Monograph on

Endemism in the Highlands and Escarpments of Angola and Namibia

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

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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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