



Original investigation

Spiny mice of the Zambezan bioregion – phylogeny, biogeography and ecological differentiation within the *Acomys spinosissimus* complex

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ABSTRACT

Despite the high degree of biological diversity in the Zambezan region, little information is available regarding the evolutionary history of its biota, and this is especially true for the fauna and flora of non-forested habitats. Here we use the most comprehensive multi-locus genetic dataset available to (1) reconstruct the phylogeny of spiny mice of the *Acomys spinosissimus* complex and to describe the spatial distribution of its genetic diversity; (2) to assess the level of reproductive isolation between genetic clades; (3) to analyse differences in climatic niche between potential species; and (4) to model their current and past distribution. The complex comprises four main genetic clades that correspond to four nominal species living in the east of the Zambezan region. Their distribution is delimited by important geographical divides including the Eastern Arc Mountains, Lake Malawi and the Zambezi River. Two species considered Tanzanian endemics, *A. ngurui* and *A. muzei*, are now known to be more widespread than previously thought and they have their centres of genetic diversity just north of the Zambezi. The first split between the extant members of the *A. spinosissimus* complex is estimated at 3 Mya. Most intraspecific diversification events are thought to have occurred in the Pleistocene, suggesting that climatic oscillations played an important role in their diversification. The climatic niches of parapatric taxa differ significantly; hence, local adaptations have likely played an important role in reproductive isolation. Species distribution modelling predicts a dramatic reduction of occurrence probability across the area during the last interglacial period, facilitating allopatric diversification of fragmented populations. Our results strongly suggest the combined role of Pleistocene climatic change, biogeographical barriers and local adaptation in forming current taxa diversity in east African savannah-like habitats. While such processes have frequently been observed in forest-living organisms (theory of allopatric diversification in forest refugia), similar mechanisms were likely also working in open ecosystems (savannah refugia).

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Introduction

The Zambezan bioregion (*sensu* Linder et al., 2012) represents a unique mosaic of ecosystems ranging from semi-arid grasslands to evergreen montane tropical forests. The majority is covered by open savannah-like habitat, mostly the so-called Mopane and

Miombo woodlands characterised by the dominant tree genera *Colophospermum* and *Brachystegia*, respectively. The main features of this ecosystem are seasonal moisture availability driven by monsoonal forcing and vegetation occurring as a mosaic of open and woody environments (Shorrocks, 2007). Despite a high degree of biological diversity in the Zambezan region (Linder et al., 2012), little relevant information is available on its evolutionary history. There is an increasing amount of phylogeographic data for taxa living in Afrotropical forests in this region (e.g. Loader et al., 2014 and references therein); however, data on the history of biota in open habitats remains scarce.

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Due to their short generation time, limited dispersal ability and strong associations with particular habitats, rodents are among the most suitable animal groups for uncovering the evolutionary history of particular ecosystems at very fine scales. Recently, large-scale rodent phylogeographic studies have provided convincing scenarios as to how open habitats in the Zambezi bioregion have been influenced by the interplay of geomorphology and Plio-Pleistocene climatic change (e.g. Colangelo et al., 2013; Mazoch et al., 2018; McDonough et al., 2015; Mikula et al., 2016). In order to assess the general applicability of their conclusions, however, comparative phylogeography approaches are needed, requiring detailed studies on multiple sympatric taxa.

Least Spiny Mice (or Southern Spiny Mice) of the *Acomys spinosissimus* complex are a monophyletic group of closely related cryptic species of the murid genus *Acomys* (Rodentia: Muridae: Deomyiinae). Originally described as a single species, taxonomic revisions based on cranial and external morphology and mitochondrial (mt) DNA data (Barome et al., 2001; Verheyen et al., 2011) suggest that the complex should be split into four distinct species with roughly parapatric distribution, i.e. *A. spinosissimus* Peters, 1852, *A. selousi* De Winton, 1896, *A. ngurui* Verheyen et al., 2011 and *A. muzei* Verheyen et al., 2011 (Monadjem et al., 2015). All four species currently recognised have similar morphological characteristics and ecology (Monadjem et al., 2015; Verheyen et al., 2011), being commonly found in the rocks and boulders of grasslands and deciduous woodlands, where they can dominate the small mammal community (Happold et al., 2013).

The whole complex is endemic to the eastern Zambezi region (Monadjem et al., 2015), with the northern distribution border represented by the divide between the Zambezi and Somali-Masai regions (*sensu* Linder et al., 2012) in northern Tanzania, where the *A. spinosissimus* complex appears to be replaced by other *Acomys* species (based on distribution maps in Monadjem et al., 2015), though precise data are scarce. The southern border coincides with the divide between the Zambezi and South-African bioregions in southern Zimbabwe and Mozambique. There are no records of the *A. spinosissimus* complex from Angola, and very few from Zambia; hence, the western limit of its distribution remains unknown (Monadjem et al., 2015). Based on a combination of available genetic and morphological data, Verheyen et al. (2011) proposed the parapatric distribution of the four species. The name *A. spinosissimus* should be retained for populations between the rivers Zambezi and Limpopo, while *A. selousi* is geographically restricted to northern South Africa and southern Zimbabwe, replacing *A. spinosissimus* from the Limpopo River southwards. Two newly described species by Verheyen et al. (2011), *A. ngurui* and *A. muzei*, are limited to open habitats of Tanzania, east or west of the Eastern Arc Mountains (EAM), respectively. Finally, the authors proposed the existence of another putative new species in southern Malawi and central Mozambique (north of the Zambezi), though its status has yet to be resolved.

Despite important progress in understanding the evolutionary history of the complex, there are still many pieces of the puzzle missing. First, genetic data from a large part of its distribution are still missing, e.g. there are no DNA sequences from the supposed distribution area of *A. spinosissimus sensu stricto* (*sensu* Verheyen et al., 2011) or from Zambia, where these spiny mice also live (Monadjem et al., 2015). Similarly, only single sequences exist from Mozambique and Malawi, where several species of this complex may co-exist (Verheyen et al., 2011). Second, previous studies concerning the phylogeny, phylogeography and taxonomy of the complex were based on morphological, cytogenetic and mtDNA data. At present, there is no genetic data available for nuclear DNA. As mtDNA introgression can be frequent between related taxa (see review by Toews and Brelsford, 2012), knowledge of variation at this marker type is not enough to delimit biological species, i.e.

reproductively isolated populations. A combination of mitochondrial and nuclear markers would better illuminate evolutionary processes, especially at contact zones between parapatrically-distributed taxa of the complex (Verheyen et al., 2011). Third, since the complex is widespread across the whole of the eastern Zambezi savanna, it represents a suitable model for the study of historical processes in the area. However, dated multi-locus phylogenetic reconstructions are unavailable and there are no model estimates of recent and past distribution for the complex. Lastly, individual species within the complex were described on the basis of skull morphology and mtDNA sequences; however, it remains unclear whether different species occupy distinct ecological niches. Detailed analysis of environmental correlates may help to assess whether inter-specific differences are the result of adaptive processes or not.

Under the framework of our recent research focussed on the evolutionary history of rodents in eastern Africa, we collected numerous samples of the *A. spinosissimus* complex from 40 localities in Tanzania, Zambia, Malawi and Mozambique. This material significantly improves previous genetic data (a total of 27 localities by Barome et al., 2001 and Verheyen et al., 2011) as (1) it includes specimens from large geographic areas not covered by DNA sequences in previous studies, and (2) it was genotyped at both mitochondrial and nuclear markers. Through a combined analysis of the newly collected samples and previously published data, we provide a detailed description of the distribution of genetic variability in the complex over the Zambezi bioregion and characterise the climatic niches of different taxa. Ecological niche modelling and dated phylogeny are then used to reconstruct historical evolutionary processes affecting open habitats in south-eastern Africa during the Plio-Pleistocene.

Material and methods

Sampling

The analysis is based on 102 *Acomys* specimens sampled from 67 localities in Mozambique, Tanzania, Zambia and Malawi (Fig. 1, Supplementary material S1). The mice were caught using a range of traps and tissue samples (usually spleens) were stored in 96% ethanol in the genetic bank of the Institute of Vertebrate Biology of the Czech Academy of Sciences, Brno (Czech Republic). Ethanol-preserved voucher specimens were deposited in the collection of the University of South Bohemia in České Budějovice (Czech Republic). All fieldwork complied with legal regulations in the respective African countries and sampling was carried out in accordance with local legislation (see Acknowledgements). The new material (64 genotyped individuals) was complemented with genetic data of 38 previously sequenced and georeferenced individuals from the *A. spinosissimus* complex (Barome et al., 2001; Colangelo et al., 2007; Verheyen et al., 2011) downloaded from GenBank (Supplementary material S1).

Genotyping

DNA was extracted using the DNeasy Blood & Tissue kit (Qiagen, Hilden, Germany) following the manufacturer's instructions. The mitochondrial gene for cytochrome *b* (*CYTB*) and parts of three nuclear genes (*IRBP*, *RAG1*, *GHR1*) were amplified by polymerase chain reaction (PCR) using the primers and protocols specified in Table S2A (Supplementary material S2). Purified PCR products were Sanger sequenced in both directions using the BigDye Terminator chemistry (Life Technologies). The new sequences are available in GenBank under accession numbers MG434378–MG434430 (*CYTB*), MG434350–MG434362 (*IRBP*), MG434431–MG434450 (*RAG1*), and MG434363–MG434377 (*GHR1*).

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