E	Conspecifics	320	Congo Basin
Yellow-mantled weaver *Ploceus tricolor*	100	–	E	Conspecifics	320	W DRC
Brown-capped weaver *Ploceus insignis*	100	–	E	Conspecifics	1,900	Albertine Rift
Crested malimbe *Malimbus malimbicus*	100	–	E	Conspecifics	320	W DRC
Woodhouse's antpecker *Parmoptila woodhousei ansorgei*	100	–	E	Conspecifics	320	W DRC
White-breasted nigrita *Nigrita fusconotus*	100	–	E	Conspecifics	320	Cabinda
Chestnut-breasted nigrita *Nigrita bicolor*	100	–	E	Conspecifics	320	Cabinda
Pale-fronted nigrita *Nigrita luteifrons*	100	–	E	Conspecifics	320	Cabinda
White-collared oliveback *Nesocharis ansorgei*	100	–	E	Conspecifics	1000	S DRC/Albertine Rift
Green twinspot *Mandingoa nitidula schlegeli*	100	–	E	Conspecifics	320	W DRC
Red-faced crimsonwing *Cryptospiza reichenovii reichenovii*	100	M	E	Conspecifics	2,000	E Zimbabwe/NE Zambia/Albertine Rift
Red-headed bluebill *Spermophaga r. ruficapilla*	100	–	E	Conspecifics	320	S DRC
Landana firefinch *Lagonosticta landanae*	90	M	E	Conspecifics	0	Parapatric
Black-and-white mannikin *Lonchura bicolor*	100	–	E	Conspecifics	320	Congo Basin
Magpie mannikin *Lonchura fringilloides*	100	–	E	Conspecifics	500	Gabon
Dusky indigobird *Vidua funerea* (Dusky Twinspot parasite)	100	M	–	Conspecifics	0	Parapatric
Mountain wagtail *Motacilla clara*	100	M	E	Conspecifics	800	NE Angola
Striped pipit *Anthus lineiventris*	100	M	–	Conspecifics	800	W Zambia
Bushveld pipit *Anthus caffer*	100	M	–	Conspecifics	800	W Zambia
Thick-billed seedeater *Crithagra burtoni tanganjicae*	100	M	–	Conspecifics	1,900	Albertine Rift

Mammal endemism in the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-palmeirim

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ABSTRACT

The highlands and escarpments of Angola and Namibia (HEAN) consist of a series of high-elevation plateaus, escarpment ridges and inselbergs. They are known for their increased capacity to promote speciation and species persistence, but the importance of this area as an endemism centre for mammals remains poorly documented. Here we describe the endemic and near-endemic mammalian taxa occurring in the HEAN. Based on a literature search, we were able to confirm 12 endemic, 13 possible endemic and 20 near-endemic mammalian taxa, of which 28 are species, 10 are possible undescribed (new) species, and 7 are subspecies. Rodents showed the highest endemism (28 taxa), followed by bats (6 taxa), with only a few other mammalian orders being represented by endemic species here: two carnivores, two bovids, one odd-toed ungulate, two shrews, one sengi, two primates and one hyrax. Most of these endemic mammals have their distribution concentrated in the Angolan section of the HEAN. However, there are considerable knowledge gaps due to the lack of mammal surveys in large parts of the region, in addition to a lack of taxonomic studies utilising modern techniques. As such, new species of bats, rodents and shrews are expected to be documented in the years ahead. Given the alarmingly rapid loss of native habitats in the region, and to avoid losing the unique biological heritage of the HEAN, we recommend the enforcement of regulations protecting native habitat relicts.

Keywords: Afromontane forest, Angola, endemism, escarpments, highlands, mammals, Namibia

INTRODUCTION

African mammals comprise a mega-diverse group, being represented by more than 1,160 species (Kingdon 2019). Some of these species have distributions restricted to a particular zone and are considered endemic if more than 85% of their range is confined to that area (Turpie & Crowe 1994), or near-endemic if marginally present elsewhere, sometimes in the form of distant satellite populations (Matthews *et al*. 1993). Endemics tend to be concentrated in areas associated with increased capacity to promote speciation or species persistence (Dynesius & Jansson 2000). Thus, although mammal diversity typically increases towards the equator, endemism centres are spread throughout the African continent (Turpie & Crowe 1994). The identification of such centres is important to efficiently allocate the usually scarce resources devoted to conservation (Reid 1998).

The most important regions for mammal endemism in Africa are found primarily at low latitudes near major elevational ranges (Herkt *et al*. 2016). Endemism centres, as recognised for mammals, generally include uplands in the western regions of the Upper Guinean forests of West Africa, the Cameroon Volcanic Line, the Lower Guinean forests of Cameroon and Gabon, the Eastern Arc Mountains of Tanzania and Kenya, the Ethiopian Highlands, the Albertine Rift in the eastern Democratic Republic of the Congo (DRC) and western Uganda, Rwanda and Burundi (Turpie & Crowe 1994, Herkt *et al*. 2016). These endemism centres do not necessarily coincide with areas of exceptional species richness (Herkt *et al*. 2016) and might further vary with the mammal group. For instance, primate endemism is mainly associated with tropical forests, whereas endemism in ungulates is linked to savanna-like biomes (Turpie & Crowe 1994). At elevations above 1,800 masl, these endemism centres typically match the Angolan Montane Forest Grasslands Ecoregion. There, habitats are comprised of temperate forests (at lower elevations) and grasslands (at higher elevations) that offer a strikingly different habitat to that of the surrounding areas which may be comprised of lowland forests, miombo woodlands or dry, fine-leafed savanna (Grimshaw 2001). The current distribution of the Afromontane habitats has resulted from past dynamics of connection and isolation between montane centres and Plio-Pleistocene glacial cycles in climate (deMenocal 1995, Maley 1996). Today, Afromontane ecosystems are highly isolated and share affinities with equivalent habitats more than 2,000 km distant across the continent. Altogether these factors have contributed to Afromontane habitats being important centres for speciation with high levels of endemism (Taylor *et al.* 2011, Huntley *et al.* 2019, Komarova *et al.* 2021), influencing the unique species composition that we observe today (Mayr & O'Hara 1986, Lézine *et al.* 2019).

The highlands and escarpments of Angola and Namibia (HEAN) consist of a series of high-elevation plateaus, escarpment ridges and inselbergs (Mendelsohn & Huntley 2023). Although they have been recognised as potentially important centres of endemism (Linder *et al.* 2012, Mills *et al.* 2013, Huntley *et al.* 2019), their significance for mammals remains poorly known (but see Krásová *et al.* 2021). In Angola the highlands correspond to a geologically old region elevated above 1,600 masl and punctuated by mountain peaks towering up to 2,600 masl, corresponding to the Angolan Planalto and the Marginal Mountain Chain (Mendelsohn & Huntley 2023: Figure 3). The most important habitats in this region are characterised by Afromontane elements (Huntley 2023). Below 1,600 masl, the scarp forests consist of impoverished representatives of the Guineo-Congolian forest biome (Huntley *et al.* 2019) and are distributed in larger blocks in the north but become scarcer at more southerly latitudes before disappearing altogether in southern Angola and Namibia. Given the suitable conditions for humans and the predicted consequences of climate change (Lézine *et al.* 2019), parts of the natural habitats within the HEAN are among the most threatened in Africa (Mills *et al.* 2013). Notwithstanding, the conditions of the HEAN have promoted the origin of unique and deeply divergent lineages, for example leading to speciation in the rodent genera *Graphiurus*, *Mastomys*, *Otomys* and *Rhabdomys*, in addition to other local variants of more widely distributed species (Krásová *et al.* 2021).

METHODS

In this chapter we describe the endemic and near-endemic mammalian taxa occurring in the HEAN. To do so, we first compiled a list of species, subspecies and those with seemingly isolated populations in the HEAN, based on both the geographic ranges made available by the IUCN (2019), a recently compiled mammal species list for Angola (Beja *et al.* 2019), the Atlas of Namibia (Atlas of Namibia Team 2022) and two comprehensive guides of African rodent (Monadjem *et al.* 2015) and bat species (Monadjem *et al.* 2020). In this review, we also include recently recorded, yet still undescribed, species as possible endemics. Finally, we conducted additional literature searches for recent surveys targeting the region. We provide a short summary of each endemic and near-endemic taxon identified for the focal region (Table 1), including taxonomy, endemism status and references to any relevant literature on the species ecology and conservation, if available. Given that most mammalian endemism is located in the Angolan section of the HEAN, we further estimated the level of endemism for this section (Beja *et al.* 2019); this is presented in Table 2. Landscape names used in this paper follow those in Mendelsohn and Huntley (2023: Figure 5).

ENDEMISM BY TAXONOMIC GROUP

Carnivora

The subspecies of Ansorge's cusimanse *Crossarchus ansorgei ansorgei* is a near-endemic to the Northern and Central Escarpment landscapes. This subspecies was initially recorded only in a limited area north of the Cuanza River (Crawford-Cabral 1989), but recent observations include the Cumbira and the Botera areas located in the Central Escarpment (Vaz Pinto *et al.* 2020), and also coastal areas in Quiçama National Park (Castells *et al.* 2021). Overall, the species is known to inhabit subtropical and tropical moist lowland forests (Angelici & Do Linh San 2015). Given the relatively few records of this subspecies of Ansorge's cusimanse obtained in bushmeat markets in Angola (Bersacola *et al.* 2014, Castells *et al.* 2021) it is thought to be uncommon, compared to other subspecies and species of cusimanses which appear more often in bushmeat markets in DRC (Colyn *et al.* 1987). It has been proposed to designate this endemic as a flagship species to promote the conservation of the remaining forests where it occurs (Vaz Pinto *et al.* 2020).

The Kaokoveld slender mongoose, *Herpestes flavescens*, is near-endemic to the HEAN, being mostly distributed from the Angolan Central Escarpment south to the Central-Western Plains of Namibia. It is possible that two subspecies exist as suggested by marked variations in the pelage of two subpopulations (Rapson *et al.* 2012): individuals with tan or yellowish pelage seem to be confined to southwestern Angola (assigned to *H. f. flavescens* or *H. flavescens sensu stricto*), while those with very dark pelage and a distinctive rufous tinge occur in the Namibian Kaokoveld, Karstveld and Central-Western Plains (*H. f. nigrata* or *H. nigratus*). Nevertheless, little is known about this species, particularly in Angola, where its distribution has been inferred from habitat-interpreted satellite imagery (Rapson & Rathbun 2015), rather than actual observations.

Cetartiodactyla (Bovidae)
The subspecies of black-faced impala *Aepyceros melampus petersi* is currently distributed in both the Southern Escarpment and Karstveld landscape units (Kingdon 2019), and thus is near-endemic to the HEAN. Notwithstanding, we urge caution in the interpretation of the near-endemic classification given to this subspecies since its historical distribution extended beyond the HEAN, including both arid coastal areas in the west and woodlands in the east (Beja *et al*. 2019). Savannas, shrublands and grasslands, ranging up to 1,700 masl in elevation, constitute the primary habitat of this water-dependent species (IUCN SSC Antelope Specialist Group 2016a).

The subspecies of blue duiker *Philantomba monticola anchietae* is considered endemic to the Angolan escarpment, yet the validity of this taxon remains unclear (Beja *et al*. 2019). This species typically thrives in a wide range of forested and wooded habitats, including primary and secondary forests, gallery forests, dry forest patches, coastal scrub farmland and regenerating forest from sea level up to 3,000 masl (IUCN SSC Antelope Specialist Group 2016b).

Chiroptera
At least three bat species are endemic or near-endemic to the HEAN. The Angolan epauletted fruit bat, *Epomophorus angolensis*, is a near-endemic species that occurs from the southern part of the Northern Escarpment to the northern part of the Southern Escarpment, extending only marginally into Namibia. The distribution of this species further extends on the west side of the Central Escarpment (Monadjem *et al*. 2020). This large bat (~90 g) is closely associated with 20 fig tree species (*Ficus* spp.) (Arumoogum *et al*. 2019). The second species is Anchieta's serotine, *Neoromicia anchietae*, which until recently was thought to have a wide distribution in southern Africa, extending from Angola eastward to Mozambique and south to South Africa and Eswatini (Monadjem *et al*. 2020). However, a recent study demonstrated that the Angolan population is genetically and morphologically distinct from the eastern population (Taylor *et al*. 2022), rendering *N. anchietae* an endemic (or possibly near-endemic) to the Central Escarpment. The exact eastern boundary of this species' distribution has not yet been established and it may extend marginally into western Zambia. The Damara horseshoe bat, *Rhinolophus damarensis*, has the bulk of its distribution in the Namibian highlands, also marginally extending northwards to Angola and southwards to South Africa (Northern Cape and North West provinces). This species resulted from a recent split of the *R. darlingi* clade into two taxa; the western populations that occur in arid habitats have been recognised as *R. damarensis*, while the populations occurring in central and eastern southern Africa were maintained as *R. darlingi* (Jacobs *et al*. 2013). Arid and warm habitats of the Damara horseshoe bat include savannas, Succulent Karoo, Nama Karoo, shrublands and deserts (Monadjem *et al*. 2017).

It is possible that there are more endemic bat taxa in the HEAN, which may be revealed by further surveys and integrative taxonomic studies, as observed in other taxonomic groups (Mills *et al*. 2013). This is clearly underlined by the results of recent surveys of both the Serra da Namba in the Marginal Mountain Chain and the nearby Cumbira Forest on the Central Escarpment (May–June 2022), which in fewer than 10 netting nights recorded several undescribed taxa, at least some of which seem new to science. These include two *Rhinolophus* spp. which differ greatly from other congeners in the peak frequency of their echolocation calls. In addition, a morphologically distinct and probably undescribed species of *Miniopterus* was also captured. This *Miniopterus* sp. is likely to be relatively common, as five individuals were captured in the same net in a single hour. Another example of potentially undescribed species involves individuals classified as the horseshoe bat *Rhinolophus eloquens* collected from Jau, Huíla Province, a location that is over 2,000 km away from the closest records in eastern DRC and in Rwanda. Since several new species have been described from the *R. eloquens/R. hildebrandtii* species complex in southern Africa (Taylor *et al*. 2018), the Jau specimens may also represent new species and it is therefore worth re-examining the original specimens, which are deposited in the American Museum of Natural History.

Eulipotyphla
The taxonomy of African shrews is particularly problematic, possibly due to the high levels of morphological conservatism in this group. In addition, shrews typically avoid the most commonly used live traps and are thus difficult to survey without directed surveys, using for instance pitfall traps. Two *Crocidura* species are endemic to the HEAN, showing restricted distributions. The heather shrew, *Crocidura erica,* is a poorly known species found in western Angola, intersecting four landscape units in the HEAN: the Northern Escarpment, the Central Escarpment, the Angolan Planalto and the Marginal Mountain Chain (Gerrie & Kennerley 2016). Records of this species were collected in the provinces of Cuanza-Norte, Malanje, Huambo, Benguela and Huíla (Beja *et al*. 2019). The black white-toothed shrew, *Crocidura nigricans,* occurs in southwestern Angola, extending over the Central Escarpment, Angolan Planalto, the Marginal Mountain Chain and the north part of the Southern Escarpment (Hutterer 2016, Beja *et al*. 2019). Neither of these *Crocidura* species has been recently captured or been subject to genetic studies so their systematic affinities are unclear.

Hyracoidea

The endemic subspecies of bush hyrax, *Heterohyrax brucei bocagei,* constitutes a large, disjoint population in west-central Angola, far removed from other subspecies (Butynski *et al.* 2015). This subspecies occurs across the entire Angolan highlands and escarpments, except Cabinda. Bush hyrax is typically found in small hills or outcrops, on sheer cliffs or precipices and in piles of large boulders. It is predominantly a browser, feeding on leaves, fruits, stems and bark (Butynski *et al.* 2015). This is also a conspicuous species, with its presence being easily noticed from the communal latrines that can be centuries old, and by its mainly nocturnal loud vocalisations (Kingdon 2019).

Macroscelidea

The endemic Namib round-eared sengi, *Macroscelides flavicaudatus,* occurs in arid areas in the highlands and escarpments of Namibia. This encompasses both the Namib Desert and the Pro-Namib. This species occurs at very low densities on gravel plains characterised by sparse vegetation and lichens which are sustained by coastal fogs; scattered bunch grasses and low bushes are also characteristic (Rathbun & Eiseb 2015).

Perissodactyla

The near-endemic Hartmann's mountain zebra, *Equus zebra hartmannae*, mostly occupies the highlands and escarpments of western Namibia, but small populations can still be found in both Angola (Iona National Park) and South Africa (Richtersveld part of the |Ai-|Ais–Richtersveld Transfrontier Park). For this subspecies too, the near-endemic classification should be interpreted with caution given that its historical distribution extended beyond the HEAN. This subspecies is water-dependent and its current distribution has been further modified from its historical range due to the establishment of artificial water sources which allow it to occupy previously unsuitable habitats. This subspecies of odd-toed ungulate has also been introduced outside of its natural range in the Western Cape, Eastern Cape, North West and Free State provinces in South Africa. Overall, mountain zebras inhabit rocky, broken mountainous and escarpment areas up to around 2,000 masl characterised by a high diversity of grass species and permanent water sources (Gosling *et al.* 2019).

Primates

The nominate subspecies of Pluto monkey, *Cercopithecus mitis mitis,* is near-endemic to the Angolan highlands and escarpments, ranging widely along the Northern Escarpment, Central Escarpment, Angolan Planalto, Marginal Mountain Chain (Machado & Crawford-Cabral 1999; Lawes *et al.* 2013) and reaching the Southern Escarpment. This subspecies also inhabits moist forests in the river basins draining into the Atlantic Ocean (Machado & Crawford-Crabal 1999, Bersacola *et al.* 2014). In terms of elevations, *C. m. mitis* is found from sea level (Barra do Cuanza) to 2,000 masl at Serra da Namba (AF Palmeirim, pers. obs.). In 2013, this was the second-most abundant species recorded in Angolan bushmeat markets (Bersacola *et al.* 2014).

The Angolan dwarf galago, *Galagoides kumbirensis*, is considered here as a HEAN endemic, known only from moist forests present along the Northern and Central escarpments (Bersacola *et al.* 2015). Although this species was discovered in Cumbira Forest (Svensson *et al.* 2017), it appears to be adapted to a wider range of habitats (Bersacola *et al.* 2015) and has subsequently been found further north. However, its geographical distribution has not yet been fully established, and it has been suggested that it might reach the Congo River in DRC (Bersacola *et al.* 2015, Svensson *et al.* 2017). The Angolan dwarf galago is mostly found in forested habitats (moist, tall primary and secondary forests), but also extends into semi-arid baobab savanna woodlands, in areas where tree-lined watercourses allow access and the elevation ranges between 285 and 910 masl (Bersacola *et al.* 2015, Svensson *et al.* 2017, 2020). Some critical habitats used by this species are under intense pressure from commercial logging and deforestation for farming and charcoal production (Hansen *et al.* 2013, Bersacola *et al.* 2015).

Rodentia

The Rodentia is the mammal order with the highest number of endemic and near-endemic taxa in the HEAN. We treat each family separately, below.

Bathyergidae

Bocage's mole rat, *Fukomys bocagei*, was recently split into *F. bocagei* and *F. vandewoetijneae*, making the former a near-endemic to three landscape units in the HEAN – Central Escarpment, Angolan Planalto and Marginal Mountain Chain – from where its distribution extends towards the eastern parts of Angola (Monadjem *et al.* 2015). This small-bodied fossorial rodent can be found in savanna, shrubland and grassland habitats (Monadjem *et al.* 2015).

Gliridae

The stone dormouse, *Graphiurus rupicola,* is the only near-endemic dormouse species described so far. This species occurs between the Marginal Mountain Chain in Angola and the Pro-Namib in Namibia and it is found either arboreal or associated with rocky outcrops and boulders (Monadjem *et al.* 2015). At least three deeply divergent (and unique) clades of *Graphiurus* were recently collected in the Central Escarpment, all of which are undescribed, and all of which may be endemic (Krásová *et al.* 2021).

Table 1: *Species and subspecies classified as endemic or near-endemic to the highlands and escarpments of Angola and Namibia, listed in systematic order. Also included are possibly new species for which genetics and morphometrics have not yet been studied.*

Order and family	**Species or subspecies**	**Endemism status**	**Reference**
Carnivora			
Herpestidae			
	Crossarchus ansorgei ansorgei	Near-endemic	Angelici & Do Linh San (2015)
	Herpestes flavescens	Near-endemic	Rapson & Rathbun (2015)
Cetartiodactyla			
Bovidae			
	Aepyceros melampus petersi	Near-endemic	IUCN SSC Antelope Specialist Group (2016a)
	Philantomba monticola anchietae	Near-endemic	IUCN SSC Antelope Specialist Group (2016b)
Chiroptera			
Pteropodidae			
	Epomophorus angolensis	Near-endemic	Mildenstein (2016)
Vespertilionidae			
	Neoromicia anchietae	Possibly endemic	Monadjem *et al*. (2020), Taylor *et al*. (2022)
Miniopteridae			
	Miniopterus sp.	Possibly endemic[1]	A. Monadjem *et al*. unpubl. data
Rhinolophidae			
	Rhinolophus damarensis	Near-endemic	Monadjem *et al*. (2017)
	Rhinolophus sp. 1	Possibly endemic[1]	A. Monadjem *et al*. unpubl. data
	Rhinolophus sp. 2	Possibly endemic[1]	A. Monadjem *et al*. unpubl. data
Eulipotyphla			
Soricidae			
	Crocidura erica	Endemic	Gerrie & Kennerley (2016)
	Crocidura nigricans	Endemic	Hutterer (2016)
Hyracoidea			
Procaviidae			
	Heterohyrax brucei bocagei	Endemic	Butynski *et al*. (2015)
Macroscelidea			
Macroscelididae			
	Macroscelides flavicaudatus	Endemic	Rathbun & Eiseb (2015)
Perissodactyla			
Equidae			
	Equus zebra hartmannae	Near-endemic	Gosling *et al*. (2019)
Primates			
Cercopithecidae			
	Cercopithecus mitis mitis	Near-endemic	Lawes *et al*. (2013), Butynski & de Jong (2019)
	Galagoides kumbirensis	Endemic	Svensson *et al*. (2017)
Rodentia			
Bathyergidae			
	Fukomys bocagei	Near-endemic	Krásová *et al*. (2021)
Gliridae			
	Graphiurus rupicola	Near-endemic	Monadjem *et al*. (2015)
	Graphiurus sp. indet. 1	Possibly endemic[1]	Krásová *et al*. (2021)
	Graphiurus sp. indet. 3	Possibly endemic[1]	Krásová *et al*. (2021)
	Graphiurus sp. indet. 4	Possibly endemic[1]	Krásová *et al*. (2021)
Muridae			
	Aethomys bocagei	Near-endemic	Krásová *et al*. (2021)
	Aethomys thomasi	Endemic	Taylor (2016), Monadjem *et al*. (2015)
	Dasymys nudipes	Endemic	Taylor & Kennerley (2017)
	Gerbilliscus angolae	Possibly endemic[1]	Krásová *et al*. (2021)
	Gerbilliscus cf. *humpatensis*	Possibly endemic[1]	Krásová *et al*. (2021)
	Hylomyscus heinrichorum	Endemic	Kennerley & Dando (2019)
	Hylomyscus carillus	Near-endemic	Schlitter & van der Straeten (2016)
	Lophuromys angolensis	Near-endemic	Monadjem *et al*. (2015)
	Mastomys angolensis	Near-endemic	Krásová *et al*. (2021)

***Table 1** (continued)*

Order and family	**Species or subspecies**	**Endemism status**	**Reference**
	Mus callewaerti	Near-endemic	Krásová *et al.* (2021)
	Mus triton B	Near-endemic	Krásová *et al.* (2021)
	Otomys anchietae	Endemic	Monadjem *et al.* (2015)
	Otomys cuanzensis	Endemic	Taylor (2016)
	Praomys coetzeei	Near-endemic	Kennerley *et al.* (2019)
	Rhabdomys sp. 1	Possibly endemic[1]	Krásová *et al.* (2021)
Nesomiydae			
	Petromyscus shortridgei	Near-endemic	Schlitter (2016)
	Petromus typicus	Near-endemic	Cassola (2016a)
	Poemys angolensis	Possibly endemic[1]	Krásová *et al.* (2021)
	Poemys leucostomus	Possibly endemic[2]	Monadjem *et al.* (2015)
	Poemys vernayi	Endemic	Monadjem *et al.* (2015)
	Poemys sp. indet. 13	Possibly endemic[1]	Krásová *et al.* (2021)
Sciuridae			
	Protoxerus stangeri loandae	Endemic	Cassola (2016b)
	Xerus princeps	Near-endemic	Cassola (2016c)

[1] Possible new species. Genetics and morphometrics have not been studied yet.
[2] This species might be conspecific with *P. melanotis*.

Muridae

Murid rodents comprise the family with the highest endemism in the HEAN, with 15 endemic or near-endemic taxa. Thomas's rock rat (*Aethomys thomasi*) is endemic to the highlands and escarpments of Angola, with a distribution restricted to the Central Escarpment, the Angolan Planalto and the Marginal Mountain Chain. This species is associated with rocky outcrops and may have recently been collected from grassland habitats in the Serra da Namba (Palmeirim *et al.* unpubl. data). Bocages's rock rat (*Aethomys bocagei*) is a near-endemic species distributed along the Northern Escarpment, Central Escarpment and the Marginal Mountain Chain, extending to the Upper Cuanza, coastal northwestern Angola, as well as neighbouring DRC (Monadjem *et al.* 2015). This species has been recently recorded in the Cumbira Forest (Krásová *et al.* 2021).

The endemic Angolan marsh rat (*Dasymys nudipes*) is mostly restricted to the Central Escarpment and Angolan Planalto, extending into the Marginal Mountain Chain and the Southern Escarpment landscapes (Monadjem *et al.* 2015). This species has not been studied using genetic methods, so its relationships to other *Dasymys* species is unclear. Animals from this genus are typically found in marshy habitats, including the moss and sedge bogs present at higher elevations. They are good swimmers and often regarded as pests in rice paddies (Kingdon 2019).

The endemic Heinrich's wood mouse (*Hylomyscus heinrichorum*) was very recently described from specimens collected in 1954 at Serra do Môco and Mount Soque in the Marginal Mountain Chain (Carleton *et al.* 2015). This species is genetically and morphologically distinct from other *Hylomyscus* species within the so-called *H. anselli* group (Peterhans *et al.* 2020). The Angolan wood mouse (*H. carillus*) is considered to be near-endemic to the HEAN, ranging from the coastal plain through the south of the Northern Escarpment, Central Escarpment, Angolan Planalto and the Marginal Mountain Chain, and further extending into western Angola (Schlitter & van der Straeten 2016). The taxonomy of this species is currently uncertain as it has never been studied using genetic methods (A Monadjem, pers. comm.). Both *Hylomyscus* species are arboreal and forest-dependent (Kingdon 2019).

The near-endemic Angolan brush-furred rat *(Lophuromys angolensis*) has only recently been described (Verheyen *et al.* 2000). This species occurs in highlands in northern Angola, encompassing the Northern Escarpment, Central Escarpment, Angolan Planalto and part of the Marginal Mountain Chain, in addition to nearby regions in the DRC (Monadjem *et al.* 2015). This terrestrial mouse is characterised by short legs and tail, in addition to prominent toes that allow it to tunnel through the vegetation.

The terrestrial Angolan multimammate mouse (*Mastomys angolensis*), previously reported as *Myomyscus angolensis* (Crawford-Cabral 1989), is endemic to the the highlands and escarpments of Angola (Krásová *et al.* 2021), having the core of its distribution centred in the Central Escarpment, Angolan Planalto and Marginal Mountain Chain (Beja *et al.* 2019). This species occurs in various woodland habitats (above 1,000 masl). Other

Mastomys species have been reported to occur at extremely high abundances and have become crop pests (Monadjem *et al.* 2015).

At least two species of the *Mus* genus are near-endemic to the HEAN: *Mus callewaerti* (Callewaert's mouse) and *Mus triton* (grey-bellied pygmy mouse) clade B. The latter is part of a species complex comprising at least two very distinct cytochrome-b clades (Lamb *et al.* 2014). The *Mus* genus has radiated widely in Africa since its arrival, about 3 mya. Today, about 20 species of *Mus* are endemic to Africa.

Two species of *Otomys* (vlei rat) are endemic to the Angolan section of the HEAN: *Otomys cuanzensis* (Cuanza vlei rat) and *Otomys anchietae* (Angolan vlei rat). The distribution of *Otomys cuanzensis* is limited to the drainage basin of the Cuanza and other rivers in northwestern Angola flowing into the Atlantic Ocean (Northern and Central escarpments), while the comparatively larger *Otomys anchietae* is confined to the highlands of central Angola, specifically to the Angolan Planalto and Marginal Mountain Chain landscape units and is associated with rivers within the Congo and Okavango catchments (Monadjem *et al.* 2015). Vlei rats typically occupy grasslands, marshes and open savannas, including those at higher elevations. It is possible that some *Otomys* species have become relict species given their persisting adaptation to moist and fireless regimes that date from times before humans started making fires and cultivating the land (Kingdon 2019). These species might be particularly affected by environmental disturbances, as observed for a congeneric species that has recently become extinct from a mountain in South Africa due to climate change (Taylor *et al.* 2015).

Coetzee's praomys (*Praomys coetzeei*) is a near-endemic species recently described that is known from just a few specimens collected in the Northern Escarpment and the Central Escarpment (van der Straeten 2008). This species is geographically separated from the rest of the species group, all of which occur outside of Angola (Nicolas *et al.* 2010). Genetic analyses have not been carried out for this species, and hence its affinities with other members of the genus are unclear.

A possibly new endemic species of the four-striped grass mouse *Rhabdomys* sp. has been recently recorded in the Angolan Planalto (*Rhabdomys* sp. 1: Krásová *et al.* 2021). This species is genetically very distinct from the rest of its congeners, including *R. dilectus* from East Africa (Krásová *et al.* 2021).

Two gerbil species are recognised as being endemic to Angola's highlands and escarpments: *Gerbilliscus angolae* and *Gerbilliscus* cf. *humpatensis*, both recorded by Krásová *et al.* (2021) in the Tundavala region, Southern Escarpment. The taxonomic status of these two species has not yet been established through integrative taxonomy, but genetically they are closely related to sister species living in parapatry in the neighbouring regions (Krásová *et al.* 2021). As gerbils, these species are typically associated with savannas and semi-arid to arid habitats (Kingdon 2019).

Nesomyidae

Shortridge's rock mouse (*Petromyscus shortridgei*) is a near-endemic species known from a few scattered localities in the Southern Escarpment and Karstveld (Monadjem *et al.* 2015). This species is found in shrubland and rocky areas, including inland cliffs and mountain peaks, ranging in elevation between 100 and 1,500 masl (Schlitter 2016). The near-endemic dassie rat *Petromus typicus* has a distribution restricted to the Namibian highlands and escarpment, intersecting all the major landscape units located in the country and further, marginally extending south into South Africa (Monadjem *et al.* 2015). In terms of habitat, this species occurs in the escarpment and adjoining mountainous areas, as well as inselbergs on the Pro-Namib plains (Cassola 2016a).

There is also endemism in the *Poemys* (African climbing mouse) genus, including the endemic *P. vernayi*, and potential endemics *P. angolensis* and *P. leucostomus*. The taxonomic status of *P. leucostomus* is unresolved and it may be conspecific with *P. melanotis* (Monadjem *et al.* 2015). Another undescribed species that may be endemic is *Poemys* sp. indet. 13 *sensu* Krásová *et al.* (2021), which has been recently recorded from Tundavala, in the Humpata Plateau (Southern Escarpment). The taxonomy of all *Poemys* species in Angola is in urgent need of revision and as a result it is unclear how these various species are related to each other (and other members of the group elsewhere in Africa) and whether some are conspecific or not.

Sciuridae

The endemic subspecies of the African giant squirrel, *Protoxerus stangeri loandae,* occurs in northwestern Angola, specifically in the south of the Northern Escarpment and north of the Central Escarpment. This subspecies comprises a geographically isolated population (Cassola 2016b). This is the largest squirrel species in Africa and can be found mostly in lowland, swamp and montane moist forests up to 2,000 masl (Happold & Kingdon 2013).

The near-endemic mountain ground squirrel (*Xerus princeps*) is confined to areas where the average annual rainfall varies from below 125 mm to just above 250 mm (Cassola 2016c). This species occurs mostly in mountains and rocky hills with sparse vegetation.

CONCLUSION

Endemism in the highlands and escarpments of Angola is relatively high (15.2%), comparing favourably with that of other endemism centres of African large mammals (Turpie & Crowe 1994). Herkt *et al*. (2016) did not find the HEAN to be an endemism centre for bats; however, this may well change following the discovery of several possible new species of bats in 2022 (as reported above). In comparison to other taxonomic groups, mammal endemism (i.e., including endemic, possible endemic and near-endemic taxa) in the highlands and escarpments of Angola was generally higher than, for example, that observed for birds (5% of endemism considering endemics, near-endemics and species having isolated populations), yet that was observed when considering only the Marginal Mountain Chain in Angola (Mills *et al*. 2013). Endemism was also exceptionally high for rodents, for which endemics, possible endemics and near-endemics account for 33% of all species in the country (22% when excluding new undescribed species; Table 1). Endemism is also high for the orders Hyracoidea (25%) and Eulipotyphla (13%), but these are represented by only one and two endemics, respectively (Table 2).

Overall, we were able to confirm 12 endemics, 13 possible endemics and 20 near-endemic mammalian taxa for the region defined as the HEAN, of which 28 are species, 10 are possible undescribed (new) species and 7 are subspecies. Rodents have the highest endemism (28 taxa), followed by bats (6 taxa), with only a few other mammalian orders having endemic species here: two carnivores, two bovids, two shrews, one sengi, one odd-toed ungulate, two primates and one hyrax. Most endemic mammals of the HEAN have their distribution concentrated in Angola. Indeed, only a few species have distributions which extend into Namibia (e.g., the fruit bat *Epomophorus angolensis* and the rock mouse *Petromyscus shortridgei*), or have distributions centred in Namibia which extend into Angola (e.g., Hartmann's mountain zebra *Equus zebra hartmannae* and the mountain ground squirrel *Xerus princeps*), or into both Angola and South Africa (e.g., the dassie rat *Petromus typicus* and the Damara horseshoe bat *Rhinolophus damarensis*). Moreover, only the Namib round-eared sengi, *Macroscelides flavicaudatus*, is restricted to the Namibian highlands and escarpments, although a handful of species are endemic to the Namib Desert west of the escarpment in both Namibia and Angola. The southern section of the HEAN is the most arid, which limits its suitability for many species that occur in other areas of the highlands and escarpments (Clark *et al*. 2011). This same pattern has also been observed for other taxonomic groups such as birds, reptiles and amphibians (Bauer *et al*. 2023, Becker *et* al. 2023, Mills & Melo 2023).

Despite its significant levels of endemism, there are significant knowledge gaps about the HEAN due to the lack of both mammal surveys in large parts of the region and of taxonomic studies utilising modern techniques. It is therefore not surprising that new species have been recorded in recent surveys, while it is very likely that additional unknown species exist, particularly on isolated mountaintops coated in forest (Taylor *et al*. 2018). Such data deficiency further precludes the estimation of the precise number of endemics, as noted for other taxonomic groups (Baptista *et al*. 2018). This is further aggravated by taxonomic ambiguities observed for many species (Monadjem *et al*. 2015), reinforcing the need for taxonomic and phylogenetic studies using integrative approaches (Krásová *et al*. 2021, Taylor *et al*. 2022).

Lack of knowledge is particularly extreme for rodents, shrews and bats, which include more than three-quarters of all mammal species currently known to science (Monadjem *et al*. 2015, 2020). This can be illustrated by the recent rodent surveys carried out by Krásová *et al*. (2021), which recorded at least five new species that might be endemic to the highlands of Angola, in a total of 12 candidate new species found across Angola. In a recent survey of small mammals in the Serra da Namba, Palmeirim *et al*. (unpubl. data) recorded four endemic species and

Table 2: *Degree of mammal endemism in the highlands and escarpments of Angola. For each order, the percentage of endemism has been calculated from the number of endemic and near-endemic species. Possible new species were also considered as endemic taxa.*

Order	**Number of species**			**Number of taxa**	**Rate of endemism (%)**
	Endemic	**Possible endemic**	**Near-endemic**		
Carnivora	0	0	2	39	5.1
Cetartiodactyla	0	0	2	33	6.1
Chiroptera	0	4	1	73	6.8
Eulipotyphla	2	0	0	15	13.3
Hyracoidea	1	0	0	4	25.0
Primates	1	0	1	24	8.3
Rodentia	7	9	11	82	32.9
Total	**11**	**13**	**17**	**270**	**15.2**

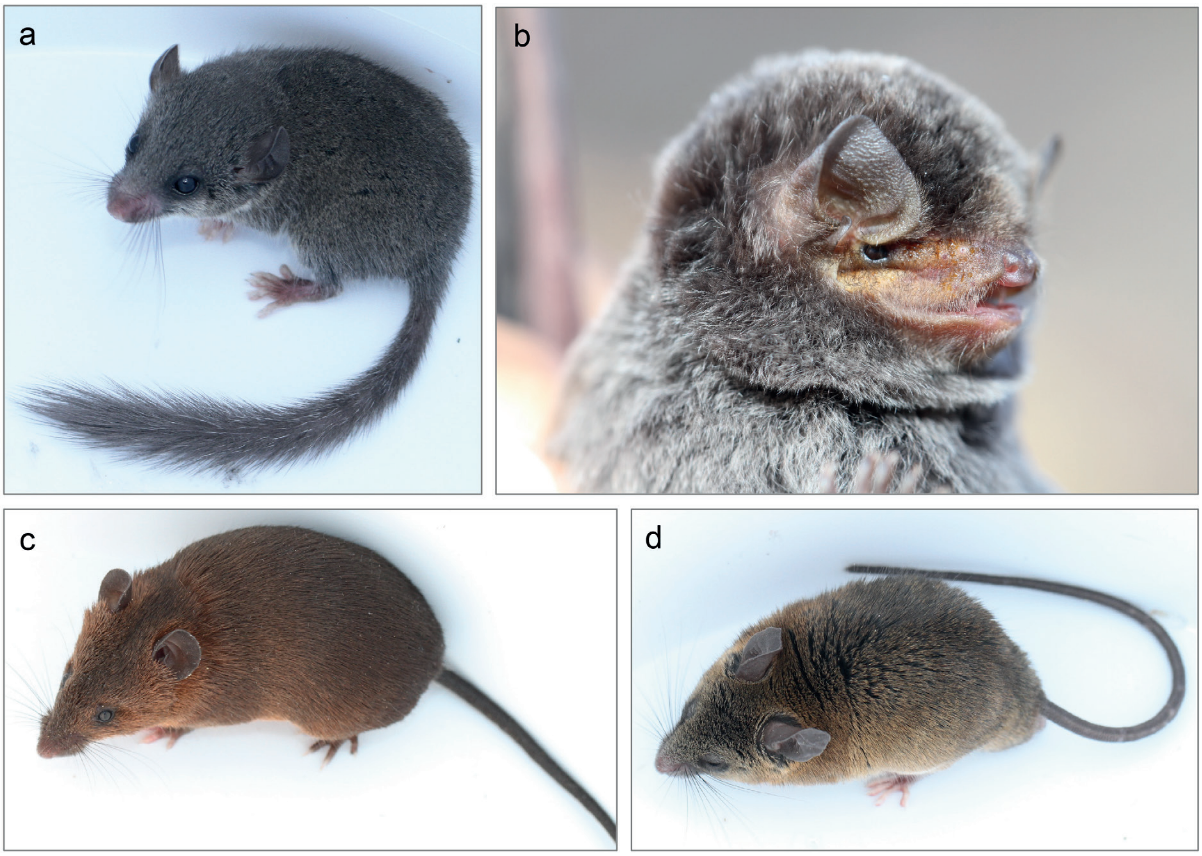

Figure 1: *Examples of endemic and possible endemic species from Angola's highlands recently recorded in the Mt Namba and Cumbira Forest surveys (AF Palmeirim unpubl. data, A Monadjem unpubl. data): a)* Graphiurus *sp., b)* Miniopterus *sp., c)* Lophuromys angolensis *and d)* Hylomyscus heinrichorum. *Photos: A Monadjem.*

perhaps three undescribed species of rodents and shrews, while Monadjem *et al.* (unpubl. data) recorded perhaps three (or more) undescribed bat species (Figure 1). We therefore suspect that future research will uncover new species endemic to the HEAN. Acquiring knowledge of the existing mammal fauna would boost the conservation value of these landscapes and should be at the top of the research agenda.

In terms of conservation status, as all the species-level endemics are either rodents, shrews or bats, it is not unexpected that information on such rare and elusive species, with small distribution ranges, is rarely sufficient to assess their status (IUCN 2019). It is also noteworthy that some rodent and bat species have isolated populations in mountains within the HEAN, which may correspond to new, as yet undescribed species. This reinforces the need to undertake more surveys specifically targeting small mammals (bats, rodents, shrews). In addition, re-examining previously collected material (including the sequencing of old museum specimens as was done by Krásová *et al.* 2021) may help to elucidate the dubious taxonomy of some species (e.g. Monadjem *et al.* 2010).

Despite the extraordinary and unique mammal species diversity inhabiting the HEAN – particularly that found in the Afromontane forests and grasslands of the Marginal Mountain Chain and Angolan Planalto, and the scarp forests of the Central Escarpment in Angola – native habitats are being replaced by slash-and-burn cultivation at unprecedent rates (e.g., Powell *et al.* 2023), as induced by the high growth rate of the human population and the consequent demand for land (see Mendelsohn & Gomes 2023: Figure 6). Additional human activities further degrade the remaining native habitats, including uncontrolled fires, logging and burning for charcoal production, and grazing of livestock. In fact, this scenario echoes that of other regions of high biodiversity and endemism in Africa, which are found to be associated with dense human settlement (Balmford *et al.* 2001). In the case of Angola, the scenario is further aggravated by the absence of well-functioning protected areas encompassing portions of its highlands and escarpments, with the exception of the few mountains inside Iona National Park. To avoid losing the unique biological heritage of the HEAN, as well as its unique ecosystems and associated ecological services, it is therefore imperative to enforce the regulations protecting the last remaining native habitats.

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Caves and their fauna in the highlands and escarpments of Angola and Namibia

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URL: https://www.nje.org.na/index.php/nje/article/view/volume8-dematos

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ABSTRACT

Several landscapes in the highlands and escarpments of Angola and Namibia (HEAN) have karstic regions with caves. Within the Northern Escarpment in Angola there are two main karstic regions. The first one includes the northern caves associated with a tropical climate and mostly concentrated in Ambuíla, Uíge Province. The second region comprises caves near the Atlantic coast, which are linked to underground flows of the Cambongo-Negunza River. An additional cluster of caves is on the Humpata Plateau and its edges within Angola's Marginal Mountain Chain landscape. Most caves in Namibia are in the Karstveld and Khomas Hochland Plateau landscapes in karstic areas of relatively high rainfall. In this paper, we provide a brief overview of the history of cave exploration, sites and fauna documented in them. We report on the fauna recorded during surveys in 2010 and 2018–2021 in the southern karst around Humpata, Huíla Province; and summarise information available on fauna from Namibia. Most species recorded in Angolan caves are trogloxene taxa observed or collected in cave sediments. Namibian caves house a diversity of invertebrates, many of which are endemic or likely to be endemic to Namibia and the HEAN. Two endemic fish in underground lakes in Namibia are critically endangered. This study emphasises the need for further field research and for strategies to conserve caves and their faunas in both countries.

Keywords: Angola, caves, escarpments, fauna, highlands, Namibia

CAVES IN ANGOLA: INTRODUCTION AND HISTORY

Few studies of Angolan caves and karstic systems have been published. Documented cave explorations are rare, and studies of the biodiversity and microenvironments of these sites are even scarcer. Most information comes from geological surveys and quarrying in the early 1900s. Mining exploration and the development of roads motivated more serious scientific inquiry in the decades prior to independence in 1975. Early studies focused on sedimentary questions, but also highlighted particular landscapes or fossil findings (Mouta & Borges 1926, Mouta & O'Donnell 1933). Caves and crevices of the highlands and escarpments received particular attention in the 1950s due to their Quaternary palaeontological fossils. The main cave sites were discovered during mining operations in the 1940s and 1950s, and their fossil contents were analysed subsequently (Arambourg & Mouta 1952, Delson *et al.* 2000, Gilbert *et al.* 2009). More recent palaeontological surveys directed by Martin Pickford and Brigitte Senut between 1989 and 1991 discovered many more sinkholes, tufa and fissures with Plio-Pleistocene to Holocene fossil-bearing sediments (Pickford *et al.* 1992, 1994, David & Pickford 1999). A few direct but brief references about the biospeleology of Angola from the work of António de Barros Machado were reported by Regala (2014); these focus largely on the ecology of Arachnida and Diptera.

The key publications about the geomorphology of the Angolan karst are from Ilídio do Amaral, a prominent Angolan geographer at the University of Lisbon. He described three main areas with caves and karst features: (i) Nova Caimpemba, Ambuíla Uíge Province (do Amaral 1973a); (ii) Cambongo-Negunza, Cuanza-Sul Province (do Amaral 2006); and (iii) Leba, Humpata, Huíla Province (do Amaral 1973b). Other small caves and crevices occur along the coast, for instance near Cabo Ledo, Lobito and Moçâmedes, but these remain mostly unstudied.

The most recent field studies have focused on the karstic features of the Leba dolomites in Humpata and Chibia *municípios* in Huíla Province. This work produced a preliminary map of 45 caves on and around the plateau, photographic records of ethnographical and biospeleological features and identified the first evidence of so-called "pseudo-karst" in the eastern flanks of the Humpata Plateau (Pinto *et al.* 2017).

The northern karst of Angola

Only a few patches of carbonate rocks occur in northern Angola and karstic areas are consequently rare (Figure 1). Precambrian rocks of the Xisto-Calcário/Schisto-Calcaire of Congo (de Carvalho *et al.* 2000) occur in the highlands of Zaire Province. The limestone there is heavily weathered and its residual formations show many of the characteristics of tropical karst.

In Zaire Province, karst features are mostly superficial and found in the upper M'bridge River basin. One cave is located at Nzau Evua hills in the Vamba River valley, about 80 km southwest of M'banza Congo city. It is locally called the *Gruta da Igreja* (Church Cave), as it once served as an improvised chapel. The cave has a cold spring with a wide dry chamber with many speleothem formations. The site has been heavily altered by recent human activities and is frequently visited by tourists. The walls of the cave are painted and local tales assign the authorship of the paintings to people of the Kongo Kingdom, who found refuge from slavery in the cave in the 15th century. Other chambers and shafts remain unexplored.

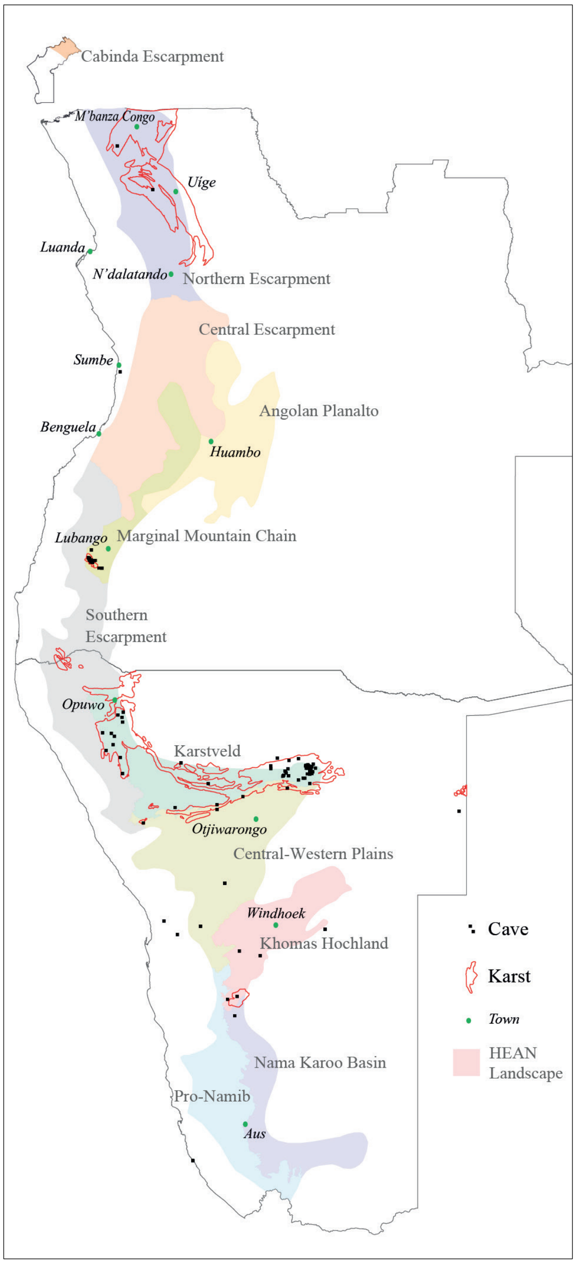

Figure 1: *Areas of karst and locations of caves in Namibia and Angola, the boundaries of the zone of highlands and escarpments of Angola and Namibia (HEAN) and their landscapes (adapted from Mendelsohn & Huntley 2023).*

Further south in Uíge Province, approximately 200 km from the coast, a tropical karst is found in the *município* of Ambuíla in the upper Loge River basin. The area is hilly with elevations between 1,100 and 1,200 masl, in mountains locally known as Serra da Mucaba, Planalto do Cau, Serra da Buela and Serra da Inga. The topography is characterised by long, dissected valleys, alternating with ridges oriented NNW–SSE and a dense dendritic network of the Loge River tributaries (see Lautenschläger *et al.* 2023).

The regional geology of the Northern Escarpment is dominated by the Upper Precambrian rocks of the Shale-Limestone Series of Sansícua and Alto Chiloango (Mouta 1954). Karstic features occur in a bedrock of dark dolomites and dolostones with cherts, oolites and stromatolites. The tropical conditions have contributed to an accelerated corrosion of the dolomites along the major fracture zones. The intense karstification in the region is expressed in a variety of depressions, dolines, uvalas and poljes, as well as many residual forms. Isolated columns and septum windows remain in the valleys as relicts of collapsed caves.

Some karst forms are overshadowed by the dense gallery forest covering the mountains, contrasting with the savanna-like vegetation of the plains. At the foothills of these poljes there are solution chambers and labyrinths. Nzenzo Cave is located in the southern flank of the Buela hills, where a limestone tower with a chamber about 10 m wide partially collapsed when the slope retreated. A waterfall drops into the cave forming a spring and a thick stalagmitic base. Most caves at Ambuíla remain unmapped but local people mentioned Kinivavua, Kulo and Nsala caves as meeting points during the first liberation movements in the 1960s.

Near Sumbe, along the coast of Cuanza-Sul Province, there is an active karstic system associated with the underground drainage of the Cambongo-Negunza river system. There, the Negunza River has carved a subterranean canyon for about 600 m with an E–W orientation, abruptly changing its direction to S–N, controlled by a fault and forming a waterfall into a circular depression, like a funnel. The waterfall has a drop of about 135 m and leads into a wide channel. The site of Furnas, also known as Sassa Caves, is a collapsed doline with two levels. In the top level, a large chamber and adjacent solution chambers are frequently visited by tourists for their scenic views of the waterfall dropping into the interior canyon, and its speleothems which include drapes, stalactites and stalagmites. Below, the channel may only be accessed during dry seasons when the phreatic level drops.

The southern karst of Leba, Humpata

The karst features in the Southern Escarpment are mostly concentrated in Huíla Province between the municipalities of Humpata and Chibia, around 30 km west of Lubango. Caves are found on the Humpata Plateau where a combination of lithology, tectonics and climate conditions allowed the development of karst features in dolomites, as well as of a pseudo-karst in quartzite-sandstone bedrocks of the Chela Group.

The Humpata Plateau is a pediplain of polygonal shape located in a sector of the Marginal Mountain Chain (Mendelsohn & Huntley 2023) that is structurally organised by systems of crossed fractures, faults and fissures (Lopes *et al.* 2016). Severe erosion shaped the hydrographic basin and formed deep valleys and canyons. At the edges, abrupt scarps and ravines over 1,200 m high (such as Fenda do Bimbe and Fenda da Tundavala) become waterfalls during torrential storms. Impressive crests of bare rock face both east and west.

In the eastern flank of the plateau, facing Lubango city, there are small fissures (fendas) in the quartzitic crests, for instance Fenda da Mapunda. At the top of the crest, many pseudo-karst forms are present at the surface. Small circular depressions, narrow chimneys and fissures give access to underground galleries. These formations are associated with the spring of Senhora do Monte which supplies water to part of the city of Lubango. Galleries with vertical development have maximum drops of 60 m. Bat populations of the genus *Rhinolophus* occupy the fissures. Other solution chambers should be present at the phreatic level.

The southwestern flank of the Humpata Plateau where the dolomites crop out is crossed by numerous fractures and faults. There are many karstic forms with subterranean development in the extensive fault of Bentiaba–Leba–Caholo–Cangalongue orientated NW–SE, which splits the plateau almost in half between Leba and Cangalongue villages. Another less extensive fault follows a NNW–SSE axis from Molo–Muange–Nuinge–Numbalo, and is partially filled by norite sills of post-Permian Age intrusive into the Chela sequence. These two main faults are structurally connected by other smaller EEN–WSW fractures and fissures at different locations, such as Leba, Bruco, Tchivinguiro, Bata-Bata and Cangalongue (Lopes *et al.* 2016).

In locations such as Leba, Bruco and M'basso, a dendritic drainage facing east follows the fractures of the Chela quartzites at the contact with the dolomites. Waterfalls can be found at the western edge of the Humpata Plateau; some are only active during wet periods, when ground saturation allows the reactivation of *mulolas* (ephemeral rivers) and interior lakes such as Nuantchite and Catende located about 20 km south of Humpata town.

Most of the known caves at Humpata are located close to the foot of the valley walls, usually 6–15 m above the talwegs. The hills usually have labyrinths of chimneys and tubules connecting the main chambers and adjacent solution chambers. Breccias and tufa deposits infill these fissures. Most of the cave entrances were exposed during the Quaternary by erosional retreat of the slopes, for instance at Leba or Malola. Others, for instance the solution chambers of Tchaticuca or Cangalongue, were connected to the surface through chimneys and were exposed only after horizontal entrances were created by quarrying. Columns and pinnacles are evident from a distance but are covered by dense shrubs.

In the upper stream of the Cudeje River (Bruco) in the Malola-Ufefua area, the dolomite hills are mostly residual and have been heavily explored for hydraulic lime until the present day. Nonetheless, important development of endokarst has been observed here. For instance, Malola II Cave is in a blind valley and has a cave mouth about 4 m wide. A vertical entrance with a talus cone of guano and silts leads to a large chamber in which the floor is covered by boulders of roof spall and guano. A few stalagmites are visible and boulders possibly cover more. The walls have travertines and speleothem drapes but the environment is dry and dusty. The chamber connects with a labyrinth of other galleries upward where eccentric flowstones and dripstones cover the walls.

Many of the solution chambers and fractures are infilled with Plio-Pleistocene breccias or younger unconsolidated deposits that yield the remains of species that lived in or near the karst habitats during prehistoric times (Pickford *et al.* 1994, Gautier 1995, Gilbert *et al.* 2009, Sen & Pickford 2022).

In the area of Tchivinguiro, several springs are tourist hotspots and support freshwater hypogean fauna. An active endorkarst developed underground is controlled by a structural faulting system with a main fault and a series of radial fractures. This geomorphology shaped the weathering of the Tchivinguiro Depression and the development of an underground network of chambers.

Tchivinguiro Cave is located at the foothills of Nandimba, a dolomite cupula with a spring fed by an underground lake. The hill has a low gradient, and

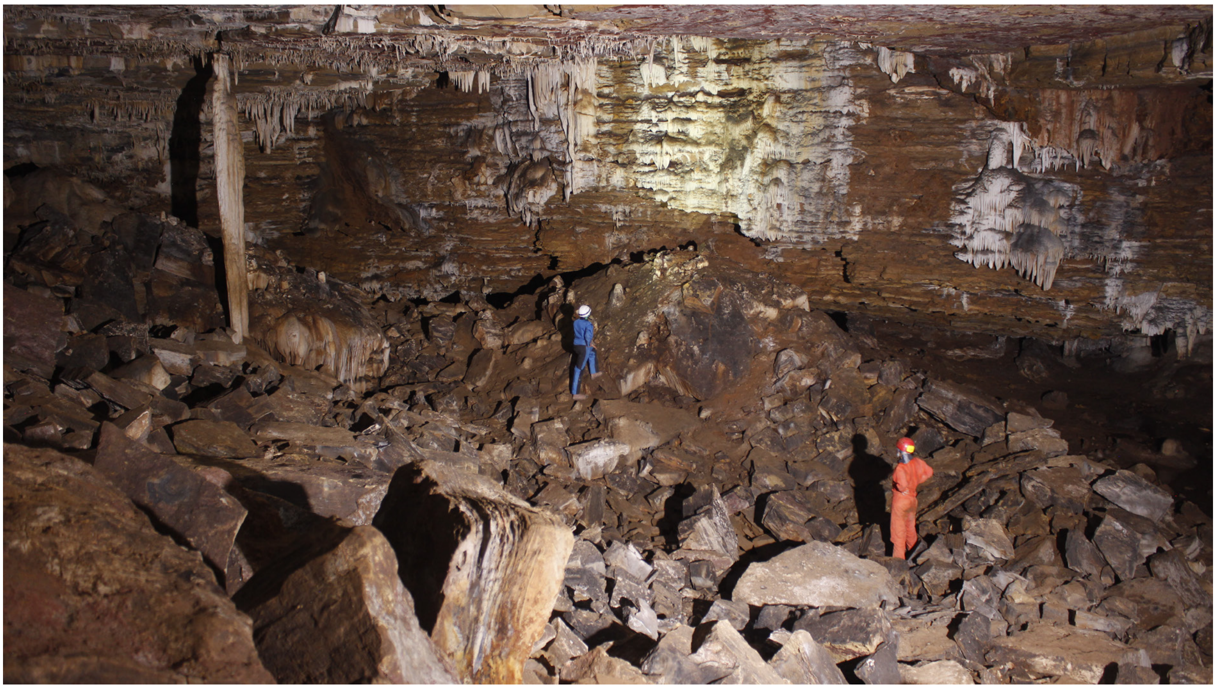

Figure 2: *The main chamber of Tchivinguiro Cave, with a column on the left. Photo: Rui Francisco, 2019.*

many chimneys and narrow sinkholes give access to the subterranean chambers. These chimneys are frequently obscured by thick thorn bushes and the channels are choked by pink–red muds and bedrock debris. Inside the cave, the environment is warm with temperatures ranging 25–28ºC, with relative humidity over 90%. The chambers are covered with the boulders of roof spall. Many stalagmites cover the upper surface of these blocks. A few speleothem columns are also present, some exceeding 4 m in height (Figure 2). The underground network surveyed at Tchivinguiro extends for about 1 km but it is likely to be longer, with a few shafts connecting to the outside. The freshwater reservoir emerges at Nandimba spring along the western foothills of the escarpment where it is used to irrigate crops. Crabs and catfish are commonly observed inside the cave pools but the aquatic fauna of Tchivinguiro cannot be regarded as stygobiotic because the pools are connected to surface pools. Areas of suction were detected and indicate pipes and chimneys to other lower bodies of water which suggest that different microenvironments and biota may be present at deeper levels.

Fauna in Angolan caves

The list of subterranean fauna presented here includes species documented during speleological surveys in 2010, and between 2018 and 2021, of the Leba caves in Humpata. The list is based on observations and skeletons collected in archaeological excavations of recent natural accumulations. Most of the species identified are trogloxene taxa. The list is notably poor in invertebrate taxa and reptiles. This should not be perceived as proof of absence but rather as an opportunity for more intensive biospeleological studies. A selection of animals found in caves is shown in Figure 3.

CRUSTACEA: Brachyuran, pigmented aquatic crab, lives in the pools of the cold spring Nandimba-Tchivinguiro.

INSECTA: Scarabaeoidea, Scarabaeinae, can be found close to the entrance of the fissures of Senhora do Monte, Malola and Cangalongue caves where there are bat roosts. *Heliocopris* sp. dung beetles have been observed in the floors of caves recently used by cattle. Orthoptera, Gryllidae, have been observed in all of the caves surveyed. They are macrophthalmic, pigmented, apterous crickets. At Leba and Cangalongue they frequent the humid shade in crevices adjacent to the main cave channels. They are typically found between large boulders coated with guano.

ARACHNIDA: Amblypygid *Damon variegatus* (whip spider) is found in dry and humid caves, and in the shade of smaller crevices. It has been observed in most of the caves of the southwestern system. Chernetidae: Chernetid pseudoscorpions have been observed in most of the Humpata caves.

GASTROPODA: *Achatina tincta*, a land gastropod, has been observed at Leba and Malola.

MYRIAPODA: Diplopoda, *Archispirostreptus gigas*, the giant African millipede, has been observed in fissures and subsurface features at Senhora do Monte, Leba and Tchivinguiro where they were probably trapped.

AVES: The remains of small owls from the genera *Glaucidium* (pygmy owls) and/or *Otus* (scops owls) spp., as well Columbiformes, Passeriformes and Piciformes have been found in caves; probably from human or carnivore prey.

REPTILIA: Testudines, Pelomedusidae: *Pelusios* spp. (turtles) have been observed in caves near water bodies or associated springs. Colubridae: *Boaedon angolensis,* the Angolan house snake, has been observed inside and in the vicinity of the caves. Agamidae: *Agama planiceps* is found in rocky areas and cliffs in the vicinity of caves. Scincidae:

Figure 3: *A selection of animals found in caves in Namibia and Angola. a) Nycteribiidae sp., bat fly found near horseshoe bat roosting deep in the caves of Senhora do Monte (photo: Renato Serôdio, 2010); b)* Amietia angolensis *observed at Algar do Tchivinguiro (photo: Renato Serôdio, 2010); c) Chernetid pseudoscorpions found at the Humpata caves (photo: Renato Serôdio, 2010); d) Groups of horseshoe bats roosting in the pseudo-karst fissures Senhora do Monte (photo: Renato Serôdio, 2010); e) Giant African millipede, Cangalongue Cave (photo: Rui Francisco, 2010); f) Amblypigi at Sumidouro Candimba Cocufima, Tchivinguiro (photo: Rui Francisco, 2010); g) Cricket (Grillidae) at Sumidouro Nandimba Cocufima (photo: Rui Francisco, 2010); h)* Clarias cavernicola *cave catfish in Aigamas cave, Namibia (photo: Francois Jacobs).*

Trachylepis sulcata ansorgii, the Ansorge's rock skink, has been seen in the fissures adjacent to most caves in the southwest.

PISCES: Ictaluridae: pigmented catfish have been observed in the Nandimba-Tchivinguiro cold spring.

AMPHIBIA: Cacosterninae, *Amietia angolensis*, the Angolan river frog, was found in springs and ponds associated with the Tchivinguiro cave system, and in crevices near rivers, ponds and lakes around Humpata, and the cold springs of Umbutu and Mewó (de Matos 2021, Robakiewicz *et al.* 2021).

MAMMALIA: Chiroptera, *Rhinolophidae* spp., horseshoe bats roost in several caves at Humpata and are the most common mammals seen inside the Humpata caves, with populations in the caves of the dolomite karst at Leba, Malola and Cangalongue, and in the fissures of the pseudo-karst of Senhora do Monte. Hystricidae: Porcupines *Hystrix africaeaustralis* are trogloxene animals; they are often found sheltering deep into many caves. Abundant Muridae (e.g., mice and rats) and Macroscelidae (e.g., elephant shrews) remains were found in prehistoric and modern sediments in caves of the Humpata Plateau (Pickford *et al.* 1992, de Matos 2022). Skeletal material originates from both the natural deaths of animals burrowing inside the cave and from skeletal fragments in regurgitated pellets produced by barn owls *Tyto alba*. Hyracoidea (the rock hyrax *Procavia capensis* and the bush hyrax *Heterohyrax brucei)* have been sighted at Leba. Remains and ichnofossils of lion (*Panthera leo*) and leopard (*P. pardus*) were collected deep inside caves before the 1950s. Spotted hyaena *Crocuta crocuta* ichnofossils have been found in cave sediments at Leba and Cangalongue. Papionini fossils were found at Leba, Malola and Cangalongue. Small groups of *Papio* spp. (baboons) can be found in the vicinity of the main caves, particularly along the western cliffs between Bimbe and Leba. They also inhabit the humid forest surrounding the spring of Senhora do Monte.

CAVES IN NAMIBIA: INTRODUCTION AND HISTORY

The first geological and hydrological survey of karst in Namibia was by Jaeger (1921), while the earliest scientific explorations and surveys of Namibian caves were by Jordan (1936), Strinati (1977) and Churchill *et al.* (1997). The South African Speleological Association undertook several expeditions to Namibia between 1968 and 1988. John Irish and colleagues established the Suid Wes Afrika Karst Navorsing Organisasie (SWAKNO) in Namibia in 1988 with the aim to promote biospeleological research. They surveyed many caves and collected biological specimens, as well as collating information on karst features and cave fauna (Irish *et al.* 2001). Pickford and Senut (2010) provide a substantial review on the geology of karst and its palaeobiology in Namibia.

Most karst in Namibia is in areas of relatively high rainfall, and the majority of underground solution features is in the form of sinkholes (Irish *et al.* 2001). Much of eastern Namibia (and Angola) is covered by young aeolian and alluvial sediments which conceal older karst features. The majority of the 76 surveyed caves (Irish *et al.* 2001) are therefore in central and northwestern Namibia (Figure 1). These 76 caves exclude small or short caves (less than 10 m in depth).

The longest caves are Arnhem (4,494 m in length) approximately 110 km ESE of Windhoek, and Pofaddergrot (2,812 m) and Ghaub (2,700 m) in the Otavi–Grootfontein–Tsumeb hills of dolomites and limestones. In the same area, Lakes Otjikoto and Guinas are open cenotes, the latter reaching a depth of 132 m. Several other large underground lakes have been found and reached through small openings on the surface, notably Aikab, Harasib, Gamkarab and Dragon's Breath. Dragon's Breath Cave contains the largest underground lake on Earth, with a surface area of about 2 ha.

Fauna in Namibian caves

The list of subterranean fauna presented here is based on the literature about Namibian biospeleology and information kindly provided by John Irish (in litt.).

CRUSTACEA: Terrestrial Isopoda, anophthalmic and pigmented, are found on the beach in the Dragon's Breath Cave and are likely to occur in areas with higher moisture in the Otavi Mountains, such as Pofadder, Ghaub, Aigamas and Johann's caves (Irish *et al.* 2001). Ostracoda, Candonidae: *Namibcypris costata,* an endemic ostracod crustacean can be found at the springs of Sesfontein. Protojaniroidea: four endemic species of depigmented crustacean isopode, stygobitic species: *Namibianira aigamensis* in Aigamas Cave; *N. aikabensis* in Aikab Cave; *N. arnhemensis* in Arnhem Cave; and *N. dracohalitus* in Dragon's Breath Cave. Amphipoda include six species of Ingolfiellidae: *Trogloleleupia dracospiritus* in Dragon's Breath Cave; *T. gobabis* in Arnhem Cave; *T. eggerti* in a borehole near Tsumeb; *T. nudicarpus* in Wondergat Cave; *T. opisthodorus* in Dragon's Breath Cave; and *Stygobarnardia caprellinoides* in groundwater in the Tsumeb area. Sternophysingidae: *Sternophysinx hibernic* was reported at Naos Cave.

ARACHNIDA: Cyatholipidae: *Cyatholipus* spp. has been recorded in Johann's Caves in the Otavi mountains. Hahniidae: *Hahnia* sp. at Scorpion's Maze. Loxoscelidae: four species of *Loxosceles* have been reported where there is low humidity. These are depigmented and troglophile species which build ground webs to entangle guanobian prey (Irish *et al.* 2001). *Loxosceles bergeri* and *L. pilosa* are reported from Arnhem Cave; *L. simillima* Lawrence, reported at Ludwig's and Kimberlite caves; and *L. vonwredei* Newlands, reported at Uhlenhorst, Otavi and Märchen Cave. Many diverse groups of Pseudoscorpiones (Cheiridiidae, Cheliferidae, Withiidae); Araneae (Cyatholipidae, Hahniidae, Loxoscelidae, Palpimanidae, Pholcidae, Prodidomidae, Segestriidae, Selenopidae, Sicariidae, Theridiidae); Opiliones (Assamidae); Amblypygi; Scorpiones (Bothriuridae); and Acari (Argasidae) have been reported at Aigamas, Nosib, Dragon's Breath, Pofadder, Obab, Ghaub, Arnhem, De Valle and Nooitgedacht caves by Irish *et al.* (2001).

MYRIAPODA: Diplopod, *Juliformia*, and other millipedes, are found mostly trapped in vertical entrances.

INSECTA: Nicoletiidae, *Lepidospora* sp., in Dragon's Breath Cave and Pofaddergat. *Katacamilla cavernicola*, at Nosib, Arnhem and De Valle caves.

ORTHOPTERA: Gryllidae are reported from caves where there are bat roosts. These macrophthalmic, pigmented, apterous crickets are typically found between large boulders coated with guano.

PISCES: The fish *Tilapia guinasana* which is endemic to Lake Guinas, and the cave catfish *Clarias cavernicola* (Figure 3h; Jacobs *et al.* 2019, 2021) which is restricted to Aigamas Cave, are both listed by IUCN as Critically Endangered (Bills 2007a, 2007b).

MAMMALIA: Soricidae: *Crocidura cyanea*, permanent troglobitic populations reported at Arhem Cave and Nooitgedacht Cave (Irish *et al.* 2001). These shrews inhabit dark zones and reportedly feed on bat carcasses and invertebrates (Irish *et al.* 2001). Chiroptera: Insectivorous bats have been recorded in Namibian caves, including *Hipposideros commersoni* at Arnhem, Aigamas and Aikab caves; *Sauromys petrophilus* at De Valle Cave; *Tadarida aegyptica* in Arnhem, De Valle and Nooitgedacht caves; and *Nycteris thebaica* in Arnhem, Gcwihaba and Nooitgedacht caves. Five species of horseshoe bats are known to roost in Namibian caves: *Rhinolophus denti* in Arnhem, Naos, Nooitgedacht and Tsumeb caves; *R. darlingi* in Arnhem and Dante caves; *R. capensis* in Arnhem Cave; *R. clivosus* in Arnhem and Nooitgedacht caves; and *R. fumigatus* in Nooitgedacht and Otgrot caves. In addition, *Miniopterus inflatus* and *M. schreibersi* roost in Arnhem, De Valle, Gifgat and Nooitgedacht caves. Medium-sized mammals such as porcupines and rock hyraxes have been found in crevices and deep caves. Leopards can be found sheltering in deep caves.

CONCLUSIONS

The diversity of cave-dwelling animals is relatively understudied in Angola and Namibia. The karst of the Northern Escarpment in Angola, in particular, has very few records as most surveys have been informal and not specialised in this field. Large areas of the northern and coastal karsts of Angola are unexplored, and it is likely that many more endemic species will be found. Understanding the processes that guide the distribution of caves and their fauna requires a complex and multidisciplinary approach with fieldwork and the involvement of local populations and stakeholders in risk assessments and conservation.

A more comprehensive spatial assessment within one or more caves in a regional context can unveil subtle variations between biotic and abiotic parameters. The remarkable connection observed between faunal groups and distinct microhabitats, as opposed to the broader range of substrate diversity, highlights the profound reliance of cave-dwelling communities on external resources. In most cases, bat guano is the main source of nutrients for cave fauna, the great majority of which are invertebrates and likely to be endemic to specific caves or karstic areas. Relative humidity is the key factor influencing the development of the underground environment, and moisture availability is therefore directly correlated to the frequency of endemic hypogean fauna. We encourage and emphasise the need for much more research on caves and their fauna in Namibia and Angola.

ACKNOWLEDGEMENTS

Fieldwork in Angola was funded by grants to D Matos by the Fundação para Ciência e Tecnologia (SFRH/BD/117162/2016), the Leakey Foundation Dissertation, and the National Geographic Society (USA). Studies were developed in partnership with the Department of Geology and Mining, the Instituto Superior Politécnico da Huíla, the Reitoria Universidade Mandume Ya Ndemufayo, Governo Provincial da Huíla, and the Humpata and Chibia Administration Offices. Thanks are due to Rui Francisco and Renato Serôdio for photographs and preliminary documentation during the 2010 Humpata Caves Survey, and to Carlos Bumba for information about the northern karst. We thank Mariana Marques and Luís Ceríaco for identification of reptiles, and Fernanda Lages and Adjany Costa for identification of fish. Special thanks to Martin Pickford for comments and corrections. John Irish kindly provided advice, and the information and geographic coordinates of caves in Namibia.

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