

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



Angola Cave-Chat *Xenocopsychus ansorgei*
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Mammal endemism in the highlands and escarpments of Angola and Namibia

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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-leaved 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 Ansoerge'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 Ansoerge'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.) (Arumogum *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			
	<i>Crossarchus ansorgei ansorgei</i>	Near-endemic	Angelici & Do Linh San (2015)
	<i>Herpestes flavescens</i>	Near-endemic	Rapson & Rathbun (2015)
Cetartiodactyla			
Bovidae			
	<i>Aepyceros melampus petersi</i>	Near-endemic	IUCN SSC Antelope Specialist Group (2016a)
	<i>Philantomba monticola anchietae</i>	Near-endemic	IUCN SSC Antelope Specialist Group (2016b)
Chiroptera			
Pteropodidae			
	<i>Epomophorus angolensis</i>	Near-endemic	Mildenstein (2016)
Vespertilionidae			
	<i>Neoromicia anchietae</i>	Possibly endemic	Monadjem <i>et al.</i> (2020), Taylor <i>et al.</i> (2022)
Miniopteridae			
	<i>Miniopterus</i> sp.	Possibly endemic ¹	A. Monadjem <i>et al.</i> unpubl. data
Rhinolophidae			
	<i>Rhinolophus damarensis</i>	Near-endemic	Monadjem <i>et al.</i> (2017)
	<i>Rhinolophus</i> sp. 1	Possibly endemic ¹	A. Monadjem <i>et al.</i> unpubl. data
	<i>Rhinolophus</i> sp. 2	Possibly endemic ¹	A. Monadjem <i>et al.</i> unpubl. data
Eulipotyphla			
Soricidae			
	<i>Crocidura erica</i>	Endemic	Gerrie & Kennerley (2016)
	<i>Crocidura nigricans</i>	Endemic	Hutterer (2016)
Hyracoidea			
Procaviidae			
	<i>Heterohyrax brucei bocagei</i>	Endemic	Butynski <i>et al.</i> (2015)
Macroscelidea			
Macroscelididae			
	<i>Macroscelides flavicaudatus</i>	Endemic	Rathbun & Eiseb (2015)
Perissodactyla			
Equidae			
	<i>Equus zebra hartmannae</i>	Near-endemic	Gosling <i>et al.</i> (2019)
Primates			
Cercopithecidae			
	<i>Cercopithecus mitis mitis</i>	Near-endemic	Lawes <i>et al.</i> (2013), Butynski & de Jong (2019)
	<i>Galagoides kumbirensis</i>	Endemic	Svensson <i>et al.</i> (2017)
Rodentia			
Bathyergidae			
	<i>Fukomys bocagei</i>	Near-endemic	Krásová <i>et al.</i> (2021)
Gliridae			
	<i>Graphiurus rupicola</i>	Near-endemic	Monadjem <i>et al.</i> (2015)
	<i>Graphiurus</i> sp. indet. 1	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
	<i>Graphiurus</i> sp. indet. 3	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
	<i>Graphiurus</i> sp. indet. 4	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
Muridae			
	<i>Aethomys bocagei</i>	Near-endemic	Krásová <i>et al.</i> (2021)
	<i>Aethomys thomasi</i>	Endemic	Taylor (2016), Monadjem <i>et al.</i> (2015)
	<i>Dasymys nudipes</i>	Endemic	Taylor & Kennerley (2017)
	<i>Gerbilliscus angolae</i>	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
	<i>Gerbilliscus</i> cf. <i>humpatensis</i>	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
	<i>Hylomyscus heinrichorum</i>	Endemic	Kennerley & Dando (2019)
	<i>Hylomyscus carillus</i>	Near-endemic	Schlitter & van der Straeten (2016)
	<i>Lophuromys angolensis</i>	Near-endemic	Monadjem <i>et al.</i> (2015)
	<i>Mastomys angolensis</i>	Near-endemic	Krásová <i>et al.</i> (2021)

Table 1 (continued)

Order and family	Species or subspecies	Endemism status	Reference
	<i>Mus callewaerti</i>	Near-endemic	Krásová <i>et al.</i> (2021)
	<i>Mus triton</i> B	Near-endemic	Krásová <i>et al.</i> (2021)
	<i>Otomys anchietae</i>	Endemic	Monadjem <i>et al.</i> (2015)
	<i>Otomys cuanzensis</i>	Endemic	Taylor (2016)
	<i>Praomys coetzei</i>	Near-endemic	Kennerley <i>et al.</i> (2019)
	<i>Rhabdomys</i> sp. 1	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
Nesomyidae			
	<i>Petromyscus shortridgei</i>	Near-endemic	Schlitter (2016)
	<i>Petromus typicus</i>	Near-endemic	Cassola (2016a)
	<i>Poemys angolensis</i>	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
	<i>Poemys leucostomus</i>	Possibly endemic ²	Monadjem <i>et al.</i> (2015)
	<i>Poemys vernayi</i>	Endemic	Monadjem <i>et al.</i> (2015)
	<i>Poemys</i> sp. indet. 13	Possibly endemic ¹	Krásová <i>et al.</i> (2021)
Sciuridae			
	<i>Protoxerus stangeri loandae</i>	Endemic	Cassola (2016b)
	<i>Xerus princeps</i>	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 prao mys (*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 *Petromyscus 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 *Petromys 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

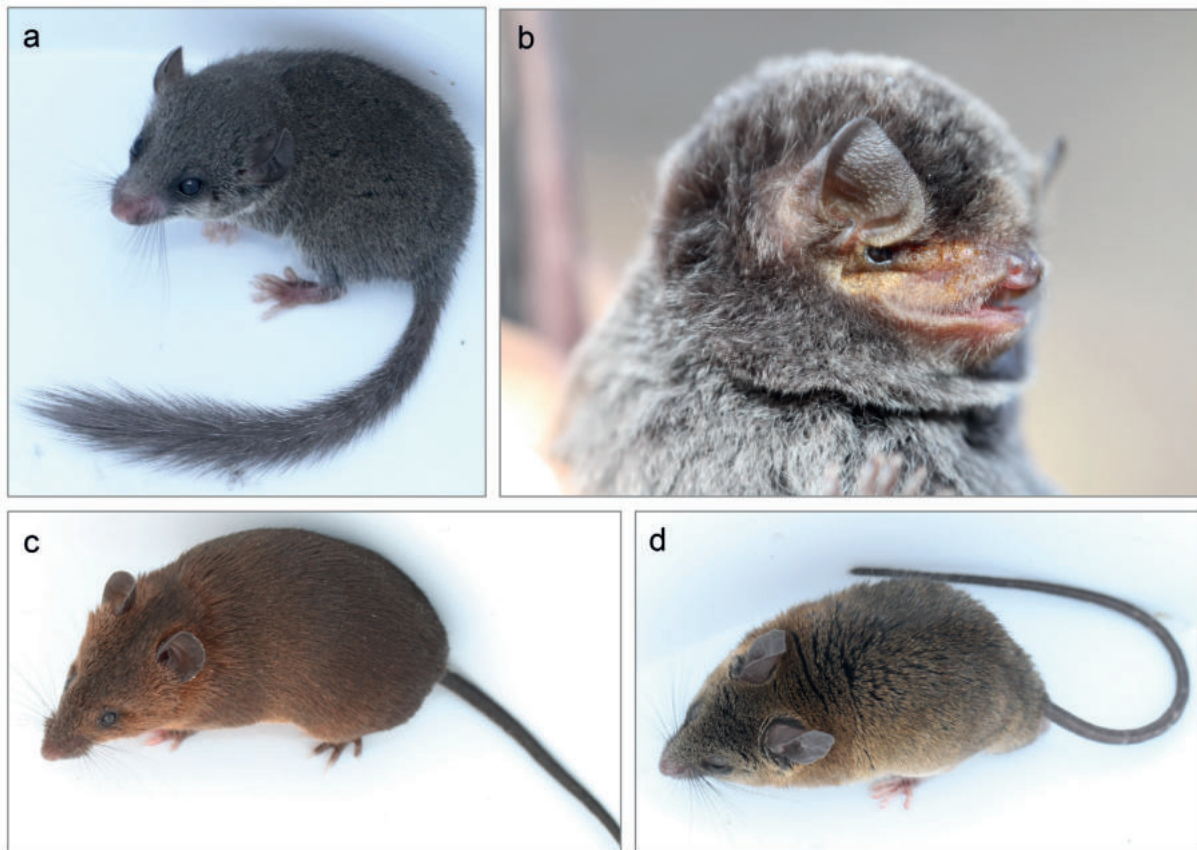


Figure 1: Examples of endemic and possible endemic species from Angola's highlands recently recorded in the Mt Namba and Cumbira Forest surveys (AF Palmeirim unpubl. data, A Monadjem unpubl. data): a) *Graphiurus* sp., b) *Miniopterus* sp., c) *Lophuromys angolensis* and d) *Hylomyscus heinrichorum*. 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 unprecedented 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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