



Reticulate Pleistocene evolution of Ethiopian rodent genus along remarkable altitudinal gradient



Josef Bryja^{a,b,*}, Danila Kostin^{c,d}, Yonas Meheretu^e, Radim Šumbera^f, Anna Bryjová^a, Mohammed Kasso^g, Ondřej Mikula^a, Leonid A. Lavrenchenko^c

^a Institute of Vertebrate Biology of the Czech Academy of Sciences, Brno, Czech Republic

^b Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

^c A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow, Russia

^d N.K. Koltsov Institute of Developmental Biology of the Russian Academy of Sciences, Moscow, Russia

^e Department of Biology, College of Natural and Computational Sciences, Mekelle University, Tigray, Ethiopia

^f Department of Zoology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

^g Department of Biology, Dire Dawa University, Ethiopia

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ABSTRACT

The Ethiopian highlands are the most extensive complex of mountainous habitats in Africa. The presence of the Great Rift Valley (GRV) and the striking elevational ecological gradients inhabited by recently radiated Ethiopian endemics, provide a wide spectrum of model situations for evolutionary studies. The extant species of endemic rodents, often markedly phenotypically differentiated, are expected to possess complex genetic features which evolved as a consequence of the interplay between geomorphology and past climatic changes. In this study, we used the largest available multi-locus genetic dataset of the murid genus *Stenocephalemys* (347 specimens from ca 40 localities across the known distributional area of all taxa) to investigate the relative importance of disruptive selection, temporary geographic isolation and introgression in their adaptive radiations in the Pleistocene. We confirmed the four main highly supported mitochondrial (mtDNA) clades that were proposed as four species in a previous pilot study: *S. albipes* is a sister species of *S. griseicauda* (both lineages are present on both sides of the GRV), while the second clade is formed by two Afro-alpine species, *S. albocaudata* (east of GRV) and the undescribed *Stenocephalemys* sp. A (west of GRV). There is a clear elevational gradient in the distribution of the *Stenocephalemys* taxa with two to three species present at different elevations of the same mountain range. Surprisingly, the nuclear species tree corresponded only a little to the mtDNA tree. Multispecies coalescent models based on six nuclear markers revealed the presence of six separate gene pools (i.e. candidate species), with different topology. Phylogenetic analysis, together with the geographic distribution of the genetic groups, suggests a complex reticulate evolution. We propose a scenario that involves (besides classical allopatric speciation) two cases of disruptive selection along the elevational ecological gradient, multiple crosses of GRV in dry and cold periods of the Pleistocene, followed by hybridization and mtDNA introgression on imperfect reproductive barriers. Spatial expansion of the currently most widespread “*albipes*” mtDNA clade was followed by population fragmentation, lineage sorting and again by hybridization and mtDNA introgression. Comparison of this genetic structure to other Ethiopian endemic taxa highlight the geographical areas of special conservation concern, where more detailed biodiversity studies should be carried out to prevent many endemic taxa from going extinct even before they are recognized.

1. Introduction

The Ethiopian highlands provide a wide spectrum of model situations for evolutionary studies. The two main blocks of the Ethiopian central plateau (900–4500 m a.s.l.), which represent the most extensive complex of mountainous habitats in Africa, are separated by the Great

Rift Valley (GRV). Its bottom is nowadays covered by dry savannah and lakes, which represent important barriers to gene flow for most Afro-montane species. Similarly, river valleys (e.g. Blue Nile or Omo Rivers) may form further geographic barriers for the dispersal of species adapted to highland conditions. The Afro-alpine ecosystem occurs above ca 3300 m a.s.l. and is currently very fragmented, which offers

* Corresponding author at: Institute of Vertebrate Biology of the Czech Academy of Sciences, Research Facility Studenec, Studenec 122, 675 02 Koněšín, Czech Republic.
E-mail address: bryja@brno.cas.cz (J. Bryja).

another opportunity for allopatric speciation of taxa adapted to this zone. Steep altitudinal gradients in environmental conditions provide strong selective forces for the evolution of morphological and physiological adaptations. In Ethiopia, such gradients, from dry lowland woodlands, through humid montane forests and ericaceous bushlands to Afro-alpine moorlands, are well developed and afford suitable conditions for parapatric ecological speciation (Nosil, 2012), which seems to be generally rare in nature. Recently radiated groups of Ethiopian organisms with low dispersal rates and strong affinities to particular habitats (like small non-flying vertebrates) can thus provide suitable models for studies of a wide spectrum of microevolutionary problems.

Climatic changes in the Plio-Pleistocene repeatedly and remarkably shifted vegetation zones along elevational gradients in Ethiopia (reviewed e.g. in Yalden and Largen, 1992), which, for example, allowed the (re-)connections of otherwise isolated patches of Afro-alpine habitats and distributional overlap among taxa adapted to various parts of the elevational gradient. If complete reproductive barriers had not yet been evolved, these contacts might have resulted in genetic admixture and introgression of genomic segments. The most frequently described example is the case of mtDNA introgression that may be adaptive in particular situations (e.g. Boratyński et al., 2014). The presence of cyto-nuclear discordances is an emerging pattern in studies of latitudinal range shifts (caused by Pleistocene glacial cycles) between hybridizing species (e.g. hares - Melo-Ferreira et al., 2005; brown vs. polar bears - Cahill et al., 2013). Much less is known about possible hybridization along a strong elevational gradient, but it is assumed that climatic changes can cause elevational shifts in the distribution of species, which may lead to similar patterns of cyto-nuclear discordance. In a recent study, Pereira et al. (2016) provided evidence of discordance between mitochondrial and nuclear markers in parapatric taxa of the fire salamanders, suggesting nuclear-mediated gene flow across contact zones at elevation gradient. These results suggest that while some genomic regions may follow morphologic species traits and retreat to isolated mountain tops, other genomic regions may flow across parapatric boundaries, sometimes leading to a complete genetic merger. Such situations offer natural laboratories to study the adaptive relevance of mtDNA evolution. The adaptive nature of mtDNA introgression has been suggested for numerous taxa, but based solely on patterns of DNA polymorphism, and disentangling the relative contribution of neutral demography and natural selection remains a challenge (Boratyński et al., 2014; Good et al., 2015).

Due to long-term evolution in geographical isolation, the Ethiopian highlands harbour numerous endemic taxa, including 36 mammal species (Bekele and Yalden, 2013). There are even several endemic mammal genera, the most emblematic being the gelada baboon (*Theropithecus gelada*). Several genera, previously considered to be endemic, were recently found to represent internal lineages of otherwise widespread African groups that considerably modified their phenotype in response to the specific environment at high elevation (Meheretu et al., 2015; Lavrenchenko et al., 2017), however there are still some mammalian lineages that evolved and differentiated only in the Ethiopian highlands. One such lineage is the rodent genus *Stenocephalemys*, which consists of four recognized species that evolved in isolation in the Ethiopian highlands (with very limited records from Eritrea; Monadjem et al., 2015) at least since the early Pliocene (5.2–7.3 Mya estimated by Lecompte et al., 2005). These rodents are widespread and abundant across the highlands, inhabiting various environments from forests to Afro-alpine moorlands, so they represent an excellent model to study evolutionary processes in the Ethiopian centre of endemism. Based on pilot studies (e.g. Lavrenchenko et al., 1999; Lavrenchenko and Verheyen, 2006), it seems that their distribution is affected principally by two main factors: (1) the elevational gradient with associated habitats/vegetation, which is the most pronounced in the Bale Mountains, and (2) the presence of the GRV, separating the western and eastern mountain blocks.

By using the largest available multi-locus genetic dataset of the

genus *Stenocephalemys*, we provide the first evidence for its very complex Pleistocene evolution. The aims of this study were: (1) to analyse the phylogeographic patterns of the genus in Ethiopia using a combination of mitochondrial, nuclear and karyological information, i.e. we described the distribution of genetic lineages in relation to elevation and geomorphological features (e.g. GRV and mountain blocks separated by river valleys). In addition, we also reviewed current taxonomic views and the distribution of particular taxa. (2) To compare mitochondrial and nuclear patterns and evaluate alternative scenarios for the evolution of mito-nuclear discordances. (3) Available pilot data from mitochondrial sequences (Lavrenchenko and Verheyen, 2006) did not support the ecological gradient speciation model (Lavrenchenko, 2011). Because the same pattern can have multiple explanations (e.g. mtDNA introgression or convergent evolution of mitochondrial genes), we reassessed the alternative scenarios of ecological vs allopatric diversification of organisms living in the Ethiopian highlands.

2. Material and methods

2.1. Sampling

For this study, we used data from 347 specimens of *Stenocephalemys* genotyped for at least one genetic marker, including seven individuals whose sequences were available in GenBank (see Supplementary data 1 for more details on analysed material). All but six specimens were collected by authors and their collaborators at ca 40 localities across the Ethiopian highlands (Fig. 1, Supplementary data 1), which represents the most comprehensive available material of all *Stenocephalemys* taxa, covering most of their known distribution area in Ethiopia. The tissue samples were stored in 96% ethanol or DMSO until DNA extraction. All fieldwork complied with legal regulations in Ethiopia and sampling was carried out with the permission of the Ethiopian Wildlife Conservation Authority and the Oromia Forest and Wildlife Enterprise (see details in Acknowledgements).

2.2. Genotyping

DNA was extracted by commercial kits and all samples were genotyped for the mitochondrial gene for cytochrome *b* (*CYTB*). Based on preliminary phylogenetic analyses of *CYTB*, we selected individuals representing each mitochondrial clade for reconstructions of nuclear phylogeny using six markers, i.e. *IRBP*, *DHCR*, *WLS*, *RAG*, *SMO*, *NADSYN*. For more details on the used markers (including primer sequences and PCR protocols) see Table S1 in Supplementary data 2. All new sequences were submitted to GenBank under accession numbers MF685433-MF685517 (*CYTB*), MF685610-MF685685 (*IRBP*), MF685518-MF685609 (*DHCR*), MF685851-MF685879 (*WLS*), MF685729-MF685793 (*RAG*), MF685794-MF685850 (*SMO*), and MF685686-MF685728 (*NADSYN*) (see Supplementary data 1). The selected specimens were karyotyped by the standard field procedure used previously for chromosome studies of Ethiopian rodents (e.g. Lavrenchenko et al., 2011). Bone marrow chromosome preparations were stained routinely by Giemsa in a phosphate buffer with pH = 7.0. Basic parameters of the newly prepared karyotypes (2n and Nfa) were then compared with previously published data (Lavrenchenko et al., 1999; Bulatova and Lavrenchenko, 2005).

2.3. Mitochondrial phylogeny, haplotype network and sequence divergence

In the first step, we reconstructed the mitochondrial phylogeny by the Bayesian Inference (BI) and maximum likelihood (ML) approaches. The *CYTB* sequences were edited and aligned in Geneious 9.0.5 (Biomatters, Ltd.) producing a final alignment of 1140 bp. The FindModel web application (<http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html>) was used to identify the most appropriate substitution model. The Akaike information criterion (AIC),

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