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Rodents of Choke Mountain and surrounding areas (Ethiopia): the Blue Nile gorge as a strong biogeographic barrier

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Abstract. Faunal studies of rodent assemblages from the areas on and around Choke Mountain (north-western Ethiopia) were conducted during two field seasons in 2012 and 2018. Here we present results of a genetic study of nine rodent species, and evaluate their genetic diversity and evolutionary relationships between conspecific populations from neighbouring montane massifs. Results of comparative analysis of phylogeographic patterns in *Lophuromys*, *Desmomys*, *Stenocephalemys* and *Tachyoryctes* have emphasized the role of the Blue Nile gorge as a strong biogeographic barrier, separating “northern” and “southern” independently evolved populations. Results of genetic analysis also revealed the presence of a new taxon of *Dendromus*, presumably belonging to a new species. Our study allows re-evaluation this area as an important “hotspot” of Ethiopian small mammal biodiversity.

Key words: biogeography, Ethiopian highlands, *Lophuromys*, *Stenocephalemys*, small mammals

Introduction

The Ethiopian highlands comprise 80% of the landmass of Africa above 3000 m a.s.l. (Siebert & Ramdhani 2004). Unusual topographic and biogeographic features of the “roof of Africa” have create conditions favouring speciation in a number of taxa. Although the species composition of the region and phylogenetic relationships among species are now relatively well known (Bryja et al. 2019 and references therein), subtle intraspecific

phylogeographic patterns in many taxa remain poorly characterised and this is especially true for rodent species, which occupy small isolated habitats. Since rodent species can be difficult to identify due to absence of diagnostic morphological features, identification based on genetic analysis often represents the only way to understand their taxonomic and genetic diversity.

Choke Mountain (with its highest peak at 4080 m a.s.l.) lies north from the Great Rift Valley at the

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north-western edge of the Ethiopian plateau. It is surrounded by the Blue Nile Valley (Fig. 1), which is hypothesized to be a biogeographic barrier, especially at the south where the walls of the canyon form an almost vertical gorge. Despite isolation of the Afro-alpine habitats of Choke Mountain from other montane massifs of the north-western plateau (e.g. Guna, Semien, Abohoy Gara; Fig. 1), a nearly continuous Afro-alpine environment to the north from the Great Rift Valley during the Last Glacial Maximum has been proposed approximately 18 kya (Bryja et al. 2018). As a consequence, a relatively high genetic similarity of conspecific populations from different montane massifs of north-western plateau is predicted. Indeed, preliminary data supports this pattern not only in different rodent groups (Bryja et al. 2018 – *Stenocephalemys*; Bryja et al. 2019 – *Arvicanthus*; Lavrenchenko et al. 2004 – *Lophuromys*) but also for several large mammals, such as the gelada baboon (Belay & Mori 2006) and Ethiopian wolf (Gottelli et al. 2004). This latter work has also shown not only genetic differences between population from the opposite sides of the Great Rift Valley, but also close relationships between mitochondrial haplotypes of Ethiopian wolf populations from the Choke and Guna Mountains.

Due to the absence of iconic large mammal species on Choke Mountain; the Ethiopian wolf went extinct several decades ago (Yalden & Largen 1992), this territory has received relatively little attention in comparison to other Ethiopian montane massifs (e.g. Simien or Bale Mountains National Parks). Available data concerning small mammal diversity of Choke Mountain are scarce (Simeneh 2016) and sometimes erroneous due to species misidentification. Nonetheless, understanding the composition and genetic diversity of the species occupying such isolated “islands” can contribute not only to addressing local conservation management questions (e.g. reintroduction of the Ethiopian wolf) but can also contribute to understanding more general evolutionary processes that have shaped contemporary biodiversity in this presumed hotspot of Ethiopian endemism.

In addition, solitary specimens of rare and morphologically distinct rodents are known from areas neighbouring Choke Mountain. One is the Ethiopian amphibious rat *Nilopegamys plumbeus*, known from a single specimen, collected near the source of the River Little Abbay in 1927. This species represents a monotypic genus possessing unique adaptations to an aquatic habit (Peterhans

& Patterson 1995) and apparently one of the few (together with *Colomys goslingi* and possibly also the genus *Malacomys*) semi-aquatic rodents in Africa. Other endemic rodent species include Cheesman’s vlei rat *Otomys cheesmani*, described on the basis of collection made in vicinity of Dangla in 1937 (Taylor et al. 2011). The phylogenetic relationships and precise systematic position of these two species remain unclear, and data on their biology are almost absent. The search for these critically endangered (if not extinct) species is, thus, critical for specific conservation projects.

This paper summarises recently collected data and provides the first comprehensive analysis of rodents living on and around Choke Mountain, including their genetic diversity and biogeographic affinities with other parts of the Ethiopian highlands. Describing the evolutionary uniqueness of mammals on Choke Mountain also serves to illustrate the necessity of nature conservation in the region without which the fragile Afro-alpine biodiversity may be irreversibly lost.

Material and Methods

Field sampling

The study was conducted on Choke Mountain (East Gojjam Zone of Amhara National Regional State) located in the north-west of the Ethiopian plateau (Fig. 1). Samples were collected at six localities at and around Choke Mountain during two expeditions in 2012 and 2018 (Table 1). Terrestrial rodents were captured using Sherman live traps (230 × 95 × 80 mm) baited with sliced carrot and sunflower oil and/or peanut butter. In 2012, some specimens were also collected using snap-traps of two different sizes baited with peanut butter. Root-rats were trapped using hand-made traps or by traditional methods following recommendations by local people. All captured specimens were weighed and measured (body, tail, ear and hind foot lengths). Preliminary species identification based on external morphology, sex and reproductive condition were also noted. Voucher specimens for each species were sacrificed by cervical dislocation and dissected. For each sacrificed individual, tissue samples from heart, kidney, spleen and muscle were preserved in 96% ethanol and deposited for further genetic work in the A. N. Severtsov Institute of Ecology and Evolution RAS (Moscow, Russia) and Institute of Vertebrate Biology CAS (Brno, Czech Republic). Representative samples of skulls and skins were deposited in the Zoological Natural

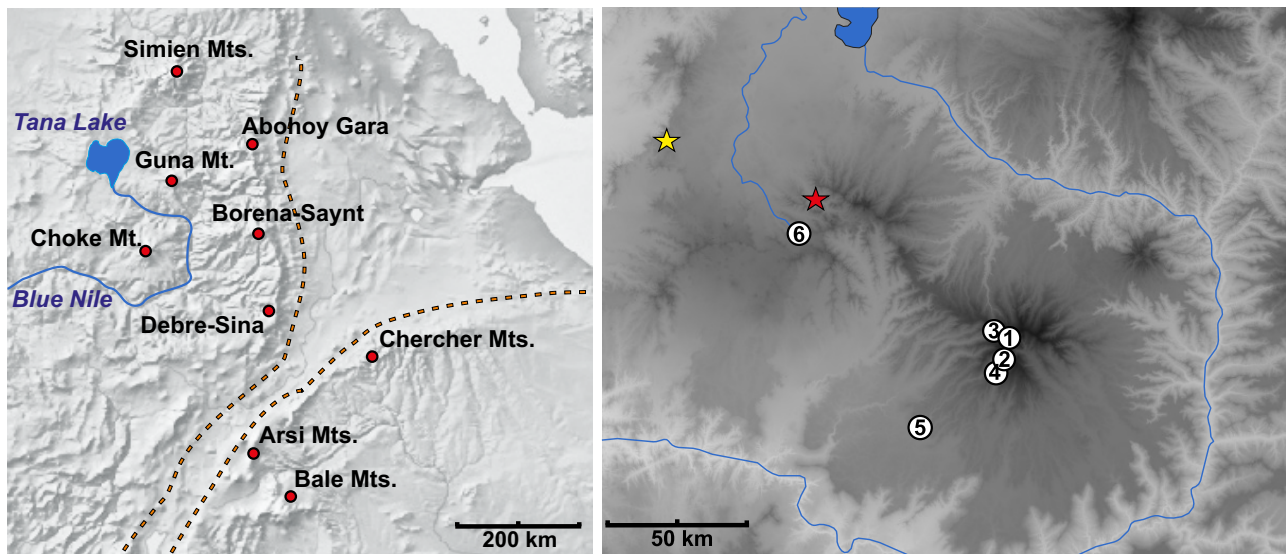


Fig. 1. Left picture: topography of the main Ethiopian montane systems mentioned in the text. Dotted orange lines schematically denote borders of the Great Rift Valley. Right picture: Choke Mountain and neighbouring areas. 1-6 – study sites (see Table 1). A red star denotes the type locality of *Nilopegamys plumbeus*, yellow star – type locality of *Otomys cheesmani*.

History Museum of Addis Ababa University and Zoological Museum of Moscow State University (Moscow). All fieldwork was performed following legal regulations in Ethiopia and permission of the Department of Biology of the Debre-Markos University, the Environment, Forest and Wildlife Protection and Development Authority of the Amhara National Regional State, and the Ethiopian Wildlife Conservation Authority.

Genotyping and mtDNA data analysis

DNA was extracted using commercial kits, and all specimens were genotyped at the mitochondrial cytochrome *b* gene (*cytb*) using a standard protocol described in Lavrenchenko & Verheyen (2006). PCR products were commercially sequenced using the Sanger method (Evrogen, Russia). To uncover phylogenetic relationships within each genus we aligned new sequences with available data from GenBank or unpublished sequences obtained by

our teams in Ethiopia over the last few years. All barcoded sequences and those used in comparative analyses are presented in Table S1 with additional information including GenBank accession numbers. A total of 168 *cytb* sequences were analysed. To assess levels of genetic differences among distinct populations we used uncorrected *p*-distances calculated in Mega X (Kumar et al. 2018). To estimate phylogenetic relationships among *cytb* sequences we constructed median-joined network using PopArt (downloaded on 15.5.2016 from <http://popart.otago.ac.nz>). Maps illustrating geographical distribution of haplogroups were constructed in QGIS.

Results and Discussion

Species composition

In total, 195 rodent specimens were collected (Table 2). Genetic analysis revealed the presence of nine rodent species: *Lophuromys simensis*, *Arvicanthis*

Table 1. Characteristics of the study sites.

| Locality | Coordinates |
|--|--------------------|
| 1 Top of Choke Mountain, Afro-alpine vegetation. 3961 m a.s.l. | 10.704 N, 37.845 E |
| 2 Southern slope of Choke Mountain, border of the Afro-alpine vegetation and ericaceous belt. 3780-3677 m a.s.l. | 10.637 N, 37.835 E |
| 3 Northern slope of Choke Mountain, village, agricultural fields. 3510 m a.s.l. | 10.728 N, 37.798 E |
| 4 Southern slope of Choke Mountain, Abaza, grazed montane meadows with ericaceous vegetation. 3421 m a.s.l. | 10.596 N, 37.804 E |
| 5 Dry forest near the town of Debre-Markos. 2342 m a.s.l. | 10.420 N, 37.563 E |
| 6 Sakalla area, riverine forest of the one of the River Blue Nile tributaries. 2372 m a.s.l. | 11.033 N, 37.180 E |

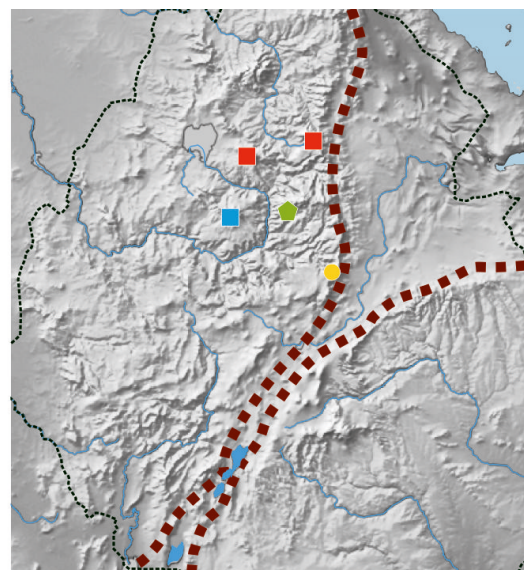
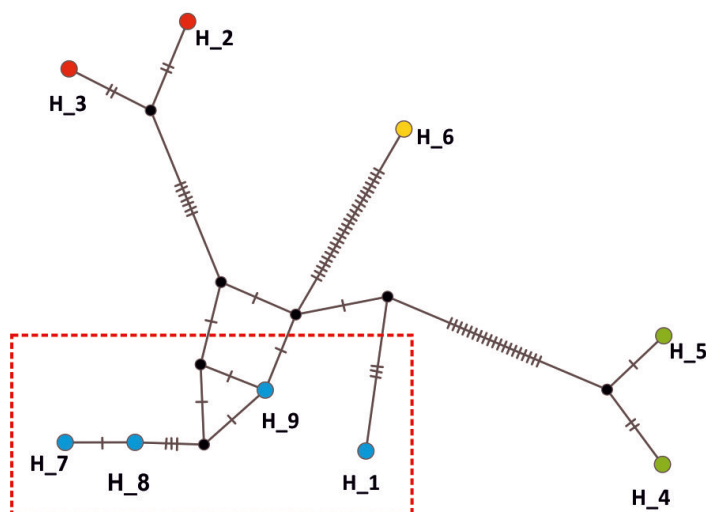


Fig. 3. Phylogenetic relationships and geographical distributions of the *Arvicanthis abyssinicus* mitochondrial lineages. Dotted lines schematically denote borders of the Great Rift Valley. Red dotted rectangle on the network denotes haplotypes from Choke Mountain. Note that population from Debre Sina with mtDNA of *A. abyssinicus* (yellow circle) requires further investigation as it might be of hybrid origin (see Bryja et al. 2019).

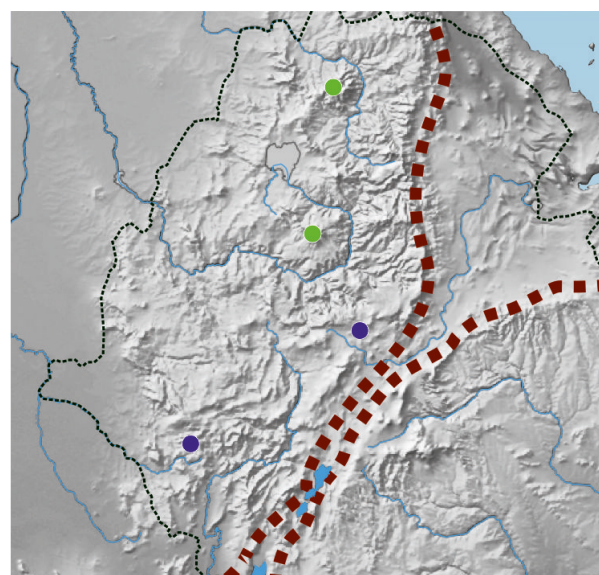
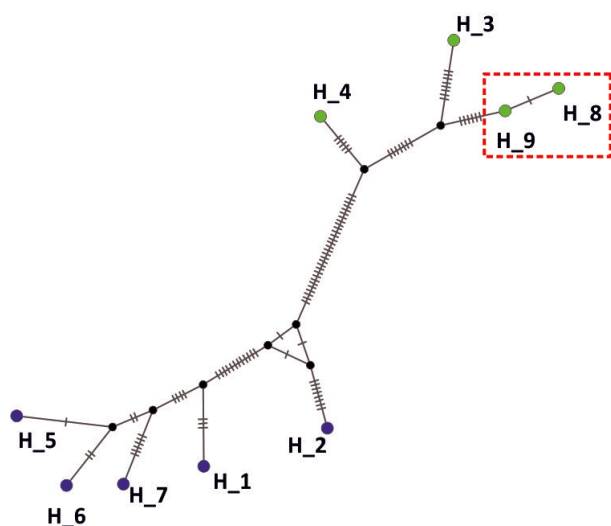


Fig. 4. Phylogenetic relationships and geographical distributions of the *Desmomys harringtoni* mitochondrial lineages. Dotted lines schematically denote borders of the Great Rift Valley. Red dotted rectangle on the network denotes haplotypes from Choke Mountain.

et al. 2019) have similar mitochondrial haplotypes, which probably reflects a result of ancient mtDNA introgression. Analysis of the *cytb* sequences of *L. simensis* individuals from Choke Mountain revealed that all specimens comprise a species-specific mitochondrial lineage 'North I' (sensu Lavrenchenko et al. 2004) (Fig. 2). Apparently introgressed from *L. menageshae*, mitochondrial lineage 'North II' (Lavrenchenko et al. 2004, 2007) likely spread along the left bank of the Blue Nile up to Guna Mountain (where it co-exists with 'North I') and the Simien Mountains (where exclusively 'North II' was found). Notably we failed to find the 'North II' lineage on and around Choke Mountain

suggesting that has probably not crossed the Blue Nile gorge (Fig. 2).

Subfamily Murinae

Ethiopian grass rat – *Arvicanthis abyssinicus* (Rüppel, 1842)

This species was abundant in the Afro-alpine habitats at the top of Choke Mountain (Table 2). The genus *Arvicanthis* represents a group of morphologically uniform species that can be differentiated mainly by their chromosomal and genetic features (Bryja et al. 2019). Molecular analysis based on *cytb* sequences allowed to assign sampled specimens to *A. abyssinicus*, a grass rat

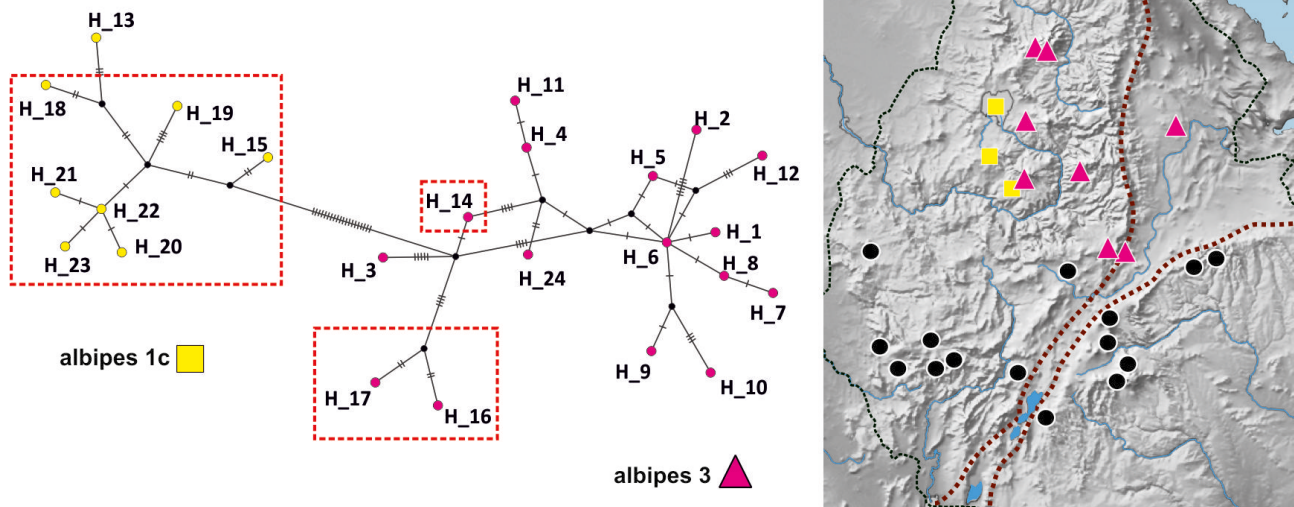


Fig. 5. Phylogenetic relationships and geographical distributions of the *Stenocephalemys albipes* mitochondrial lineages. Dotted lines schematically denote borders of the Great Rift Valley. Other mitochondrial lineages of this species are shown by black circles. Red dotted rectangles on the network denote haplotypes from Choke Mountain. Names of lineages are given according to Bryja et al. (2018).

species abundant on high elevation plateaus in the north-western part of the Ethiopian highlands. Haplotypes from the Choke Mountain form a separate haplogroup, but are closely related ($p = 2.04 \pm 0.39\%$ at *cytb*) with populations from neighbouring mountain massifs (Guna and Abohoy Gara), separated by the Blue Nile Valley (Fig. 3).

Harrington's scrub rat – *Desmomys harringtoni* (Thomas, 1902)

Molecular analysis of the two trapped individuals revealed that they are much closer to conspecifics from the Simien Mountains ($p = 1.79 \pm 0.33\%$) than to populations from the Menagesha and Tepi Forests in central and south-west Ethiopia, respectively ($p = 6.04 \pm 0.69\%$). Thus, it seems that the Blue Nile gorge again represents strong biogeographic barrier defining genetic variability within species (Fig. 4).

Natal multimammate mouse – *Mastomys natalensis* (A. Smith, 1834)

Ethiopian *Mastomys* include three morphologically indistinguishable species differentiating only on the basis of genetic differences (Martynov & Lavrenchenko 2018, Martynov et al. 2020). *Mastomys natalensis* is widespread throughout sub-Saharan Africa except deserts, tropical moist forests, and highlands (Bryja et al. 2019). It represents one of the major vertebrate agricultural pests (Leirs 1994) and can serve as a reservoir and vector of important pathogens like arenaviruses and plague bacteria (Isaacson et al. 1981, Gratz 1997, Lecompte et al. 2006, Göuy de Bellocq et al.

2020). In Ethiopia, *M. natalensis* is widespread on the north-western plateau and it was also found in a single locality at the bottom of the Ethiopian Rift Valley (Martynov et al. 2020). During our survey we captured two individuals of *M. natalensis* at site 5, which is the highest documented altitude (2330 m a.s.l.) for this species in Ethiopia. The species has a clear intraspecific structure with six main mtDNA haplogroups with parapatric distribution. Captured individuals, as well as all other Ethiopian populations of *M. natalensis*, belong to the haplogroup A-III (sensu Colangelo et al. 2013, see also Martynov et al. 2020).

Ethiopian white-footed narrow-headed rat – *Stenocephalemys albipes* (Rüppel, 1842)

The species is widespread throughout Ethiopian highlands (Bryja et al. 2019). Individuals captured at site 1 represent the highest documented altitudinal record (3840 m a.s.l.) for this species. Notably, all previous records of this species at high altitudes (the Simien Mountains, 3800 m. a.s.l.; see Bryja et al. 2018) represent commensal populations. Analysis of *cytb* revealed that individuals inhabiting Choke Mountain belong to two distinct haplogroups ($p = 3.66 \pm 0.7\%$, Fig. 5). The first, 'albipes-1c' (sensu Bryja et al. 2018), is restricted to the River Blue Nile Valley to the south of Lake Tana (including one island in the lake itself). The second, 'albipes-3' (sensu Bryja et al. 2018) is widespread in the north of the Ethiopian highlands and was found at the top of Choke Mountain (Fig. 5). Obtained results allow to suggest at least two independent colonization events of Choke Mountain by this species.

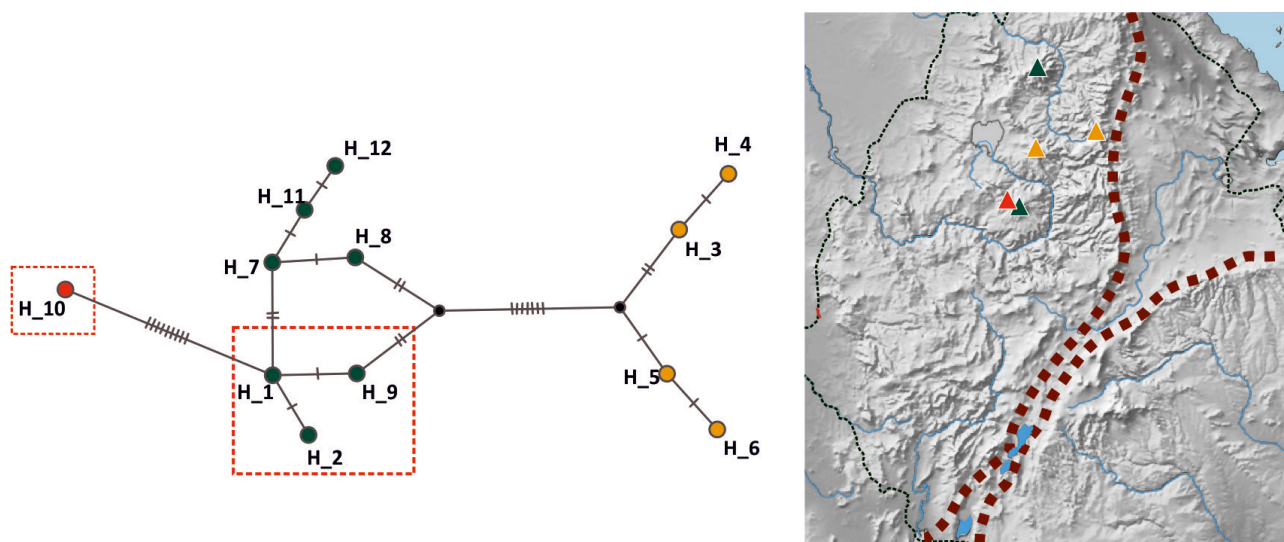


Fig. 6. Phylogenetic relationships and geographical distributions of the *Stenocephalemys* sp. A mitochondrial lineage. Dotted lines schematically denote borders of the Great Rift Valley. Red dotted rectangles on the network denote haplotypes from Choke Mountain.

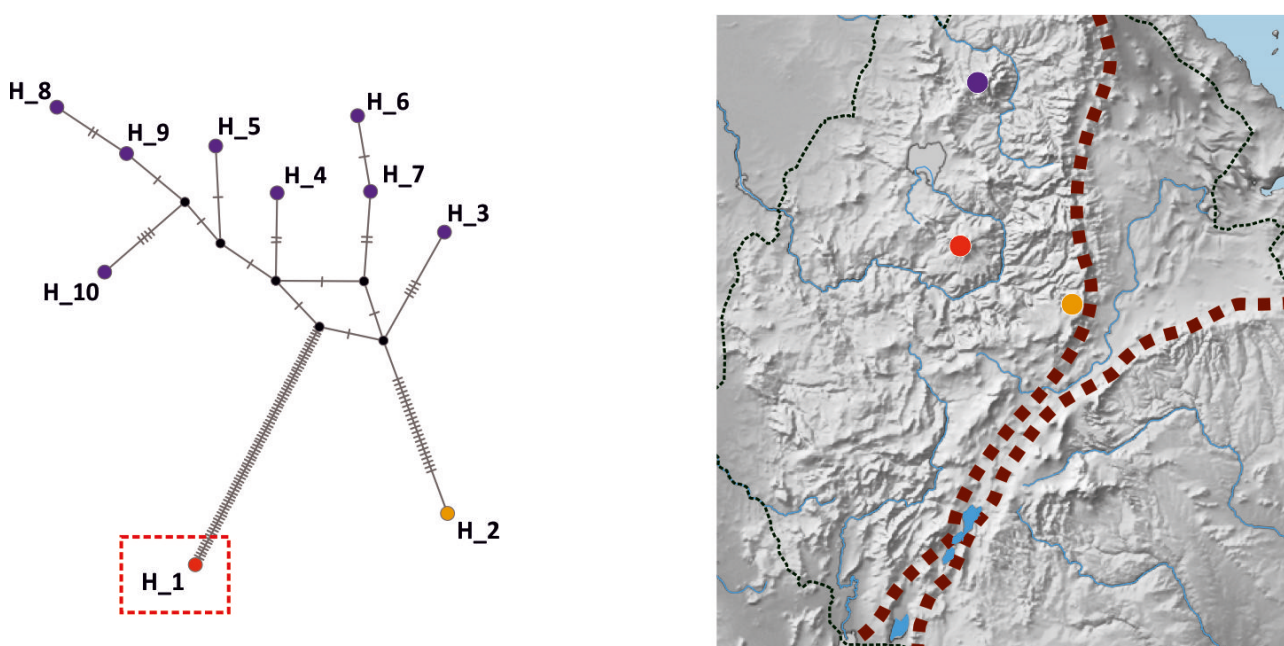


Fig. 7. Phylogenetic relationships and geographical distributions of the *Dendromus lovati* mitochondrial lineages. Dotted lines schematically denote borders of the Great Rift Valley. Red dotted rectangles on the network denote haplotypes from Choke Mountain.

Narrow-headed rat – *Stenocephalemys* sp. A (sensu Lavrenchenko & Verheyen 2006)

This species is confined to high-elevation ericaceous and Afro-alpine habitats of the north-western plateau (see Mizerovská et al. 2020, for more details and a formal description of this taxon). Results from analysis of *cytb* are in agreement with previously published data (Bryja et al. 2018). Thus, individuals from Choke Mountain show similarity with conspecifics from the Simien Mountains while the geographically closer population from Guna Mountain, on the opposite bank of the Blue Nile, clustered with specimens from Abohay Gara (Fig. 6). It is worth noting that these two

groups (green and orange at Fig. 6, differing from each other at $p = 1.93 \pm 0.42\%$ based on *cytb*) also showed differences in their chromosomal sets (Bulatova & Lavrenchenko 2005, see also Bryja et al. 2018). Interestingly, three individuals expressed a distinct haplotype ($p = 1.54 \pm 0.46\%$) representing a new mitochondrial lineage (haplogroup 'H_10' at Fig. 6).

Ethiopian vlei rat – *Otomys typus* (Heuglin, 1877)

Three representatives of this species were captured at sites 1 and 2. Preliminary molecular analysis demonstrated that specimens from Choke Mountain clustered with *O. typus* s.str. from the Simien

Mountains (not shown). However, it is worth recognising that the phylogeny and taxonomy of Ethiopian *Otomys* still remains unresolved and requires further research (Taylor et al. 2011).

Family Nesomyidae

Subfamily Dendromurinae

Lovat's African climbing mouse – *Dendromus cf. lovati* (de Winton, 1900)

One small individual of the African climbing mouse was trapped at the top of Choke Mountain (site 1). Although this specimen showed external resemblance with *D. lovati* (three black stripes on the dorsal side of the body), its *cytb* sequence revealed striking differences ($p = 9.74 \pm 1\%$) compared to other populations of *D. lovati* from Simien and Debre-Sina (blue and orange circles at Fig. 7). It is, therefore, possible that the Choke Mountain population represents a new species in this poorly studied genus. Detailed analysis of this form including chromosomal and multilocus data will be published elsewhere.

Family Spalacidae

Subfamily Tachyoryctinae

African root-rat – *Tachyoryctes splendens* (Rüppel, 1835)

Twenty individuals of this fossorial species were trapped in colonies throughout Choke Mountain (Table 2). Results of molecular analysis were in agreement with previous research (Šumbera et al. 2018) showing genetic resemblance of the Choke Mountain population with those from the north of the Blue Nile gorge ('splendens 2' sensu Šumbera et al. 2018).

Behavioural features of root-rats from Choke Mountain population were noteworthy. Unlike representatives of other *T. splendens* populations, individuals from Choke Mountain regularly use direct visual assessment of their environment and even go above ground to feed (Fig. 8). Similar behaviour is known only for morphologically distinct *T. macrocephalus* living in Afro-alpine habitats in the Bale Mountains. In their recent study, Šumbera et al. (2018) showed that *T. splendens* form a paraphyletic group, with *T. macrocephalus* as one of its internal lineages. Strikingly, populations of *T. splendens* from the Chercher Mountains belonging to the mitochondrial lineage 'splendens 1' (sensu Šumbera et al. 2018), which is sister to *T. macrocephalus*, do not possess these behavioural features (our unpublished data). Thus, there may be independent parallel evolution of this



Fig. 8. Individuals of *Tachyoryctes splendens* demonstrating behavioural elements of partially terrestrial life style. Upper picture – *Tachyoryctes splendens* feeding together with *Arvicanthis abyssinicus*. Choke Mountain, 3960-3780 m a.s.l.

behaviour, which is potentially adaptive in the open Afro-alpine habitats of root-rats from the Choke and Bale Mountains.

Complex biogeography of Ethiopian highlands and the role of the Blue Nile gorge as biogeographic barrier

Montane habitats of the Ethiopian highlands are split into two major plateaus, i.e. the north-western plateau (Abyssinian massif) and the south-eastern plateau (Harar massif), divided by the Great Rift Valley. Now covered by dry savannah, the Great Rift Valley appears to be partially or completely impassable to small-sized species adapted to Afromontane ecosystems (Mairal et al. 2017). This is reflected in the pattern of genetic diversity of different groups inhabiting Ethiopian highlands: plants (Kebede et al. 2007), frogs (Evans et al. 2011, Reyes-Velasco et al. 2018), large mammals (Gottelli et al. 2004, Belay & Mori 2006) and rodents (i.e. Lavrenchenko et al. 2004, Bryja et al. 2018, 2019, Šumbera et al. 2018). At the same time, cases of species having traversed the Great Rift Valley have been shown, even for highly specialized Afro-alpine species (*Stenocephalemys albocaudata* – Bryja et al. 2018; *Arvicanthis blicki* – Bryja et al. 2019; *Lophuromys melanonyx* – Lavrenchenko et



Fig. 9. Highly disturbed natural habitat at the type locality of *Nilopegamys plumbeus* – “small stream tributary to the Little Abbay, between Sakalla and Njabara, Gojjam, Abyssinia. Altitude 8500 ft.” (Osgood, 1928).

al. 2007). Such dispersal events may have led to secondary contacts of partially differentiated populations, hybridization and partial genomic introgression. Cases of such introgression (especially mitochondrial genomes) have been repeatedly observed at the eastern side of the north-western plateau of the Debre-Sina and Borena Saynt mountain massifs (see e.g. references for *Stenocephalemys* or *Arvicanthis* above). However, the Blue Nile gorge, lying to the north-west of the Great Rift Valley, seems to efficiently prevent gene flow between conspecific populations of Afromontane taxa (at least rodents). This pattern, more or less obvious in *Lophuromys* (Fig. 2), *Arvicanthis* (Fig. 3), *Stenocephalemys* (Fig. 6) and *Tachyoryctes* (see Šumbera et al. 2018) implicates the Blue Nile gorge as a strong biogeographic barrier for Afromontane taxa, to some extent more effective than the Great Rift Valley. In this light, the area at and around Choke Mountain, on the right bank of the Blue Nile, can be considered as the southernmost stronghold of populations representing the original genetic diversity of the north-western plateau, not affected by the introgression from the south-eastern plateau.

Two emblematic Ethiopian rodents likely extinct

The vicinity of Choke Mountain encompasses type localities of two emblematic Ethiopian endemic

rodent species: the Ethiopian amphibious rat *Nilopegamys plumbeus* Osgood, 1928 and Cheesman's vlei rat *Otomys cheesmani* Taylor et al., 2011. During our fieldwork in 2018 we surveyed the type locality of *Nilopegamys plumbeus* (Sakalla area, 11.122 N, 37.211 E, 2300 m a.s.l., Fig. 1). While impassable to cars, we reached the location on horseback. However, instead of a “small mountain stream near the source of Little Abbay or Blue Nile”, as depicted by Osgood (1928), we found significantly altered habitats (Fig. 9), obviously unfavourable for any aquatic or semiaquatic rodent. *Nilopegamys plumbeus* has thus likely disappeared from this area or even become globally extinct. The same might be true for another endemic species known from this area – *Otomys cheesmani*, described in 2011 on the basis of specimens collected by Cheesman R.E. in the vicinity of Dangla (11.266 N, 36.58 E, 2100 m a.s.l., Fig. 1). During our survey we failed to capture any specimens of *O. cheesmani* or even locate any suitable habitats for this species in the region between the southern shore of Lake Tana and the vicinity of Debre-Markos. Taking into account that this species is associated with meadows at relatively low altitudes (2000-2500 m a.s.l., Lavrenchenko & Bekele 2017), which today are significantly altered by anthropogenic pressure, we presume that *O. cheesmani* may also be extinct.

Conservation implication

Identification and delimitation of so-called biodiversity “hot spots” is important, not only for further genetic and evolutionary studies, but also as a crucial step in the prioritisation of biodiversity conservation in the tropics. Twenty years ago, Fjeldså et al. (1999) reported a correlation between centres of endemism and ancient human cultures, suggesting that both are located in areas of long-term climatic stability. This association is especially true for Ethiopia, which is a well-known cradle of one of the most ancient sub-Saharan African cultures. Owing to an exponentially growing human population, Ethiopia now represents the second most populous country in Africa after Nigeria (<http://worldpopulationreview.com>). An outcome is a sustained loss of the natural environment. Despite the ongoing anthropogenic pressure several regions have received conservation attention and are designated as conservation areas (e.g. the Simien and Bale Mountains National Parks). Choke Mountain, in contrast, has no legal conservation status and currently suffers from overgrazing. An effect of overgrazing is likely to be local extinctions and, as a consequence, irreversible loss of Ethiopian endemic diversity. There is an increasing trend to re-examine natural history museum collections (Patterson 2001), potentially revealing cryptic species that are unrecognizable without molecular genetic data (Baker & Bradley 2006). Faunal surveys of regions showing high biodiversity are imperative for improve our understanding

of the complex interactions between evolution and ecology that drive taxonomic diversity. Finally, a welcome development is that Choke Mountain has recently been officially protected as a community-based conservation area by the regional government. This change offers hope that this unique natural area and its remaining biodiversity will be preserved in the face of rapid environmental modification.

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Supplementary online material

Table S1. List of sequenced individuals, GenBank numbers, and sampling details (<https://www.ivb.cz/wp-content/uploads/JVB-vol.-69-2-2020-Kostin-et-al.-Table.S1.xlsx>).