Biogeography of Angolan rodents: The first glimpse based on phylogenetic evidence

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Abstract

Aim: Assessment of phylogenetic diversity and biogeographical affinities of the rodent fauna from one of the most neglected areas in Africa.

Location: Angola (with biogeographical implications in adjacent areas).

Methods: Inference of mitochondrial phylogenies for rodent genera occurring in Angola, delimitation of molecular operational taxonomic units (MOTUs), assessment and comparative analysis of their geographical distribution.

Results: We provide the first genetic evidence for the presence of 44 rodent taxa from 19 genera and 5 families in Angola, including twelve MOTUs endemic to Angola, and 12 candidate new species, pending integrative taxonomic revisions. The endemic MOTUs were found almost exclusively in the Angolan Miombo Woodlands and in Angolan montane forest-grassland mosaic.

Main conclusions: The highly diverse Angolan rodent fauna is mostly composed of and shows affinities with taxa originating from three major biogeographical regions of sub-Saharan Africa (Zambezian, South African and Congolian). It is also composed of a unique fauna comprising palaeoendemics from the Angolan Highlands. The species richness and the endemism detected in the Angolan montane forest-grassland mosaic and in the Angolan escarpment forests suggest that these are relevant for conservation, but more studies including other biological groups are needed to fundament this.
1 | INTRODUCTION

The shortage of high-quality data on the distribution of organisms is one of the biggest challenges of conservation biogeography (Richardson & Whittaker, 2010). Many areas of the world remain heavily under-sampled for most taxa as a result of unfavourable conditions for field surveys, including political instability. Even in areas with good sampling coverage, distributional data are often affected by geographical sampling bias: much of our distributional data are limited to political geographical units (state borders) (Hughes et al., 2021) or lacking biological meaning (Farooq et al., 2021). Besides geographical sampling bias, the quality of the collected data is another factor limiting our knowledge about species diversity of a particular area. An essential source of data on species distribution consists of historical inventories (museum collections; Ferguson, 2020). In assessing diversity distribution, this kind of data should be used with caution mainly due to two drawbacks: (1) historical data do not necessarily reflect current species distribution, e.g., due to habitat loss; and (2) this type of information is often restricted to morphological description and does not sufficiently recognize cryptic diversity, i.e., the occurrence of distinct evolutionary lineages that are otherwise morphologically indistinguishable to a human observer. These are usually reliably detected only by genetic data obtained by molecular techniques (Chenuil et al., 2019).

In Africa, south-western Africa, represented roughly by Angola and adjacent parts of neighbouring countries, is, in general, one of the most understudied regions concerning biodiversity (Clark et al., 2011; Huntley et al., 2019). More than forty years of instability related to the colonial and civil wars in Angola (1961–2002) prevented field studies and the collection of biological samples. Despite the revival of biodiversity research in some Angolan regions (e.g., Conradie et al., 2012; Mills et al., 2013) in the last two decades, genetic data reflecting evolutionary diversity is still scarce. For example, the only large-scale study of Angolan mammalian biogeography is solely based on records of morphologically identified species (Rodrigues et al., 2015).

Because of its geological, topographical and climatic diversity, Angola has seven biomes and 15 terrestrial ecoregions within its borders, ranking first and second in Africa, respectively (Burgess et al., 2004; Huntley, 2019), being therefore particularly interesting for biogeographers. Three major biogeographic regions of sub-Saharan Africa meet in Angola: the moist forests and savannahs of the Congolian region; the woodlands, savannahs and floodplains of the Zambezian region; and the arid savannahs, dwarf shrublands and desert of the Karoo-Namib region (Linder et al., 2012). Although there are several areas of great global conservation importance and putative centres of endemism in Angola, such as the Angolan Escarpment Zone, the evolutionary history of most biological groups occurring there is virtually unknown (Huntley et al., 2019).

Rodents are well suited for detection of phylogeographic patterns owing to their short generation time, limited dispersal ability and strong association with particular habitats. For instance, periodic fragmentation of African forests during the Plio-Pleistocene caused by palaeoclimatic changes resulted in remarkable genetic differentiation of forest dwelling rodents (e.g., Bohoussou et al., 2015; Demos et al., 2014; Nicolas et al., 2011). Moreover, their populations were not substantially modified by hunting as with large mammals, which have been significantly affected during the civil war until now. A few recent surveys of large mammals confirm that many species once common in Angola only persist currently in remote areas, usually having small and fragmented populations (Funston et al., 2017; Monterroso et al., 2020; Overton et al., 2017).

Current knowledge of Angolan rodent fauna stands mostly on a foundation laid by the detailed studies by Crawford-Cabral (1966a, 1966b, 1983, 1989, 1998). According to the most recent species list of Angolan rodents (Beja et al., 2019), there are 10 rodent families in Angola, represented by 85 rodent species, 13 of which are considered endemic either to the country or to south-western Africa. However, this compilation is exclusively based on morphological identifications and would greatly benefit from the inclusion of genetic data. This type of data allows to test for the distinctiveness of the currently recognised species, the presence of cryptic diversity and the existence of intraspecific phylogeographic lineages. In addition, such studies can also provide information about phylogenetic position, evolutionary uniqueness and biogeographical affinities if performed at a broader geographical scale and not limited by borders of a single country.

The aim of this study was to perform the first-ever phylogeographic assessment of Angolan rodent diversity based on cytochrome b sequences. It is based on four sources of genetic information from Angolan rodents: (1) Material collected in our recent survey conducted in three provinces of western Angola (Namibe, Huila and Cuanza-Sul) supplemented with (2) other donated material; (3) museum samples and (4) publicly available sequences (GenBank, African Mammalia). The results provide the most comprehensive information about the evolutionary diversity and biogeographical affinities of Angolan rodents based on genetic data and indicate taxa worthy of further taxonomic studies. They also highlight areas with evolutionary uniqueness and local endemism, which might contribute to the identification of regions deserving formal protection.

KEYWORDS
DNA barcoding, endemism, mice, molecular operational taxonomic units, Muridae, phylogeography, rats, South African region, Zambezian region
2 | METHODS

2.1 | Sampling

The trapping survey was conducted in July 2017 at nine localities in south-western Angola (Figures 1 and 2). Animals were trapped using snap traps and Sherman traps. To maximize trapping success and diversity of the captured rodents, we set the trap lines to cover a representative proportion of each habitat rather than using a fixed distance or grid. In addition, one cane rat (Thryonomys) was obtained from local people by the road to Sumbe, and one house mouse (M. m. domesticus) was captured in the city of Lubango (Table S1.1). Standard body measurements (body weight and lengths of head + body, tail, ear and hind foot without claws) were taken from all specimens, and a tissue sample (spleen where possible) from each of them was preserved in 96% ethanol and stored at −20°C until DNA extraction. Voucher specimens were preserved in 70% ethanol for further taxonomic work and deposited at the University of South Bohemia, České Budějovice, Czech Republic, and in the ZC-IICA, Angola.

To cover a broader geographical area of Angola, we took tissue samples from 58 dry skins from the collection of ZC-IICA (collected in 1962–1974). Preferably toes were cut and stored dry in Eppendorf tubes until DNA extraction with the Invisorb Spin Forensic Kit (Stratec). In addition, we used sequences of eight specimens collected recently by Taylor in central Angola (Taylor et al., 2018) and two tissue samples from the collection of the Field Museum of Natural History, Chicago, U.S.A.

To reveal the phylogenetic position of Angolan taxa with a particular focus on their biogeographic affinities, we sequenced 674 rodent specimens from our previous expeditions to eastern Africa (GenBank accession numbers and other details are provided in Table S1.1). Additionally, 69 samples were obtained from various museum collections. For details about the collected specimens and origin of the museum samples, see Table S1.1. The obtained data were combined with sequences from GenBank (N = 1584) and the African Mammalia (Van de Perre et al., 2019) database (N = 92).

2.2 | Genotyping, phylogenetic analysis and biogeographical assessment

The captured individuals were classified to genera and tentatively to species based on their physical attributes and the measurements. At least one specimen per species (“morphotype”) and locality was chosen for sequencing of the mitochondrial gene for cytochrome b (CYTB). For more information on the DNA extraction, polymerase chain reaction (PCR) and Sanger sequencing see Krásová et al. (2019).

In the material from ZC-IICA, we targeted specific short fragments of CYTB using high-throughput amplicon sequencing on the Illumina MiSeq platform (Illumina, San Diego, CA, USA) as described in Šmid et al. (2020). Short fragments of CYTB from the additional 69 museum samples were obtained by 454-pyrosequencing on the GS Junior Roche platform (Roche, Basel, Switzerland) as described in Aghová et al. (2017).

Based on their CYTB sequences, the individuals were classified to genera using the BLAST tool (Altschul et al., 1990) at the NCBI GenBank website (www.ncbi.nlm.nih.gov/genbank). To put the Angolan specimens into an appropriate phylogenetic context, for each genus, we made a separate CYTB alignment comprising relevant sequences available in public databases (see above), as well as our previously collected and unpublished data (Table S1.1). In a few cases, we relied on unpublished data of other research groups (Table S1.1).

Every genus was subjected to a separate phylogenetic analysis, which followed the same protocol, wherever it was possible. First, we conducted a preliminary analysis using FastTree (Price et al., 2009) and created a representative CYTB alignment covering the phylogenetic diversity of the genus (or species) in question as much as possible. Then, we obtained an unrooted tree with branch lengths in substitution units using Bayesian inference as implemented in MrBayes 3.2.6 (Ronquist et al., 2012). The same setting was used in all cases: uniform prior overall topologies and HKY nucleotide substitution model (Hasegawa et al., 1985) with Gamma distributed variation in substitution rates and a proportion of invariant sites and 12–3 partitioning according to the codon position. Three outgroups were included in every tree for their post
hoc rooting (Table S1.2). Four independent Markov Chain Monte Carlo simulations were conducted to test for the convergence, which was done visually in Tracer 1.7 (Rambaut et al., 2018). After discarding burn-in, the four posterior samples were pooled, the trees rooted and outgroups removed not to bias subsequent analyses. The Maximum Clade Credibility (MCC) tree, as defined by Drummond and Bouckaert (2015, p. 162), was then calculated to represent the pooled sample. Its branch lengths were based on the common ancestor heights (Drummond & Bouckaert, 2015, p. 92). The MCC tree was calculated in R (R Core Team, 2019) using packages ape (Paradis & Schliep, 2019), phangorn (Schliep, 2011) and custom functions written by one of the authors (OM; https://github.com/onmikula/mctree_mrbayes).

The haplotypes included in the tree were classified into molecular operational taxonomic units (MOTUs), which can be considered as approximations of species or deeply divergent intraspecific (phylogeographic) clades. We used the maximum likelihood-based mPTP algorithm of Kapli et al. (2017), which partitions the tree into $K + 1$ components, one interspecific backbone and $K$ MOTUs, each with its own exponential distribution of branch lengths. The resulting classification is fully reported in Table S1.1, but we focused on the Angolan taxa and their relatives. Only these focal MOTUs are, therefore, shown as distinct, while the others were collapsed into larger monophyletic lineages. Where appropriate, the existing species (or intraspecific lineages) names were assigned to the MOTUs. Distribution of the MOTUs was assessed by phylogenetic placement of all available georeferenced sequences, including the short CYTB sequences obtained by high-throughput sequencing of old museum samples. Given the fact that the tree covers the whole phylogenetic diversity of the genus/species, we used simple nearest-neighbour classifier based on uncorrected genetic distances to place the sequences into MOTUs. The distribution of every MOTU was visualised in QGIS (QGIS Development Team, 2019). The biogeographical affinities of Angolan MOTUs were assessed by visual examination of the maps and described separately.

### 3 | RESULTS

#### 3.1 | Trapping success and genotyping summary of Angolan material

In total, 307 rodents representing 16 genera were collected in 2017 during our fieldwork in Angola. Details about trapping success and genera captured at particular localities are summarised in Tables S1.3 and S1.4, respectively. In total, we sequenced the CYTB gene for 135 of the 307 captured individuals. Additionally, short fragments of CYTB (147 base pairs) were successfully obtained for 35 of 58 specimens from ZC-IICA from additional 25 localities (Figure 1), which provided the first genetic data of three genera (Grammomys, Lemniscomys, Zelotomys) not trapped during our 2017 expedition. Further, 69 CYTB minibarcodes (135 base pairs) from various museum collections were obtained by 454 sequencing. Finally, two more taxa (Graphiurus sp. indet. 2 and Rhabdomys sp. 1) were revealed by genetic analysis of specimens obtained in the upper Okavango catchment (Table S1.1).

#### 3.2 | Intragenic diversity in a biogeographical context

In total, the genetic data allowed the identification of 44 taxa (i.e., MOTUs or potential species) of rodents in Angola,
belonging to 19 genera (Table S1.1). For the majority of them, CYTB sequences represent the first genetic information from the country. Specific accounts for particular genera, including phylogenetic trees, distributional maps and taxonomic comments are available in Data S1. We were able to assign names to three out of 12 taxa not listed in the most recent species list of Angolan rodents (Beja et al., 2019) (Lemniscomys rosalia, Mus cf. kasaicus, Mus sp. "Nyiika"). Based on the phylogenetic analysis (i.e., monophyletic clades, sufficiently distinct from their sister lineages), we propose to resurrect from synonymy five species, specifically Poemys angolensis, Dendromus cf. whytei, Gerbilliscus angolae, Gerbilliscus cf. humpatensis and Grammomys surdaster. However, this will require further quantification of phenotypic differences and comparison with the type material. Two taxa are possibly new and require further taxonomic work (Table S2.1). Poemys sp. indet. 13 (sensu Voelker et al., 2021) was found solely at Tundavala, while Rhabdomys sp. 1, was found exclusively at the Lungwebungu River locality. Mastomys angolensis recorded solely at the 20 km SW Cassongue locality was previously reported as Myomyscus angolensis (Crawford-Cabral, 1989). For some taxa
We defined four major biogeographical patterns based on the distributional patterns of Angolan MOTUs in Angola and neighbouring countries and the analysed phylogenetic trees including clades related to the Angolan MOTUs (see phylogenetic trees and distributional maps for particular taxa in Data S1) (Figure 3 and Figure 4). (1) 13 MOTUs have a wide distribution in the Zambezian region; (2) 7 in the Congolian; (3) 4 in the South African and (4) 12 MOTUs are endemic to Angola (Table 1). Altogether, eight Angolan MOTUs were not assigned to any region because of data deficiency or unclear pattern (in a single case of *M. minutoides* MOTU 24).

The distribution of the endemic taxa is concentrated in the Angolan Miombo Woodlands and Angolan montane forest–grassland mosaic (Figure 4). Two endemic taxa (*Aethomys bocagei* and *Mus minutoides* MOTU 20) were captured in forest habitat, whilst the others were recorded in open habitats (Table S1.3).

### 4 | DISCUSSION

#### 4.1 | Diversity of Angolan rodents

The most recent checklist of Angolan rodents presented in Beja et al. (2019) counts 10 families and 85 species, thirteen of them being endemic or near-endemic to the country. This checklist is largely a summary of morphological studies pre-dating the molecular revolution in taxonomy (e.g., Crawford-Cabral, 1966a). Pending future integrative taxonomic revisions, the present study records 23 species from the list and suggests the existence of up to 12 others, including two endemics (Table S2.1).

Given that rodent diversity has never been surveyed in a large part of Angola, it is not surprising that additional species were recorded. An updated checklist of Angolan rodents based on the findings of the present study could contain more than 90 species, which would be more than, for instance, the number of species found in the combined South Africa, Swaziland and Lesotho region (74 species; Child et al., 2016) or Mozambique (51 species; Neves et al., 2018), which is, however, similarly understudied as Angola. Among African countries, only Ethiopia (104 species; Bryja et al., 2019) and Kenya (106 species; Musila et al., 2019) host more rodent species than Angola. However, they are both better surveyed than Angola and, especially Ethiopia, has an extremely heterogeneous landscape with high mountains separated by substantial migration barriers such as the Rift valley, which may promote speciation (Huhndorf et al., 2007).

Even though our sampling represents just a snapshot of the rodent fauna in south-western Angola, we covered an important part of the country’s rodent diversity. During only ten trapping nights, 26 rodent taxa were recorded, which corresponds to one-third of the total count (75) after exclusion of *Hyrictidae*, *Pedetidae* and

| **Biogeographic affinity** | **Family** | **MOTU** |
|---------------------------|-----------|---------|
| Zambezian                 | *Gliridae*| *Graphiurus* sp. indet. 3 |
| Zambezian                 | *Nesomyidae*| *Poemys* sp. indet. 13 |
| Zambezian                 | *Nesomyidae*| *Dendromus cf.* whytei |
| Zambezian                 | *Nesomyidae*| *Steatomys parvus* |
| Zambezian                 | *Nesomyidae*| *Steatomys pratensis* |
| Zambezian                 | *Muridae*  | *Aethomys nyika* |
| Zambezian                 | *Muridae*  | *Aethomys chrysophilus* |
| Zambezian                 | *Muridae*  | *Gerbilliscus leucogaster* |
| Zambezian                 | *Muridae*  | *Lemniscomys rosalia* B |
| Zambezian                 | *Muridae*  | *Mastomys natalensis* lineage BVI |
| Zambezian                 | *Muridae*  | *Mus sp.* “Nyika” |
| Zambezian                 | *Muridae*  | *Mus triton* lineage D |
| Zambezian                 | *Muridae*  | *Thallomys paederulus* |
| Congolian                 | *Nesomyidae*| *Poemys pecilei* |
| Congolian                 | *Bathyergidae*| *Fukomys “Kinshasa-Quimbango”* |
| Congolian                 | *Muridae*  | *Grammomys surdaster* lineage su5 |
| Congolian                 | *Muridae*  | *Lophuromys angolensis* |
| Congolian                 | *Muridae*  | *Mastomys angolensis* |
| Congolian                 | *Muridae*  | *Mus cf.* Kasaicus |
| Congolian                 | *Muridae*  | *Mus triton* lineage B |
| South African             | *Nesomyidae*| *Petromyscus collinus* |
| South African             | *Nesomyidae*| *Saccostomus campestris mashonae* |
| South African             | *Nesomyidae*| *Steatomys krebssii* |
| South African             | *Muridae*  | *Thallomys nigricauda* |
| Endemic to Angola         | *Gliridae*| *Graphiurus* sp. indet. 1 |
| Endemic to Angola         | *Gliridae*| *Graphiurus* sp. indet. 2 |
| Endemic to Angola         | *Gliridae*| *Graphiurus* sp. indet. 4 |
| Endemic to Angola         | *Bathyergidae*| *Fukomys bocagei* |
| Endemic to Angola         | *Nesomyidae*| *Poemys angolensis* |
| Endemic to Angola         | *Muridae*  | *Aethomys bocagei* |
| Endemic to Angola         | *Muridae*  | *Gerbilliscus cf.* humpatensis |
| Endemic to Angola         | *Muridae*  | *Hylomyscus heinrichorum* |
| Endemic to Angola         | *Muridae*  | *Micaelamys namaquensis* MOTU 2 |
| Endemic to Angola         | *Muridae*  | *Mus minutoides MOTU 20* |
| Endemic to Angola         | *Muridae*  | *Rhabdomys dilectus* MOTU 6 |
| Endemic to Angola         | *Muridae*  | *Rhabdomys sp.* 1 |
Sciuridae, the groups not targeted by our trapping method. It is clear, therefore, that even such limited field studies are very valuable, especially in poorly documented areas like Angola.

Any assessment of biodiversity relies on the estimates of species boundaries and/or phylogenetic relationships. In the present study, we employed single-locus methods of phylogenetic and species delimitation inference and used sequences of the mitochondrial cytochrome b gene as our data (135 bp in museum samples, 1,140 bp otherwise). Thanks to its frequent use as a mammalian barcode marker (DeSalle & Goldstein, 2019), it allowed us to combine our sequences with the largest possible amount of data from public databases. The use of a single marker with matrilinear inheritance has its inherent limitations. We checked for the presence of unusually conservative sequences (Puechmaille et al., 2011) and the presence of stop codons (Song et al., 2008) to remove possible nuclear pseudogenes, but these signs may not always be apparent in short museum barcodes. Also, cytonuclear discordance can mislead single gene analyses, whether it is due to mitochondrial introgression or incomplete lineage sorting. Therefore, the kind of trees presented in Data S1 cannot be conclusive about the phylogenetic relationships in a particular genera, but it is known to provide a sound basis for biodiversity assessment (e.g., Boubli et al., 2018).

4.2 | Biogeographic affinities

Although an increasing body of papers focuses on the biodiversity of Angolan mammals, only a few have used genetic approaches (e.g., Bock et al., 2014; Pitra et al., 2006; Vaz Pinto, 2018) and none of them dealt with rodents. Here, we begin to fill this gap, allowing for putting Angolan rodents into a pan-African phylogeographic context for the first time. More specifically, we asked in what other African regions do Angolan taxa occur, or where are their closest relatives. These biogeographic affinities are assumed to reflect ancient or more recent historical connections of the faunal assemblages. Even though we relied on mtDNA, which gene trees may be discordant with population-level history (Degnan & Rosenberg, 2009; Toews & Brelsford, 2012), the observed phylogeographic patterns are surprisingly consistent among different taxa. Based on the results of the phylogenetic analyses, the definition of MOTUs and analysis of their distribution, it seems obvious that the high biodiversity of Angolan rodents is at least partly caused by the overlap of fauna originating from three biogeographic regions as defined by Linder et al. (2012): Zambezian, Congolian and South African (summarised in Figure 3). Accordingly, it is possible to divide Angolan rodent taxa into the following major groups:

1. **Taxa with affinities to the Zambezian region** (summarised by blue crosses in Figure 3). This group consists of lineages (species or deep intraspecific groups) widely distributed in the Zambezian region, either in Miombo woodlands (Aethomys nyikae, Steatomys pratensis, Mus triton clade D, Mastomys natalensis clade B-VI and partly also G. leucogaster and Aethomys chrysophilus) or in the higher elevations of Afromontane ecosystems from northern Zambia/Malawi (Mus sp. “Nyika”, Poemys sp. indet. 13, Dendromus cf. whytei), some of them being found in Kenya (Rhabdomys ditectus) or even Ethiopia (Graphiurus MOTU 11). Miombo woodlands form a continuous unit covering the major part of central and eastern Angola, extending across Zambia and the south-eastern DRC up to northern Tanzania and southern Mozambique (White, 1983). It is therefore not surprising that taxa associated with this ecosystem exhibit wide and continuous distributions. Their internal phylogenetic structure is relatively homogeneous, reflecting only a few existing significant biogeographic barriers, the most important being the Zambezi River and the large rift lakes (e.g., Krásová et al., 2019; Mazoch et al., 2018; McDonough et al., 2015; Mikula et al., 2016). The existence of gene flow between Angola and Zambia is also suggested by the distribution of many avian taxa, although this is not yet verified by molecular data (Beja et al., 2019). The presence of corridors between Afromontane populations from Angola and East Africa in the past is more surprising because these two mountain blocks are currently separated by more than 2000 km of Zambezian savannah and woodland. On the other hand, it is thought that Afromontane pockets, which are currently very localized and isolated, used to be more widely distributed in humid periods of the Pleistocene (Diamond & Hamilton, 1980), allowing stepping-stone colonization of the Angolan highlands from the East African Afromontane hotspot, probably through the highlands in Katanga (DRC). This pattern, with sister populations in western Angola and Katanga, respectively, was recently proven by molecular data and distribution modelling in multiple bird species (Vaz da Silva, 2015). Unfortunately, genetic data about rodents in Katanga are almost completely missing.

2. **Taxa with affinities to the savannah/forest mosaic in southwestern DRC** (red crosses in Figure 3). There is a significant lack of data from large areas of the south-western DRC compared to other regions of sub-Saharan Africa, but our study suggests that part of the Angolan taxa is evolutionarily close or identical to the fauna distributed southwards of the continuous forest belt in the south of the Congo Basin. They are represented by species associated with relatively open habitats (e.g., Mus cf. kasaicus, Mus triton B, Mastomys angolensis) or margins of tropical forests (Lophuromys angolensis). Most of these taxa are restricted to the north-western part of the country, but some occur further south, near the Namibian border (e.g., M. triton B; Figure 3, Figure S2.12). We hypothesize that this southward colonization occurred due to the presence of relatively moist gallery forests along the Kunene River during more humid periods. A similar pattern is known for several bird species (e.g., Dryoscopus angolensis and Apalis cinerea) that occur in western Angola and have disjoint populations in eastern DRC and/or in
Cameroon/Gabon (Diamond & Hamilton, 1980). Further sampling in poorly known areas of southern DRC would be necessary to test this hypothesis with genetic approaches.

3. Taxa with affinities to the South African region (green circles in Figure 3). This group is represented by species adapted to arid habitats found along the Atlantic coast (Petromyiscus collinus) or in Botswana (Thallomys nigricalaude) and by taxa more widely distributed in southern Africa (Saccostomus campestris masho-nae, part of Gerbilliscus leucogaster). The south-western coast of Africa is covered by a continuous belt of desert (the Namib Desert) extending from the Carunjamba River in Angola, southwards through Namibia, to the Western Cape in South Africa (Andersen & Cernek, 2018). Inland, the Kalahari Desert covers the major part of south-western Botswana, eastern Namibia and the northern portion of South Africa. The distribution of species adapted to arid conditions, like P. collinus and T. nigricalaude, reflect the occurrence of suitable habitats, as with the distribution of other vertebrates associated with xeric habitats, e.g., skinks (Portik et al., 2011), but also other mammalian species such as Antidorcas marsupialis (Cain et al., 2004). More widely distributed taxa from Angola associated with the South African region (e.g., Saccostomus, Gerbilliscus) inhabit other types of open savannah-like habitats south of the Zambezi River (Data S1).

Importantly, these affinities are apparent on different phylogenetic scales. While some of them likely reflect recent colonization events (i.e., Angola shares the same MOTUs with neighbouring countries), others have a more ancient basis (i.e., Angola and neighbouring regions) and are occupied by different but closely related MOTUs corresponding either to conspecific phylogeographic lineages or sister species. For instance, in rodents of savannah-like habitats, the affinity to the South African region is revealed by five shared MOTUs (Table 1) and two MOTUs endemic to Angola, but having the most closely related counterparts in southern Africa (Micaelamys namaquensis MOTU 2, Rhabdomys sp. 1).

The fact that the genetic data used in the present study revealed a clear biogeographic pattern is even more intriguing when compared with a similar study based on morphologically determined museum records. Rodrigues et al. (2015) used museum records of three mammalian groups (carnivores, rodents and ungulates) to develop a biogeographical regionalization of Angolan mammals. Four biogeographical subdivisions emerged from ungulate data: a northern region (Zaire-Lunda-Cuanza), a central region (Central Plateau) and two regions in the south (Namibe and Cunene-Cuando Cubango), whilst rodent and carnivore data were largely uninformative (Rodrigues et al., 2015).

The study hypothesised that this could be explained by the lower number of records available for rodents and carnivores or by a stronger association of ungulates with specific vegetation types. Our study does not support this, because a smaller dataset of rodent records was used, and revealed strong biogeographic divisions. This highlights the fact that the quality of data used for biogeographical assessments (i.e., data including genetic information) is crucial in determining spatial patterns of biodiversity. This also questions the broad use of morphologically determined species in biogeographic studies of rodents and other groups.

4.3 | Endemism in Angola

Numerous vertebrate species have been described as endemic or nearly endemic to Angola, although the precise number of Angolan endemics is difficult to estimate due to data deficiency and taxonomic ambiguities (Beja et al., 2019). Recently published studies have shown that especially the use of genetic material represents a valuable tool for identifying Angolan endemics and their phylogenetic position (Ceríaco, Agarwal et al., 2020; Ceríaco, Heinicke et al., 2020; Ceríaco et al., 2018; Ceríaco, Tolley et al., 2020; Hallermann et al., 2020; Krásová et al., 2021; Marques et al., 2019, 2020). The results presented in this study might serve as a starting point for a re-assessment of Angolan rodent fauna, including the level of endemism.

Our phylogenetic analysis revealed the presence of 12 MOTUs endemic to Angola (Table 1, Figure 4). Despite the lack of detailed phenotypic and ecological data, seven of them can be safely considered distinct species. Aethomys bocagei represents a genetically distinct species sister to A. kaiser from Eastern Africa. Fukomys bocagei is a small-bodied species more widespread than the large-bodied F. mechowii. Rhabdomys sp. 1 from the Bié plateau in central Angola is genetically very distinct from the rest of the genus (including R. diluctus from the East African mountains, which also occurs in Angola), and all three Graphiurus MOTUs represent deeply divergent lineages not yet found in other countries. Hylomyscus heinrichorum was proven to be genetically and morphologically distinct from other Hylomyscus species from the so-called H. anselli group (Carleton et al., 2015; Peterhans et al., 2020). The taxonomic status of dendromus angolensis, Gerbilliscus angolae and Gerbilliscus cf. humpatensis crucially depends on the applied species concept, as they are closely related to similar sister species living in parapatry in the neighbouring regions. The endemic MOTUs of Micaelamys namaquensis, Rhabdomys diluctus and Mus minutoides are likely to represent specific phylogeographic lineages, not separate species, but integrative taxonomic work is required. More details about the distribution and phylogenetic position of Angolan endemics are available in Data S1.

4.4 | Western Angola as a centre of diversity—conservation implications

Although our results do not allow to identify areas of high endemism and diversity, the observation of 12 unique MOTUs endemic to Angola justify further conservation efforts, even in the absence of up-to-date comprehensive surveys. Our data suggest
that some parts of western Angola are especially important centres of biological diversity, crucial for the persistence of Angolan endemics.

The Tundavala site is located in the Humpate plateau in the southern region of the Angolan Escarpment and is the southern-most representative of the Angolan montane forest-grassland mosaic ecoregion (Burgess et al., 2004) (Figure 4). These highlands have a peculiar combination of features, high elevations, and a much colder and moister climate than the surrounding areas, thus functioning as an important endemic center. Tundavala comprises a mosaic of diverse vegetation types including miombo woodlands, relic montane grasslands and Afromontane forests, shrublands with elements of the South African fynbos such as Proteas and Ericas. During two trapping nights, we captured five MOTUs endemic to Angola (Fukomys bocagei, Gerbilliscus cf. humpatensis, Graphiurus sp. indet. 1, Rhabdomys dilectus MOTU 6, Miciaelamys namaquensis MOTU 2). Three of them (Gerbilliscus cf. humpatensis, Graphiurus sp. indet. 1 and Rhabdomys dilectus MOTU 6) were found exclusively at this site.

The locality 20 km SW of Cassongue is located in the south of Cuanza-Sul province at the northern part of the Marginal Mountain Chain (mostly 1,600–1,850 m a.s.l.) (Huntley, 1974). The habitat at this locality included grassland and degraded miombo. During one trapping night, ten species from six genera were captured (Table S1.4), including two Angolan endemics (Dendromus angolensis, Hylomyscus heinrichorum) and three taxa with affinities to the savannah/forest mosaic in south-western DRC (Lophuromys angolensis, Mastomys angolensis and Mus cf. kasaicus). Interestingly, two species of Mastomys and four different species of Mus were present at this single locality.

Kumbira Forest is a localized patch of forest between dry coastal vegetation and the moist savannahs of the Angolan interior plateau located in the central part of the Angolan Escarpment (Mills, 2010). It represents a remnant of a forest with close affinities to the Guineo-Congolian biome (Gonçalves & Goyder, 2016). Recently, a new species of bushbaby (Galagoides kumbirensis) was described from the forest (Svensson et al., 2017), which is an endemism centre for many bird species (Cáceres et al., 2015). In a single trapping night, we captured one Angolan endemic species (Aethomys bocagei), one near-endemic (Lophuromys angolensis) and a distinct clade of Mus minutoides (MOTU 20) known only from Angola.

Taken together, our records suggest that the Angolan montane forest-grassland mosaic ecoregion supports a variety of habitats hosting numerous species with high phylogenetic diversity, including several endemics. It is therefore of critical importance to introduce regulations protecting this diversity and unique biological heritage of Angola and south-western Africa. The new taxa suggested in this study should be formally delimitated and described. Detailed information about their distribution and ecology will then be used for their IUCN Red List assessment, which should be the way to go to advocate for protection of the most valuable parts of the montane forest-grassland mosaic ecoregion.

5 | CONCLUSIONS

Our study brings two significant findings. First, Angola apparently hosts core populations of several phylogenetically distinctive rodent species. Even though Angola does not host palaeoendemics comparable, for instance, to the endemic genera from the Albertine Rift (Plumptre et al., 2007) or from the Ethiopian highlands (Bryja et al., 2019), its rodent fauna bears an imprint of the country’s geo-morphological and climatic diversity, which allowed long-term survival of several unique deeply divergent lineages (e.g., in genera Graphiurus, Mastomys, Rhabdomys) and many local variants of more widely distributed rodent taxa. Nevertheless, a full appreciation of the uniqueness of Angolan rodents would require further sampling, as the rodent fauna has never been surveyed in many regions of Angola. Second, the remarkable diversity of rodent species is related to habitat diversity and the confluence of three major biogeographical regions (Linder et al., 2012), six biomes and 14 terrestrial ecoregions (Burgess et al., 2004; Huntley, 2019) within the political borders of Angola. Further phylogeographic studies should address specific hypotheses, for example, it seems that there was a recent colonization wave coming from the Zambezian savannah, while a connection of montane forests with both the southern part of the Congo basin and Southern Rift Mountains in Zambia/Malawi existed a long time ago. Similarly, the Escarpment may have acted as a refuge for lowland forest species as previously hypothesised for bird taxa (Diamond & Hamilton, 1980).

From a conservation perspective, our study reinforces the idea that several habitats within the Angolan montane forest-grassland ecoregion deserve legal protection as they host many endemic species and can be understood as a living archive of the country’s evolutionary and ecological past. For instance, Tundavala’s grasslands host a rodent community adapted to this open and cold habitat. The last remnants of these once large forests require strict protection. Attention should also be paid to seemingly indistinctive environments of low- and mid-altitudes, whose species may be seriously threatened by rapid and large-scale conversion of their natural habitats for agriculture. Currently, no region of the Angolan Escarpment falls into any protected area. Conservation efforts in this area are urgent as the local environment is threatened by progressively increasing human activities, especially logging and burning for charcoal production, and grazing of livestock (Baptista et al., 2018).

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CONFLICTS OF INTEREST
The authors have no conflicts of interest to declare. All fieldwork complied with legal regulations in Angola and sampling was carried out under permission of the Instituto Superior de Ciências de Educação, Luango (see Acknowledgements).

PEER REVIEW
The peer review history for this article is available at https://publo ns.com/publon/10.1111/ddi.13435.

DATA AVAILABILITY STATEMENT
Details on all individuals used in the phylogenetic analyses (including the GenBank accession numbers of CYTB sequences) and details on all localities (including GPS coordinates) are provided in Table S1.1. New sequences were submitted to GenBank under accession numbers MW470670-MW470846, MW512116-MW512239, MW537105-MW537578, MW544573-MW544612 and MW556239-MW556263.

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