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Annotated checklist, taxonomy and distribution of rodents in Ethiopia

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Abstract. We provide an annotated checklist of rodents of Ethiopia. For each species we show a distributional map based on critically revised data from: (1) published literature; (2) museum collections, including records in the Global Biodiversity Information Facility (GBIF); and (3) recent field surveys performed in the last three decades as part of the Joint Ethio-Russian Biological Expedition (JERBE) and Ethio-Czech Research Projects. In most cases recent material was analysed in detail using genetic and/or morphometric approaches. In total, the Ethiopian rodent fauna consists of 104 species (40 genera, 10 families). Compared to previous studies we were not able to confirm the presence of 12 species, probably due to a lack of data from arid lowland areas, though some of these species may be extinct. We report the occurrence of > 40 species not previously included in a checklist published in 1996 (with many species still requiring formal description). Of the total number of species recorded, a high proportion are endemics of Ethiopian Highlands (43 species = 41.3 %), followed by those living in Somali-Masai (27) and Sudanian (13) savanna. The checklist confirms an unusually high level of Ethiopian rodent biodiversity, which should serve as a basis for conservation.

Key words: biodiversity, Ethiopian Highlands, biogeography, Somali-Masai savanna, Sudanian savanna, Rodentia

Introduction

Importance of accurate knowledge of the distribution of biodiversity

Biodiversity is not distributed equally on the Earth. Some geographical areas have higher diversification rates than others (due to diverse geomorphology, the important role of climate change in past diversification, steep ecological gradients, etc.) or they harbour higher diversity simply because they have been stable over long periods of time (i.e. the extinction rate is low). These areas are referred to as biodiversity hot-spots and they should be priority sites for nature conservation (Mittermeier et al. 2011). However, the estimation of spatial biodiversity patterns and predictions of future changes are most often based on species distributions, which can be wrong for several reasons: (i) they are based on incorrect/incomparable species delimitations, even in well studied taxa like mammals; and (ii)

distributional data for well-delimited species are scarce and frequently not correct.

Rodents are generally good indicators of local biodiversity levels, because of their specialization to particular types of ecosystems and their low dispersal ability. Despite intensive progress in recent decades the alpha-taxonomy of small mammals in tropical Africa is still dynamically changing and the distribution of taxa defined by integrative taxonomy is poorly known (Monadjem et al. 2015). This lack of knowledge is likely to affect subsequent analyses of spatial biodiversity patterns, and it is therefore important to have reliable information on the distributions of particular taxa. Besides the protection of areas with high and endemic biodiversity, this knowledge can have other practical consequences for humans, e.g. in the epidemiology of rodent-borne diseases. The correct host identification and knowledge of

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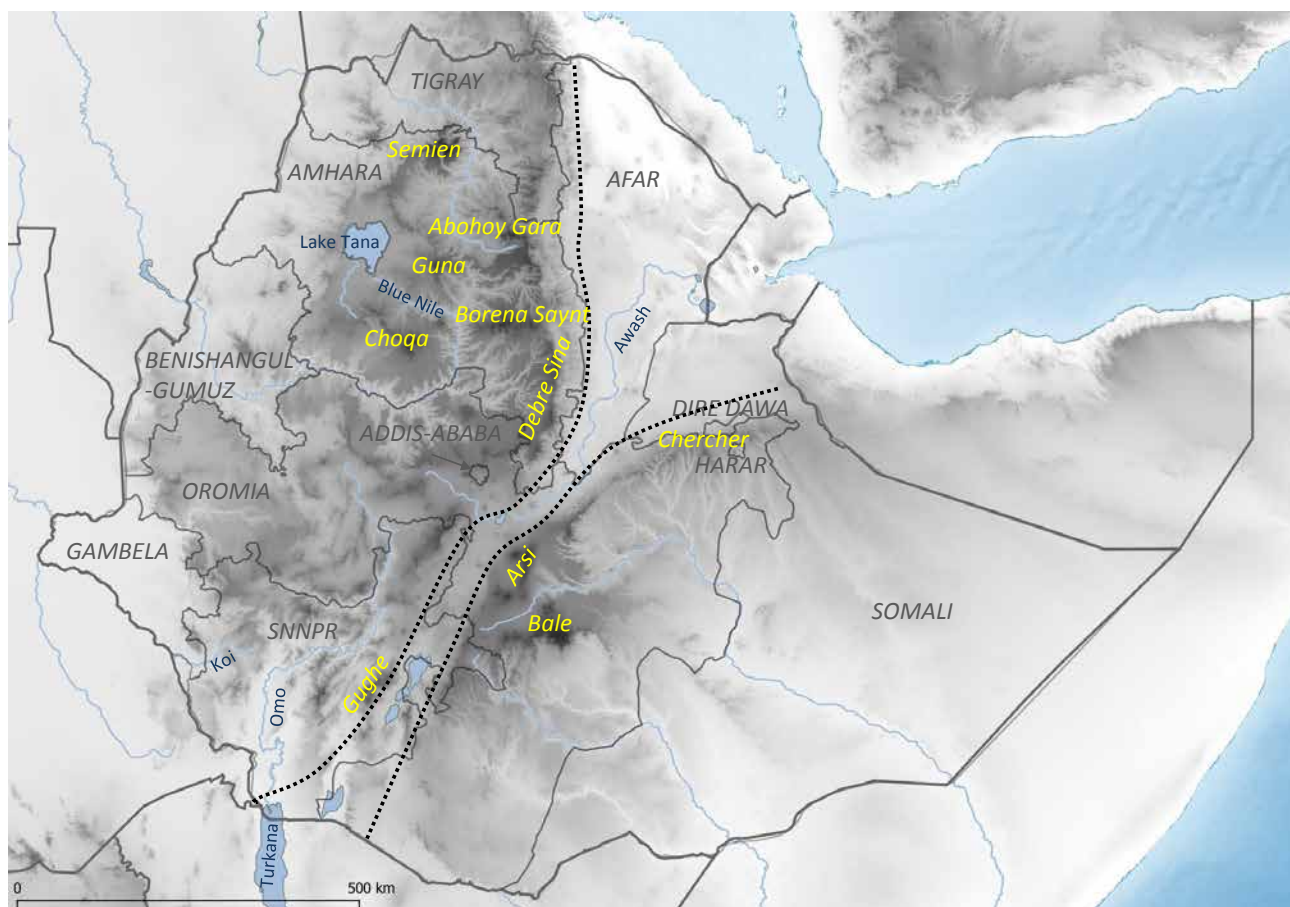


Fig. 1. Geographical map of Ethiopia with major geomorphological features. Dark grey lines and corresponding names in capitals indicate 11 regional states of Ethiopia (SNNPR = Southern Nations, Nationalities, and Peoples' Region); major mountain ranges are in yellow; large rivers and lakes are in dark blue. Two dotted lines delimit the Great Rift Valley, separating the Ethiopian Highlands into south-eastern and north-western blocks.

its distribution are necessary for predictions of occurrence of host-specific pathogens and disease outbreaks (e.g. Gryseels et al. 2017). Rodents are also important agricultural pests and the use of species-specific pest-control methods (e.g. contraceptives) is the most promising way in managing such damages (e.g. Massawe et al. 2018).

Biogeography of Ethiopia

Ethiopia (Fig. 1) is a geomorphologically very diverse country, which is reflected in the diversity of ecosystems and vegetation types. The most conspicuous feature of Ethiopian geomorphology is the large area of mountains. More than 15 % of Ethiopia is above 2000 m a.s.l. and 2 % above 3000 m a.s.l. In other words, 50.4 % of the Afrotropics above 2000 m a.s.l. (and 79.7 % above 3000 m a.s.l.) is located in the territory of Ethiopia (Yalden 1983). The potential natural vegetation (Lillesø et al. 2011) can be grouped into several major types (Fig. 2). The Ethiopian Highlands (green, grey and white in Fig. 2) have a well-developed elevational gradient.

Various types of forests dominate at lower elevations (with evergreen bushland and thicket at the lower margin), while the highest elevations are covered by Afroalpine habitats, with the montane Ericaceous belt occurring in transitional elevation zones. The lower and drier western part of the country falls under Sudanian savanna (orange in Fig. 2), dominated by wooded grasslands with *Combretum*. In the Great Rift Valley, Afar region and south-eastern Ethiopia, the Somali-Masai savanna (yellow-beige in Fig. 2) predominates with *Acacia-Commiphora* deciduous bushland and thickets as the main vegetation types. These major types of vegetation correspond to the main biogeographical regions defined by Linder et al. (2012) on the basis of the distribution of higher vertebrates and vascular plant species. The Ethiopian Highlands belong to the Ethiopian region (subregion Ethiopia), *Combretum* savanna represents the easternmost part of the Sudanian region, and Somali-Masai savanna is the northern part of the Somalian region (subregion Somalia). Furthermore, Linder et al. (2012) also distinguished the subregion Horn within

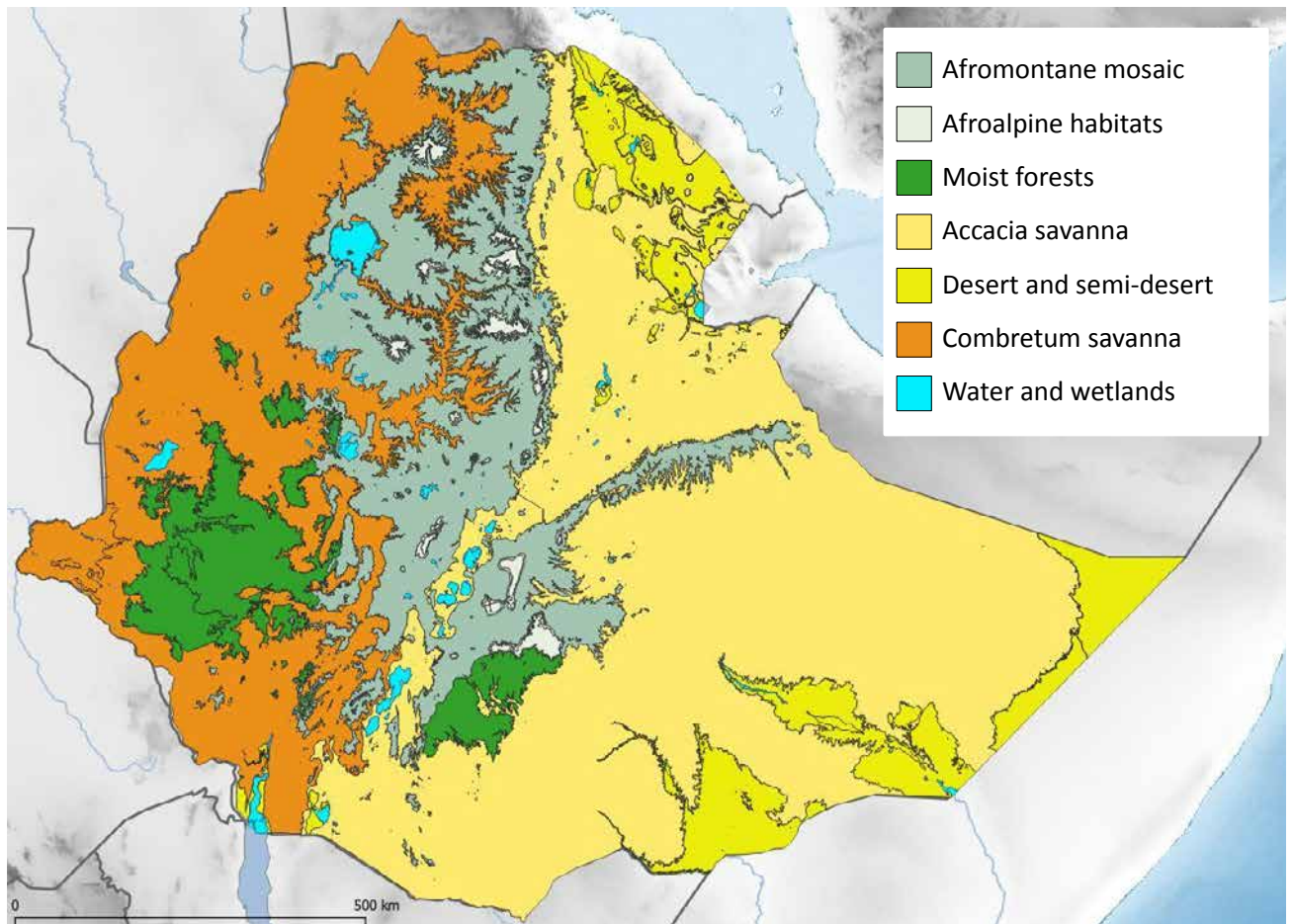


Fig. 2. Distribution of major potential natural vegetation types in Ethiopia (based on Lillesø et al. 2011). Individual vegetation types were grouped as follows: *AFROMONTANE MOSAIC*: Complex of Afromontane undifferentiated forest with wooded grasslands and evergreen or semi-evergreen bushland and thicket at lower margins. *AFROALPINE HABITATS*: Afroalpine vegetation, Montane Ericaceous belt. *MOIST FORESTS*: Afromontane rain forest, Afromontane moist transitional forest. *ACCACIA SAVANNA* (= Somali-Masai savanna): Somalia-Masai *Acacia* (= *Vachellia*)-*Commiphora* deciduous bushland and thicket, Upland *Acacia* wooded grassland, *Vachellia tortilis* wooded grassland and woodland. *DESERT AND SEMI-DESERT*: Desert, Somalia-Masai semi-desert grassland and shrubland. *COMBRETUM SAVANNA* (= Sudanian savanna): Dry *Combretum* wooded grassland, Edaphic wooded grassland on drainage-impeded or seasonally flooded soils. *WATER AND WETLANDS*: Water bodies, Freshwater swamp, Lakes with halophytic shoreline vegetation.

the Somalian region, which roughly corresponds to “Deserts and semi-deserts” in Fig. 2.

Rodents of Ethiopia

As a part of the diverse natural history, the Ethiopian vertebrate fauna is also very diverse. First, there are multiple major biogeographical regions in the Ethiopian territory (Linder et al. 2012), which is reflected in the high species diversity of the country as a whole. Second, Ethiopia is geographically close to the Afro-Arabian late Miocene land-bridge, through which the ancestors of many African groups colonized the continent from Asia (see e.g. Aghová et al. 2018 and references therein), and after the colonization they were effectively stopped from spreading further by the Ethiopian Highlands, where they diversified (e.g. genus *Mus*; Bryja et al. 2014). Third, the complex

geomorphology of the Ethiopian Highlands, e.g. the presence of the Great Rift Valley (we will use only the Rift Valley hereafter) and large rivers (e.g. the River Blue Nile), also promoted diversification processes. This was intensified by climate changes, especially during the Pleistocene, causing elevational shifts of ecosystems and leading to secondary contacts of populations evolved in allopatry, which further increased the diversity by the form of so-called reticulate evolution. The presence of glaciers and the spatially largest Afroalpine ecosystem are other important factors promoting the evolution of endemic biodiversity in Ethiopia, which is especially high in mammals and amphibians (Jacobs & Schloeder 2001, Lavrenchenko & Bekele 2017).

Compared to other parts of sub-Saharan Africa the knowledge of mammal diversity of Ethiopia is

relatively good. Zoological expeditions had already started in the 18th century and the unique nature of the country has attracted many researchers since that time (see the overview of history of zoological research in Ethiopia in Bekele & Yalden 2013). The diversity and distribution of rodent species were summarized in the excellent and comprehensive papers of Yalden et al. (1976, 1996), with more details on endemic taxa in Yalden & Largen (1992). However, the most recent checklist (Yalden et al. 1996) is now almost 25 years old (the book of Bekele & Yalden 2013 is more recent, but it is largely based on Yalden et al. 1976, 1996). Since that time intensive fieldwork has been performed in various parts of Ethiopia and valuable new material has been collected and analysed (e.g. Lavrenchenko & Bekele 2017). Furthermore, the last two decades are characterized by the unprecedented use of genetics in the description of biodiversity, which have provided new views on evolutionary processes in Ethiopian taxa and highlighted their uniqueness. The description of evolutionary diversity of Ethiopian rodents thus crucially requires the integration of genetic data. This has been done recently for some taxa, but a summarized checklist of all rodents with distributional maps reflecting the current state of knowledge is still missing.

Aims of the study

The main aim of this study is to provide up-to-date information about biodiversity of rodents in Ethiopia. For this purpose, we use updated knowledge of evolutionary processes, integrative species delimitations, and the most recent taxonomic classification. For all species we provide distributional maps based on three data sources. Firstly, we reviewed and revised relevant published data, especially those reported in summarizing works of Yalden and his collaborators (Yalden et al. 1976, 1996). Secondly, we critically revised data from the Global Biodiversity Information Facility (GBIF) based mostly on museum collections. Finally, the most original part of this review is based on our own field research performed in the last three decades within the activities of the Joint Ethio-Russian Biological Expedition (JERBE; see Lavrenchenko & Bekele 2017) and Ethio-Czech Research Projects. This recent material was in most cases analysed in detail by genetic (e.g. barcoding of mitochondrial DNA and allozymes), karyological and/or morphometric approaches.

We hope that this work will be used by students and researchers in zoology, epidemiology and ecology as a basic source of information about the current state

of the taxonomic and biogeographical knowledge of Ethiopian rodents. We also believe that it will promote further research of understudied taxa and regions of the country. It is clear that the taxonomy of African rodents is still in flux and we highlight the groups in which we feel, pending careful revision, new species may be discovered. Similarly, we show that hitherto research in some Ethiopian regions (e.g. Afar, Somali or Benishangul-Gumuz) has been unsatisfactory and its intensification will result in new and important data emerging on Ethiopian biodiversity. The raw distributional data (that we plan to make available online) can be used as a direct source for conservation management, e.g. by highlighting the areas of unique biodiversity and/or intensive ongoing evolutionary processes.

Methods

The individual species accounts are composed of taxonomic, ecological and distributional annotation, followed by a distributional map based on georeferenced records. In most cases, we adopted the taxonomic information (i.e. species delimitations, authors of descriptions of species and genera, and classification of higher rodent taxa) from the most recent volumes of *The Handbook of the Mammals of the World* (Wilson et al. 2016, 2017). However, in some groups our recent evolutionary research indicated that the taxonomy is likely to be modified in the light of new integrative taxonomic data. For such groups we report provisional names and references to more detailed publications, awaiting formal taxonomic revisions and species descriptions.

The distribution maps of species are in most cases composed of three data types. (1) We reviewed all available published georeferenced data, the majority of which were taken from Yalden et al. (1976, 1996). We used the geographic coordinates reported in gazetteers of Yalden et al. (1976, 1986, 1996) or from the map (in a few cases when the geographic description was unequivocal and the locality was missing in the gazetteer). (2) Additional records were obtained from the GBIF portal (www.gbif.org) (conducted on 18th September 2018), which contained 4299 georeferenced occurrences of rodents in Ethiopia. These data were carefully evaluated and evident misidentifications were removed (see more details about the use of GBIF data in Taylor et al. 2018). The GBIF points are mostly based on museum vouchers and they significantly overlap with Yalden et al.'s (1976, 1996) data, as these authors explored available museum collections. (3) We summarized the

Table 1. Checklist and taxonomy of Ethiopian rodents. Column “Yalden et al. (1976, 1996)” indicates whether the species was included in Yalden et al. (1976, 1996) checklists. “?” means that the species was not previously recognized. Column “This study” confirms occurrence (“x”) after Yalden et al. (1996). We were not able to confirm the presence of 12 species mentioned in previous studies (“-”). The column “Distribution” corresponds to Fig. 4.

Taxon	Yalden et al. (1976, 1996)	This study	Distribution
Family Nesomyidae (pouched rats, climbing mice and fat mice)			
Genus <i>Saccostomus</i> Peters, 1846			
<i>Saccostomus mearnsi</i> Heller, 1910	x	x	Somali-Masai
Genus <i>Dendromus</i> A. Smith, 1829			
<i>Dendromus mystacalis</i> (Heuglin, 1863)	x	x	Ethiopian endemic
<i>Dendromus lovati</i> (de Winton, 1900)	x	x	Ethiopian endemic
<i>Dendromus</i> sp. indet. 1 (sensu Voelker et al., in lit.)	?	x	Ethiopian endemic
<i>Dendromus</i> sp. indet. 2 (sensu Voelker et al., in lit.)	?	x	Ethiopian endemic
<i>Dendromus</i> sp. indet. 3 (sensu Voelker et al., in lit.)	?	x	Ethiopian endemic
Genus <i>Megadendromus</i> Dieterlen & Rupp, 1978			
<i>Megadendromus nikolausi</i> Dieterlen & Rupp, 1978	x	x	Ethiopian endemic
Genus <i>Steatomys</i> Peters, 1846			
<i>Steatomys parvus</i> Rhoads, 1896	x	-	Somali-Masai
<i>Steatomys pratensis</i> Peters, 1846	x	-	Somali-Masai
Family Muridae (mice and rats)			
Subfamily Murinae			
Tribe Otomyini			
Genus <i>Otomys</i> F. Cuvier, 1824			
<i>Otomys cheesmani</i> Taylor et al., 2011	?	-	Ethiopian endemic
<i>Otomys fortior</i> Thomas, 1906	?	x	Ethiopian endemic
<i>Otomys helleri</i> Frick, 1914	?	x	Ethiopian endemic
<i>Otomys simiensis</i> Taylor et al., 2011	?	x	Ethiopian endemic
<i>Otomys typus</i> (Heuglin, 1877)	x	x	Ethiopian endemic
<i>Otomys yaldeni</i> Taylor et al., 2011	?	x	Ethiopian endemic
Tribe Arvicanthini			
Genus <i>Desmomyys</i> Thomas, 1910			
<i>Desmomyys harringtoni</i> (Thomas, 1902)	x	x	Ethiopian endemic
<i>Desmomyys yaldeni</i> Lavrenchenko, 2003	-	x	Ethiopian endemic
Genus <i>Arvicanthis</i> Lesson, 1842			
<i>Arvicanthis abyssinicus</i> (Rüppel, 1842)	x	x	Ethiopian endemic
<i>Arvicanthis blicki</i> Frick, 1914	x	x	Ethiopian endemic
<i>Arvicanthis somalicus</i> Thomas, 1903	x	x	Somali-Masai
<i>Arvicanthis niloticus</i> (É. Geoffroy Saint Hilaire, 1803)	x	x	Nubian
<i>Arvicanthis niloticus</i> “C2-C4” (sensu Bryja et al. 2019)	?	x	Sudanian
<i>Arvicanthis mearnsi</i> Frick, 1914	?	x	Somali-Masai
<i>Arvicanthis saturatus</i> Dollman, 1911	?	x	Ethiopian endemic
<i>Arvicanthis raffertyi</i> Frick, 1914	?	x	Somali-Masai
Genus <i>Mylomys</i> Thomas, 1906			
<i>Mylomys rex</i> (Thomas, 1906)	?	-	Ethiopian endemic
Genus <i>Aethomys</i> Thomas, 1915			
<i>Aethomys hindai</i> (Thomas, 1902)	x	x	Sudanian
<i>Aethomys kaiseri</i> (Noack, 1887)	-	x	Somali-Masai

Genus <i>Dasymys</i> Peters, 1875			
<i>Dasymys griseifrons</i> Osgood, 1936	x	x	Ethiopian endemic
Genus <i>Grammomys</i> Thomas, 1915			
<i>Grammomys minnae</i> Hutterer & Dieterlen, 1984	x	x	Afromontane
<i>Grammomys</i> sp. "m4" (sensu Bryja et al. 2017)	?	x	Afromontane
Genus <i>Lemniscomys</i> Trouessart, 1881			
<i>Lemniscomys zebra</i> (Heuglin, 1864)	x	x	Sudanian
<i>Lemniscomys macculus</i> (Thomas & Wroughton, 1910)	x	x	Sudanian
Genus <i>Oenomys</i> Thomas, 1904			
<i>Oenomys hypoxanthus</i> (Pucheran, 1855)	x	x	Afromontane
Genus <i>Thallomys</i> Thomas, 1920			
<i>Thallomys paedulcus</i> (Sundevall, 1846)	x	-	Somali-Masai
Tribe Murini			
Genus <i>Mus</i> Linnaeus, 1758			
<i>Mus musculus</i> Linnaeus, 1758	x	x	Introduced (commensal)
<i>Mus imberbis</i> Rüppel, 1842	x	x	Ethiopian endemic
<i>Mus mahomet</i> Rhoads, 1896	x	x	Ethiopian endemic
<i>Mus proconodon</i> Rhoads, 1896	x	x	Ethiopian endemic
<i>Mus</i> sp. "Harena" (sensu Bryja et al. 2014)	x	x	Ethiopian endemic
<i>Mus minutoides</i> A. Smith, 1834	?	x	Widespread sub-Saharan
<i>Mus musculoides</i> Temminck, 1853	?	x	Sudanian
<i>Mus tenellus</i> Thomas, 1903	x	x	Nubian
<i>Mus</i> sp. "Koi River" (sensu Bryja et al. 2014)	-	x	Sudanian
Tribe Praomyini			
Genus <i>Stenocephalemys</i> Frick, 1914			
<i>Stenocephalemys albipes</i> (Rüppel, 1842)	x	x	Ethiopian endemic
<i>Stenocephalemys albocaudatus</i> Frick, 1914	x	x	Ethiopian endemic
<i>Stenocephalemys griseicauda</i> Petter, 1972	x	x	Ethiopian endemic
<i>Stenocephalemys "pseudogriseicauda"</i> (sensu Bryja et al. 2018a)	?	x	Ethiopian endemic
<i>Stenocephalemys ruppi</i> Van der Straeten & Dieterlen, 1983	x	x	Ethiopian endemic
<i>Stenocephalemys</i> sp. "A" (sensu Lavrenchenko & Verheyen 2006)	?	x	Ethiopian endemic
Genus <i>Mastomys</i> Thomas, 1915			
<i>Mastomys awashensis</i> Lavrenchenko et al., 1998	?	x	Ethiopian endemic
<i>Mastomys natalensis</i> (A. Smith, 1834)	x	x	Widespread sub-Saharan
<i>Mastomys erythroleucus</i> (Temminck, 1853)	x	x	Sudanian
<i>Mastomys kollmannspergeri</i> (Petter, 1957)	-	x	Sudanian
Genus <i>Myomyscus</i> Shortridge, 1942			
<i>Myomyscus brockmani</i> (Thomas, 1906)	x	x	Somali-Masai
<i>Myomyscus</i> sp. "South"	?	x	Somali-Masai
Genus <i>Nilopegamys</i> Osgood, 1928			
<i>Nilopegamys plumbeus</i> Osgood, 1928	x	-	Ethiopian endemic
Tribe Rattini			
Genus <i>Rattus</i> G. Fischer, 1803			
<i>Rattus rattus</i> (Linnaeus, 1758)	x	x	Introduced (commensal)
Subfamily Deomyinae			
Genus <i>Acomys</i> I. Geoffroy Saint-Hilaire, 1838			
<i>Acomys cahirinus</i> (É. Geoffroy Saint-Hilaire, 1803)	x	x	Nubian

<i>Acomys</i> sp. “Cah7” (sensu Aghová et al. 2019)	?	x	Nubian
<i>Acomys</i> sp. “Cah8” (sensu Aghová et al. 2019)	?	x	Nubian
<i>Acomys mullah</i> Thomas, 1904	?	x	Somali-Masai
<i>Acomys louisae</i> Thomas, 1896	?	x	Somali-Masai
<i>Acomys kempfi</i> Dollman, 1911	?	x	Somali-Masai
<i>Acomys</i> sp. “Ign1” (sensu Aghová et al. 2019)	?	x	Somali-Masai
<i>Acomys</i> sp. “Ign2” (sensu Aghová et al. 2019)	?	x	Somali-Masai
<i>Acomys percivali</i> Dollman, 1911	?	x	Somali-Masai
<i>Acomys wilsoni</i> Thomas, 1892	x	x	Somali-Masai
Genus <i>Lophuromys</i> Peters, 1874			
<i>Lophuromys chrysopus</i> Osgood, 1936	?	x	Ethiopian endemic
<i>Lophuromys melanonyx</i> Petter, 1972	x	x	Ethiopian endemic
<i>Lophuromys flavopunctatus</i> Thomas, 1888	x	x	Ethiopian endemic
<i>Lophuromys brunneus</i> Thomas, 1906	?	x	Ethiopian endemic
<i>Lophuromys brevicaudus</i> Osgood, 1936	?	x	Ethiopian endemic
<i>Lophuromys simensis</i> Osgood, 1836	?	x	Ethiopian endemic
<i>Lophuromys menageshae</i> Lavrenchenko et al., 2007	?	x	Ethiopian endemic
<i>Lophuromys chercherensis</i> Lavrenchenko et al., 2007	?	x	Ethiopian endemic
<i>Lophuromys pseudosikapusi</i> Lavrenchenko et al., 2007	?	x	Ethiopian endemic
Genus <i>Uranomys</i> Dollman, 1909			
<i>Uranomys ruddi</i> Dollman, 1909	x	x	Sudanian
Subfamily Gerbillinae			
Tribe Taterillini			
Genus <i>Gerbilliscus</i> Thomas, 1897			
<i>Gerbilliscus giffardi</i> (Wroughton, 1906)	x	x	Sudanian
<i>Gerbilliscus robustus</i> (Cretzschmar, 1826)	x	x	Somali-Masai
<i>Gerbilliscus</i> sp. “Babile” (sensu Aghová et al. 2017)	?	x	Somali-Masai
<i>Gerbilliscus phillipsi</i> (de Winton, 1898)	x	x	Somali-Masai
<i>Gerbilliscus nigricaudus</i> (Peters, 1878)	x	x	Somali-Masai
Genus <i>Taterillus</i> Thomas, 1910			
<i>Taterillus emini</i> (Thomas, 1892)	x	x	Somali-Masai
Tribe Ammodillini			
Genus <i>Ammodillus</i> Thomas, 904			
<i>Ammodillus imbellis</i> (de Winton, 1898)	x	-	Horn of Africa
Tribe Gerbillini			
Genus <i>Gerbillus</i> Desmarest, 1804			
<i>Gerbillus dunni</i> Thomas, 1904	x	-	Horn of Africa
<i>Gerbillus pulvinatus</i> Rhoads, 1896	x	-	Somali-Masai
<i>Gerbillus pusillus</i> Peters, 1878	x	x	Somali-Masai
Genus <i>Microdillus</i> Thomas, 1910			
<i>Microdillus peeli</i> (de Winton, 1898)	-	-	Horn of Africa
Subfamily Lophiomyinae			
Genus <i>Lophiomyys</i> Milne-Edwards, 1867			
<i>Lophiomyys imhausi</i> Milne-Edwards, 1867	x	x	Afromontane
Family Sciuridae (squirrels)			
Subfamily Xerinae			

Tribe Xerini (African ground squirrels)			
Genus <i>Xerus</i> Hemprich & Ehrenberg, 1933			
<i>Xerus rutilus</i> (Cretzschmar, 1828)	x	x	Somali-Masai
Genus <i>Euxerus</i> Thomas, 1909			
<i>Euxerus erythropus</i> (E. Geoffroy, 1803)	x	x	Sudanian
Tribe Protoxerini (African tree squirrels)			
Genus <i>Heliosciurus</i> Trouessart, 1880			
<i>Heliosciurus gambianus</i> (Ogilby, 1835)	x	x	Sudanian
Genus <i>Paraxerus</i> Forsyth Major, 1893			
<i>Paraxerus ochraceus</i> (Huet, 1880)	x	-	Somali-Masai
Family Gliridae (dormice)			
Genus <i>Graphiurus</i> Smuts, 1832			
<i>Graphiurus</i> sp. "A"	?	x	Sudanian
<i>Graphiurus</i> sp. "B"	?	x	Ethiopian endemic
<i>Graphiurus</i> sp. "C"	?	x	Afromontane
Family Dipodidae (jerboas)			
Genus <i>Jaculus</i> Erxleben, 1777			
<i>Jaculus hirtipes</i> (Lichtenstein, 1823)	x	-	Nubian
Family Spalacidae (muroid mole rats)			
Subfamily Rhizomyinae			
Tribe Tachyoryctini			
Genus <i>Tachyoryctes</i> Rüppel, 1835			
<i>Tachyoryctes splendens</i> (Rüppel, 1835)	x	x	Ethiopian endemic
<i>Tachyoryctes macrocephalus</i> (Rüppel, 1842)	x	x	Ethiopian endemic
Family Heterocephalidae (naked mole rats)			
Genus <i>Heterocephalus</i> Rüppel, 1842			
<i>Heterocephalus glaber</i> Rüppel, 1842	x	x	Somali-Masai
Family Hystricidae (Old World porcupines)			
Genus <i>Hystrix</i> Linnaeus, 1758			
<i>Hystrix cristata</i> Linnaeus, 1758	x	x	Widespread sub-Saharan
Family Thryonomidae (cane rats)			
Genus <i>Thryonomys</i> Fitzinger, 1867			
<i>Thryonomys gregorianus</i> (Thomas, 1894)	x	x	Widespread sub-Saharan
Family Ctenodactylidae (gundis)			
Genus <i>Pectinator</i> Blyth, 1856			
<i>Pectinator spekei</i> Blyth, 1856	x	x	Horn of Africa

available data from recent field work and publications after Yalden et al. (1996). The most important part of these data comes from two sources. First, for over thirty years, the Mammal Research Group of the Joint Ethio-Russian Biological Expedition (JERBE; coordinated by A. N. Severtsov Institute of Ecology and Evolution RAS in Moscow and Addis Ababa University) studied the diversity and evolution of Ethiopian mammals (see more details in Lavrenchenko & Bekele 2017). Second, numerous material and data were collected within the Joint Ethio-Czech Research Projects

(coordinated by the Institute of Vertebrate Biology CAS in Brno, Mekelle University and University of South Bohemia in České Budějovice), since 2012. Most of the material collected by these joint research programmes was characterized by a combination of morphometric, molecular genetic and/or karyological approaches. Voucher specimens are available in the collections of the Zoological Museum of the Moscow University (Russia), University of South Bohemia in České Budějovice and Institute of Vertebrate Biology CAS in Brno (Czech Republic) and Mekelle

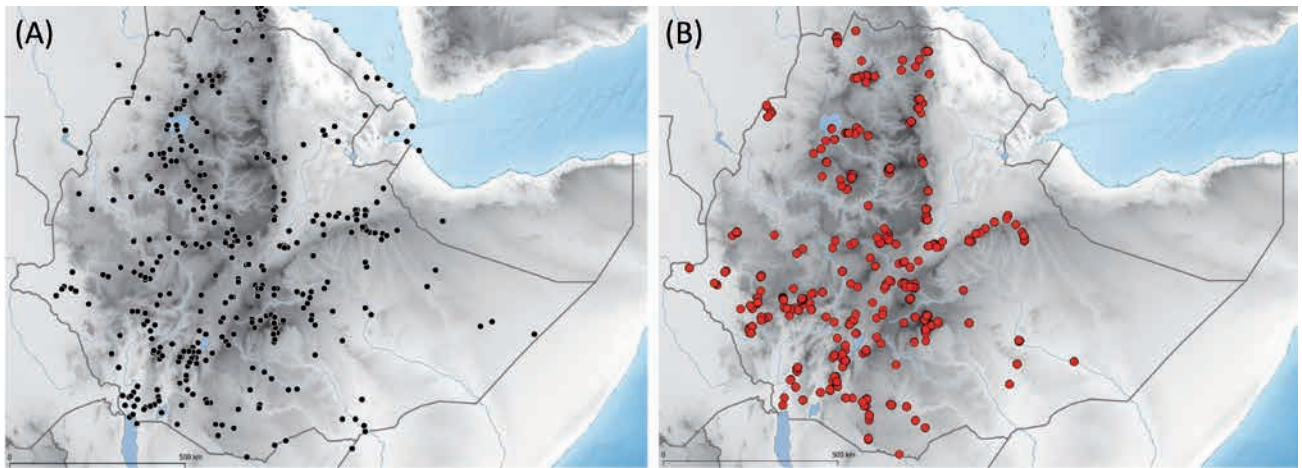


Fig. 3. (A) Distribution of data from Yalden et al. (1976, 1996). (B) Distribution of data collected within JERBE, Ethio-Czech expeditions and papers published after 1996.

University (Ethiopia). Ethiopian material has often been analysed in a wider geographical context and we can therefore reliably assess the level of evolutionary uniqueness of Ethiopian populations (see references in individual species accounts).

Results

Summary of the Ethiopian rodent fauna

An overview of distributional data (Fig. 3) suggests that most intensive research on Ethiopian rodents has so far focussed on the Ethiopian Highlands, Rift Valley and southern Ethiopia. There is an evident lack of data from arid lowland regions like Afar and Somali, but also in the westernmost part of the country close to the Sudan and South Sudan borders (e.g. Benishangul-Gumuz region).

In total, we document the presence of 104 rodent species in Ethiopia belonging to 40 genera and 10 families (Table 1). Compared to Yalden et al. (1976, 1996) we were not able to confirm the presence of 12 species, mostly due to lack of recent data from arid lowland habitats (for further details see the Discussion). On the other hand, the updated checklist provides numerous species (> 40) that were not reported by Yalden et al. (1996). These are either cryptic, i.e. recognized only recently by a combination of genetics and skull morphometry (e.g. genera *Otomys* or *Lophuromys*), or were overlooked or not captured during former times (e.g. *Desmomyys yaldeni*, *Aethomys kaiseri*, *Microdillus peeli*).

Biogeographic summary

Based on the distributional patterns, we defined eight biogeographic categories of Ethiopian rodents (Table 1, Fig. 4), roughly following Linder et al. (2012). Ethiopian endemics living mostly in the Highlands

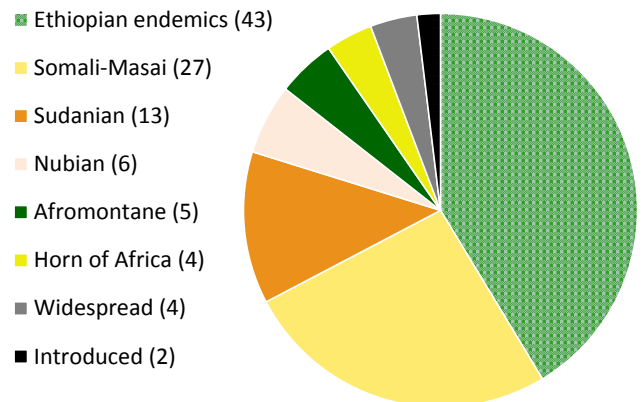


Fig. 4. Biogeographic affinities of the Ethiopian rodent fauna. See text for more details of category definitions.

represent the highest proportion of rodent diversity (43 of 104 species, 41.3%), followed by species living in the Somali-Masai (27 species) and Sudanian (13 species) savanna. Six species are probably distributed in the Nubian region and four in the Horn of Africa (sensu Linder et al. 2012), but the distribution of these requires further study. Five species are more widely distributed across the Eastern Afromontane region and four species are widespread across sub-Saharan Africa. The only commensal rodents (*Mus musculus* and *Rattus rattus*) have both been introduced.

Individual species accounts

The individual accounts for 104 species of Ethiopian rodents are composed of a map (Figs. 5-108) and a short annotation including brief taxonomic and distributional comments. Each map is composed of up to three types of data (see Methods) visualized by different symbols. For many species one or two data types are missing, but we have kept the uniform legend and specify further details in the text.

Family Nesomyidae (pouched rats, climbing mice and fat mice)

This is an old African family, currently distributed in 68 living species (Goodman & Monadjem 2017) in sub-Saharan Africa and Madagascar. Four genera (*Saccostomus*, *Dendromus*, *Megadendromus*, *Steatomys*) have been reported from Ethiopia (Monadjem et al. 2015).

Genus *Saccostomus* Peters, 1846

African pouched mice of the genus *Saccostomus* are small to medium-sized slowly moving rodents, which are locally abundant in the seasonal environments of grasslands, savanna, scrublands and woodlands of southern and eastern Africa (Monadjem et al. 2015). The genus is morphologically well defined by heavily built bodies with short limbs and short tails as well as by the presence of cheek pouches. Two major clades are defined in the genus, the *campestris* group and the *mearnsi* group, with the latter occurring in the Somali-Maasai bioregion and consisting of two species (Mikula et al. 2016). Only one species, *S. mearnsi*, occurs in Ethiopia, where it reaches the northern border of the genus distribution (Mikula et al. 2016).

Saccostomus mearnsi Heller, 1910

This species occurs in the Somali-Maasai bioregion, from northernmost Tanzania across Kenya to southern Ethiopia and Somalia, South Sudan and eastern Uganda (Mikula et al. 2016). The precise distribution in South Sudan, Uganda and Somalia is unresolved. It has a parapatric distribution with *S. umbriventer* in north-eastern Tanzania and south-western Kenya, where the two species could possibly meet, but evidence for such contact is missing. In Ethiopia, it was found in grasslands and acacia savanna in the southernmost part of the country.

Genus *Dendromus* A. Smith, 1829

The genus *Dendromus* represents a group of relatively small rodents with a very long tail, living in tall grass habitats. The taxonomy of the genus is not well resolved. Based on Goodman & Monadjem (2017) there are several species (e.g. *nyikae*, *mystacalis*, *melanotis*, *mesomelas*) with large discontinuous distributions, but this is very likely an artefact of cryptic diversity and unresolved taxonomy (Monadjem et al. 2015). Recent genetic work (Lavrenchenko et al. 2017, Voelker et al., in lit.) identified a monophyletic clade of the subgenus *Dendromus* clustering all Ethiopian taxa

plus one species from South Sudan (*ruppi*; see Dieterlen 2009) and one still undescribed species from Mountain Kilimanjaro (Voelker et al., in lit.). There are five genetic lineages in Ethiopia, potentially representing five species, but only two of them have available names (*mystacalis*, *lovati*). All species of Ethiopian *Dendromus* are endemic to the country. The morphology of Ethiopian material was reviewed by Dieterlen (2009), but he included only three of the five genetic clades. See the account of *Megadendromus* for the details about recent taxonomic changes. The GBIF records of South African *D. melanotis* (locality Didessa in western Ethiopia) and East African *D. nysae* (two specimens from Arsi Mountains) are not considered here as they are very likely misidentifications and probably represent other species (most likely *D. mystacalis* and *D. sp. indet. 1*, respectively).

Dendromus mystacalis (Heuglin, 1863)

This is the most widespread species of *Dendromus* in Ethiopia. Its type locality is Eifag (Eifaz), north of Lake Tana and Dieterlen (2009) examined numerous specimens across the Ethiopian Highlands with most records from 2000-3000 m a.s.l. No material of this species from the eastern plateau has been genotyped, so its presence there is still to be confirmed. All genetically analysed specimens of single-striped *Dendromus* from the Bale, Arsi and Chercher Mountains belong to different taxa (in most cases, however, this material originated from much higher elevations than that preferred by *D. mystacalis*).

Dendromus lovati (de Winton, 1900)

This species can be easily identified by three dark stripes over the back and rump, while all other Ethiopian *Dendromus* taxa have at most one stripe. It lives in the elevation zone 2500-3550 m a.s.l. (Yalden et al. 1976, 1996), but recent sampling in the Semien Mts. reported it from 3990 m a.s.l. (Craig et al., in lit.). In the Semien Mts. it may overlap with *D. mystacalis* at 3200-3300 m; with *D. mystacalis* generally occurring below this elevation, and *D. lovati* above it (Craig et al., in lit.). It occurs on plateaux on both sides of the Rift Valley.

Dendromus sp. indet. 1 (sensu Voelker et al., in lit.)

All animals in this clade (sister to *D. lovati*) were captured at high elevations on both sides of the Rift Valley (3200-3600 m a.s.l.; e.g. Kostin et al. 2019). Populations on either side of the Rift Valley form monophyletic subclades, i.e. the Rift Valley caused the

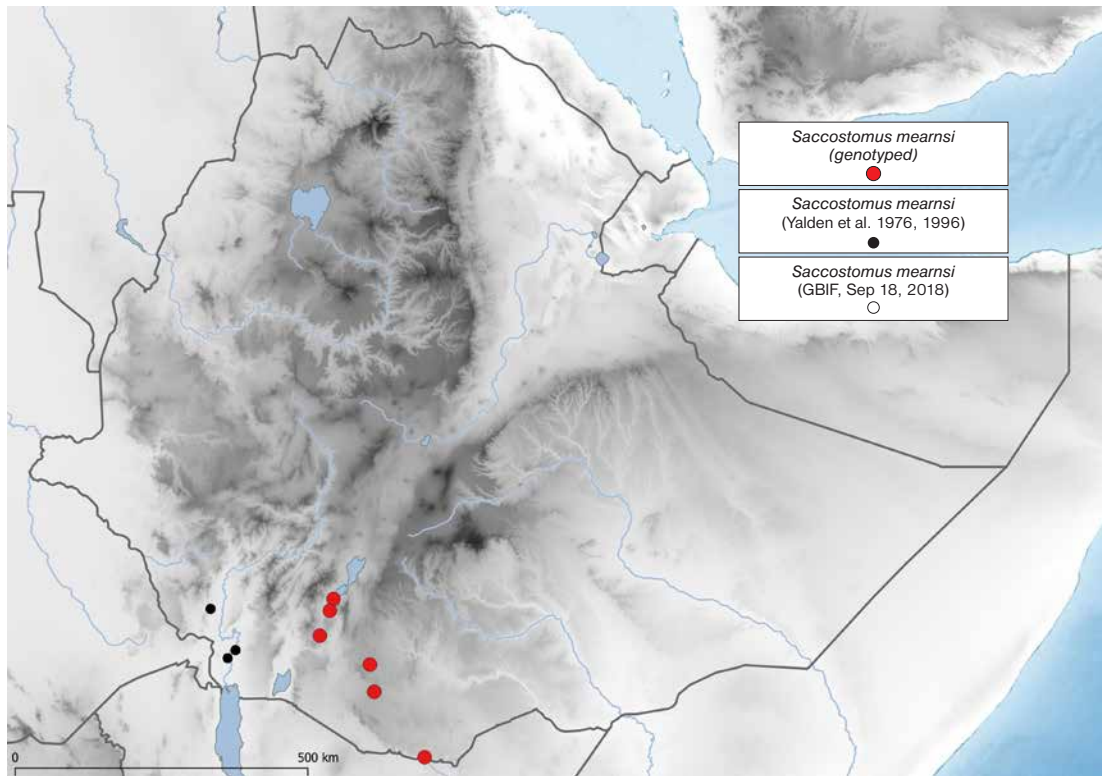


Fig. 5. Distribution of *Saccostomus mearnsi*. The Ethiopian populations west of the River Omo (Hubert 1978a; the northernmost one is also in GBIF) were not genetically characterized, but genotyped individuals from South Sudan and north-western Kenya suggest that they are all *S. mearnsi* (see Mikula et al. 2016).

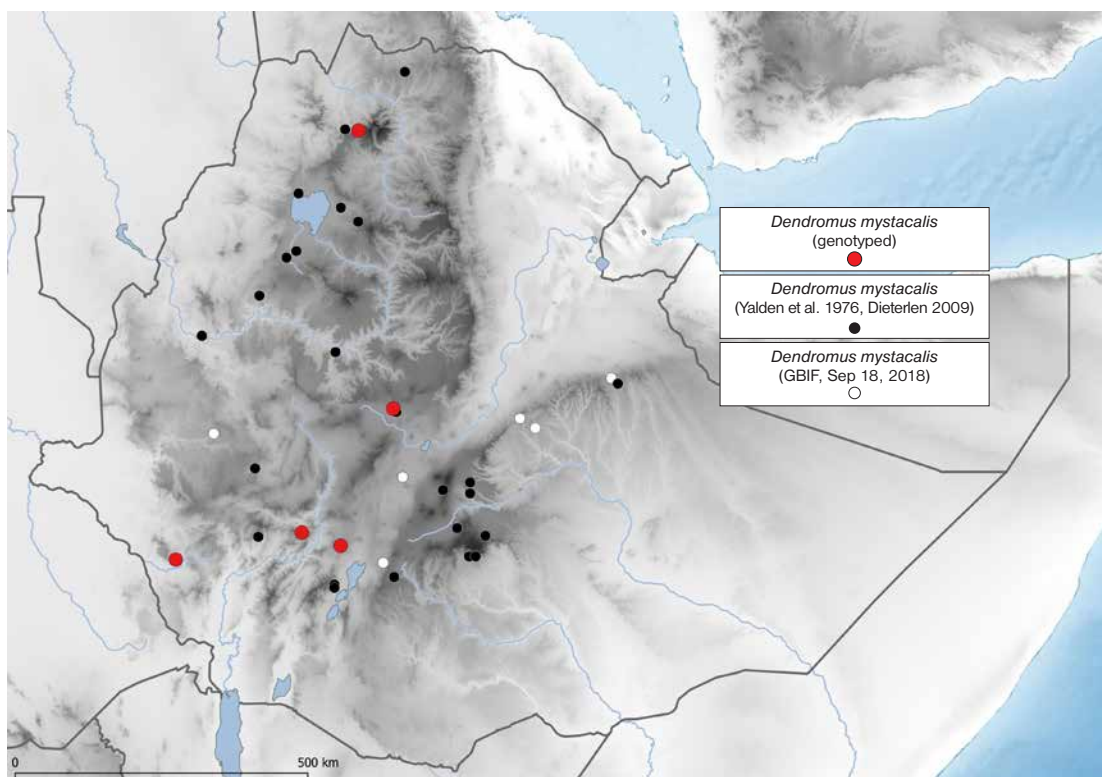


Fig. 6. Distribution of *Dendromus mystacalis*. The specimens east of the Rift Valley originate from altitudes 2000-3000 m a.s.l. and were probably correctly assigned to *D. mystacalis* by Dieterlen (2009) (except locality Ladjo 3850 m, which might represent *D. sp. indet. 1*). However, this exception needs to be confirmed genetically.

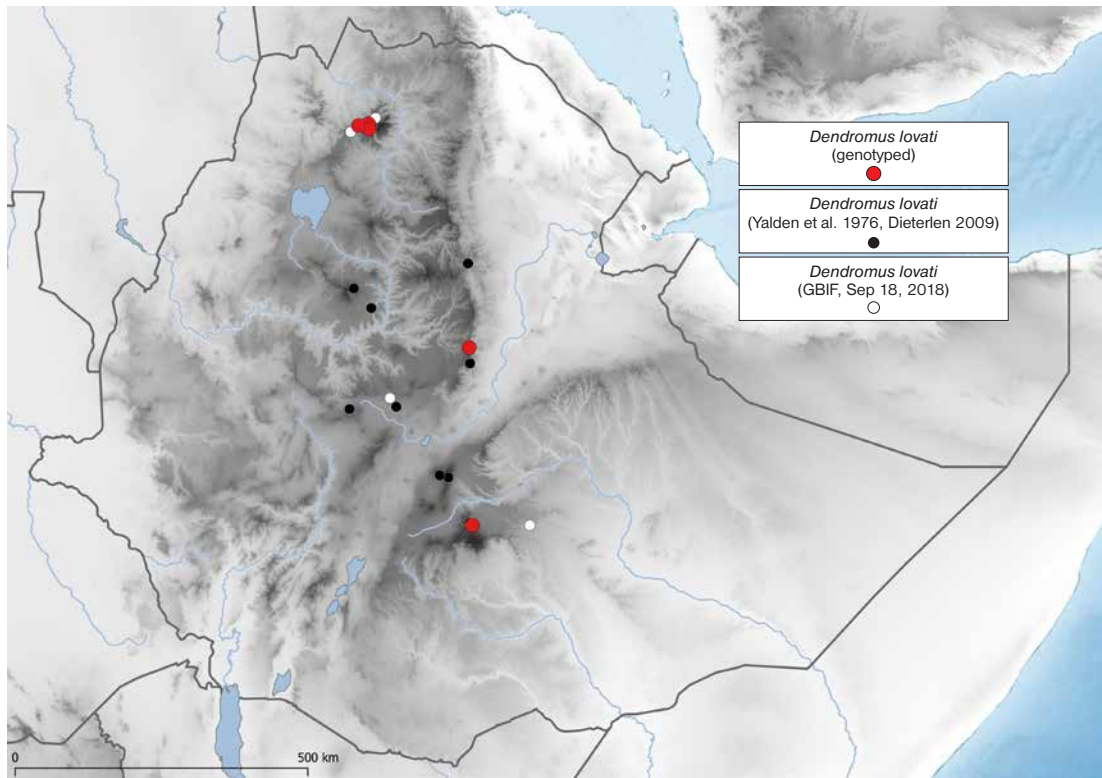


Fig. 7. Distribution of *Dendromus lovati*. The specimen from Bale Mts. was identified based on morphology, because only a short cytochrome *b* sequence was obtained. The role of the Rift Valley on the genetic structure of this taxon remains to be explored.

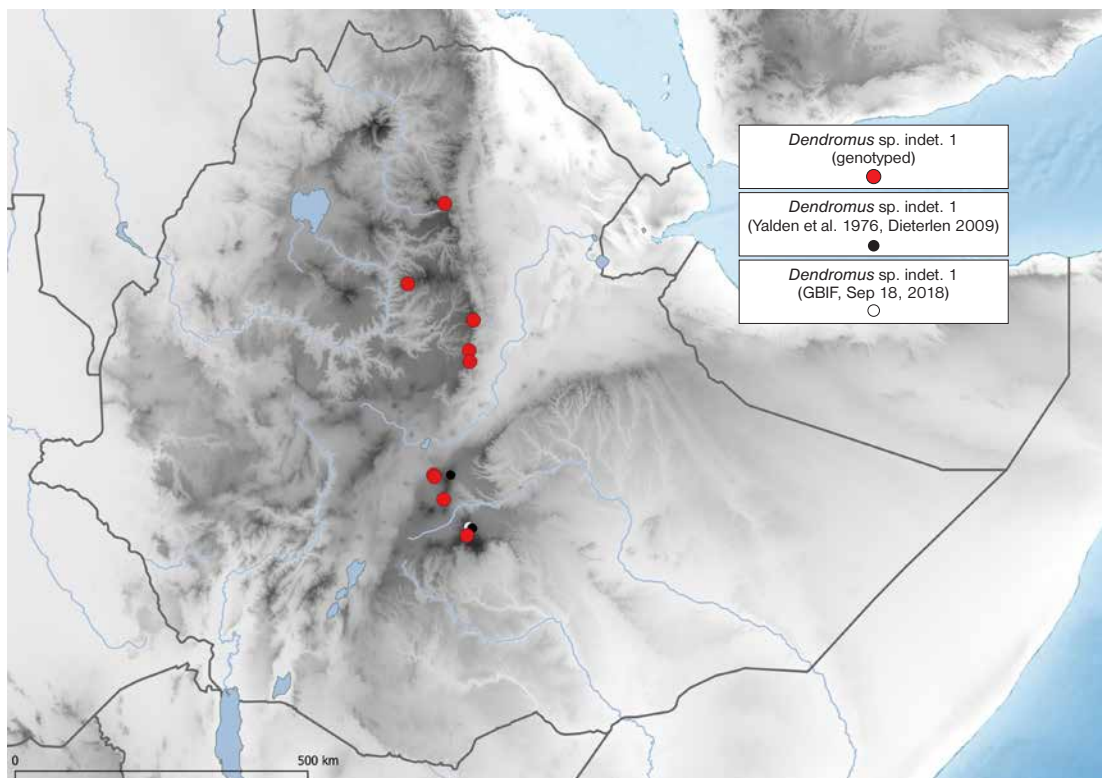


Fig. 8. Distribution of *Dendromus* sp. indet. 1. Individuals from the same side of the Rift Valley form monophyletic groups in the mtDNA phylogeny. GBIF and Dieterlen's (2009) records of *D. insignis* are assigned to this species.

deepest split in intraspecific mitochondrial phylogeny (unpublished data). This taxon may represent *D. insignis abyssinicus* (see Dieterlen 2009). Dieterlen (2009) states that specimens from Bale-Dinsho (above 3000 m) are unmistakably *D. insignis*, so they are probably morphologically clearly distinct from true *D. mystacalis*, but integrative taxonomic revision, especially the comparison with the type of *abyssinicus*, is required. They are also genetically very distant from true *D. insignis*, in fact belonging to a different genetic clade of *Dendromus* (Voelker et al., in lit.).

Dendromus sp. indet. 2 (sensu Voelker et al., in lit.)
This taxon is represented only by three known specimens – two of them are from Kuni Muktar in the Chercher Mts. (ca. 2400 m a.s.l.) and these are morphologically distinct with conspicuously small body size. The only individual from Mekane Selam close to Borena Saynt NP (2900 m a.s.l.) was not analysed morphologically, but genetically is very close to the specimens from the Chercher Mts., despite the large geographical distance between them. It is also possible that some of the *D. mystacalis* reported by Dieterlen (2009), especially those from Chercher Mts., belong to this species. This taxon is genetically

sister to lowland *Dendromus* sp. indet. 3 (at mtDNA; Voelker et al., in lit.).

Dendromus sp. indet. 3 (sensu Voelker et al., in lit.)
This taxon probably represents the lowland Ethiopian *Dendromus* as it was found only at two localities: the border of Sheko forest at 1200 m a.s.l. (J. Bryja et al., unpublished data) and Dhati-Welel NP at 1400 m a.s.l. (Lavrenchenko et al. 2017). This clade is not the sister of topotypic *D. ruppi* (Voelker et al., in lit.), but they should be compared with the material of “*D. mystacalis lineatus*” from South Sudan (Dieterlen 2009). On the first view, however, the Ethiopian specimens have a much less developed black dorsal stripe compared to individuals from Fig. 2 in Dieterlen (2009).

Genus *Megadendromus* Dieterlen & Rupp, 1978
The Ethiopian endemic genus *Megadendromus* was recently analysed genetically by Lavrenchenko et al. (2017) who found that it is an internal lineage of *Dendromus* in the current sense. Ongoing pan-African revision of *Dendromus* (Voelker et al., in lit.), however, confirms three major clades of current *Dendromus* with unique morphological traits (*Dendromus*, *Megadendromus*, *Poemys*) that will be upgraded to

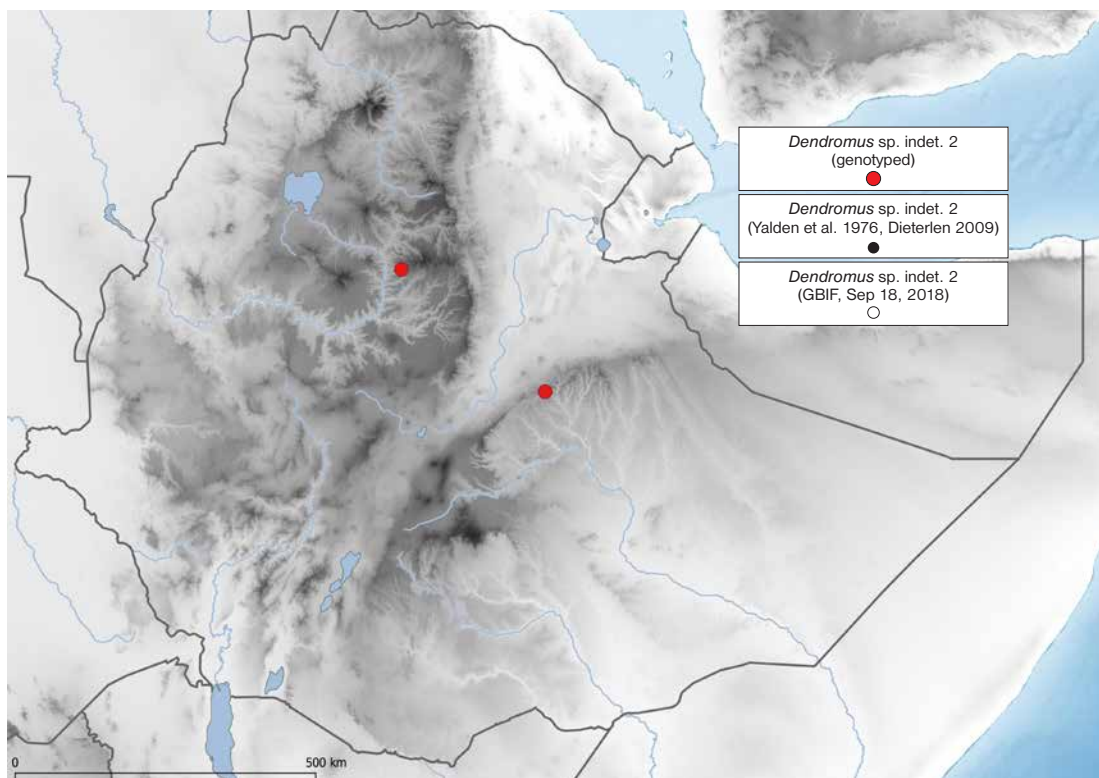


Fig. 9. Distribution of *Dendromus* sp. indet. 2. Both known populations are genetically similar based on mtDNA, despite their separation by the Rift Valley.

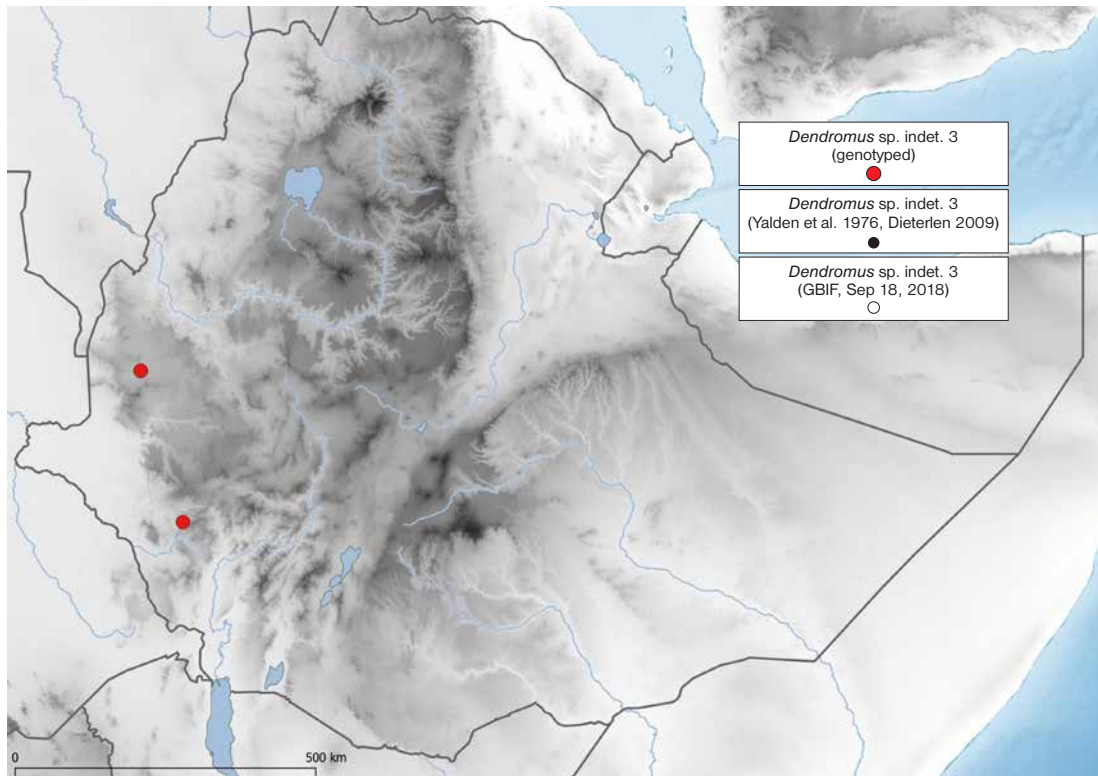


Fig. 10. Distribution of *Dendromus* sp. indet. 3. Genetic and morphological comparison with material from South Sudan (reviewed by Dieterlen 2009, but without genetic data) is required to resolve its taxonomy.

generic level (see also discussion in Lavrenchenko et al. 2017). Here we follow this suggestion and keep *Megadendromus* as a separate genus, endemic to Ethiopia.

Megadendromus nikolausi Dieterlen & Rupp, 1978

This species represents one of the most enigmatic rodents endemic to Ethiopia. It was described on the basis of the holotype from south of Goba (Bale Mountains), and two more specimens plus some remains from owl pellets collected on Mt. Badda (Arsi Mountains) (Dieterlen & Rupp 1978). Subsequently, Demeter obtained a further specimen near Dinshu, also in the Bale Mountains (Demeter & Topal 1982). Despite a superficial resemblance to *Dendromus*, this species differs from all representatives of the genus by significantly larger size and shorter tail. Its dentition is also distinctive in having additional internal cusps on rows two and three on the first and second molars (Dieterlen & Rupp 1978). All known specimens of *M. nikolausi* were collected in *Erica arborea* scrub, at altitudes between 3000 and 3800 m a.s.l. (see a review of all known specimens in Lavrenchenko et al. 2017; since this publication another specimen was captured on the western slopes of the Galama ridge in

the Arsi Mts., at 3400 m a.s.l.; see Kostin et al. 2019). The diploid chromosomal set of *M. nikolausi* consists of 36 bi-armed chromosomes combined into 18 pairs, thus the chromosome arm number doubles the diploid number, $2N = 36$, $FN = 72$ (Lavrenchenko et al. 2017).

Genus *Steatomys* Peters, 1846

The genus is distributed in various types of savanna in sub-Saharan Africa. They are difficult to capture and generally very few records exist from eastern Africa. No genetic study of *Steatomys* is available, so the taxonomic position of the two Ethiopian records is questionable. No specimens of this genus have been collected in the last 30 years in Ethiopia.

Steatomys parvus Rhoads, 1896

The species is distributed from South Sudan, north-eastern Uganda, southern Ethiopia and Somalia to South Africa. The only Ethiopian record remains its type locality, Rusia, on the north shore of Lake Turkana (Yalden et al. 1976).

Steatomys pratensis Peters, 1846

Demeter (1982) reported a collection of owl pellets, from the Sabober Plains in the Awash National Park,

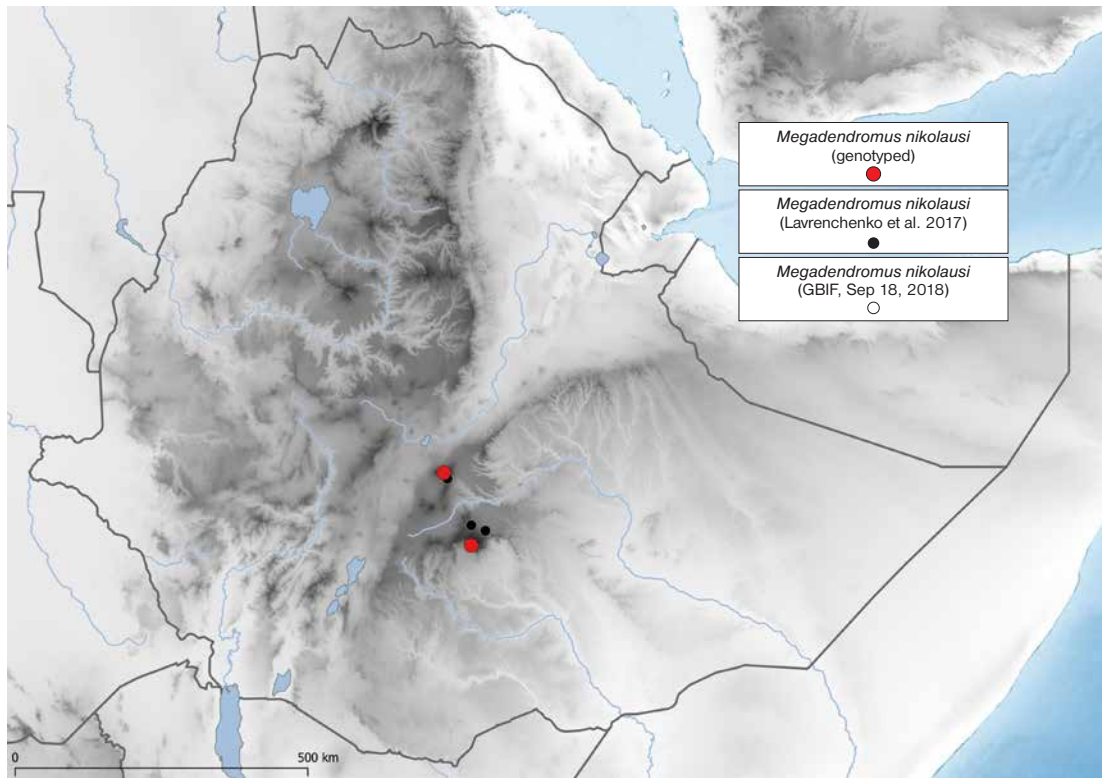


Fig. 11. Distribution of *Megadendromus nikolausi*. The species is known only from high elevations of the eastern massif (for details see Lavrenchenko et al. 2017).

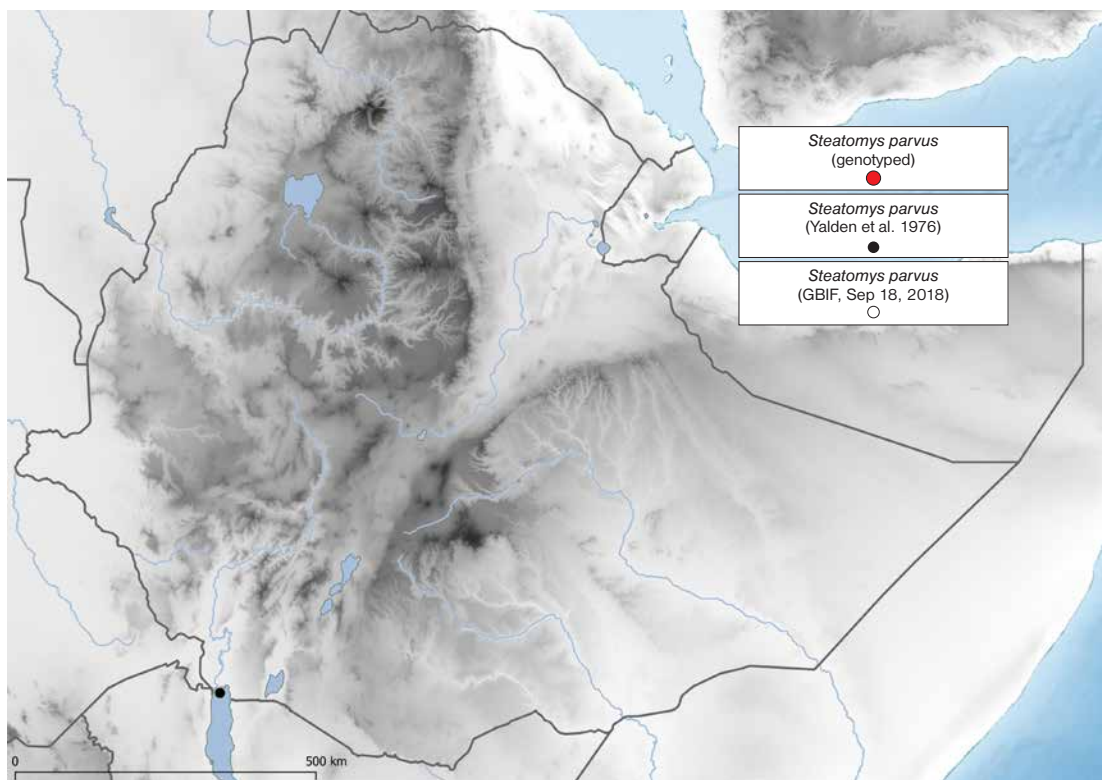


Fig. 12. Distribution of *Steatomys parvus*. The species is known only from its type locality in the extreme south of the country.

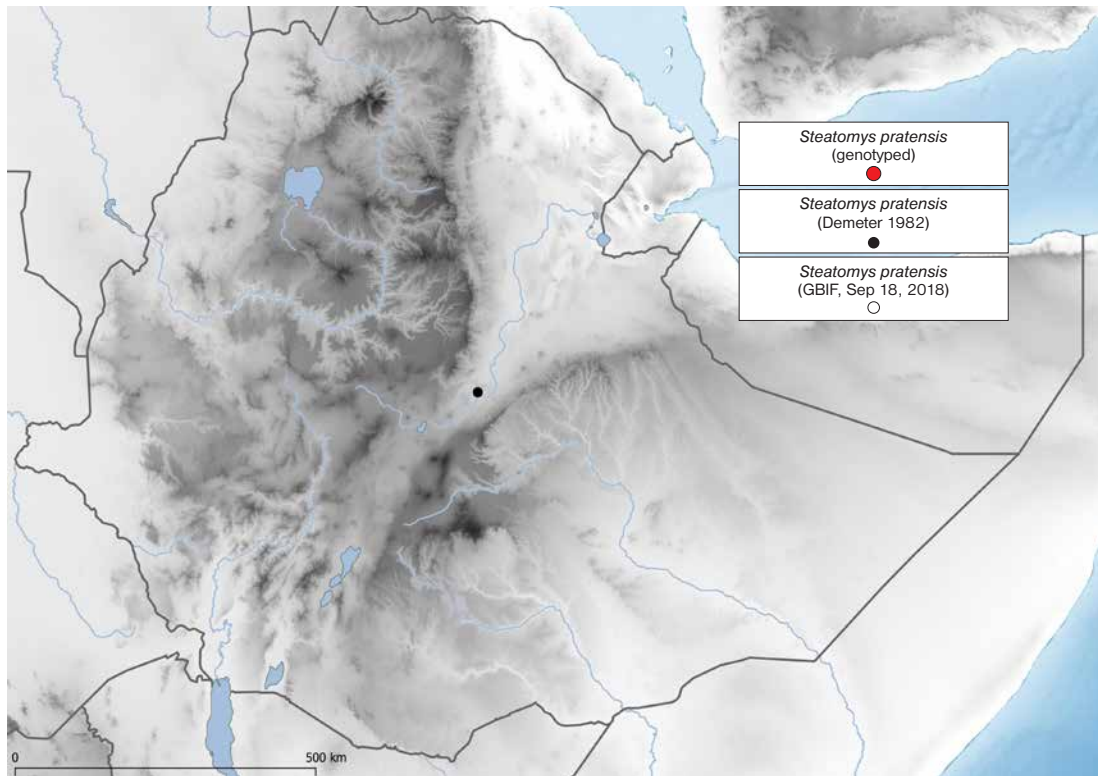


Fig. 13. Distribution of *Steatomys pratensis*. The only record is from owl pellets in the Awash NP (Demeter 1982).

which contained *Steatomys* skulls appreciably larger than those of *S. parvus*. He did not assign a specific name to these skulls, but noted that they are comparable in size with the type of *S. gazellae* Thomas & Hinton, 1923 from southern Sudan. This name is considered to be a synonym of *S. pratensis*, so Yalden et al. (1996) tentatively retained this species on the Ethiopian faunal list. Demeter (1982) notes that the Awash National Park lies about 600 km northeast of the nearest collection site for *S. parvus* and even further from Sudanese localities for *S. pratensis*, but he speculates that such gaps may not represent genuine isolation, in view of the fact that these small mice are so notoriously difficult to capture (Yalden et al. 1996).

Family Muridae (mice and rats)

Subfamily Murinae

Tribe Otomyini

Genus *Otomys* F. Cuvier, 1824

The genus *Otomys* has a wide but highly fragmented distribution in sub-Saharan Africa, often restricted to highlands. This fragmentation has resulted in intensive allopatric diversification and populations, which inhabit different mountain ranges, are usually considered separate species (based on genetic and morphological differences). Ethiopian taxa had been treated as a single species, *O. typus*, until the taxonomic revision by Taylor

et al. (2011), who showed that it is a complex of at least six species, differing in their ecology, morphology and genetics. Available genetic data suggests that Ethiopian *Otomys* are divided in two major genetic clades (*O. simiensis* vs. others; Taylor et al. 2011). Two species can co-occur in some mountains (e.g. Simien or Bale Mts.), but they usually prefer different elevations and habitats (e.g. Craig et al., in lit.). All Ethiopian species seem to be endemic to the country.

Otomys cheesmani P.J. Taylor et al., 2011

This is the largest representative of the *O. typus* species complex, known only from two localities in north-western Ethiopia. It occupies lower elevations (2100-2500 m a.s.l.) than other Ethiopian *Otomys* species (excluding the rainforest dweller *O. fortior*). Nevertheless, the habitat requirements of this species remain unclear. The type locality currently represents an agricultural landscape, presumably much transformed from the time when the type series was collected (Taylor et al. 2011). No genetic data are available for this taxon and no new material has been collected since 1968.

Otomys fortior Thomas, 1906

Restricted to evergreen forests in the south-western regions of the country, west of the River Omo. It is the

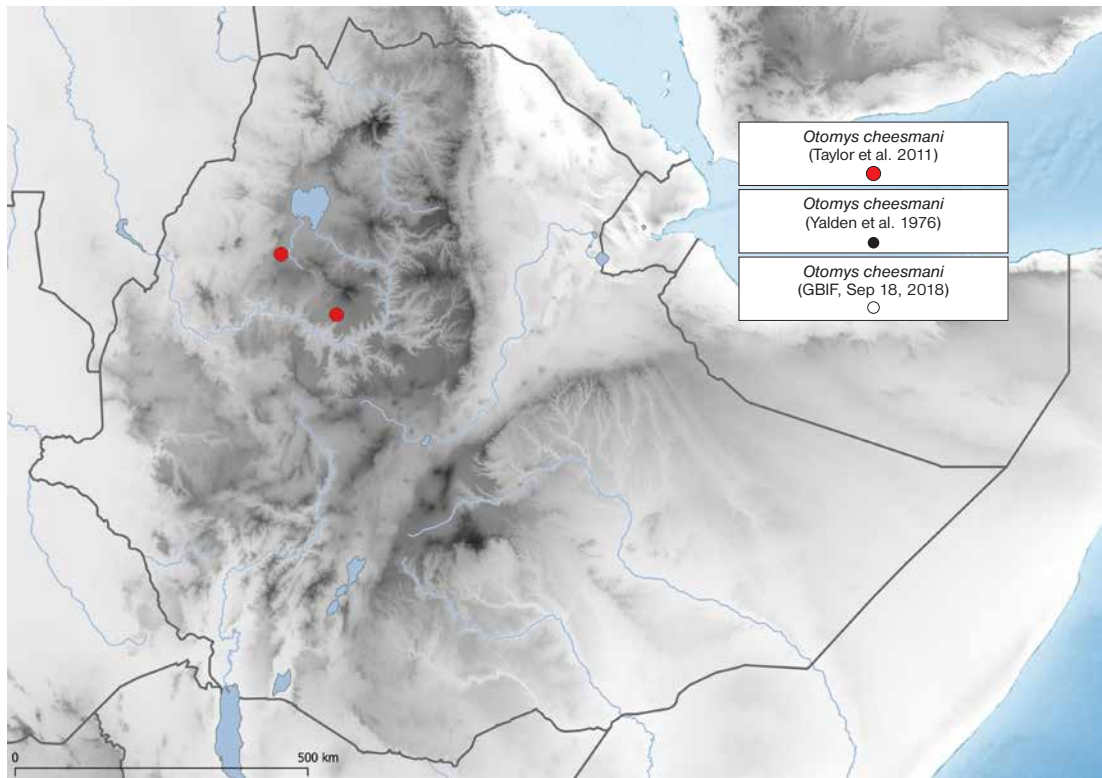


Fig. 14. Distribution of *Otomys cheesmani*. The species is known only from two localities south of Lake Tana (collected in 1926–1937 and 1968). Note that the GPS coordinates of Dangila are incorrect in Taylor et al. (2011) and are corrected here.

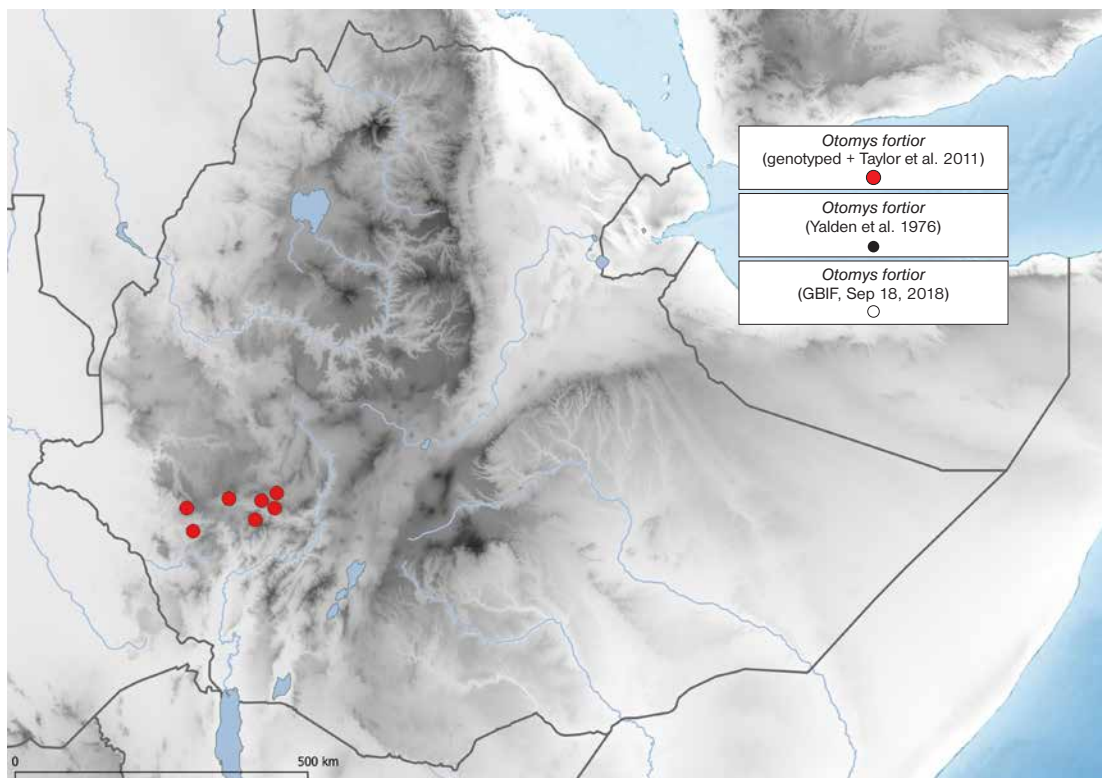


Fig. 15. Distribution of *Otomys fortior*. The species is distributed in tropical rainforests in south-western Ethiopia.

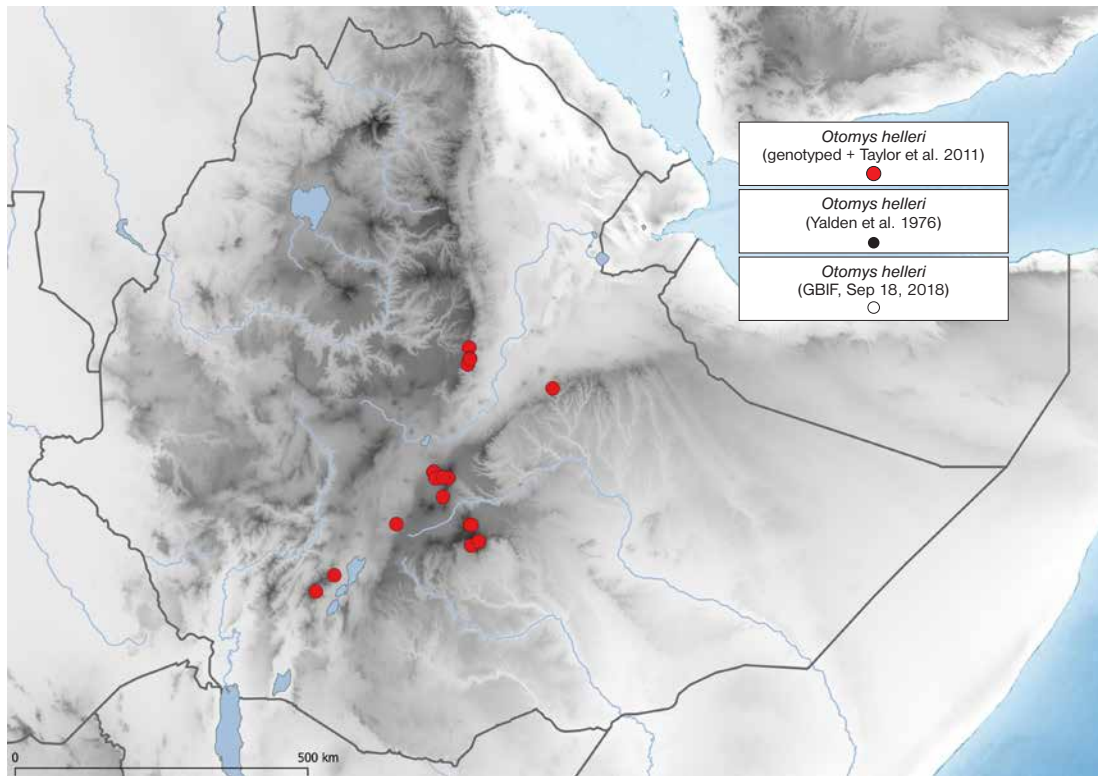


Fig. 16. Distribution of *Otomys helleri*. The species is best documented from the Bale and Arsi Mts. Material from other localities was assigned to this species based on skull morphometry and genetic confirmation is required.

only species of *Otomys* in this region. Specimens from Jimma were assigned to *O. fortior* based on geographic and ecological proximity, but morphologically this species is characterized by large cranial size making them comparable with *O. cheesmani* (Taylor et al. 2011). Genetic data are needed from this population.

Otomys helleri Frick, 1914

The species occupies Afroalpine habitats in the Bale and Arsi Mts. The populations from Ankober-Debre Sina (west of the Rift Valley), Chercher Mts. (eastern Ethiopia) and Bonke-Chencha (southern Ethiopia) were assigned to this species based on cranial morphology (Taylor et al. 2011), but need to be confirmed genetically.

Otomys simiensis P.J. Taylor et al., 2011

A small-sized member of the *O. typus* species complex, described from the vicinity of the Sankaber campsite (3250 m a.s.l.) in the Semien Mts. The type series was collected in tree-heather forest (trees: *Erica arborea*, *Hypericum revolutum*; shrub: *Rosa abyssinica*) with open grassy patches. At higher altitudes, this species seems to be replaced by *O. typus*, a common inhabitant of the Afroalpine zone in the Simien Mts. (Taylor et al. 2011, Craig et al., in lit.). We recently found a similar

distributional pattern in the Aboye (Abohoy) Gara Mts., where both species co-occur in ca. 3500 m a.s.l., but only *O. typus* was found at higher altitudes (Meheretu et al., unpublished data). The populations from mid-elevation altitudes around Kombolcha (2600 m a.s.l.) and Ankober (3100 m a.s.l.) form separate mitochondrial clades and should be further investigated.

Otomys typus (Heuglin, 1877)

After Taylor's et al. (2011) revision (see above), the name *O. typus* is restricted to populations at high elevations in the north-western Highlands. This species may co-occur with *O. simiensis* in several mountain blocks, but the latter species usually prefers lower elevations (see *O. simiensis* account). The analysis of mitochondrial DNA showed very high genetic diversity of populations considered here as *O. typus* s. str. (our unpublished data) suggesting the presence of additional cryptic species that need to be examined using integrative taxonomy (see e.g. Bryja et al. 2018a). Taylor et al. (2011) mentioned that the species occurs also at one locality east of the Rift Valley (Hirna in the Chercher Mts.), but this is based on morphological assignment with weak probability and should be confirmed by genetic data (the locality is not shown on the map).

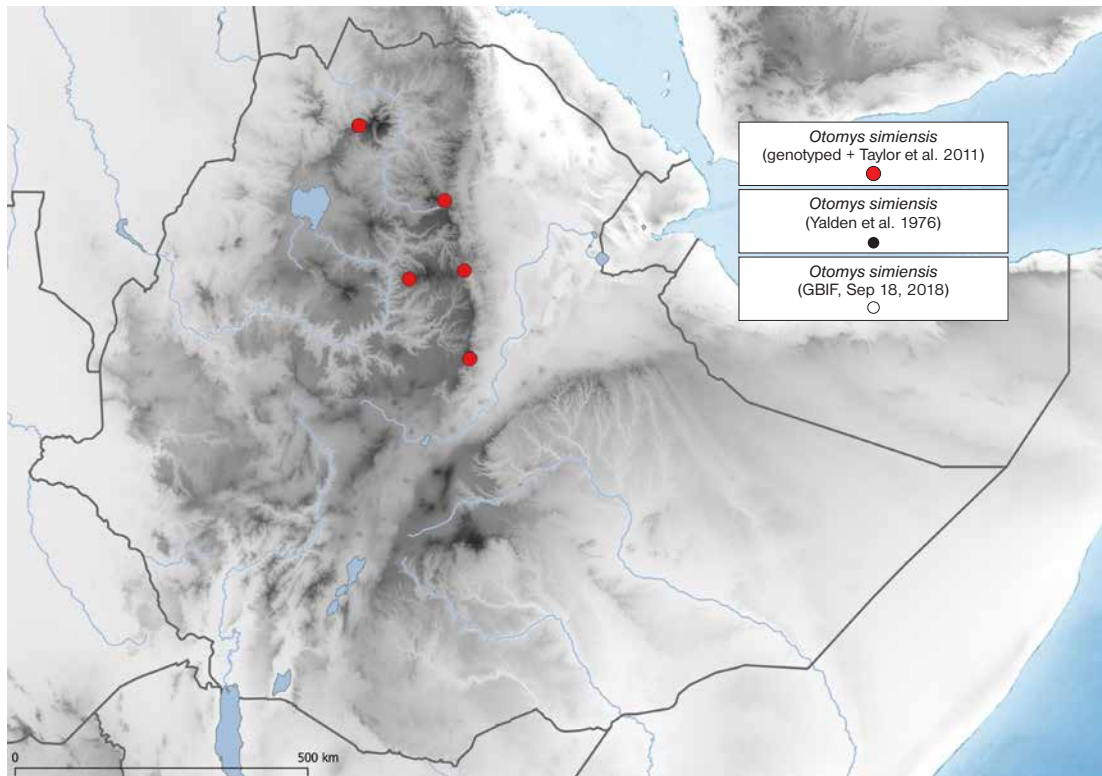


Fig. 17. Distribution of *Otomys simiensis*. The species was described from Semien Mts., but our analysis of mtDNA also confirmed genetically similar populations from other mountains west of the Rift Valley.

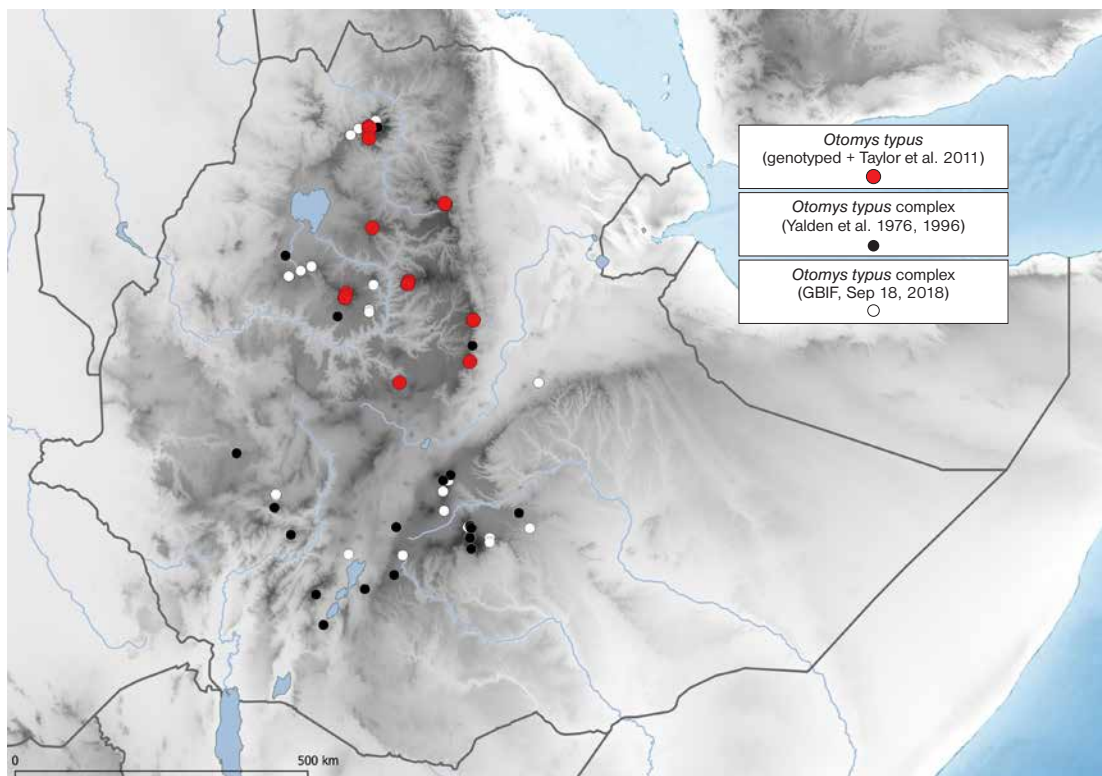


Fig. 18. Distribution of *Otomys typus*. Before revision by Taylor et al. (2011) all specimens of the genus *Otomys* from Ethiopia were assigned to the single species, *O. typus* (shown on this map). However, it is now clear that animals from localities in the southern half of Ethiopia represent other species (*O. fortior*, *O. helleri*, and *O. yaldeni*).

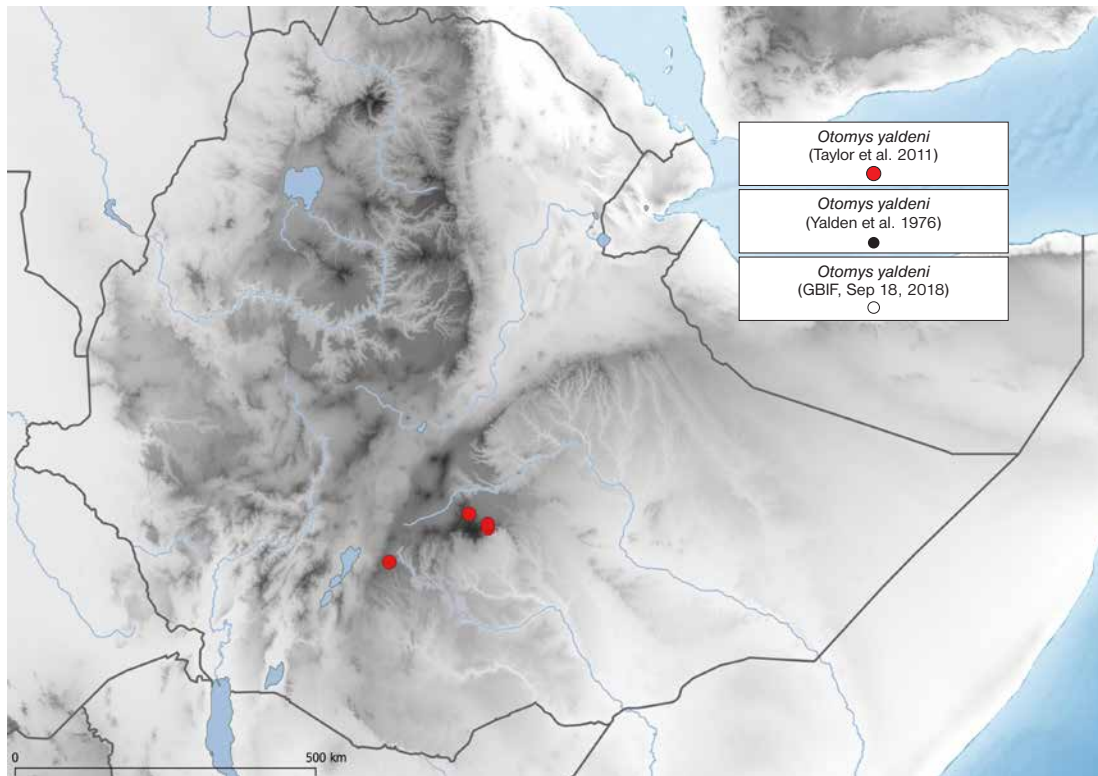


Fig. 19. Distribution of *Otomys yaldeni*. The species was recorded only from northern and south-western slopes of the Bale Mts. (2650–3800 m a.s.l.).

Otomys yaldeni P.J. Taylor et al., 2011

A small-sized *Otomys* with a relatively short tail. Lavrenchenko et al. (1997) demonstrated the genetic distinctness (on allozyme data and karyotypes) of *O. yaldeni* (= their “Sp. A”) and *O. helleri* (= their “Sp. B”) in the Bale Mountains. Morphological analysis by Taylor et al. (2011) documented *O. yaldeni* from the northern (Dinsho and Goba areas) and south-western (70 km north-west of Kebre Mengist) slopes of the Bale Massif. All known specimens of *O. yaldeni* were collected in mosaic habitats of grassland and forest between 2650 and 3800 m a.s.l. (Taylor et al. 2011). There are no DNA sequences of this species and its phylogenetic position is thus unresolved. Based on morphology, it is the most similar to *O. simiensis* (Taylor et al. 2011).

Tribe Arvicanthini

Genus *Desmomys* Thomas, 1910

This is an endemic Ethiopian genus, related to *Rhabdomys* (Eastern African mountains and southern Africa) and *Lamottemys* (endemic to Mount Oku in Cameroon) (see Lavrenchenko & Verheyen 2005, Missouf et al. 2016, Mikula et al., in lit.). Two species have been described from Ethiopia, one is widespread, while the second has a highly restricted distribution.

Desmomys harringtoni (Thomas, 1902)

This is a widespread species across the Ethiopian Highlands on both sides of Rift Valley, but it has never been captured in high numbers, which may be a reflection of its semi-arboreal habits as hypothesized by Yalden et al. (1976). It occurs at elevations from 1350 m a.s.l. (Tepi in south-western Ethiopia) to 3300 m a.s.l. (at Wuchacha and Semien Mts.) (our unpublished data, Yalden et al. 1996, Craig et al., in lit.).

Desmomys yaldeni Lavrenchenko, 2003

This species was distinguished from *D. harringtoni* on the basis of karyotype, external and cranial morphology, and mitochondrial DNA (Lavrenchenko 2003, Lavrenchenko & Verheyen 2005). It is an endemic taxon with a restricted distribution, captured only at three localities in forests of south-western Ethiopia at elevations 1250–1930 m a.s.l. In addition to Lavrenchenko (2003), another specimen was captured in 2017 near the Dembi dam (1250 m a.s.l.), at the border of Sheko forest (our unpublished data). The two *Desmomys* species may co-occur in south-western Ethiopia, but they can be differentiated e.g. by a significantly longer tail in *D. yaldeni* (see Lavrenchenko 2003 for more details).

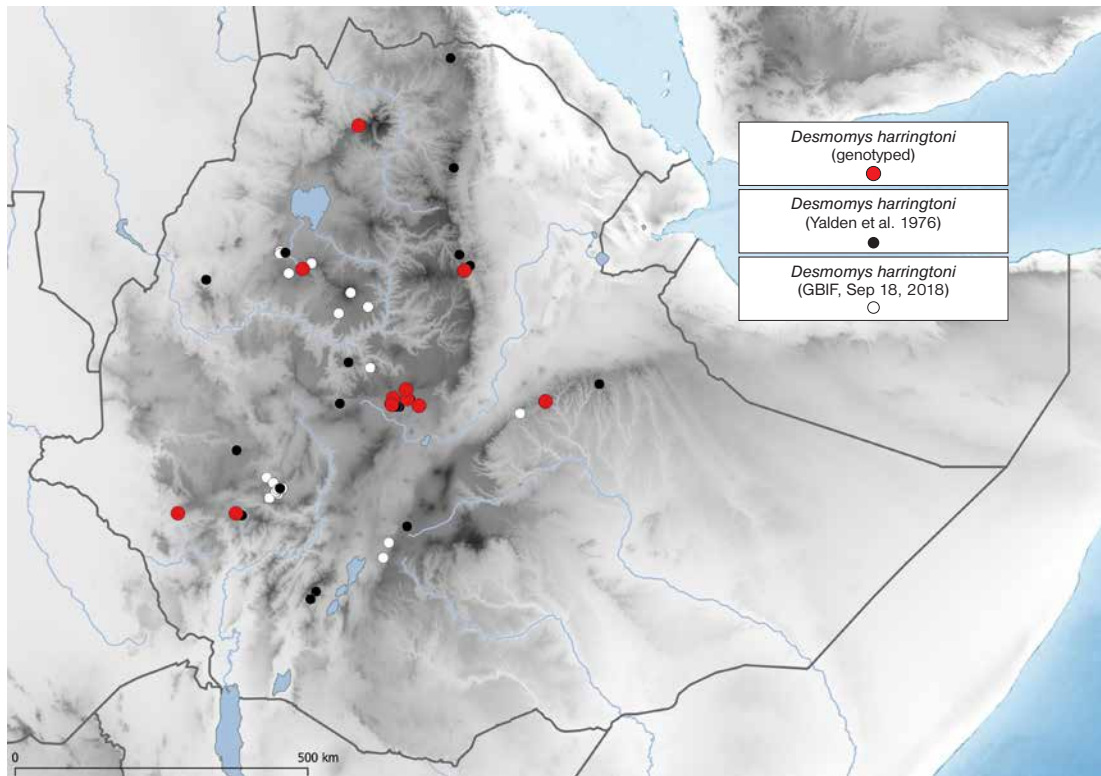


Fig. 20. Distribution of *Desmomys harringtoni*. This is a widespread species across the Ethiopian Highlands, albeit never abundant. Some of the GBIF records are under the name “*Pelomys harringtoni*”.

Genus *Arvicanthis* Lesson, 1842

This genus includes primarily diurnal rodents, often very abundant in various types of open grassland habitats (from arid lowland savanna to Afroalpine grasslands). The taxonomy of this genus is still far from resolved, but a recent multilocus genetic study (Bryja et al. 2019) has shed light on the evolutionary history of this important group and described diversity patterns. There are eight genetic clades in Ethiopia, occupying different regions and habitats of the country and they are considered here as separate species. Bryja et al. (2019) proposed names for particular Ethiopian taxa based on the analysis of original species descriptions and we follow this work here. However, these names need to be confirmed by comparison with the type material, which is unfortunately impossible for some of them as they have been destroyed (see Bryja et al. 2019). Three species are endemic to the Ethiopian Highlands (*A. abyssinicus*, *A. blicki*, *A. saturatus*), and two to lowland savanna mainly in the Ethiopian Rift Valley (*A. mearnsi*, *A. raffertyi*). The remaining three species (*A. somalicus*, *A. niloticus*, *A. niloticus* “C2-C4” sensu Bryja et al. 2019) have wide distributions extending to other parts of Africa.

Arvicanthis abyssinicus (Rüppel, 1842)

This species was described from Semien Mts. (Entschetgab = Entschetqab). The only species of *Arvicanthis* repeatedly captured in the Semien Mts. during three recent expeditions has mtDNA very similar to *A. blicki*, but is very distinct at nuclear markers and very likely not conspecific with *A. blicki* (see similar situation in *Stenocephalemys albocaudatus* vs. *S. sp. “A”*; Bryja et al. 2018a). All genotyped *Arvicanthis* from the Semien Mts. were captured at 3600-3900 m a.s.l. and no *Arvicanthis* was captured below 3600 m (Craig et al., in lit.). This is in contradiction to the original description of *A. abyssinicus*, because the type locality lies at the elevation of 3250 m a.s.l. (Bryja et al. 2019; but incorrect in Yalden et al. 1976). Yalden et al. (1976, 1996) reported *A. abyssinicus* as a very common species over a wide elevational range 1300-3400 m a.s.l., which is not confirmed by genetic data. The type material of *A. abyssinicus* is unfortunately damaged to the extent that it cannot be used for any multivariate analysis of skull morphology (O. Mikula, pers. comm.; see also Yalden et al. 1976). Here we follow Bryja et al. (2019) and use the name *A. abyssinicus* only for the high-elevation taxon, which was (besides the Semien Mts.) genetically confirmed also in other high mountains in north-western Ethiopia (Guna, Choqa, Aboye Gara and Borena Saynt).

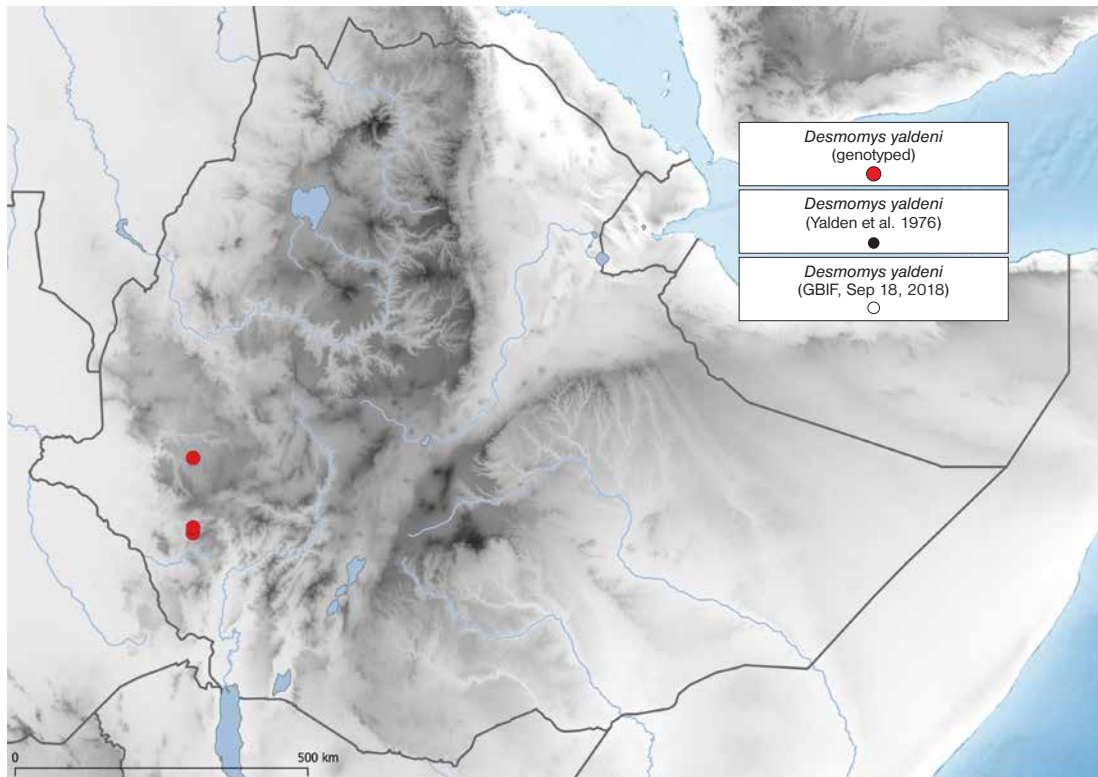


Fig. 21. Distribution of *Desmomys yaldeni*. The species is known only from rainforests in south-western Ethiopia at elevations 1250-1930 m a.s.l. The specimen from the northernmost locality of Gore (BMNH 72.419) was not genotyped, but assigned to this species with high probability based on skull morphometry.

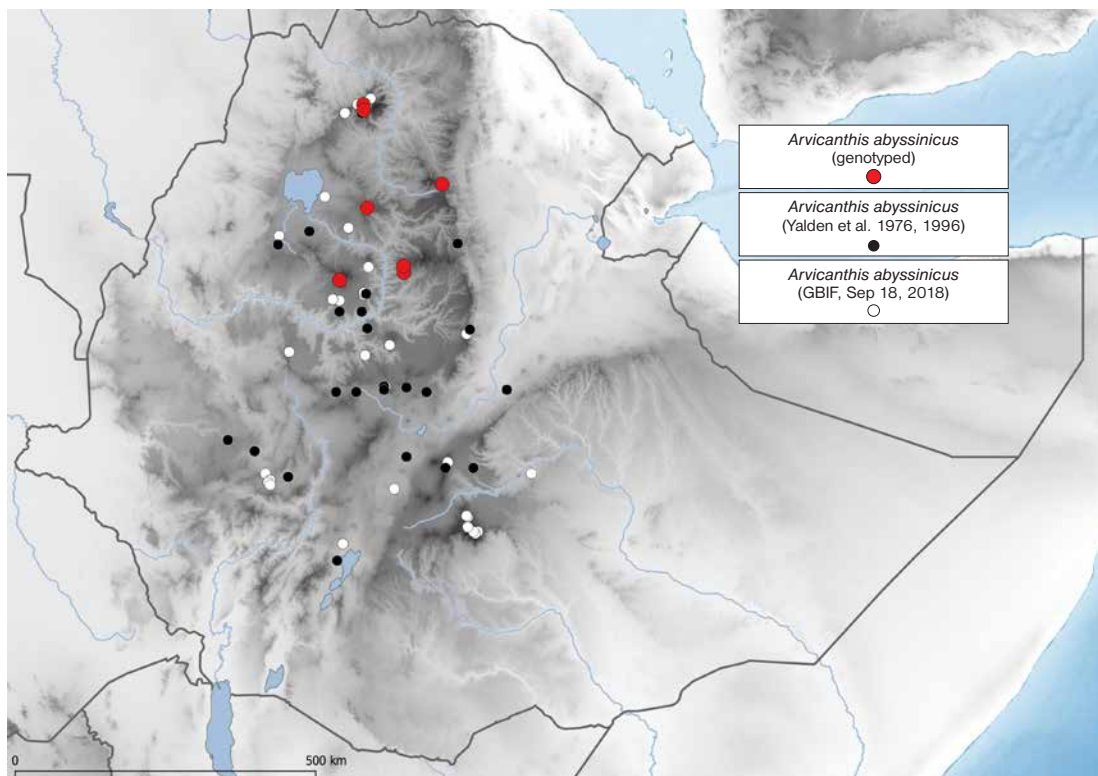


Fig. 22. Distribution of *Arvicanthis abyssinicus*. Numerous previous records (Yalden et al. 1976, 1996, GBIF database) likely represent other species; i.e. *A. saturatus*, *A. niloticus*, *A. blicki*, or *A. raffertyi*. Here we consider *A. abyssinicus* as a high-altitude species occurring in fragmented populations in north-western Ethiopia, following Bryja et al. (2019).

Arvicanthis blicki Frick, 1914

This is a high altitude species with relatively large body size, typical for the Afroalpine moorland zone above 3500 m a.s.l., but it also descends to grasslands at lower altitudes (Yalden et al. 1976). It is very distinct at skull morphology (Fadda & Corti 2001). It was considered to be distributed only in the Bale and Arsi Mts., east of the Rift Valley, but the population in Debre Sina west of the Rift Valley is genetically similar especially at nuclear markers and very likely represents this species as well, possibly affected by hybridization with *A. abyssinicus* (Bryja et al. 2019). The understanding of possible reticulate evolution of Ethiopian highland taxa (*A. abyssinicus*, *A. blicki*, *A. saturatus*) would require the use of genomic approaches and new material especially from west of the Rift Valley.

Arvicanthis somalicus Thomas, 1903

This is a low altitude, arid habitat species with small body size. It may occur together with larger *A. mearnsi* in the southern part of the Afar triangle (e.g. in Awash NP; Corbet & Yalden 1972, Demeter 1983, our data), but it is probably the only species of *Arvicanthis* living in the large Somali region in south-eastern Ethiopia. The species was described from northern Somaliland and genetically confirmed also from northern and central Kenya (Bryja et al. 2019). It has been considered as a synonym of *A. neumanni*, another small-bodied species living in arid habitats of the Masai steppe in Tanzania. The two taxa, however, are genetically very distinct at both nuclear and mitochondrial markers (Bryja et al. 2019), differ significantly in the shape of the skull (Fadda & Corti 2001) and karyotype (Castiglia et al. 2006), and should be considered as two different species (see also suggestions in Musser & Carleton 2005, Monadjem et al. 2015, Denys et al. 2017a).

Arvicanthis niloticus (É. Geoffroy Saint-Hilaire, 1803)

This species has been reported as *A. dembeensis* in previous studies (Yalden et al. 1976, 1996). It corresponds to *A. niloticus* clade C1 in Dobigny et al. (2013), but it seems to be a valid species, genetically very distinct from (and not sister to) *A. niloticus* “C2-C4” (sensu Dobigny et al. 2013) at both mitochondrial and nuclear markers (Bryja et al. 2019). The samples from Egypt (i.e. type locality of *A. niloticus*) belong to the mitochondrial clade C1 and the name “*niloticus*” should be therefore used for the species distributed along the Nile River, in northern Ethiopia and Yemen.

On the other hand, the widely distributed species in the belt of Sudanian savanna from Senegal to southern Ethiopia and western Kenya (genetically structured from west to east) should receive another name; here we follow Bryja et al. (2019) by using provisionally the name *A. niloticus* “C2-C4” (see below). Recent genetic results therefore support previous views, e.g. based on skull morphology (Fadda & Corti 2001), that populations living along the Nile valley, in northern Ethiopia and Yemen represent the same species (see also taxonomic discussion in Musser & Carleton 2005), distinct from the Sudano-Sahelian taxon, i.e. *A. niloticus* “C2-C4”. There are two mitochondrial lineages of *A. niloticus* in Ethiopia. The first one was found around Lake Tana and Alatish NP and it also occurs along the Nile Valley in Sudan (Abdel Rahman et al. 2008), while the second is distributed in the Tigray Region and along the eastern escarpment of the Abyssinian massif (Bryja et al. 2019).

Arvicanthis niloticus “C2-C4” (sensu Bryja et al. 2019)

This is a typical species of the Sudanian savanna/Sahel ecosystem (Bryja et al. 2019). Its phylogeographic structure was studied by Dobigny et al. (2013), who defined four main clades within *A. niloticus* sensu lato (C1-C4). The easternmost clade C1 is considered here as *A. niloticus* s. str. (see above), while the remaining clades represent species that should receive another scientific name. Numerous descriptions originate from Kenya and Uganda (see Allen 1939), from where substantial morphological variability has been reported (Fadda & Corti 2001) and where this taxon clearly occurs. It will be necessary to perform combined genetic and morphological analysis from this region to answer the question of how many species exist there and how they are related to *A. niloticus* “C2-C4” in central and western Africa. Similarly, there are at least four descriptions from “Anglo-Egyptian Sudan” (Allen 1939), i.e. current Sudan and South Sudan, which is a potential contact zone of *A. niloticus* s. str. and *A. niloticus* “C2-C4”. Detailed analysis of the type material and genomic analysis of potential contact zone, especially in Sudan, is required to correctly delimit these taxa (Bryja et al. 2019). The clade C2 of *A. niloticus* “C2-C4” is distributed in Sudanian savanna from northern Cameroon to southern Ethiopia and western Kenya. Very likely, it is also the species present in the Gambella region, west of the River Omo, from where DNA data are missing (Orlov et al. 1992, Bulatova et al. 2002). The localities of *A. dembeensis* (= *A. niloticus* s. str.) from

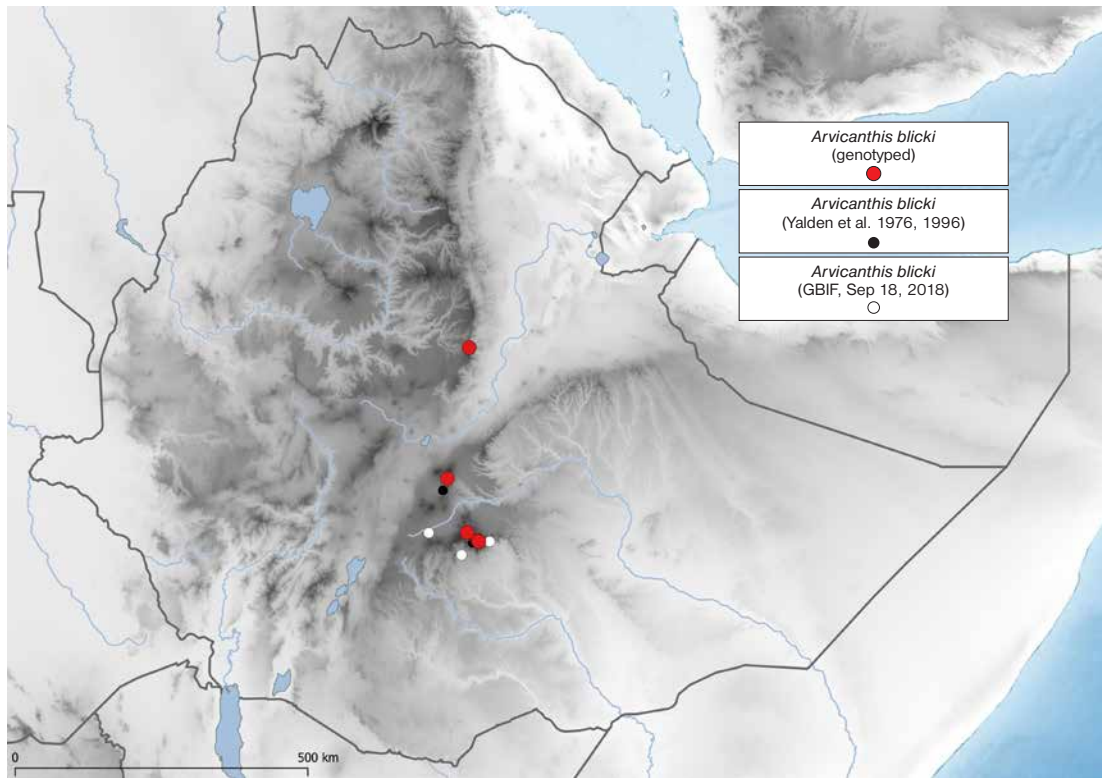


Fig. 23. Distribution of *Arvicanthis blicki*. The occurrence of the species in Debre Sina, west of the Rift Valley, was suggested based on the analysis of genetic markers (Bryja et al. 2019), but an understanding of its relationships with *A. abyssinicus* requires further study.

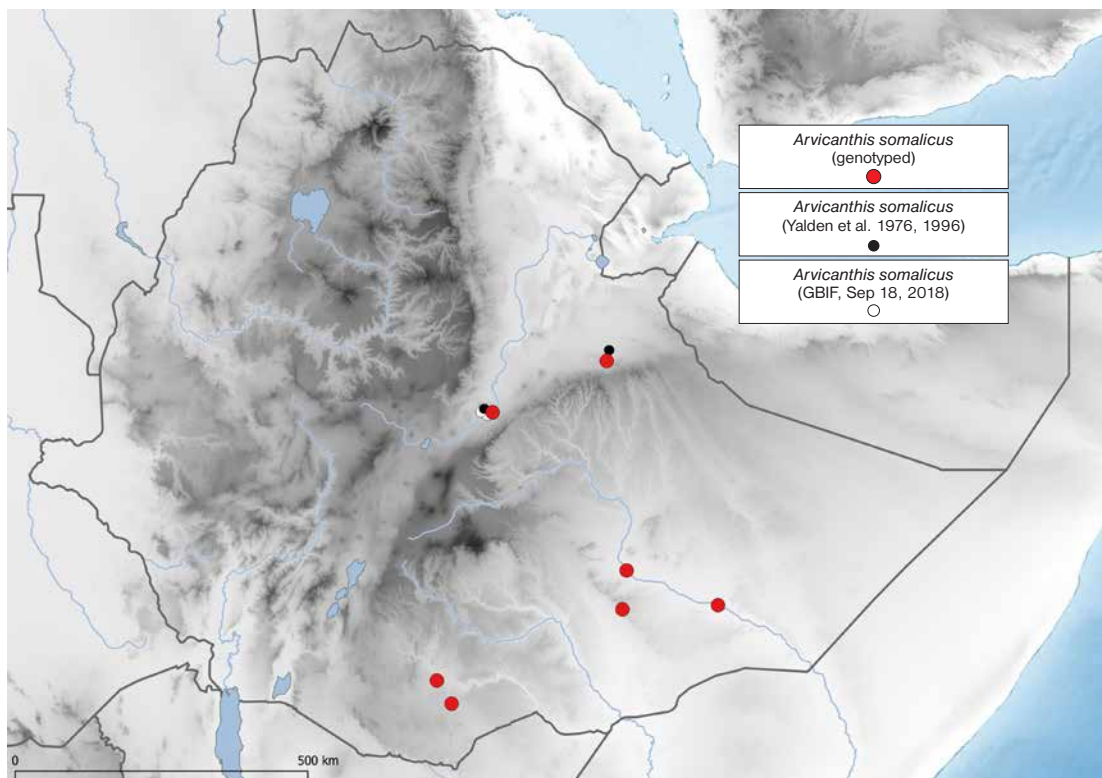


Fig. 24. Distribution of *Arvicanthis somalicus*. The records from the lower Omo River valley (Hubert 1978b, Roche 1979) require verification and are not shown here.

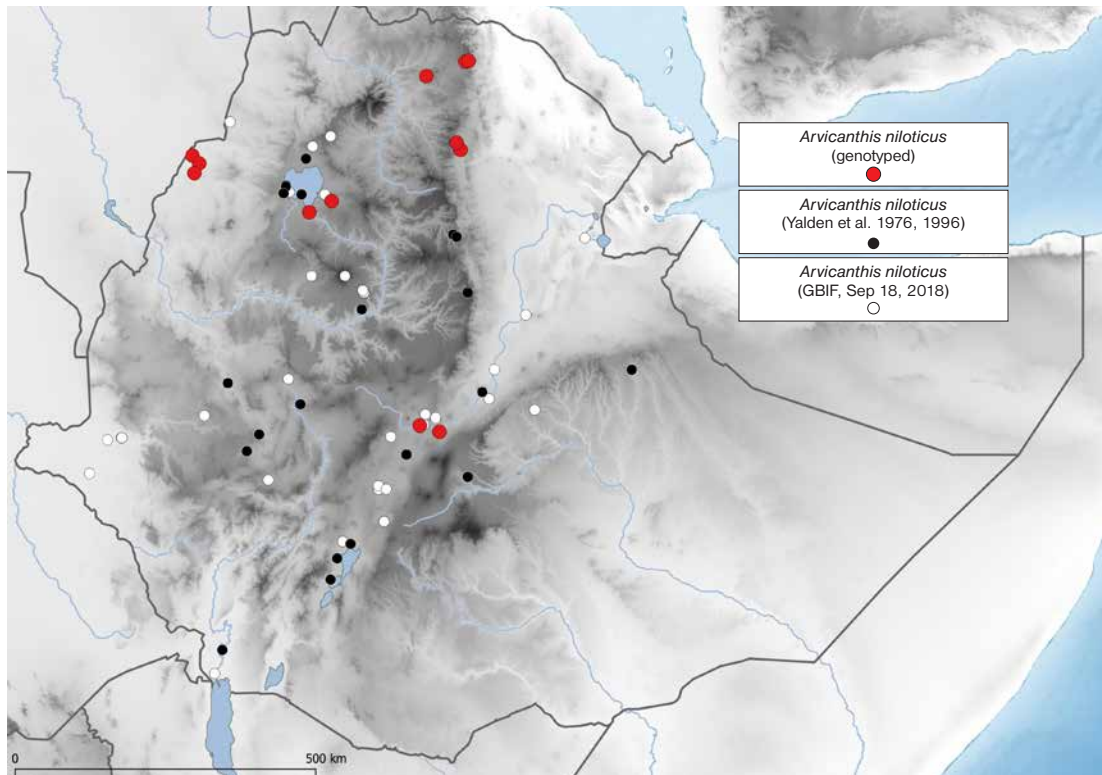


Fig. 25. Distribution of *Arvicanthis niloticus*. The localities from Yalden et al. (1976, 1996) were reported under the name *A. dembeensis*, while those from GBIF as *A. niloticus*. In both cases, some of these are likely to represent other taxa; i.e. *A. niloticus* “C2-C4” (in south-western part of the country), *A. mearnsi* (in lowlands along the River Awash), or *A. raffertyi* (in southern part of Rift Valley and south of Chercher Mts.).

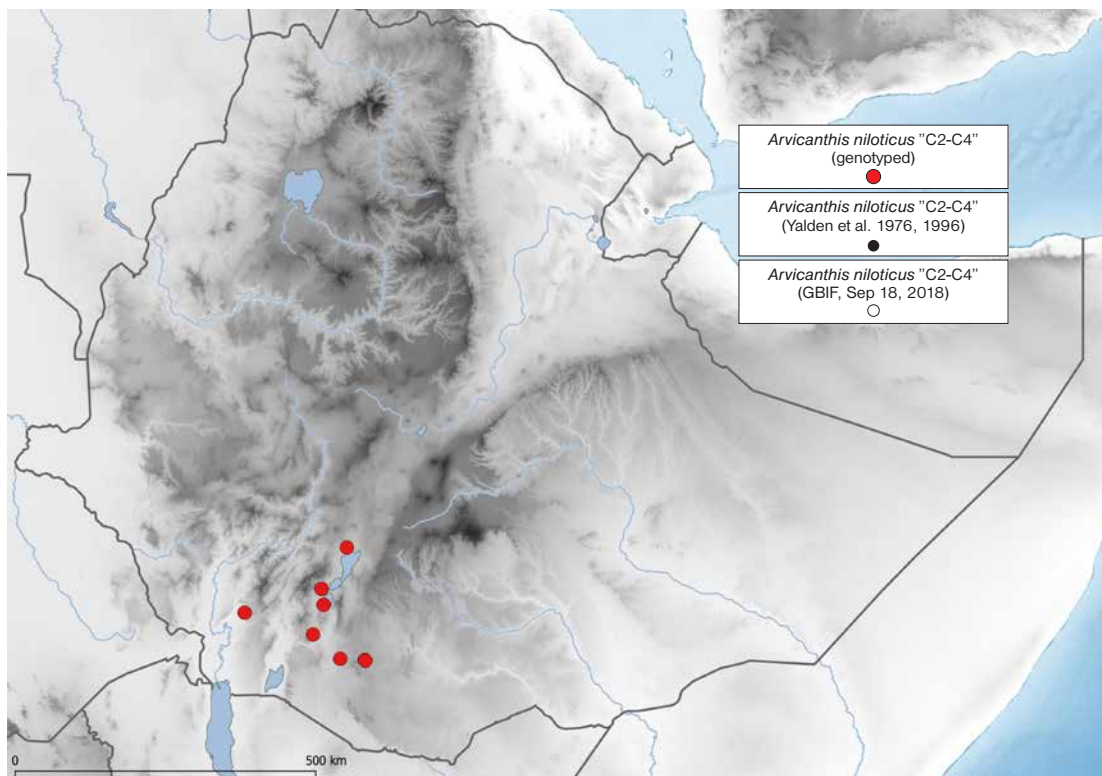


Fig. 26. Distribution of *Arvicanthis niloticus* “C2-C4”. All genotyped individuals belong to the clade C2 (sensu Dobigny et al. 2013). Some localities of *A. dembeensis* reported by Yalden et al. (1976) probably represent *A. niloticus* “C2-C4” (they are shown on the map of *A. niloticus*).

the southern part of the Rift Valley reported by Yalden et al. (1976) very likely represent *A. niloticus* “C2-C4”.

Arvicanthis mearnsi Frick, 1914

Besides the genetically very distinct species *A. raffertyi* (belonging to the so-called ANSORGEI group, sensu Bryja et al. 2019), there are three additional species occurring in the Rift Valley in Ethiopia (Bryja et al. 2019): *A. mearnsi*, *A. somalicus*, and *A. niloticus* s. str. The latter probably prefers higher altitudes (confirmed from Koka and Dera Dilfekar, ca. 1700 m a.s.l.), but *A. mearnsi* and *A. somalicus* co-occur e.g. in the Awash NP (Demeter 1983). *Arvicanthis abyssinicus mearnsi* Frick, 1914 was described from “Sadi Malka, the River Awash, 2800 ft (853 m a.s.l.)”, close to the current Awash NP. The name is reported as a synonym of “*niloticus*” in Musser & Carleton (2005), but Bryja et al. (2019) suggested it as the most suitable name for the larger lowland species living (at least) in the northern part of the Rift Valley and at the southern margin of the Afar triangle. All genetically confirmed individuals of *A. mearnsi* are from the central and northern part of the Rift Valley. It is likely that previous records of larger *Arvicanthis* from this area (Corbet & Yalden 1972, Demeter 1983; some of them reported as *A. dembeensis* by Yalden et al. 1976) represent this taxon. Its precise distributional limits and phylogenetic relationships with *A. niloticus* s. str. should be further investigated, but the two species seem to be closely related as suggested by shared insertion at one nuclear gene and sister relationship in the species tree (Bryja et al. 2019).

Arvicanthis saturatus Dollman, 1911

Arvicanthis abyssinicus saturatus Dollman, 1911 was described from the River Didessa near Guma and it is the oldest available name for this taxon, reported in most previous works (except the original description, see above) as *A. abyssinicus* (Bryja et al. 2019). The original description by Dollman (1911) perfectly fits this taxon, i.e. general colour dark blackish, backs of feet dark brown, toes black and dorsal stripe (usually) well marked, and it also corresponds well in morphometric analysis of skulls (Fadda & Corti 2001). All genetically characterized specimens of this species originate from central Ethiopia, not far from Addis Ababa (e.g. crop fields near Menagesha). Yalden et al. (1976) mentioned that the mid-dorsal dark stripe, lack of the reddish suffusion on the hindquarters and rather dark agouti fur on the venter is typical colouration of “*A. abyssinicus*”. This suggests that most localities of

A. abyssinicus from Yalden et al. (1976) in fact might represent *A. saturatus*. Genetic analysis of more numerous material especially from lower elevations of the Abyssinian massif (where genetic data are largely lacking) is required to delimit the distribution of this taxon.

Arvicanthis raffertyi Frick, 1914

This is genetically the most distinct *Arvicanthis* in Ethiopia, sister to *A. ansorgei* from western Africa (Bryja et al. 2019). Despite this fact, it has been overlooked and not recognized as a separate species. Compared to all other Ethiopian taxa it has a very distinct karyotype called ANI-6 or ANI-6a (Orlov et al. 1992, Corti et al. 2005, Castiglia et al. 2006). It is very likely an Ethiopian endemic species (even though its occurrence in northern Kenya, South Sudan and Somalia cannot currently be ruled out) with two genetic (mitochondrial) sublineages distributed in parapatry (north vs. south). The species lives at lower elevations along mountain escarpments and in the Rift Valley. Part of the material reported by Yalden et al. (1976) as *A. abyssinicus* or *A. dembeensis* very probably belongs to this species (ditto for GBIF – see maps for *A. abyssinicus* and *A. niloticus*). The taxonomic relationships with the populations in Gambella (ANI-7 karyotype) and Afgoi, Somalia (ANI-8 karyotype) should be further analysed (Castiglia et al. 2006, Bryja et al. 2019).

Genus *Mylomys* Thomas, 1906

These are large rodents (80-200 g, head + body 160-210 mm) living in grasslands in the forest-savanna mosaic. There are only two species included in this genus; one is widespread from Guinea to western Kenya, the second is known only from the holotype captured more than 110 years ago in the Kaffa region in Ethiopia.

Mylomys rex (Thomas, 1906)

This species, previously reported as *Pelomys rex* (Yalden et al. 1976) or *Mylomys dybowski* (Yalden et al. 1996) is known only from the type specimen, collected in the Charada forest in south-western Ethiopia by Peter Zaphiro in 1904-1905. Only the skin of an adult male is preserved (see more details in Lavrenchenko 2003), based on which it was assigned to the genus *Mylomys* by Musser & Carleton (1993). More intensive research in south-western Ethiopia should be done to assess, whether this species is still a member of Ethiopian fauna and what its taxonomic position is.

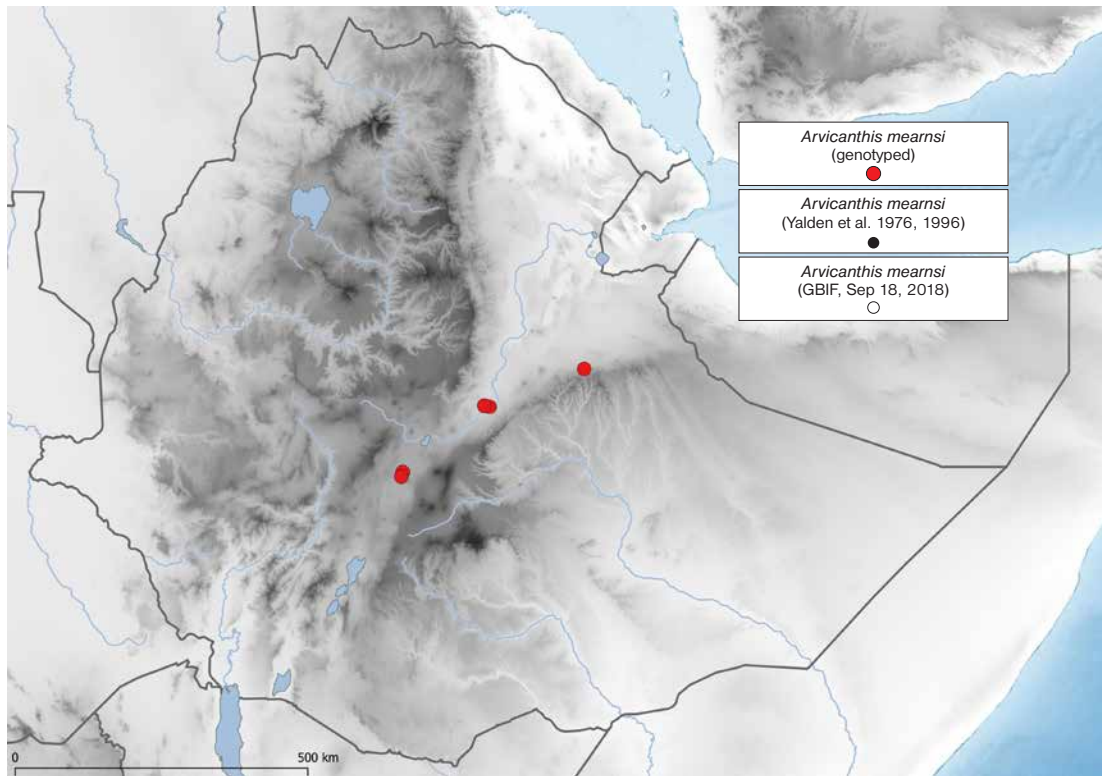


Fig. 27. Distribution of *Arvicanthis mearnsi*. Some localities of *A. dembeensis* from Yalden et al. (1976) and *A. niloticus* from GBIF database may represent this lowland taxon (see the map for *A. niloticus*).

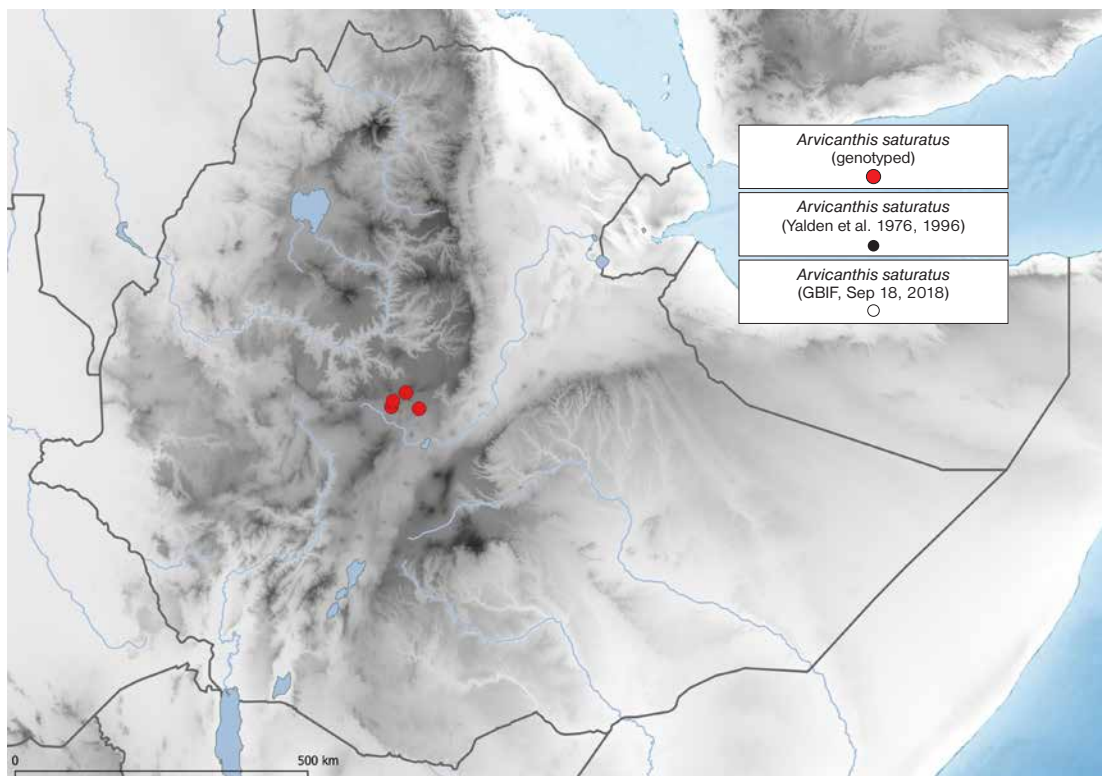


Fig. 28. Distribution of *Arvicanthis saturatus*. The species is probably more widespread in the Abyssinian massif west of the Rift Valley, and numerous records of *A. abyssinicus* in Yalden et al. (1976) and GBIF database might belong to this species (see the map for *A. abyssinicus*).

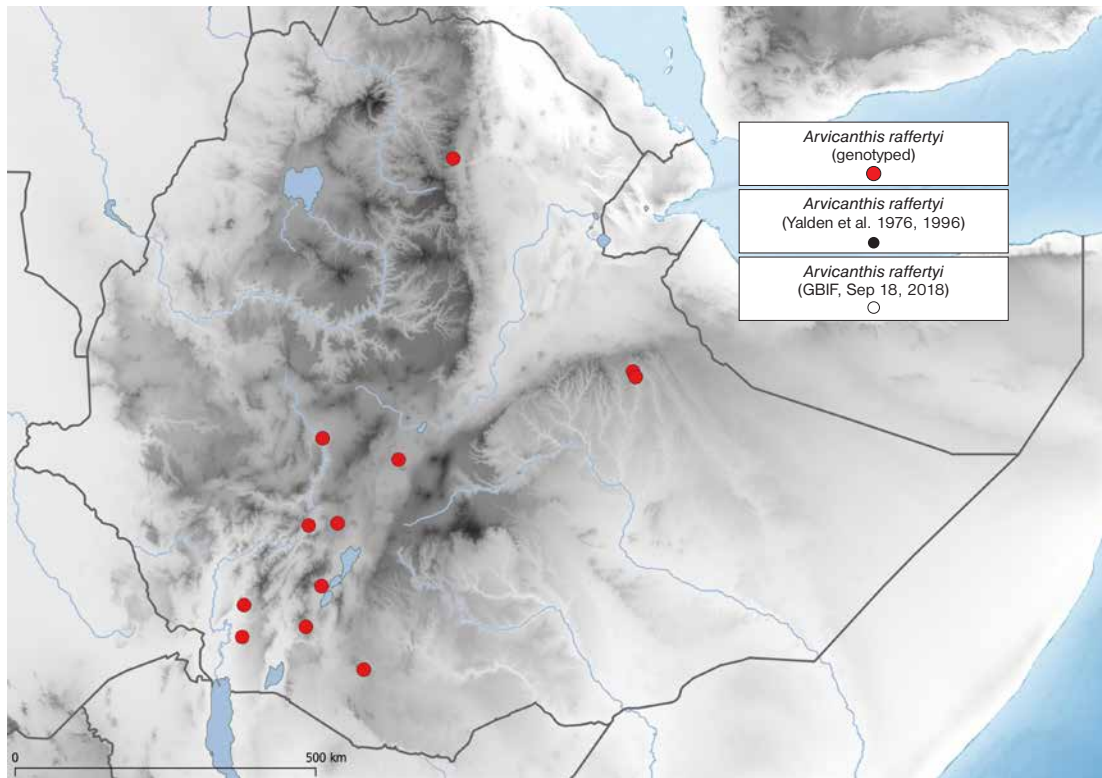


Fig. 29. Distribution of *Arvicanthis raffertyi*. Part of localities of *A. abyssinicus* and *A. dembeensis* in Yalden et al. (1976) and *A. abyssinicus* and *A. niloticus* in GBIF database might represent this species (see the maps for *A. abyssinicus* and *A. niloticus*). The specimens from Alamata (northern Ethiopia) and Babile (eastern Ethiopia) form a distinct mtDNA sub-lineage separated from populations in the bottom of Rift Valley. The population with ANI-7 karyotype from the Gambella region is not shown here, as its taxonomic status should be further studied (Bryja et al. 2019).

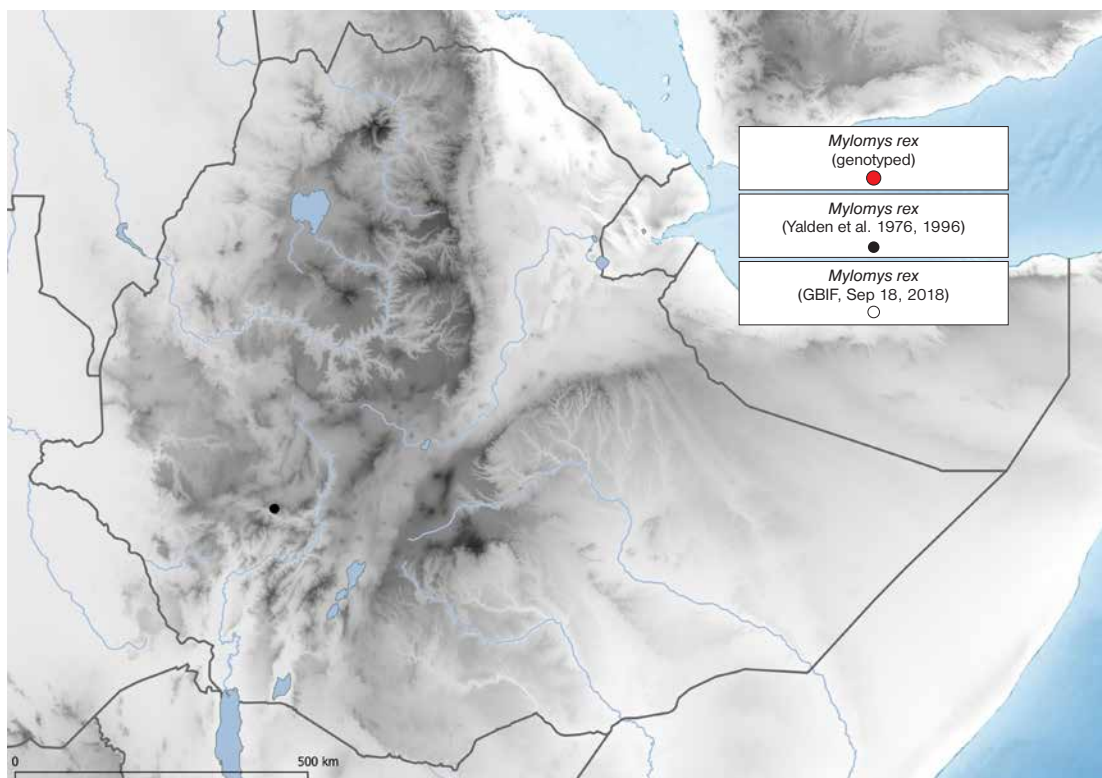


Fig. 30. Distribution of *Mylomys rex*. The species is known only from the holotype (skin without skull) collected by Peter Zaphiro in 1904-1905.

Genus *Aethomys* Thomas, 1915

A widely distributed genus, typically living in various savanna-like habitats. Two species are known from Ethiopia, both at their distributional limits.

Aethomys hindei (Thomas, 1902)

This species is distributed in the southern part of the Sudanian savanna belt from Cameroon to western Kenya. Genotyping of Ethiopian material revealed a separate genetic clade (also confirmed in neighbouring regions of South Sudan), sister to all other *A. hindei* from the rest of its distribution. In Ethiopia, it is known from the Sudanian savanna in the south-western part of the country. Three specimens collected at the River Gato, south of Gardula in 1912, in the Rift Valley (Bekele & Schlitter 1989) may represent *A. kaiseri*.

Aethomys kaiseri (Noack, 1887)

The species is widespread on the savanna of eastern Africa. Ongoing genetic work has found two genetically very distinct clades: one is distributed mainly in the Zambezi savanna in Tanzania and Zambia, and the second in the Somali-Masai savanna east of the Rift Valley, from north-eastern Tanzania to southern Ethiopia (Mikula et al., in lit.). Morphological comparison of both clades is necessary and their potential reproductive isolation needs to be studied in the presumed contact zone in the Rift Valley in south-western Kenya. In Ethiopia, it was reported only recently from two localities in the southernmost part of the country. Three specimens collected at the River Gato, south of Gardula (Bekele & Schlitter 1989) may also represent this species (they were reported as *A. hindei* by Yalden et al. 1996; see the map and account of this species). On the other hand, the GBIF record from Godare in western Ethiopia is questionable. It is based on a series of seven specimens of *Aethomys* in BMNH from this locality; six were identified as *A. hindei* and one as *A. kaiseri*, but the two species are not known to overlap anywhere in their distribution. All *Aethomys* collected by Lavrenchenko and colleagues in the Godare forest were *A. hindei*.

Genus *Dasymys* Peters, 1875

This genus represents the group of arvicanthine rodents adapted for living in moist habitats (riverine, swampy, wetlands), which possibly explains its disjunctive distribution throughout its wide range across sub-Saharan Africa. Once regarded as monotypic (*D. incommutus* sensu lato), reviews based mainly on morphology of skulls (Verheyen et al. 2003, Mullin et al. 2004a, b) recognized up to 14 species (Monadjem

et al. 2015). However, integrative taxonomic revision of the whole genus, including genetic data, is urgently required. One species is currently considered to occur in Ethiopia.

Dasymys griseifrons Osgood, 1936

As with all members of the genus, *D. griseifrons* is usually associated with riverine and swampy habitats with long grass at altitudes of 1200–2500 m a.s.l. (Yalden et al. 1976, 1996). It has been known only from localities west of the Rift Valley (Yalden et al. 1996). However, Lavrenchenko (2000) discovered an isolated population in a small swamp on the River Shawe in the centre of the Harenna forest, east of the Rift Valley. The species, as currently delimited, is endemic to Ethiopia (Mullin et al. 2005). Sequenced individuals form genetically very distinct lineages from East and West Africa, supporting the endemic status. However, genetic data are still scarce and it is possible that more species occur in Ethiopia as suggested by Monadjem et al. (2015). The chromosome number of animals from Ethiopia is variable with $2n = 38-40$, $FN = 44$ (Volobouev et al. 2000).

Genus *Grammomys* Thomas, 1915

The genus comprises of partially arboreal taxa, widespread in woodlands and forests in sub-Saharan Africa. Its taxonomy is not well resolved and there is much confusion over the use of species names. However, the recent comprehensive phylogenetic analysis by Bryja et al. (2017) has shed light on the evolutionary relationships among major groups and their distribution. In Ethiopia, two lineages from the *macmillani* group were confirmed, but detailed analysis of the Kenyan populations (where they co-occur) is required to decide whether they represent two biological species.

Grammomys minnae Hutterer & Dieterlen, 1984

This species was described as an Ethiopian endemic from the Bulcha forest in the Rift Valley, based on a chromosome count ($2n = 32$) and snow white (rather than yellowish-white) underside (Hutterer & Dieterlen 1984). Recent genetic analysis of material from the Arero forest ($2n = 32$; L. Lavrenchenko et al., unpublished data) showed that *G. minnae* is genetically very close to *G. sp. "m7"* (sensu Bryja et al. 2017), which is distributed in isolated forest patches from northernmost Tanzania to central Kenya. This lineage is sympatric with *G. sp. "m4"* at several localities in Kenya and taxonomic analysis of this group (= the *macmillani* group sensu Bryja et al. 2017) is required.

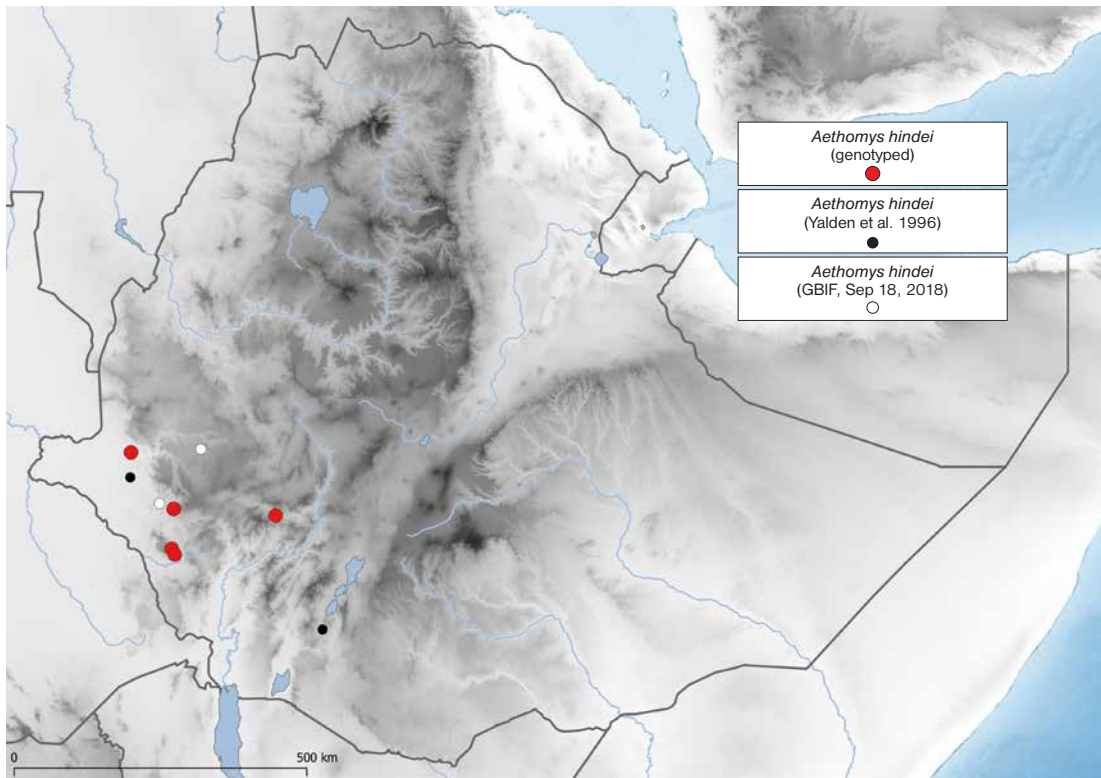


Fig. 31. Distribution of *Aethomys hindei*. The southernmost locality in the Rift Valley (the River Gato, Yalden et al. 1996) may represent *A. kaiseri*.

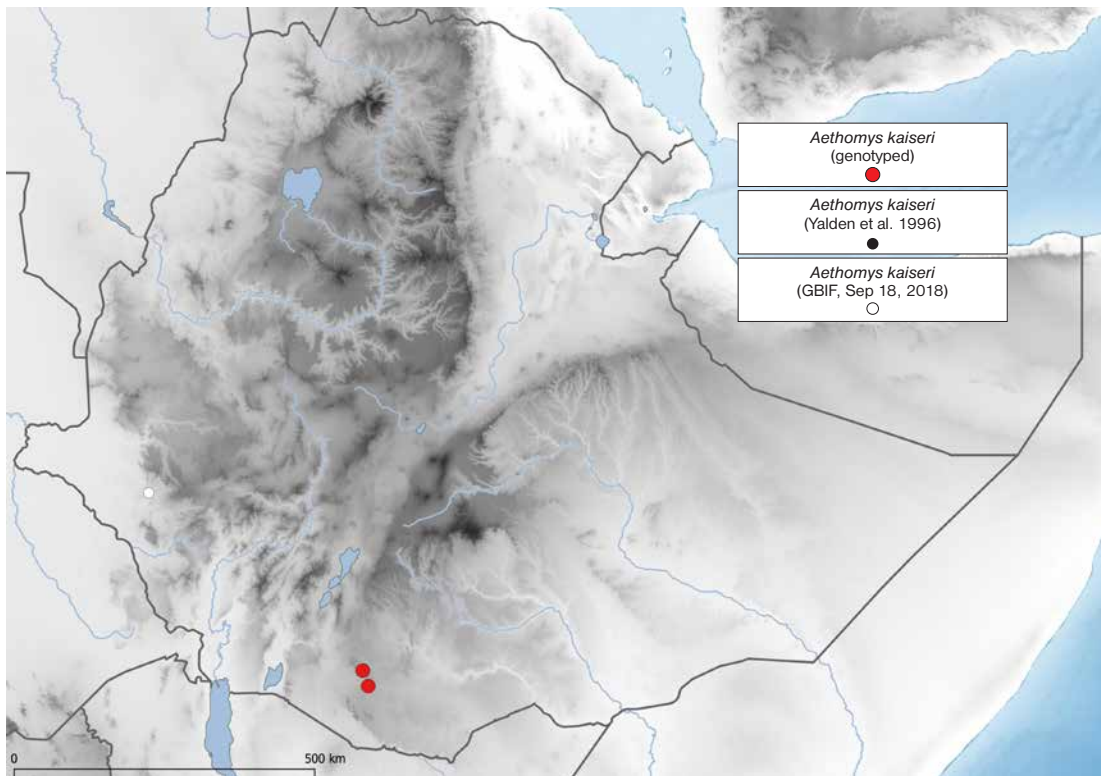


Fig. 32. Distribution of *Aethomys kaiseri*. The species may potentially occur even in southern part of the Rift Valley as suggested by the records of *Aethomys* in the River Gato and reported as *A. hindei* by Yalden et al. (1996) – see the map for *A. hindei*. In contrast, the GBIF record from Godare in western Ethiopia is questionable (see text).

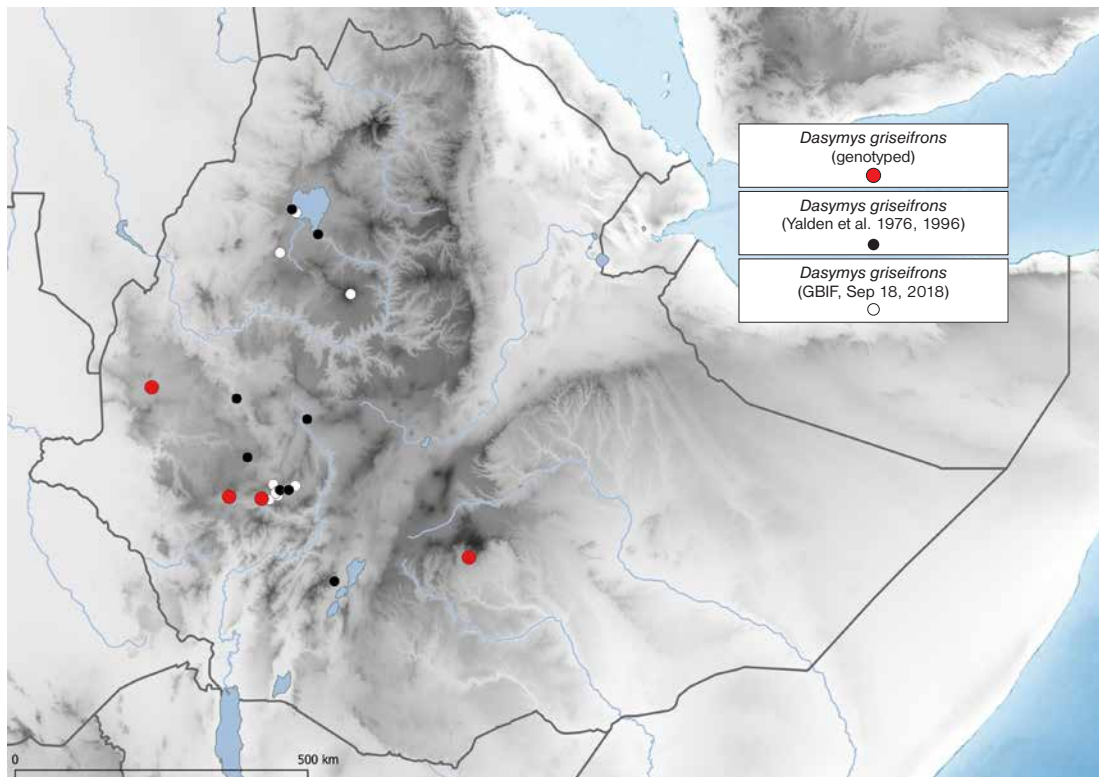


Fig. 33. Distribution of *Dasymys griseifrons*. All known localities of *Dasymys* in Ethiopia are from swampy areas. Until more data become available we consider this to be a single species.

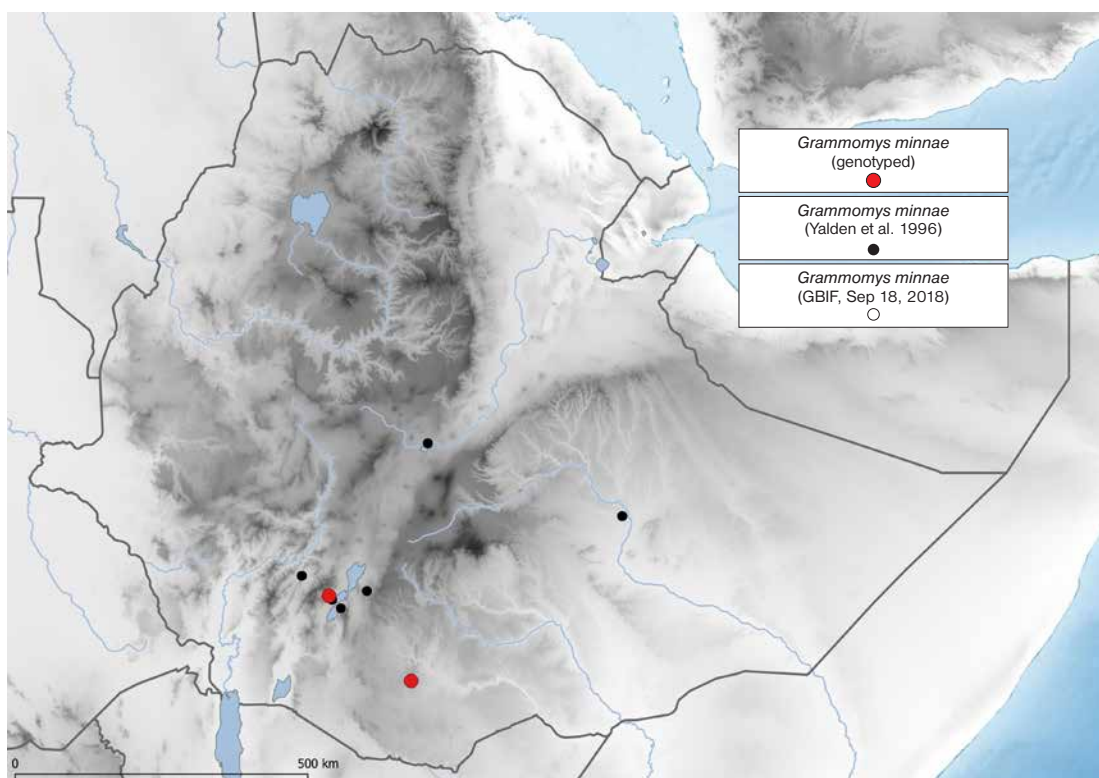


Fig. 34. Distribution of *Grammomyss minnae*. The easternmost record from the River Darde (Rhoads 1896) requires verification, as well as the material from USNM collected in Koka (the Awash River valley). Yalden et al. (1976) reported this species under the name *G. dolichurus*.

All records from the Rift Valley are reported here as *G. minnae*, although Yalden et al. (1996) cited Duckworth et al. (1993) who claimed that a single individual from the River Sermale forest (Nechisar NP) is distinct from *G. minnae* in both size and colour. Another specimen from the River Darde (Rhoads 1896) was identified as *Mus arborarius* and put in synonymy with *Grammomys* (Yalden et al. 1976). This old record, however, is questionable and requires verification (it may represent *Myomyscus*). The species *G. macmillani* (Wroughton, 1907) was described from “Wouida, north of Lake Rudolf (= Turkana) at altitude of 6200 feet”. If the coordinates of this locality are correct in Yalden et al. (1976), it is very close to the known localities of *G. minnae* in the Arba Minch region. Because *G. minnae* was described mainly on the basis of a very distinct karyotype and there is no karyotype available from the type locality of *G. macmillani*, it is possible that the two taxa are conspecific (with *G. minnae* being an earlier synonym).

Grammomys sp. “m4” (sensu Bryja et al. 2017)

This genetic lineage is widespread in the Kenyan Highlands (included Mt. Kenya and Elgon), and has also been confirmed from the Imatong Mts. in South Sudan and isolated dry forests in the Ilemi triangle (between Kenya, South Sudan and Ethiopia) (Bryja et al. 2017). In 2017, it was captured in Sheko forest (Dembi dam) in south-western Ethiopia (J. Bryja et al., unpublished data). The record from the lower Omo valley (Hubert 1978b) is considered here as belonging to this species as well. The available names for this lineage can be *G. macmillani* (see *G. minnae* account) or *G. ibeanus* (Osgood, 1910) described from Molo in Kenya. Most material of this clade from Kenya has been reported under the latter name in previous studies based on morphological species identifications. The whole *macmillani* group (sensu Bryja et al. 2017) requires taxonomic revision, including analyses of the type material and a study of potential hybridization between multiple mitochondrial genetic lineages in central Kenya.

Genus *Lemniscomys* Trouessart, 1881

This genus is closely related to *Arvicanthis* (e.g. Aghová et al. 2018) and is characterized by conspicuous dark stripes on the back, whose pattern is often species-specific. There are two genetically confirmed species in Ethiopia.

Lemniscomys zebra (Heuglin, 1864)

Yalden et al. (1976) reported this species under the name *L. barbarus* (Linnaeus, 1767), which is now

considered endemic to regions north of the Sahara by most authors (Monadjem et al. 2015, Denys et al. 2017a). However, recent genetic data suggest that *L. barbarus* is conspecific with populations of *L. zebra* from the western Sudanian savanna from Senegal to Benin (Hánová et al., in lit.), while “true” *L. zebra* (described from South Sudan) is distributed in the same vegetation belt but further east from Chad to central Tanzania. A single individual collected by Lavrenchenko and his colleagues in the Gambella Region in western Ethiopia has the phenotype of *L. zebra*. We genotyped this sample using dry skin tissue and obtained a short *cytb* sequence, which is more similar to *L. zebra* than to any other species. The northernmost record from Gallabat at the Sudanese border (Yalden et al. 1976) may be *L. hoogstraali* Dieterlen, 1991, known only from the holotype collected in Upper Nile Province in South Sudan, and considered by some authors as an aberrant specimen of *L. zebra* (Monadjem et al. 2015). Genetic analysis of new material, especially from northern Ethiopia, is urgently needed to resolve the species status and distribution of *L. hoogstraali*.

Lemniscomys macculus (Thomas & Wroughton, 1910) Yalden et al. (1976) reported numerous localities of *L. striatus* (Linnaeus, 1758), especially from south-western Ethiopia. Van der Straeten & Verheyen (1979) have shown that some of this material in fact represents a smaller species *L. macculus* and that the two taxa are broadly sympatric in Ethiopia. Recent genetic analysis confirmed only genetically uniform *L. macculus* in Ethiopia, which is phylogenetically very distant from *L. striatus*, despite a similar stripe pattern (Hánová et al., in lit.). A phylogeographic study by Nicolas et al. (2008) genetically confirmed *L. striatus* in large areas of tropical Africa, mostly in the transitional zone between tropical forest and savanna. Its occurrence in Ethiopia is therefore questionable and we consider here all previous records in the country as *L. macculus*. This species is genetically almost identical to *L. bellieri* Van der Straeten, 1975 from the western Sudanian savanna, and they should be considered synonymous (Monadjem et al. 2015, Hánová et al., in lit.).

Genus *Oenomys* Thomas, 1904

This is an old lineage of Arvicanthini, sister to all other African genera in this tribe (Mikula et al., in lit.). The two recognized species live in forests of western and central Africa. They can be easily recognized by the pelage colouration with a conspicuously orange nose patch.

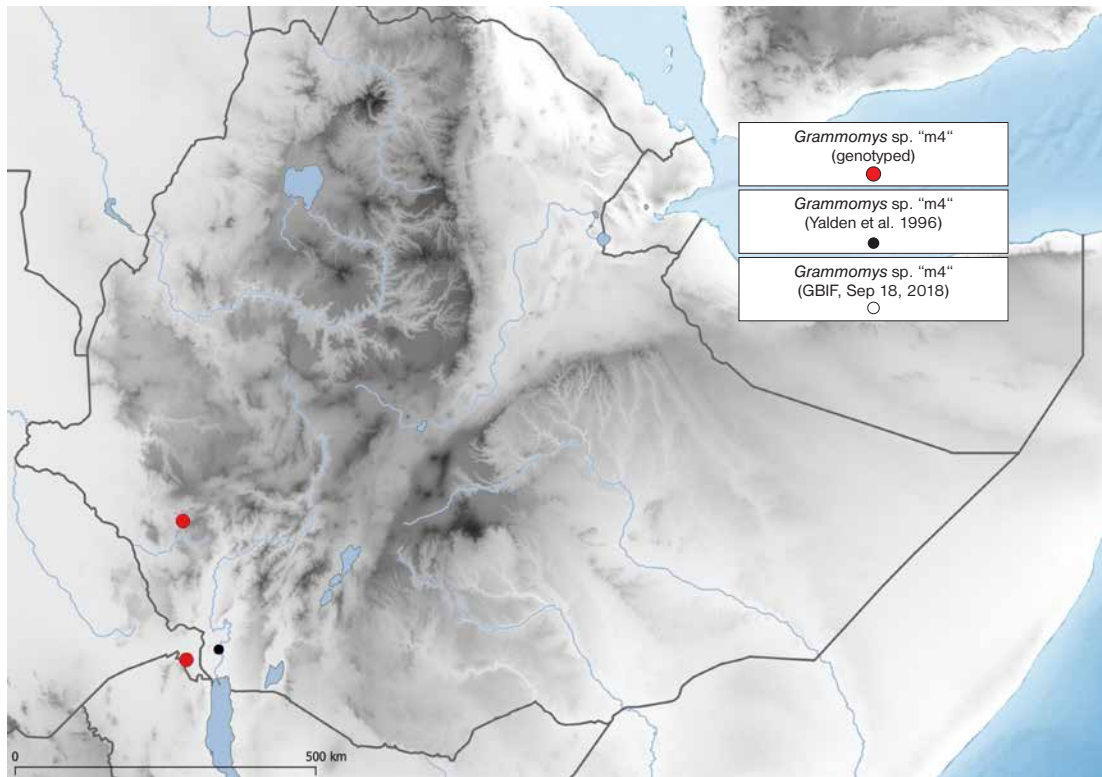


Fig. 35. Distribution of *Grammomys* sp. "m4". The record from the lower Omo valley (Hubert 1978b; listed under *G. minnae* account in Yalden et al. 1996) is reported here as this species because it is close to the Ilemi triangle (on the map here as part of South Sudan), from where this lineage was also confirmed genetically (Bryja et al. 2017).

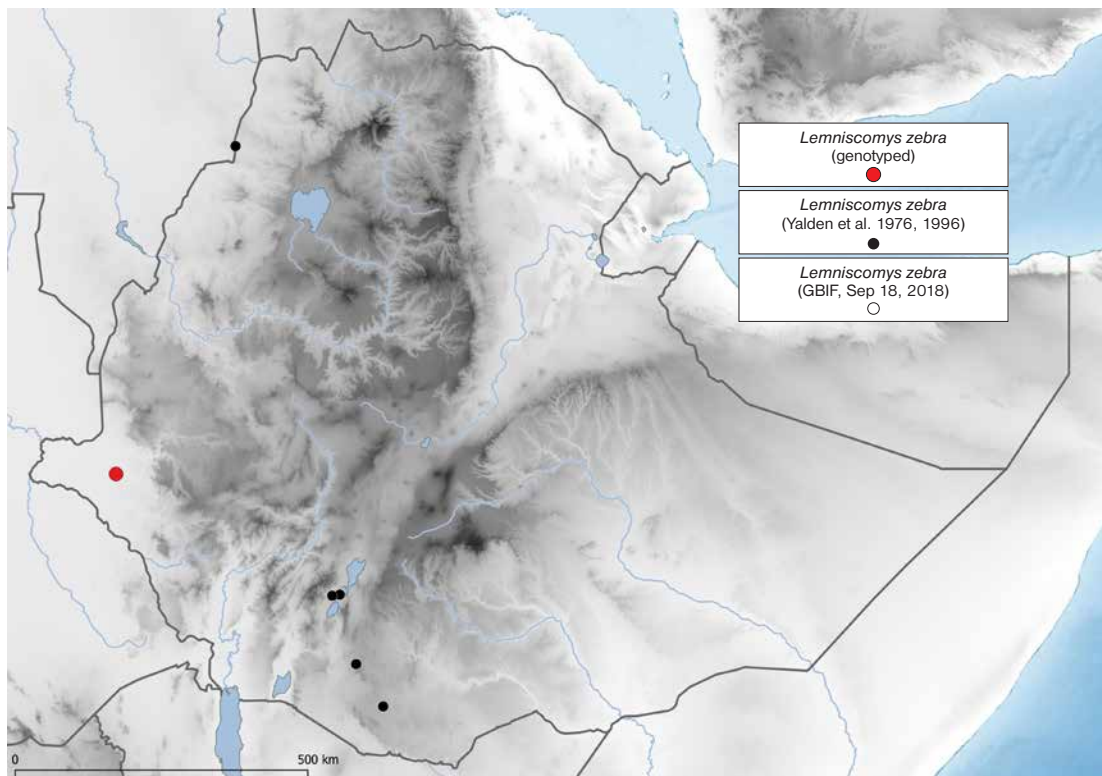


Fig. 36. Distribution of *Lemniscomys zebra*. The northernmost record from Gallabat (Yalden et al. 1976) may represent the poorly known *L. hoogstraali*. Other records reported by Yalden et al. (1976, 1996) as *L. barbarus* from the Rift Valley need confirmation as they may represent *L. macculus*, which is relatively abundant in neighbouring localities (see below).

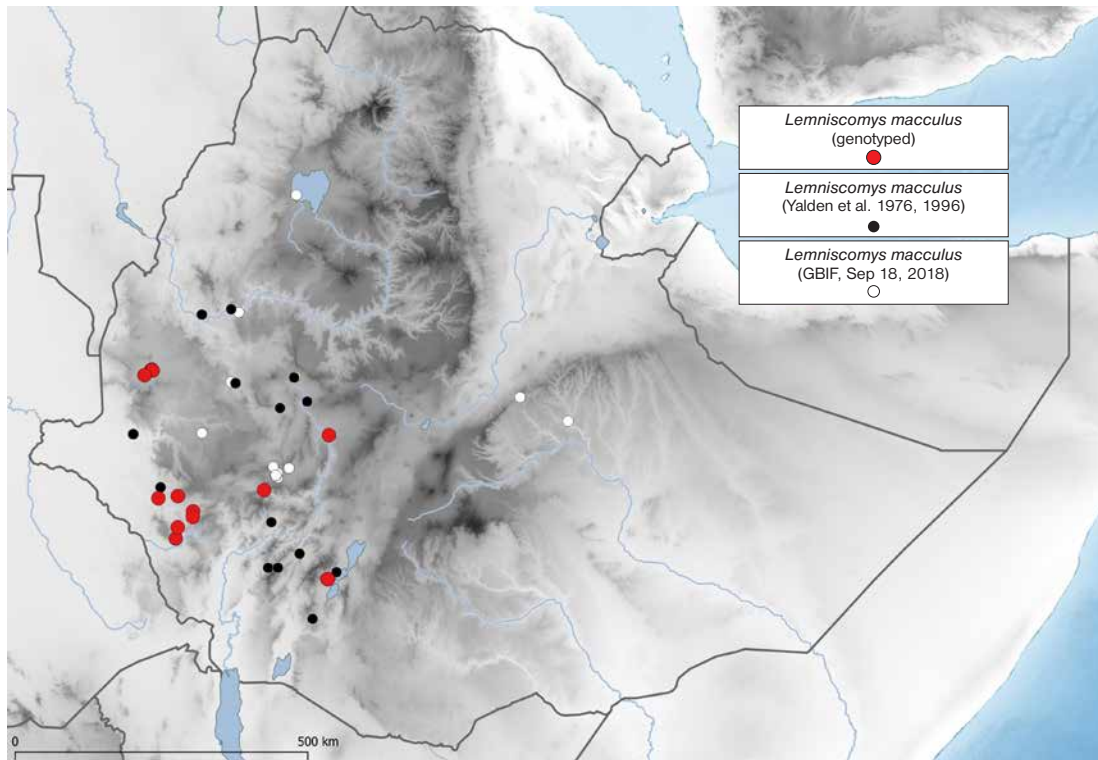


Fig. 37. Distribution of *Lemniscomys macculus*. Yalden et al. (1976) reported this species as *L. striatus* (ditto for part of GBIF records), which should be widely sympatric with *L. macculus* in Ethiopia (see Van der Straeten & Verheyen 1979, Yalden et al. 1996). All genotyped Ethiopian records, however, represent *L. macculus* and the occurrence of *L. striatus* in Ethiopia is therefore questionable (all previous records of *L. striatus* are here shown as *L. macculus*). The most remote GBIF records (Lake Tana in northern Ethiopia, Galampso and Sagatta in eastern Ethiopia) are the only Ethiopian *Lemniscomys* from the FMNH collection (collected in 1927) and their identification should be taken with caution and await confirmation.

Oenomys hypoxanthus (Pucheran, 1855)

This is primarily a forest species, widespread throughout the Guineo-Congolian forests, Albertine Rift Mts. and Kenyan Highlands. In Ethiopia it is limited to forest regions in the south-west of the country, where it has been found at altitudes of 500-2600 m a.s.l. It is probably rare as it was not captured during several recent expeditions. It seems that the Ethiopian population is geographically isolated from the more continuous distribution in central Africa, but a detailed genetic study of the Ethiopian population remains to be done.

Genus *Thallomys* Thomas, 1920

These large (mass ca. 60-80 g; head + body ca. 130-150 mm) rodents have a coarse buffy-brown to grey dorsal pelage and pure white ventral pelage as well as chin and throat, with a well-furred black tail that is longer (110-145 %) than the head and body (Monadjem et al. 2015). They are arboreal and they can be seen climbing on acacia bushes during daylight. They typically occur in acacia savanna from northern South Africa, Botswana, Namibia and south-western Angola to Tanzania, Kenya and Ethiopia in

the north. However, records, especially from eastern Africa, are very scarce and there is no detailed genetic study of the genus. One species has been recorded in southern Ethiopia.

Thallomys paedulus (Sundevall, 1846)

Misonne (1968) reported this species from “southern Ethiopia” without any details. The only reliable georeferenced record of this species (otherwise widespread in southern and eastern Africa) in Ethiopia is reported by Petter (1973) from Javello (Yabello). This species has been poorly diagnosed and its relationships with other congeners are currently unclear or even confused (Monadjem et al. 2015). It is likely that populations from the Somali-Masai savanna (including Ethiopia) are a different species to those from the Zambezian savanna (similar patterns are shown by other genera, e.g. *Gerbilliscus* or *Acomys*; Aghová et al. 2017, 2019).

Tribe Murini

Genus *Mus* Linnaeus, 1758

Rodents of the genus *Mus* represent one of the most valuable biological models for biomedical

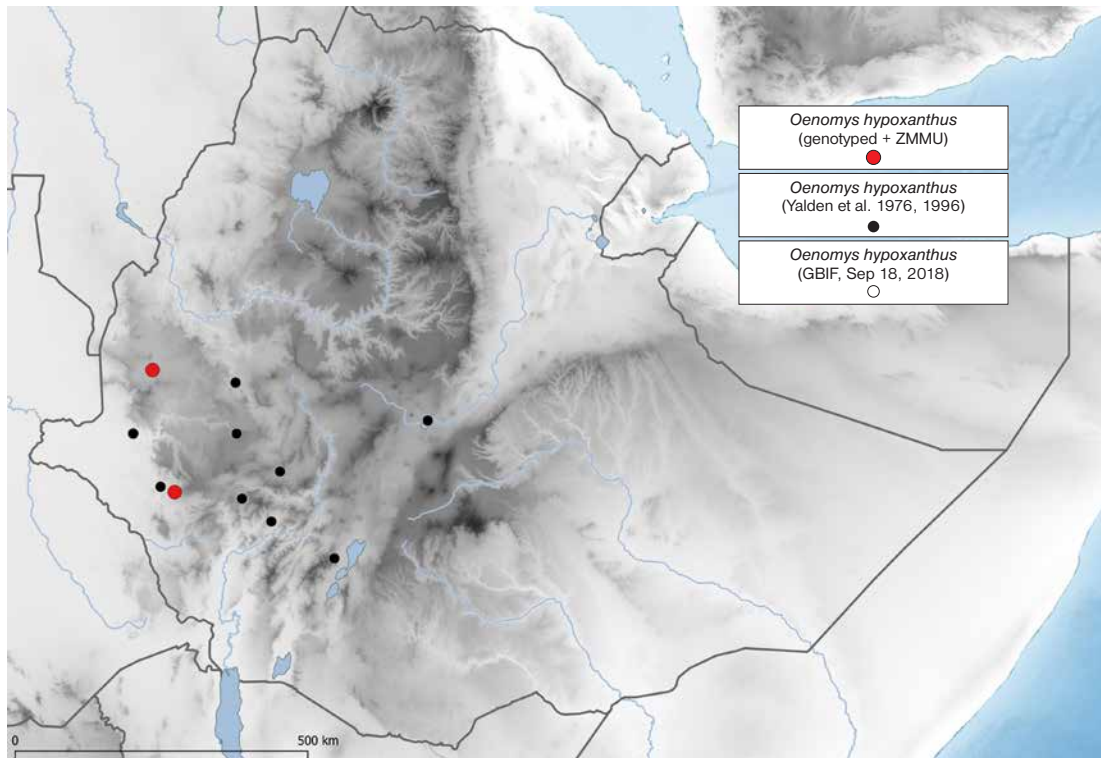


Fig. 38. Distribution of *Oenomys hypoxanthus*. The easternmost record from the locality of Koka (Yalden et al. 1976, based on material from USNM; also in GBIF database) in the Awash River valley requires confirmation as this region is ecologically different from forested areas in south-western Ethiopia.

and evolutionary research (Macholán et al. 2012). Out of the four currently recognized subgenera, i.e. *Mus*, *Coelomys*, *Pyromys* and *Nannomys*, the last mentioned comprises the African pygmy mice (Chevret et al. 2005). These are small rodents (4–12 g in most taxa), endemic to sub-Saharan Africa. The phylogenetic relationships, species diversity, ecology and chromosomal evolution of *Nannomys* were recently reviewed (Britton-Davidian et al. 2012, Bryja et al. 2014), but there are still numerous unresolved taxonomic issues. While predominantly savanna dwellers (Veyrunes et al. 2005), several species have also been found in forest (Bryja et al. 2014 and references therein). The genus *Mus* diverged in Asia approximately 6.7 to 7.8 Mya and shortly after this time the ancestors of *Nannomys* colonized Africa through the Arabian Peninsula and Miocene land bridges. The highly heterogeneous environment of Eastern Africa can thus be considered as the place of first diversification of African *Mus* in Early Pliocene, followed by a radiation caused by climatic oscillations and habitat modification (Bryja et al. 2014). The subgenus *Nannomys* is represented in Ethiopia by eight species, five of them are endemic to the country (*M. imberbis*, *M. mahomet* and *M. sp.* “Harena” in the Highlands, *M. proconodon* and *M. sp.*

“the River Koi” in open savanna-like habitats at lower elevation). Furthermore, the synanthropic species with worldwide distribution, *M. musculus* (from subgenus *Mus*) has also been documented in Ethiopia as an alien species.

Mus musculus Linnaeus, 1758

This is a worldwide distributed commensal species, often used as a model for various biological studies (e.g. Macholán et al. 2012). The rodents living in towns and villages have important zoonotic potential, but there is still a lack of studies of non-indigenous Ethiopian taxa. The species has been reported from several towns and villages in Ethiopia (Yalden et al. 1976). The results of allozyme analysis (L. Lavrenchenko, unpublished data) revealed that one specimen from Addis Ababa belongs to the subspecies *Mus m. domesticus*. Recently, we also confirmed it genetically from the town of Imi in the Somali region in south-eastern Ethiopia. At this locality, mtDNA is very diverse and corresponds to two subspecies, *M. m. castaneus* and *M. m. domesticus* (J. Piálek, unpublished data).

Mus imberbis Rüppel, 1842

It is an easily distinguished taxon, very large compared to other *Nannomys* (sequenced individual weighted

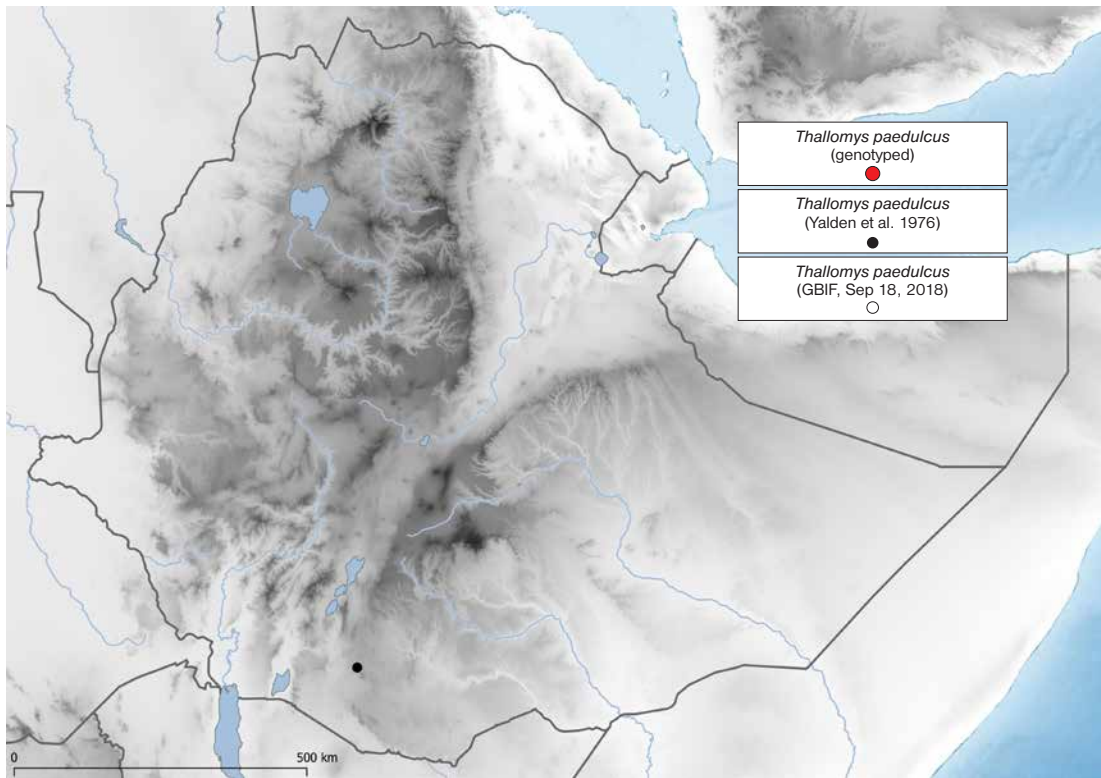


Fig. 39. Distribution of *Thallomys paedulcus*. The record from Misonne (1968) from “southern Ethiopia” is not shown here.

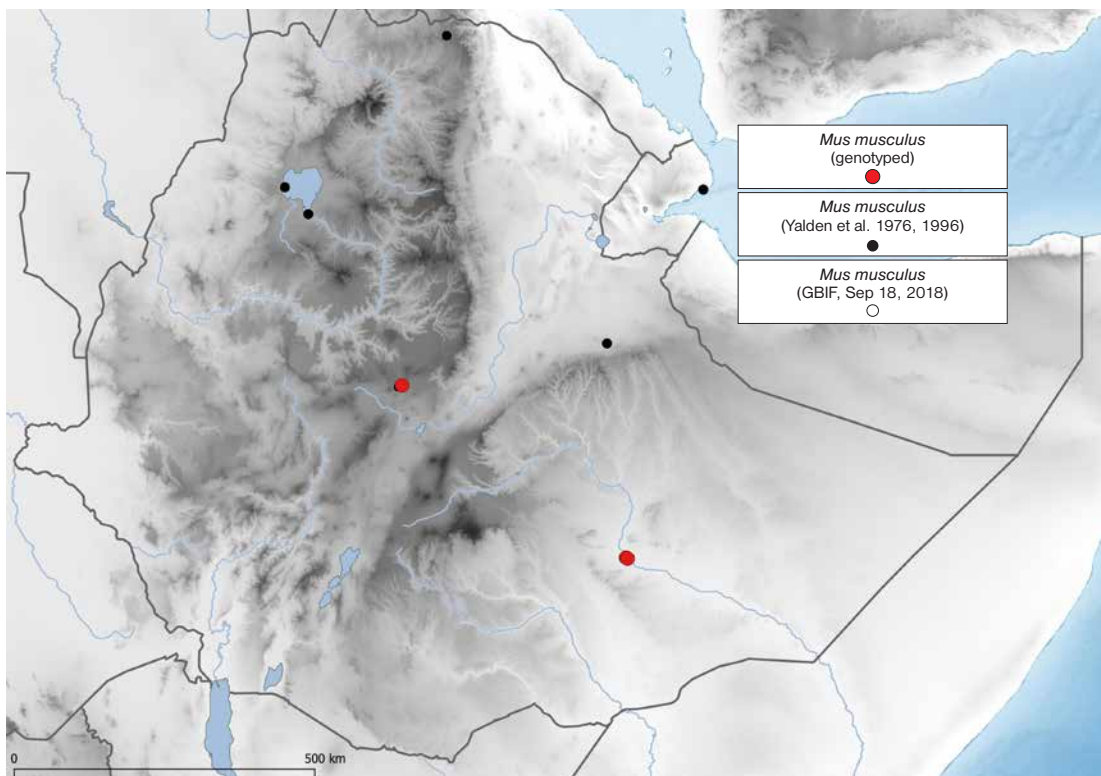


Fig. 40. Distribution of *Mus musculus*. The species is probably more widespread, but there is a lack of data for commensal mammals in Ethiopia.

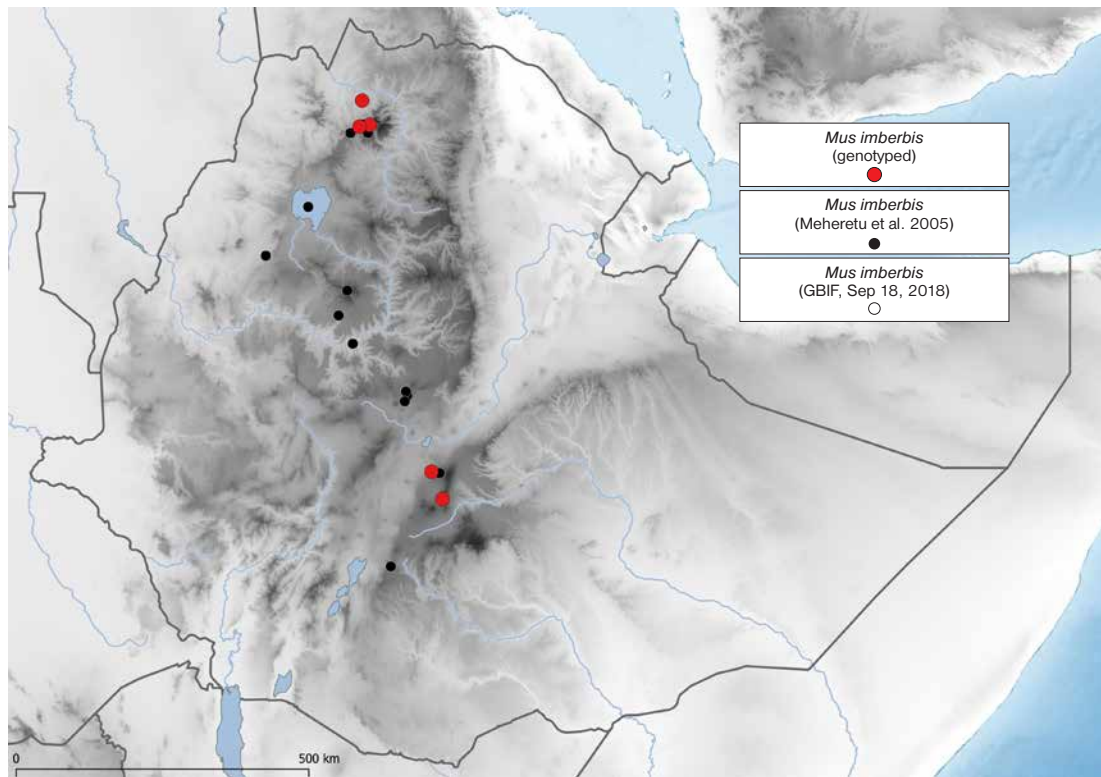


Fig. 41. Distribution of *Mus imberbis*. Some records, especially those below 3000 m reported by Assefa & Zerihun (1980), require verification as no vouchers were preserved.

25 g) and with a black dorsal stripe. It was previously considered as a separate genus *Muriculus*, but genetic analysis clearly showed that it is an internal lineage of *Mus* (Meheretu et al. 2015). It is an endemic species of the high plateaux of Ethiopia, known only from a few individuals. Until the study of Meheretu et al. (2015), only 34 specimens of this species had been known, 12 of them captured before 1940 (Yalden 2013) and the remaining 22 reported by a single study (Assefa & Zerihun 1980; unfortunately, no vouchers from this study were preserved, so the species identification cannot be confirmed). The type locality of this species is characterized as open upland grasslands in the Semien Mts., at 2800 m a.s.l. Assefa & Zerihun (1980) collected the species from bushes and grassland habitats at the edges of farmlands close to streams, between 2490 and 2900 m a.s.l. Some specimens have also been collected from anthropogenic habitats around the type locality (Yalden et al. 1996). The specimen reported by Meheretu et al. (2015), as well as recently collected material from Mt. Chilalo (Kostin et al. 2019) and Semien Mts. (Craig et al., in lit.), were all collected in fragmented ericaceous shrub growth, suggesting that this species might have a wider ecological distribution than previously thought. However, because several attempts to trap the species from its presumed natural habitats have not been successful,

including the extensive sampling from 1968 to 1998 by Yalden and colleagues, it has been suggested that the species has become rarer in its natural habitat since 1940 in response to habitat destruction (Yalden et al. 1976, 1996, Lavrenchenko & Schlitter 2008). Assefa & Zerihun (1980) captured most of the specimens by flooding burrows with water, and they stated that the species was not attracted to peanut butter bait and was rarely captured in snap traps even at localities where flooding was very successful. Two recent specimens in the Arsi Mts. (Meheretu et al. 2015, Kostin et al. 2019; both at 3200 m a.s.l.) were captured in a snap trap and a Sherman live trap, respectively, while in the Semien Mts. (Craig et al., in lit.; 3250 and 3600 m a.s.l.) the species was captured in Sherman traps (n = 2) and pitfall traps (n = 2). The low trapping success by conventional methods may also be related to its partly fossorial lifestyle (Yalden 2013).

Mus mahomet Rhoads, 1896

It is an abundant and widespread species with a distribution range restricted to the Ethiopian Plateau (but see the discussion in Yalden et al. (1976) about the description of *M. kerensis* from Eritrea, which is probably conspecific with *M. mahomet*). Bryja et al. (2014) provided the first genetic data of this taxon, confirming its position within the *setulosus* group

as a strongly supported monophyletic lineage. This supports the view of Yalden & Largen (1992), who considered *M. mahomet* as an Ethiopian endemic, contrary to previous opinions merging it with Kenyan and Ugandan populations, which form a significantly supported sister group to *M. mahomet* (Bryja et al. 2014). It can be relatively easily recognized, as it has a whitish belly separated from the greyish upperpart by a narrow orange band. It lives in various habitats, but predominantly at the border of forests covered by high undergrowth.

Mus proconodon Rhoads, 1896

It represents one of only a few endemic Ethiopian mammals living in savanna-like habitats (Lavrenchenko & Bekele 2017). This species was synonymised with *M. setulosus* (Musser & Carleton 2005), but genetically it represents the most distinct lineage in the whole *setulosus* group (sensu Bryja et al. 2014). We therefore view it as a separate species, but not that its relationships with other taxa in the *setulosus* group need further study. After *M. imberbis*, this is the largest Ethiopian *Nannomys*, differing from *M. mahomet* in having a clear white ventral surface and no orange dividing line on the flank (Yalden et al.

1976). It also lives in lower elevation and generally drier and more open habitats (Yalden et al. 1976).

Mus sp. “Harena” (sensu Bryja et al. 2014)

It is a large species of *Mus* (ca. 16 g), endemic to moist montane forest in Ethiopia. Bryja et al. (2014) considered it endemic to the Harena forest in the Bale Mts. Based on morphometry this taxon was previously reported as *M. triton* (or *M. cf. triton*) (e.g. Yalden et al. 1996) and in most phylogenetic topologies in Bryja et al. (2014) it is the sister taxon to the *triton* group. Genetically, however, it is a very distinct lineage (13.5-14.4 % K2P distance to taxa of the *triton* group) with a remarkably different karyotype than *M. triton* (Aniskin et al. 1998). Earlier studies have already suggested that this taxon represents a valid species (Lavrenchenko 2000), but it is not yet formally described. It can be sympatric with *M. mahomet*, but differs in habitat preferences; *M. sp. “Harena”* lives mostly in the forest margins, while *M. mahomet* inhabits more open grassy habitats (Yalden et al. 1996; our unpublished data). Recently (November 2017), a single individual of this species was captured in the Chingawa (Inegawa) forest in south-western Ethiopia (our unpublished data).

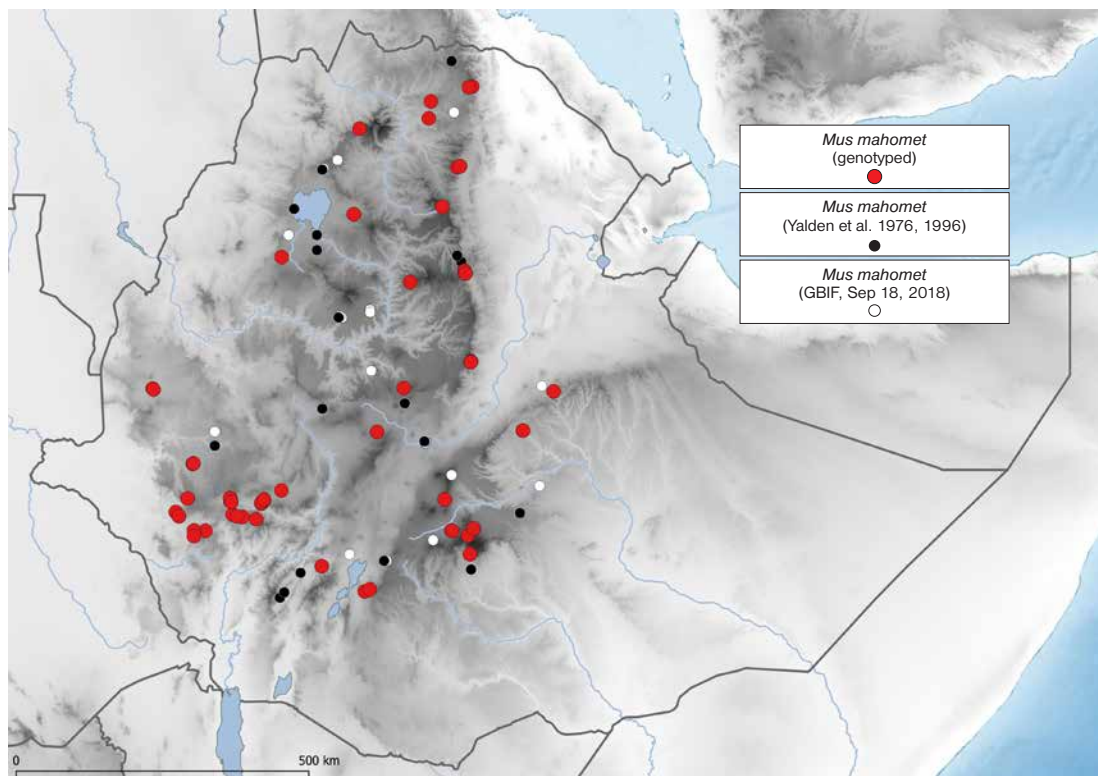


Fig. 42. Distribution of *Mus mahomet*. This is the most widespread and abundant indigenous species of *Mus* in the Ethiopian Highlands.

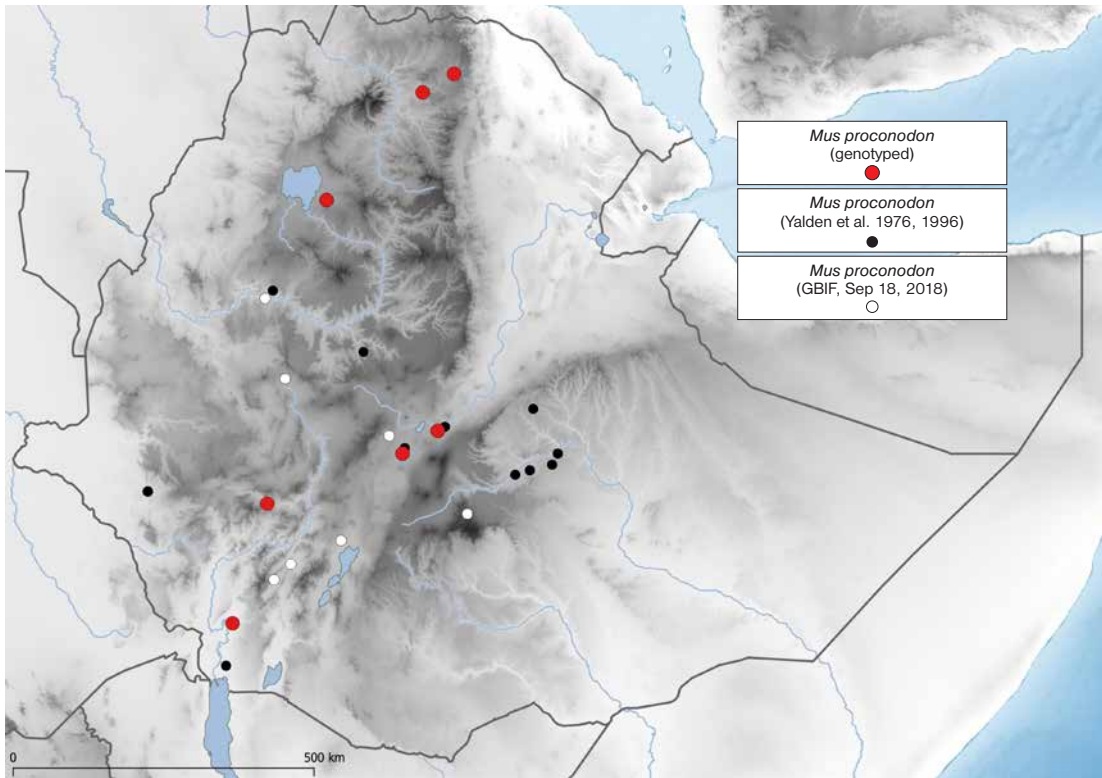


Fig. 43. Distribution of *Mus proconodon*. Records from the Harar massif (as well as other Highland records) need genetic confirmation as they might represent *M. mahomet*. The GBIF records are under the name *M. setulosus*.

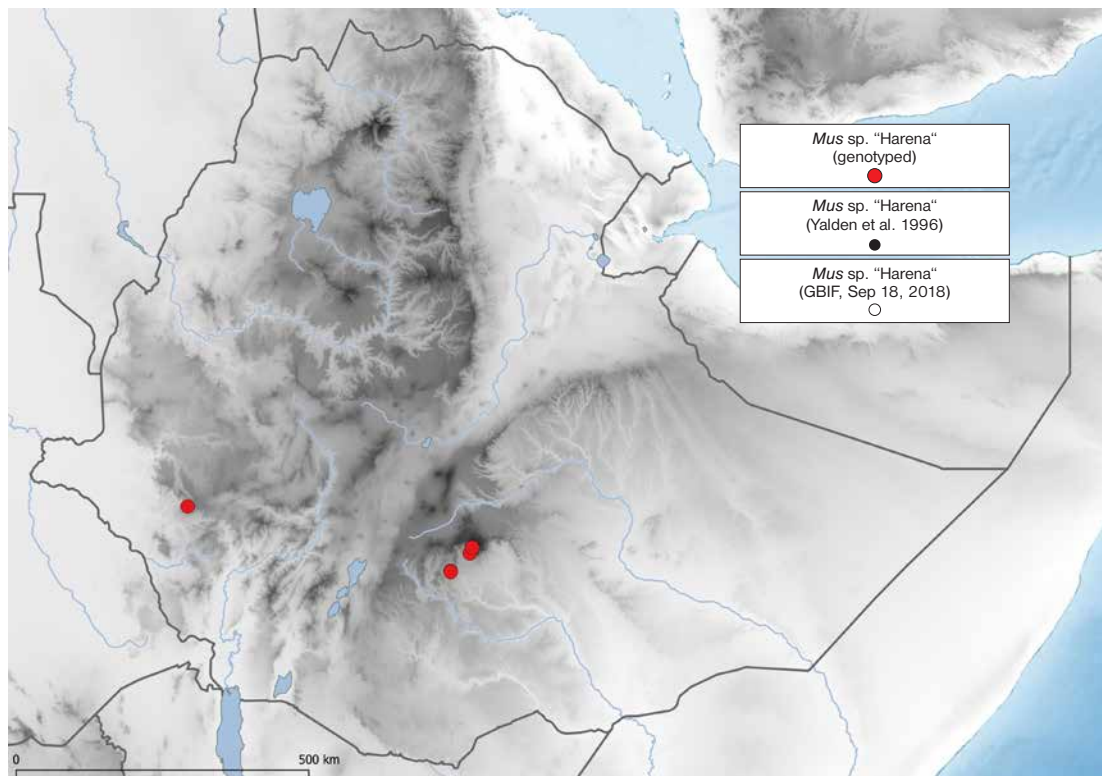


Fig. 44. Distribution of *Mus* sp. "Harena". Recent sampling in the Chingawa forest in south-western Ethiopia revealed the disjointed distribution of this rare forest species.

Mus minutoides A. Smith, 1834

It is a widely distributed species in most of sub-Saharan Africa (probably except continuously forested areas in the Congo basin and deserts; Bryja et al. 2014) and it includes specimens from southern Ethiopia, some of which were previously called *M. tenellus* (Musser & Carleton 2005, Britton-Davidian et al. 2012). There are two other species from the *minutoides* group (sensu Bryja et al. 2014) in Ethiopia, all of them have very small body size (ca. 5 g) and have been reported under the name *M. tenellus* (e.g. Yalden et al. 1976, 1996). Whether or not one of them represents true *M. tenellus* is still under debate (see account of *M. tenellus*).

Mus musculoides Temminck, 1853

It is a typical species of the Sudanian savanna belt. It was previously reported from western Africa and northern Cameroon (see references in Bryja et al. 2014). Bryja et al. (2014) provided a new very distant record from western Ethiopia (Gambella region), representing the easternmost genetically confirmed locality of the species. Very probably it is also present in poorly sampled countries such as Chad, northern CAR and South Sudan. Some of the previous records of “*M. tenellus*” from Ethiopia (Yalden et al. 1976, 1996, GBIF database), especially those from Sudanian savanna in western part of the country, might represent this species.

Mus tenellus Thomas, 1903

This clearly distinct genetic lineage was found at two close localities in northern Ethiopia – in Hagere Selam and in the Mekelle University campus. It may represent true *M. tenellus*, described from the River Blue Nile in Sudan, but comparison with the type material is necessary. On the contrary, morphological studies of museum material suggest that most published Ethiopian records of *M. tenellus*, especially those from southern Ethiopia, were actually *M. minutoides* (Musser & Carleton 2005, Bryja et al. 2014; see the account of *M. minutoides*).

Mus sp. “Koi River” (sensu Bryja et al. 2014)

A single specimen from moist savanna near the River Koi in south-western Ethiopia clearly belongs to the *sorella* group (sensu Bryja et al. 2014), but is genetically very divergent (K2P-distance at *cytb* gene between this species and other lineages of the *sorella* group are 9.72-9.83 %). Further work is necessary to resolve the taxonomic rank of this lineage. This is the first record of a member of the *sorella* group in Ethiopia. It was found in sympatry with *M. minutoides*.

Tribe Praomyini

Genus *Stenocephalemys* Frick, 1914

This genus is endemic to Ethiopia and Eritrea, where it often represents the most abundant component of the small mammal community in the Highlands. Four species of *Stenocephalemys* with valid names are currently recognized in Ethiopia (Yalden et al. 1976, 1996, Musser & Carleton 2005, Happold 2013, Monadjem et al. 2015, Wilson et al. 2017): *S. albipes*, *S. ruppi*, *S. griseicauda* and *S. albocaudata* (the first two species have historically been included in the genera *Praomys*, *Myomyscus* or *Myomys*; reviewed e.g. in Musser & Carleton 2005), but we recognize two additional (and undescribed) species: *S. “pseudogriseicauda”* and *S. sp. “A”* (sensu Bryja et al. 2018a). Previous genetic studies of this genus (Fadda et al. 2001a, Lavrenchenko & Verheyen 2006) used only a limited number of individuals (12 and 11, respectively) genotyped at a single mitochondrial marker (*16S-rDNA* or *cytb*, respectively), and the geographical distribution of the analysed samples was restricted. Bryja et al. (2018a) genotyped 341 specimens representing all known species. The combined analysis of mitochondrial and nuclear loci allowed the mapping of the main genetic lineages and provided the first data on elevational ranges of particular taxa.

Stenocephalemys albipes (Rüppel, 1842)

It is the most widespread of the four named species of the genus. It prefers various forest types at lower elevations, but it is probably more opportunistic, as it was also recorded in deforested areas, fields and even in human settlements. It can be sympatric with other taxa (e.g. with *S. griseicauda* in the Arsi Mts. or *S. cf. ruppi* in the Chingawa forest), but at most localities it is the only species of the genus. It has a wide elevational distribution range (800-3300 m a.s.l. according to Yalden et al. 1976, 1996). The lowest (genetically confirmed) elevation records are from the humid forests of south-western Ethiopia (Godare forest 1220 m), where many typical species of the Ethiopian Highlands reach their lower elevational limits (Yalden et al. 1976). On the contrary, numerous Ethiopian endemics reach their highest elevation records in the much drier mountains of northern Ethiopia. This is true also for *S. albipes* which was recorded around the Sankaber camp in the Semien Mts. at an elevation ca. 3250 m a.s.l. A small commensal population (represented by three specimens in Bryja et al. 2018a) was found even higher, at the Chennek camp site (3800 m a.s.l.). Similarly, Müller (1977)

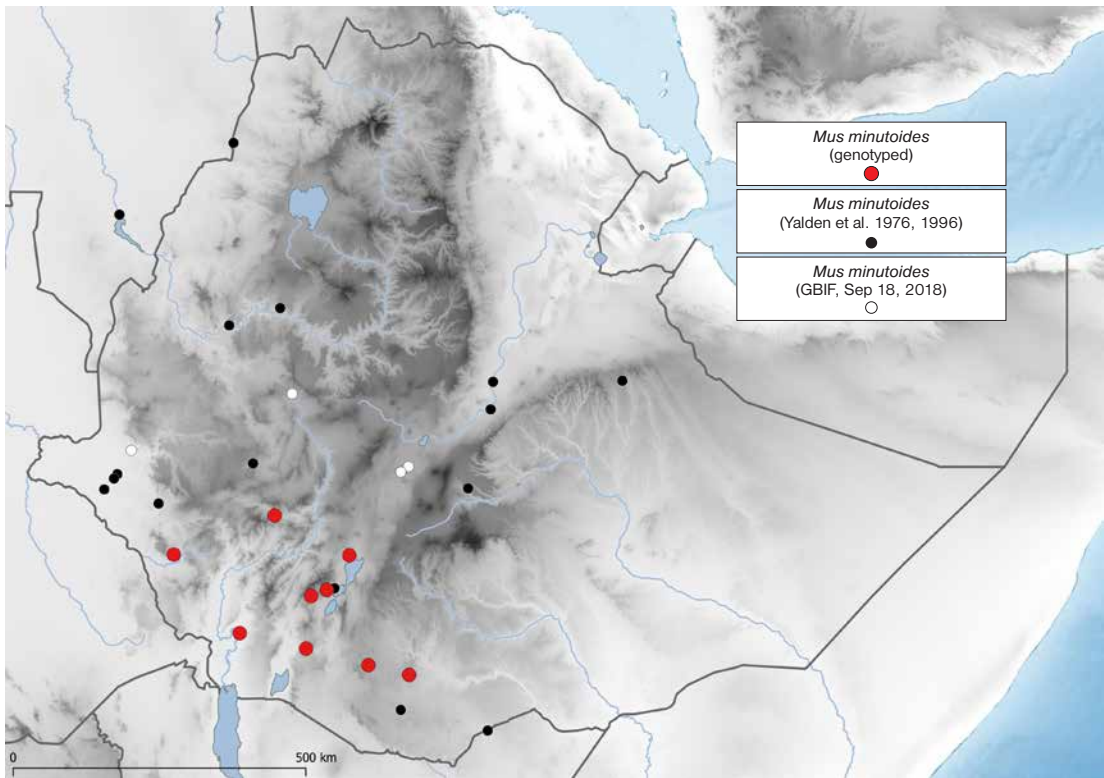


Fig. 45. Distribution of *Mus minutoides*. Yalden et al. (1976, 1996) reported small *Nannomys* as *M. tenellus* (black dots), which might represent three different species (*M. minutoides*, *M. musculooides*, *M. tenellus*). Genetically confirmed *M. minutoides* seems to be restricted to savannas in the southern part of the Rift Valley. GBIF records reported under the names *M. tenellus* or *M. musculooides* are included in this map, but they may also represent other species. The localities in the Highlands of the Harar massif are questionable and the species status of individuals from the Awash River valley should also be further explored.

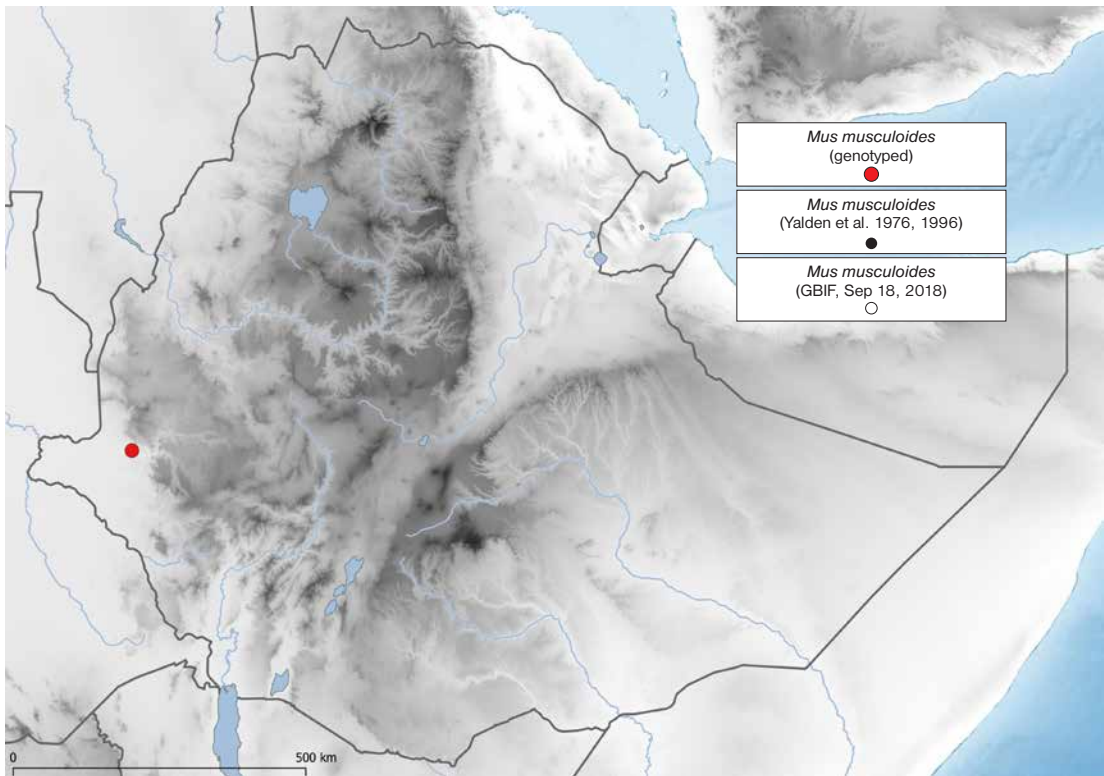


Fig. 46. Distribution of *Mus musculooides*. The species may be more widespread in Sudanian savanna in the western part of the country and some localities of *M. tenellus* in Yalden et al. (1976, 1996) might represent this taxon (see the account of *M. minutoides*).

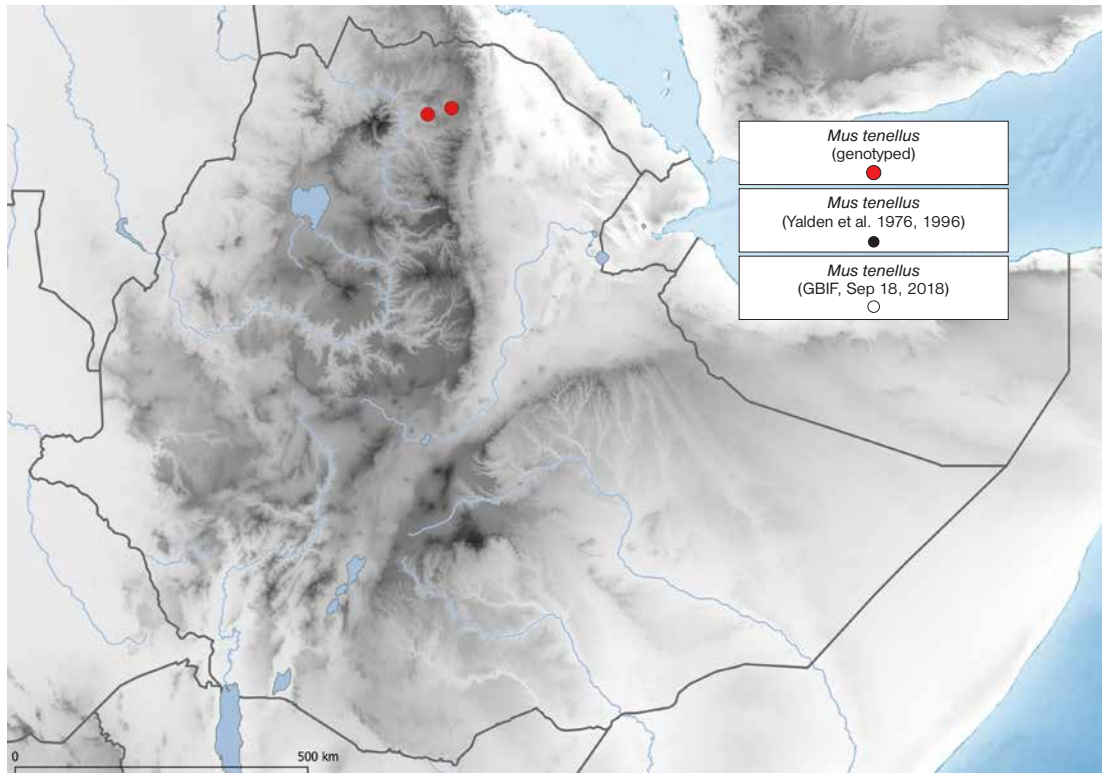


Fig. 47. Distribution of *Mus tenellus*. It is possible that some records reported by Yalden et al. (1976, 1996) under this name (especially those from the north-western part of the country or the Awash River valley; see the map of *M. minutoides*), are true *M. tenellus*, but need to be confirmed genetically. These records are not shown on this map.

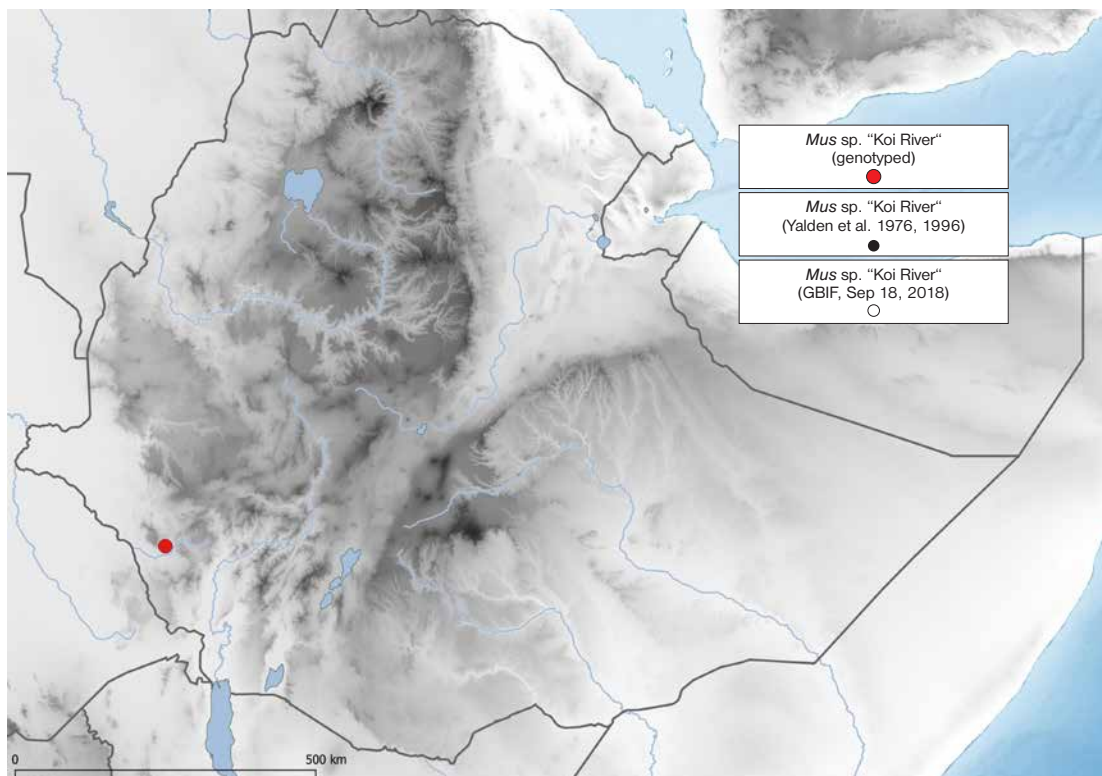


Fig. 48. Distribution of *Mus* sp. "Koi River". This is the only record of *Mus* (*Nannomys*) from the *sorella* group (sensu Bryja et al. 2014) in Ethiopia.

found it absent from grassland areas in the Semien Mts. (3700 m a.s.l.), and encountered it there only in buildings. At such high elevation, usually covered by non-forest vegetation, it appears to be replaced by other congeners (Müller 1977, Rupp 1980, Yalden 1988, Bryja et al. 2018a). Bryja et al. (2018a) described a profound intraspecific geographical structure of *S. albipes* in mtDNA, but very low intraspecific divergence at the nuclear markers. This suggests the rapid spread of this species across most Ethiopian Highlands followed by fragmentation of suitable forest habitats during the dry Pleistocene periods and intensive lineage sorting of mtDNA in small fragmented populations. During the expansion of its range in the humid interglacial periods of the Pleistocene, *S. albipes* encountered other congeners of the genus and occasionally hybridized with them. As a result, Bryja et al. (2018a) observed population of *S. "pseudogriseicauda"* in high elevation of Borena Saynt NP, and *S. cf. ruppi* in the Chingawa forest in south-western Ethiopia with introgressed mtDNA of *S. albipes*. Therefore, caution is needed when using only mitochondrial sequences for identification of *Stenocephalemys* species. The chromosomal data on *S. albipes* (Lavrenchenko et al. 1997, 1999, Corti et al. 1999, Bulatova & Lavrenchenko 2005) shows a diploid number $2n = 46$ and differ in the autosomal arm number (NFa = 58, 50-53 or 50 respectively). The variation in the number of bi-armed autosomes (from 3 to 7 pairs) may be associated with different degrees of chromosomal contraction carrying very short arms in different studies. To exclude this uncertainty, Bryja et al. (2018a) compared NFa counts only for "true" metacentrics and submetacentrics against one-armed groups, which comprised acro- and subacrocentrics. On this basis, the karyotype of *S. albipes* can be described as $2n = 46$, NFa = 50 or 51, which is widespread across Ethiopia (see more details in Bryja et al. 2018a).

Stenocephalemys albocaudatus Frick, 1914

This species (formerly known as *S. albocaudata* and changed for gender agreement by Denys et al. 2017a) is the most specialized species of the genus to life in Afroalpine habitats (3000-4050 m a.s.l. according to Yalden et al. 1996). Our records confirm that it is the most common *Stenocephalemys* species in the Afroalpine zone of the Bale and Arsi Mts., living in grasslands between 3300-4150 m a.s.l. At some localities, mainly in the Arsi Mts., it may be sympatric with *S. griseicauda*, i.e. a species which generally prefers lower elevation and higher shrub cover. Bryja et al. (2018a) reported

the first reliable record of *S. albocaudatus* west of the Rift Valley (Guwassa area). This population was found at about 3300 m a.s.l. and was genetically remarkably similar to the one in the Arsi Mts. at both mitochondrial and nuclear markers. It occurs in sympatry (or rather micro-allopatry) with the taxon that Bryja et al. (2018a) called *S. "pseudogriseicauda"*. Yalden et al. (1996) cited D. Schlitter (pers. comm.) who claimed the capture of *S. albocaudatus* on Mt. Entoto, north of Addis Ababa, but that record was considered a clear misidentification (D. Yalden, pers. comm.). Similarly, the material captured by Osgood in 1927 in Sakalla, Gojjam (FMNH collection, unpublished data) was probably misidentified. The chromosomal sets of *S. albocaudatus* ($2n = 54$, NFa = 62) from Arsi ($N = 17$) were identical to those from Bale (Lavrenchenko et al. 1997, 1999, Bryja et al. 2018a). The karyotype of *S. albocaudatus* from Guwassa (the only known population of the species to the west of the Rift Valley) remains unknown.

Stenocephalemys griseicauda Petter, 1972

The species was considered to occur on both sides of the Rift Valley (e.g. Monadjem et al. 2015, Wilson et al. 2017), but Bryja et al. (2018a) showed a more complex situation with several (as yet undescribed) taxa. The species *S. griseicauda* was described from Dinsho in Bale Mts., east of the Rift Valley. Multilocus nuclear genetic data suggest that the Bale and Arsi Mts. represent the only region with "true" *S. griseicauda*, where it lives at elevations of 3000-3800 m a.s.l. The only exception is probably the isolated population in the clearing of Harena forest at Katcha, where this species was repeatedly captured at 2400 m a.s.l. (Lavrenchenko 2000). Genetically very distinct populations west of the Rift Valley (previously reported as *S. griseicauda*, but here considered as *S. "pseudogriseicauda"* and *S. sp. "A"* based on Bryja et al. 2018a) require more detailed integrative taxonomic revision using morphological and genomic data. The karyotype of *S. griseicauda* from Arsi ($N = 20$) was similar to those from Debre Sina (= *S. "pseudogriseicauda"*, $N = 2$) located on the opposite side of the Rift Valley (Bryja et al. 2018a). This karyotype ($2n = 54$, NFa = 58) has been described earlier for *S. griseicauda* from Bale (Lavrenchenko et al. 1997, 1999).

Stenocephalemys "pseudogriseicauda" (sensu Bryja et al. 2018a)

Populations west of the Rift Valley with mtDNA belonging to the *S. griseicauda* clade (i.e. lineage

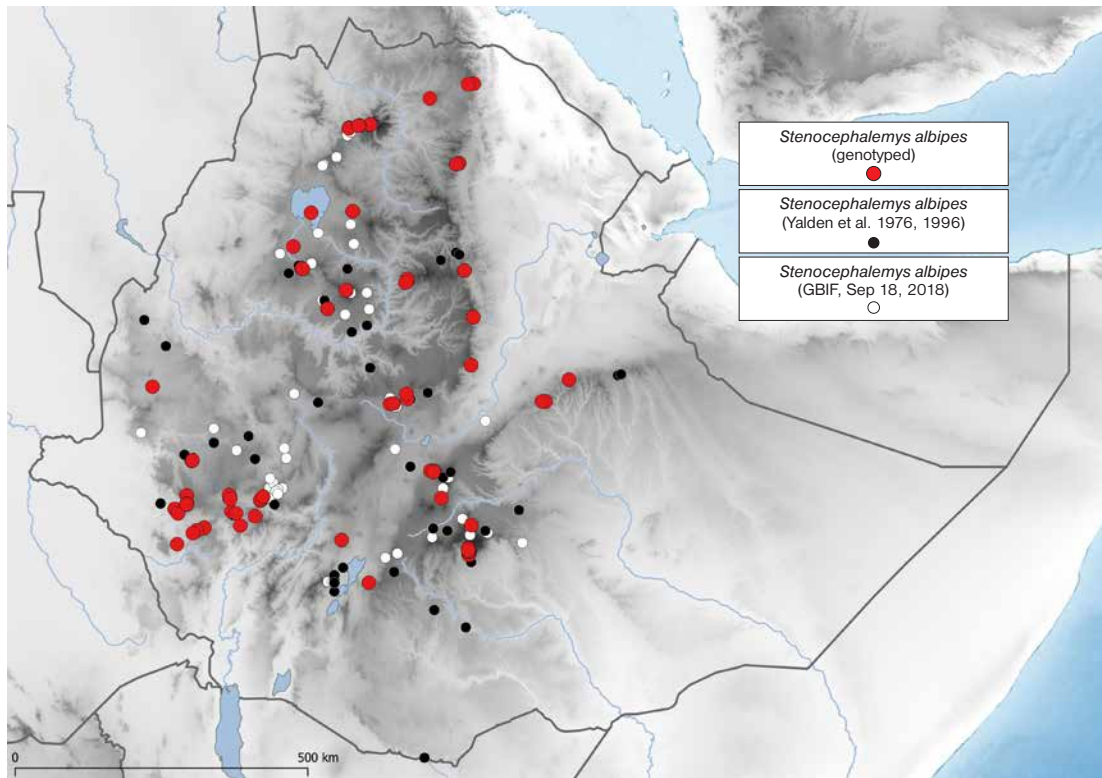


Fig. 49. Distribution of *Stenocephalemys albipes*. It is a widespread and abundant species in the Ethiopian Highlands. The record from the Kenyan border at Moyale (from BMNH) is probably erroneous (see also discussion about Sof Omar individuals in Yalden et al. 1976).

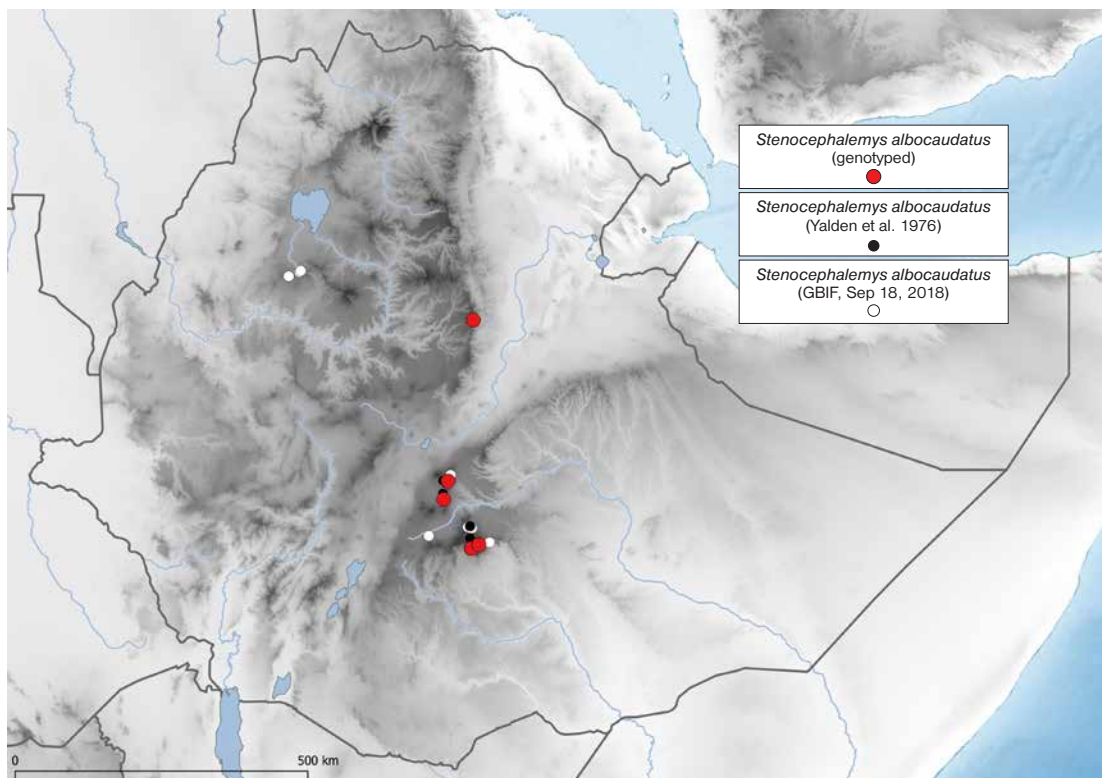


Fig. 50. Distribution of *Stenocephalemys albicaudatus*. The population from Afroalpine habitats in the Guwassa area west of the Rift Valley was genetically confirmed (e.g. Bryja et al. 2018a). In contrast, records from Sakalla, Gojjam, in north-western Ethiopia (GBIF database) likely represent misidentification and require verification.

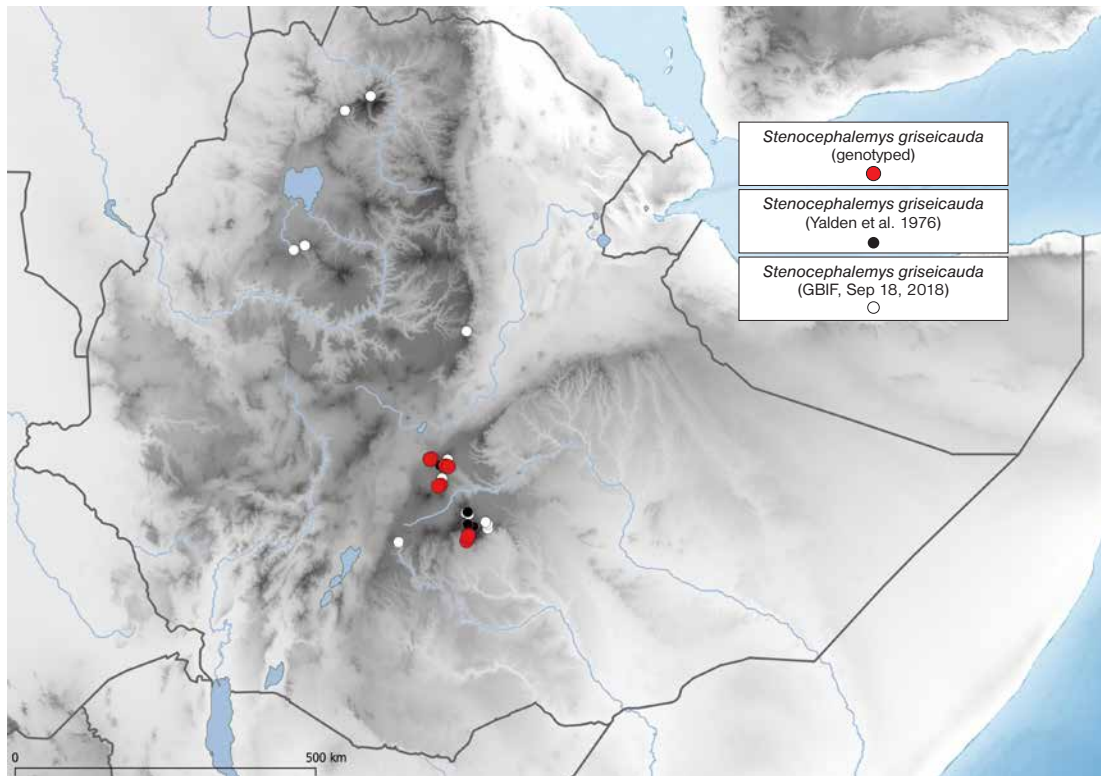


Fig. 51. Distribution of *Stenocephalemys griseicauda*. Previous records of this species from the north-west of the Rift Valley (on this map some of those from GBIF database) are either *S. "pseudogriseicauda"* or *S. sp. "A"*, based on Bryja et al. (2018).

gr_2 from Debre Sina and Guwassa in Bryja et al. (2018) are genetically very distinct at six nuclear markers from true *S. griseicauda* from the Bale and Arsi Mts. and Bryja et al. (2018a) provisionally called this taxon *S. "pseudogriseicauda"*, which we follow here. Genetic data suggest past hybridization of *S. "pseudogriseicauda"* and *S. griseicauda*, during which the mtDNA of *S. griseicauda* has been introgressed west of the Rift Valley. The taxonomic status should be critically revised using an integrative taxonomic approach and the formal description will be published elsewhere. The distribution of this taxon is not completely known, but based on nuclear genetic markers it also includes the population from higher elevations in Borena Saynt NP with introgressed mtDNA of *S. albipes* (Bryja et al. 2018a). The karyotype of this taxon from Debre Sina ($2n = 54$, $NFa = 58$) is similar to *S. griseicauda* from Bale and Arsi Mts. (Lavrenchenko et al. 1997, 1999, Bryja et al. 2018a).

Stenocephalemys ruppi Van der Straeten & Dieterlen, 1983

Bryja et al. (2018a) discovered two clearly distinct taxa living in sympatry in the very humid Chingawa

(= Inegawa) forest in south-western Ethiopia (but not in other forests despite intensive recent surveys). The two species differed significantly at all nuclear markers (Bryja et al. 2018a) as well as in external morphology (J. Bryja et al., unpublished data), suggesting the lack of contemporary hybridization. Despite the fact that mtDNA of both of them belongs to the *S. albipes* clade, they possessed different mitochondrial haplogroups (Bryja et al. 2018a). The first haplogroup (ap_1a) is typical of *S. albipes*, widely distributed at numerous other localities of south-western Ethiopia, while the second (ap_2) was almost identical with the mtDNA of the paratype of *S. ruppi*. Bryja et al. (2018a) therefore assumed that the latter taxon in Chingawa forest might represent *S. ruppi*, so far recorded only at two localities in the Gughe Highlands west of the Rift Valley, and always in sympatry with *S. albipes* (Van der Straeten & Dieterlen 1983). The type locality of *S. ruppi* was explored recently by L. Lavrenchenko, but all suitable forest habitats had been destroyed by human activity, so it is possible that *S. ruppi* is extinct in Gughe Highlands (Lavrenchenko & Bekele 2017). The known elevational distribution of *S. ruppi* (2800-3200 m a.s.l.; Yalden et al. 1996) is higher than the locality in Chingawa forest

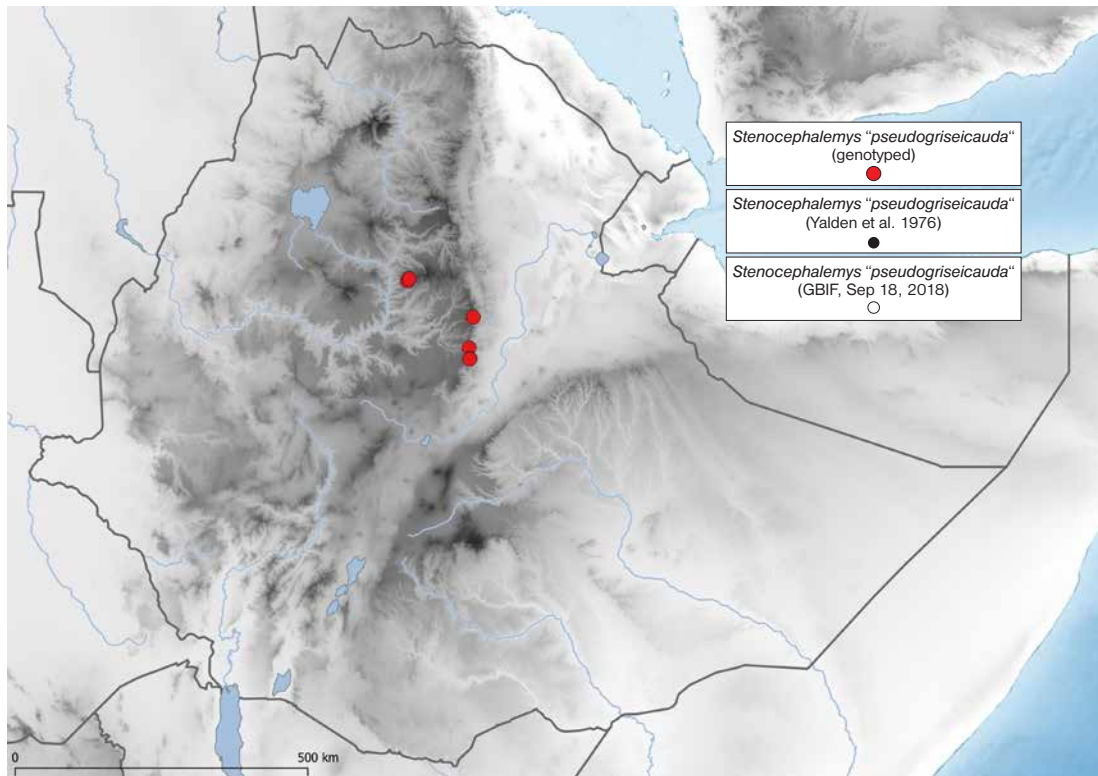


Fig. 52. Distribution of *Stenocephalemys* “*pseudogriseicauda*”. The northernmost population at high elevation in the Borena Saynt NP has mtDNA introgressed from *S. albipes* (see more details in Bryja et al. 2018a).

(2340 m). *Stenocephalemys albipes* and *S. rupp*i in the Chingawa forest have identical karyotypes ($2n = 46$, $NFa = 50$), which may have facilitated past hybridization and mtDNA introgression in southern Ethiopia (Bryja et al. 2018a). Detailed morphological analysis and comparison with type material is now required to shed light on the taxonomy of the poorly known *S. rupp*i.

Stenocephalemys sp. “A” (sensu Lavrenchenko & Verheyen 2006)

High-elevation localities (3400-4000 m a.s.l.) in the northern part of the Ethiopian Highlands are inhabited by the clearly distinct *Stenocephalemys* sp. “A” (sensu Lavrenchenko & Verheyen 2006). This taxon is well distinguished from *S. griseicauda* by its karyotype and both mitochondrial and nuclear markers, and very likely represents a new species, awaiting formal description (Bryja et al. 2018a). Its current populations seem to be isolated from each other at the tops of the highest mountains and their divergence into two groups based on their mtDNA (Semien + Choqa vs. Aboye Gara + Guna) is supported by the presence of two distinct karyotypes (Bryja et al. 2018a). The population from the Semien Mts. has a karyotype ($2n = 50$, $NFa = 52$) differing

from populations in the Guna Mt. ($2n = 50$, $NFa = 56$; Bulatova & Lavrenchenko 2005) in the proportion of acrocentric and metacentric chromosomes and the presence of a very large acrocentric pair.

Genus *Mastomys* Thomas, 1915

The multimammate mice of the genus *Mastomys* are widespread in sub-Saharan Africa and occur in a wide array of open habitats; they avoid only deserts, continuous tropical moist forests and the highest parts of mountains (e.g. Monadjem et al. 2015). Species of this genus are often the most abundant African rodents and the main vertebrate agricultural pests (Leirs 1995). They are also reservoirs of important human pathogens, e.g. Lassa arenavirus (Lecompte et al. 2006). The taxonomy of the genus has long been dependent on analyses of karyotypes (see Granjon et al. 1997 for a review), because many species are morphologically indistinguishable. More recent studies (e.g. Dobigny et al. 2008, Mouline et al. 2008, Brouat et al. 2009, Colangelo et al. 2010, 2013) provided mitochondrial markers allowing DNA barcoding of these common rodents and a reliable description of their geographic distribution. Four species are reported from Ethiopia, up to three of which were found to occur in sympatry at one locality

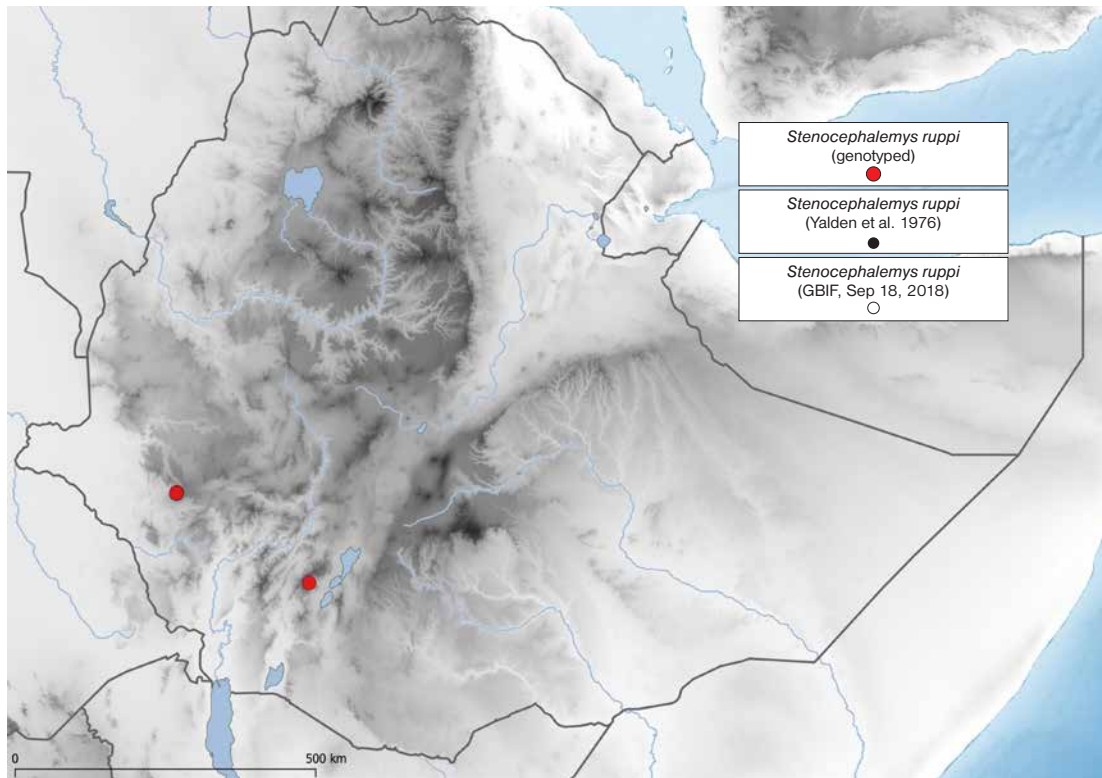


Fig. 53. Distribution of *Stenocephalemys ruppi*. The population from the Chingawa forest is reported here as *S. ruppi* is awaiting morphological comparison with the type series from the Gughe Mountains, close to the Rift Valley.

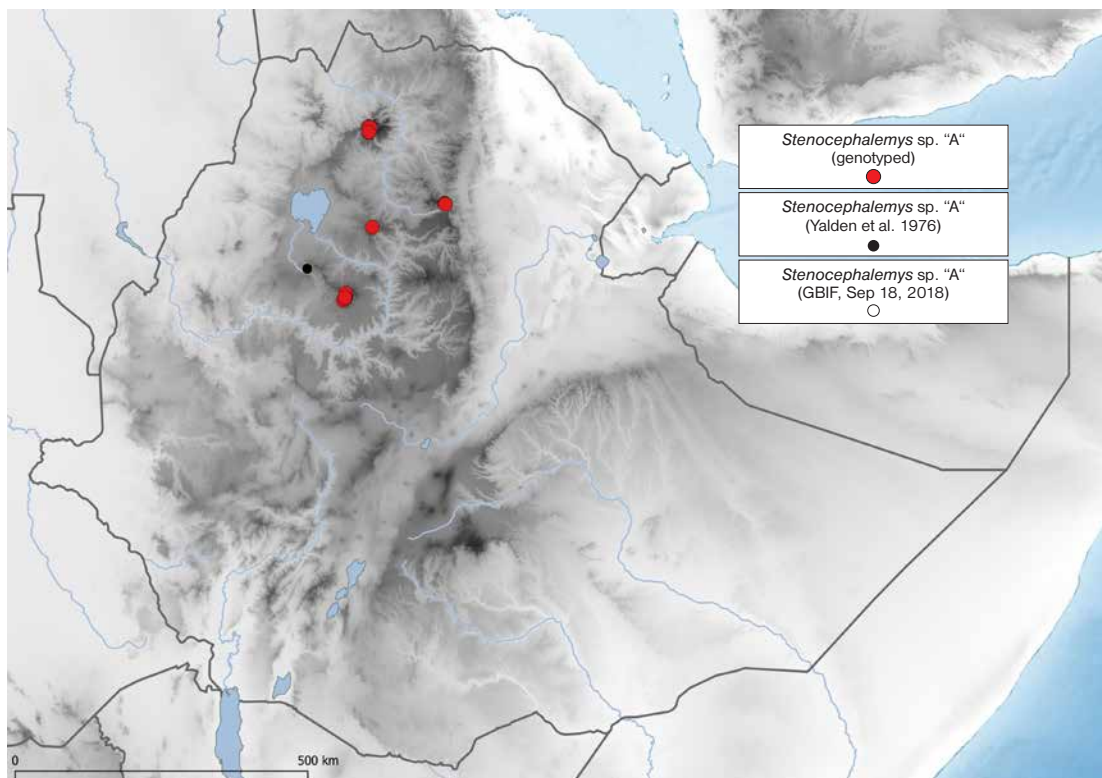


Fig. 54. Distribution of *Stenocephalemys* sp. "A". The population from Semien Mts. is genetically more similar to that on Mt. Choqa, rather than the geographically closer Mts. Guna or Aboye Gara (Bryja et al. 2018a).

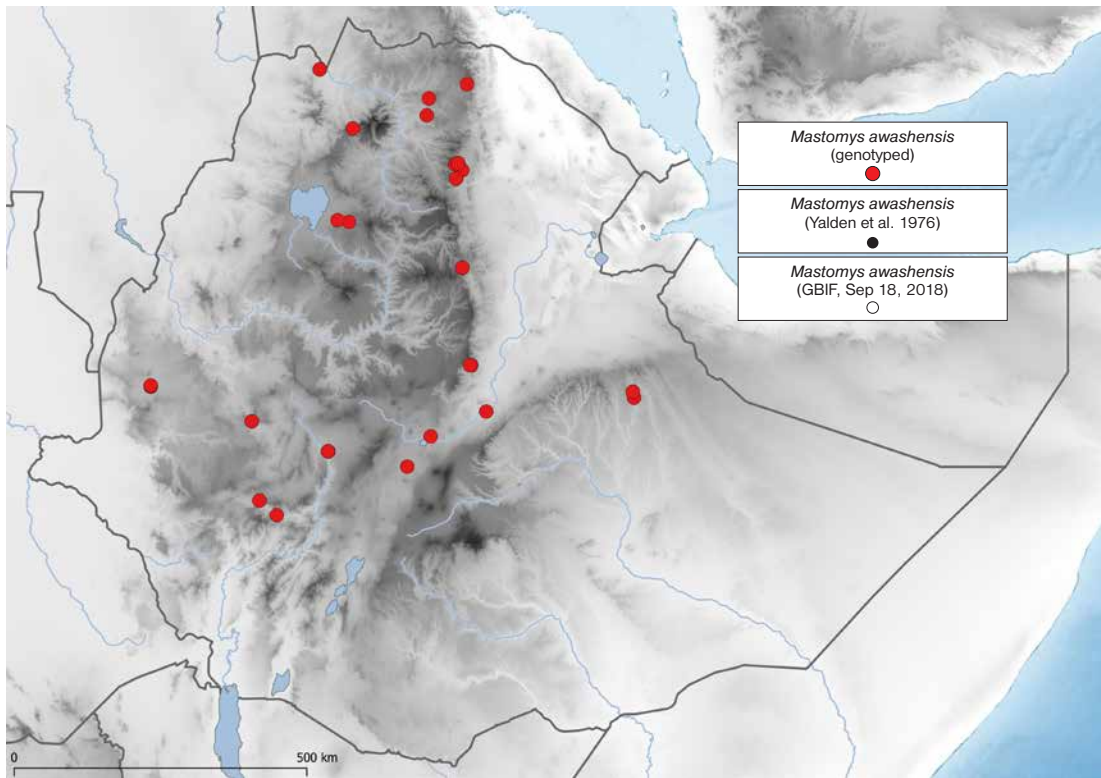


Fig. 55. Distribution of *Mastomys awashensis*. The species was originally considered an Ethiopian endemic, but its presence in neighbouring countries such as Eritrea, is possible.

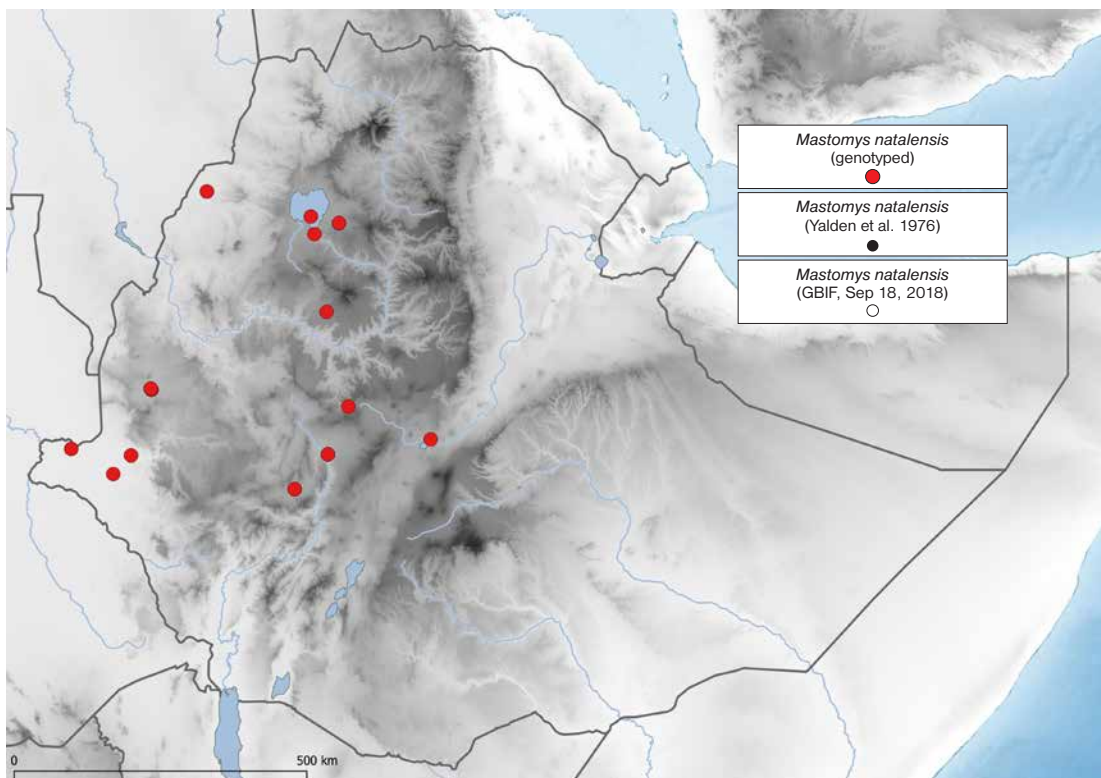


Fig. 56. Distribution of *Mastomys natalensis*. The distribution in Ethiopia is restricted to lower altitudes west of the Rift Valley.

in the Rift Valley (for more details see Martynov et al., in litt.). Previous reviews reported only one (as “*Praomys natalensis*” in Yalden et al. 1976) or two (as “*Praomys erythroleucus*” and “*P. hildebrandtii* = *M. natalensis*”) species of *Mastomys* in Ethiopia, because the authors were not able to sufficiently diagnose individual taxa. For this reason, we do not show the distributional data from the Yalden et al. (1976, 1996) studies and our distribution maps are conservative and require updating as new surveys are conducted.

Mastomys awashensis Lavrenchenko et al., 1998

This species was described on the basis of genetic data, genital morphology and karyotypes (Lavrenchenko et al. 1998). It shares the same chromosomal formula with *M. natalensis* ($2n = 32$) but differs by some structural changes (Lavrenchenko et al. 1998, Colangelo et al. 2010). It has been previously considered as an Ethiopian endemic in the Awash valley (type locality), but increasing genetic data suggests its wider distribution in Ethiopia (Colangelo et al. 2010, Lavrenchenko et al. 2010, Martynov et al., in litt.) and perhaps spilling over into neighbouring countries, e.g. Eritrea. It is distributed mainly in the north-western plateau and in the Rift Valley near the Koka and Ziway lakes and the Awash NP. To date, it has only been reported in the south-eastern plateau from the Babile Elephant Sanctuary (Lavrenchenko et al. 2010, Martynov et al., in litt.). The elevational range of the species varies from 967 to 3145 m a.s.l. (Martynov et al., in litt.).

Mastomys natalensis (A. Smith, 1834)

This species is one of the most widespread mammals in sub-Saharan Africa. It is structured into six genetic lineages with parapatric distributions (Colangelo et al. 2013). These lineages can form narrow zones of hybridization at secondary contacts (Gryseels et al. 2017). All studied Ethiopian populations belong to the phylogroup A-III (Colangelo et al. 2013, Martynov et al., in litt.). *Mastomys natalensis* is widely distributed at lower elevations of the north-western plateau. It was also found in a single locality in the Rift Valley (Lake Koka), but has not been documented in the south-eastern plateau. The elevational range of the species varies from 420 to 2190 m a.s.l. (Martynov et al., in litt.).

Mastomys erythroleucus (Temminck, 1853)

This species is a typical inhabitant of northern Sudanian savanna extending from Senegal in the West to Ethiopia in the East, and the shores of Lake Victoria

in the South-east. Similarly to the previous species, *M. erythroleucus* has a pronounced intraspecific genetic structure with four distinct phylogroups distributed in parapatry in a west-east direction (Brouat et al. 2009). Only phylogroup D (sensu Brouat et al. 2009) was found in Ethiopia (Martynov et al., in litt.). The species is common in the southern part of the country including the southern part of the Rift Valley, but it was recorded also from two localities (vicinities of Lakes Koka and Ziway) in the northern part of the Rift Valley. Its occurrence in the north-western plateau is sporadic, but it was found relatively abundant in the Alatish NP in north-western Ethiopia (based on *cytb* barcoding). The species prefers lower altitudes, but was found within a relatively wide range from 380 to 1945 m a.s.l. (Martynov et al., in litt.).

Mastomys kollmannspergeri (Petter, 1957)

This species represents one of the first offshoots in the diversification of the genus *Mastomys*. In previous studies it has been sometimes reported as *M. verheyeni*, but Dobigny et al. (2008) unambiguously showed that it is a junior synonym of *M. kollmannspergeri*. The species was recorded at relatively few localities in the eastern part of the Sudanian savanna from central Niger to eastern South Sudan (see review of known records in Dobigny et al. 2008). Martynov et al. (in litt.) provided the first genetically confirmed finding of this species in Ethiopia. It was captured in a field with tall teff crop in Mai-Temen in the northernmost part of the country. It was sympatric with *M. awashensis*, but the latter was captured in a wet stream bank in green shrubs.

Genus *Myomyscus* Shortridge, 1942

This genus contains four species, but recent genetic analyses showed that it is a polyphyletic taxon grouping unrelated species with probably ancestral morphology of the Praomyini tribe (e.g. Lecompte et al. 2008, J. Bryja et al., unpublished data). The type species of the genus is *M. verreauxii* (A. Smith, 1834) from the Cape Region and the genus name *Myomyscus* should be kept only for this taxon (Monadjem et al. 2015). There are two very distinct genetic lineages in Ethiopia that morphologically resemble *Myomyscus*. Awaiting taxonomic revision of the tribe Praomyini, we still keep the generic name *Myomyscus* for them.

Myomyscus brockmani (Thomas, 1906)

This species was described from Upper Sheikh in Somalia (British Somaliland), which is geomorphologically the continuation of the Chercher Mountains in eastern Ethiopia. We use this name for the

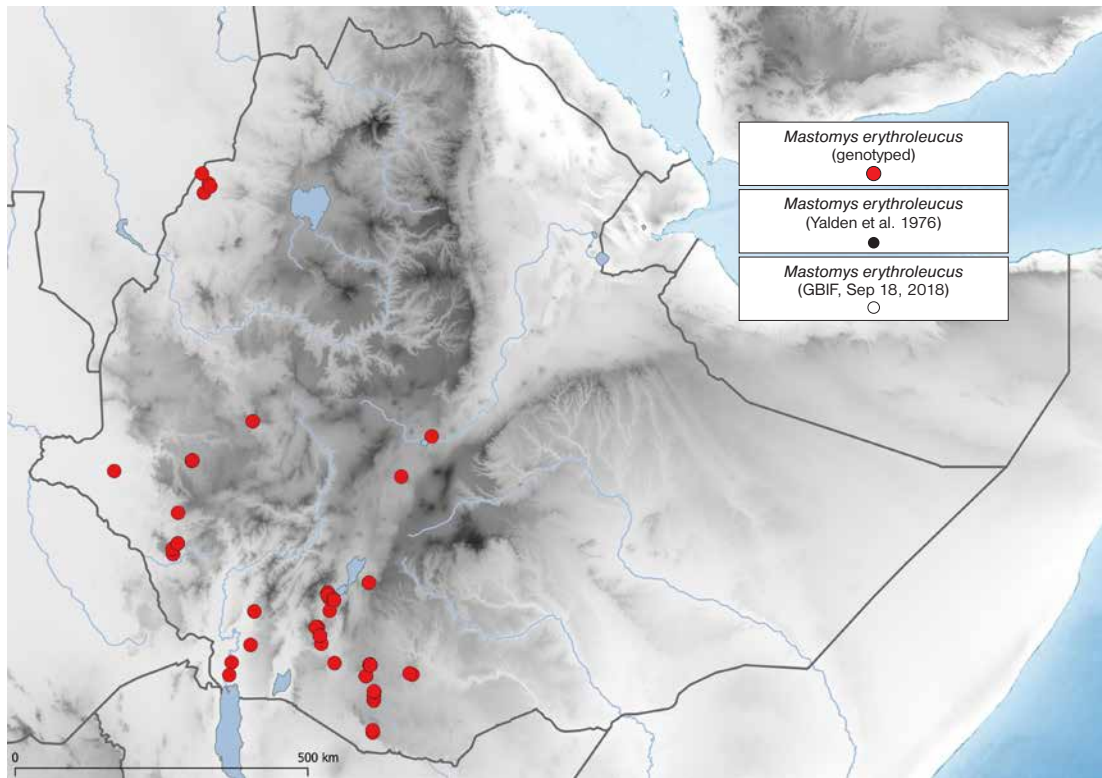


Fig. 57. Distribution of *Mastomys erythroleucus*. The species prefers relatively dry savanna agricultural mosaics in the southernmost part of the country, where it can be abundant.

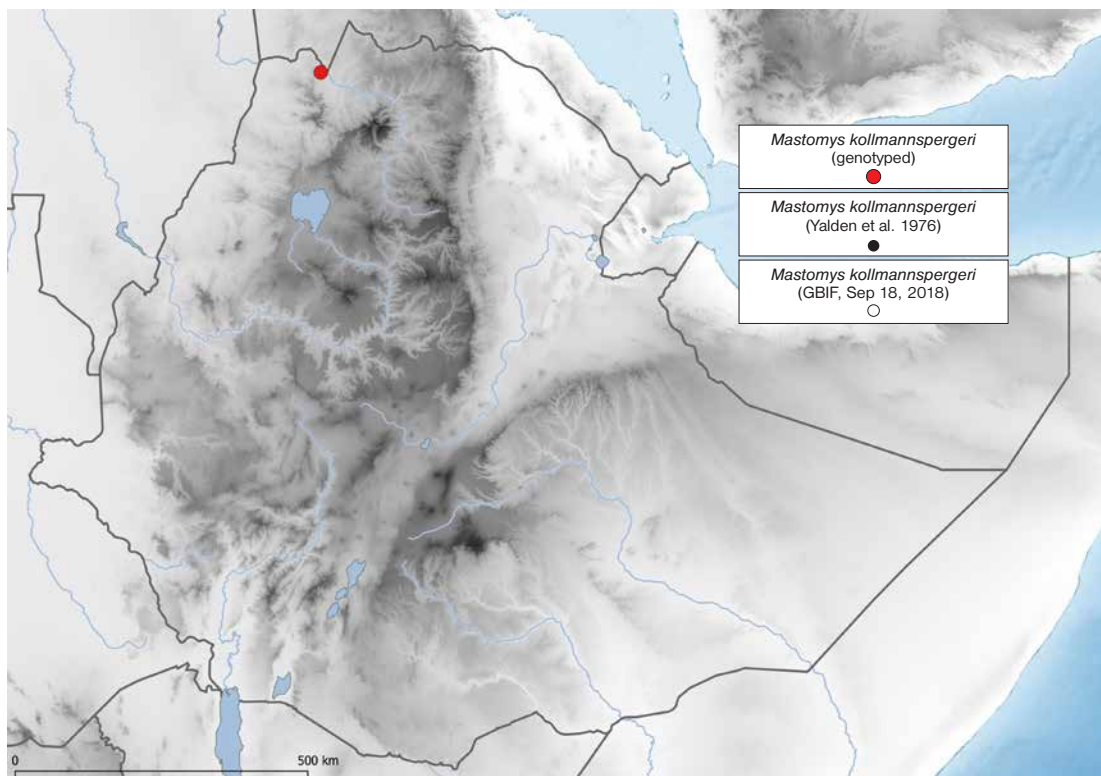


Fig. 58. Distribution of *Mastomys kollmannspergeri*. The only record of this species is from Mai-Temen, where it is sympatric with *M. awashensis*.

genetic clade that we found in Harar, Alamata and Sof Omar. There is a remarkable genetic structure in this taxon as each locality contains a separate and distinct genetic subclade. The species is sister to *M. yemeni* (Sanborn & Hoogstraal, 1953) from the southern part of the Arabian peninsula. The species was reported by Yalden et al. (1976, 1996) under the name *Praomys fumatus* (ditto for GBIF database), but localities from southern Ethiopia and the bottom of the Rift Valley probably represent another taxon here provisionally called *Myomyscus* sp. “South” (see below).

Myomyscus sp. “South”

This genetically very distinct mitochondrial lineage (at the level of separate genus) has been previously reported as *M. brockmani* or *Praomys/Myomys fumatus*. However, given the type locality of *M. brockmani* (see that account), this taxon very likely represents an unnamed species. Based on a few genetic markers at both nuclear and mitochondrial DNA, this species is not the sister of *Myomyscus brockmani* + *M. yemeni* (J. Bryja et al., unpublished data), but phylogenomic analysis is required to solve the radiation and generic classification of Praomyini. Its distribution in Ethiopia is restricted to the southern part of the country (dry woodlands in Somali-Massai savanna), but it is also relatively widespread in Kenya and northernmost Tanzania.

Genus *Nilopegamys* Osgood, 1928

A monotypic genus occurring only in the Highlands of Ethiopia. Described as a genus by Osgood (1928), but subsequently included in *Colomys* by Hayman (1966). Later, Kerbis Peterhans & Patterson (1995) re-examined the type specimen and showed that *Nilopegamys* can be distinguished from *Colomys* by a unique set of external, cranial, dental and postcranial traits, and is even more highly specialized for a semi-aquatic lifestyle than *Colomys*. Sequence analysis of a mitochondrial 16S rRNA gene fragment of the type specimen revealed sister relationships between *Nilopegamys* and *Praomys* s. str. (Dillen et al. 2001). This should be taken with caution because it may be a result of contamination (E. Verheyen, pers. comm.). We follow the view of Denys et al. (2017b) and include the genus in the tribe Praomyini.

Nilopegamys plumbeus Osgood, 1928

This species possesses unique adaptations to life in the water (Kerbis Peterhans & Patterson 1995). The species is known only by the holotype which was collected near the source of the River Little Abbay

(tributary of the River Blue Nile) in 1927. Repeated attempts were made to recollect this species, but without any success. During our survey of the type locality (11°07'20" N; 37°12'40" E; 2300 m a.s.l.) in 2018 we found only significantly degraded natural habitat (L. Lavrenchenko et al., unpublished data), and the area now seems unfavourable for any aquatic or semiaquatic rodent. Hence, this unique endemic rodent may be extinct.

Tribe Rattini

Genus *Rattus* G. Fischer, 1803

This genus reaches its highest diversity in south-eastern Asia, but three species were introduced to Africa, where they live commensally with humans in towns and villages. One of them is widespread across Africa (*R. rattus*), while two others (*R. norvegicus* and *R. tanezumi*) have much more limited distributions. Only the black rat (*R. rattus*) is reported from Ethiopia. The Norwegian rat (*R. norvegicus*) lives in several harbours in the Red Sea coast and neighbouring islands (Yalden et al. 1976, 1996), but has not yet been documented from Ethiopia.

Rattus rattus (Linnaeus, 1758)

This is a commensal species, widely distributed at elevations below 2500 m a.s.l. It can, however, also colonize higher elevations, e.g. at Borena Saynt NP, where we captured it in a house at 3270 m a.s.l.

Subfamily Deomyinae

Four genera (*Deomys*, *Acomys*, *Lophuromys*, *Uranomys*) were assigned to this subfamily based on genetic data (e.g. Wilson et al. 2017, Aghová et al. 2018). Three of them were reported from Ethiopia. While *Uranomys* seems to be a rare (or difficult to trap) taxon, *Acomys* and *Lophuromys* form dominant members of small mammal communities in dry lowland habitats and moist highlands, respectively.

Genus *Acomys* I. Geoffroy Saint-Hilaire, 1838

The genus *Acomys* was described as a separate taxon at the beginning of the nineteenth century, but the first synthetic revision of genetic diversity covering the whole genus was published only very recently (Aghová et al. 2019). Although the study significantly improved our knowledge of the evolutionary history and phylogenetic patterns in the genus, the taxonomic revision remains to be finalized. Descriptions and available names are plentiful (Ellerman 1941, Setzer 1975, Honacki et al. 1982, Musser & Carleton 2005, Monadjem et al. 2015, Denys et al. 2017a). There

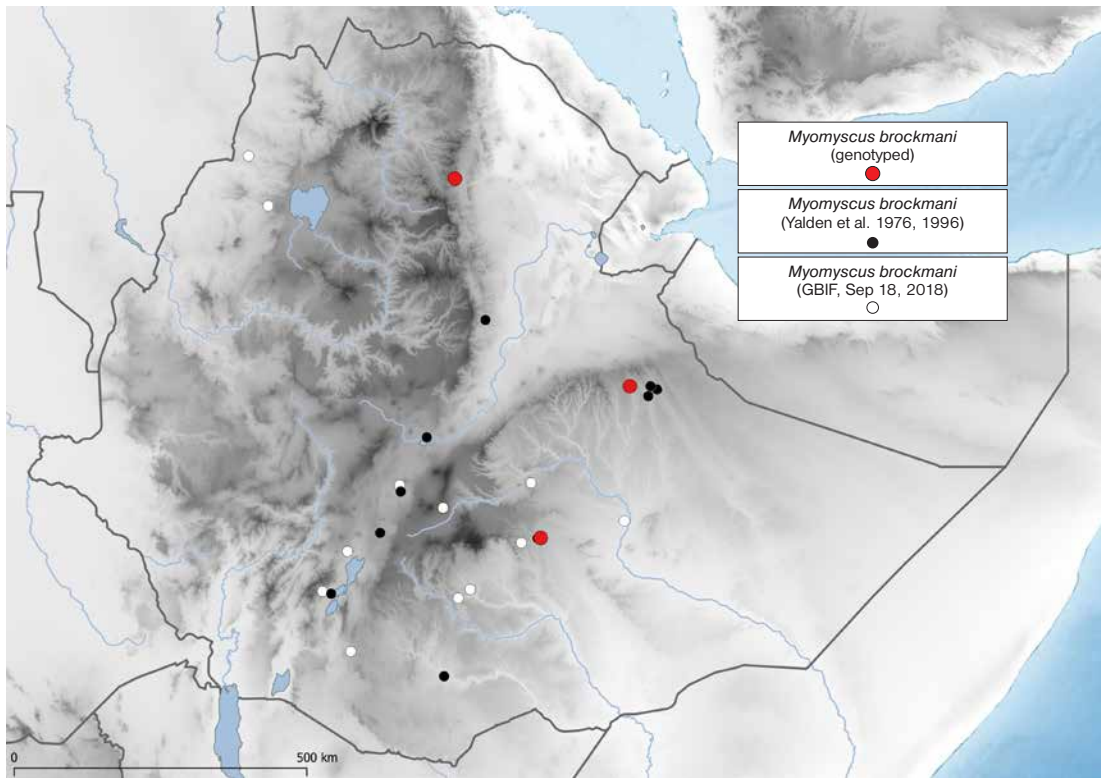


Fig. 59. Distribution of *Myomyscus brockmani*. Localities in southern Ethiopia and the Rift Valley probably represent *M. sp.* "South". Two GBIF records west of the Lake Tana require verification.

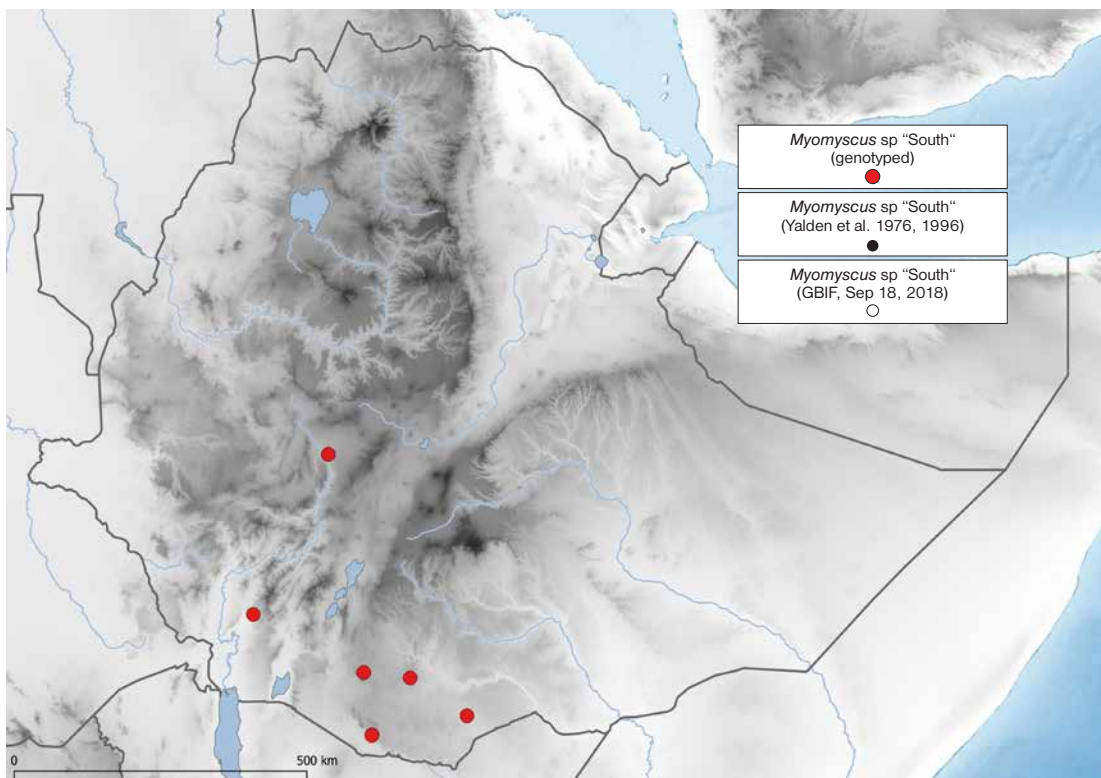


Fig. 60. Distribution of *Myomyscus sp.* "South". The species is also widespread in dry forests in Kenya down to northern Tanzania.

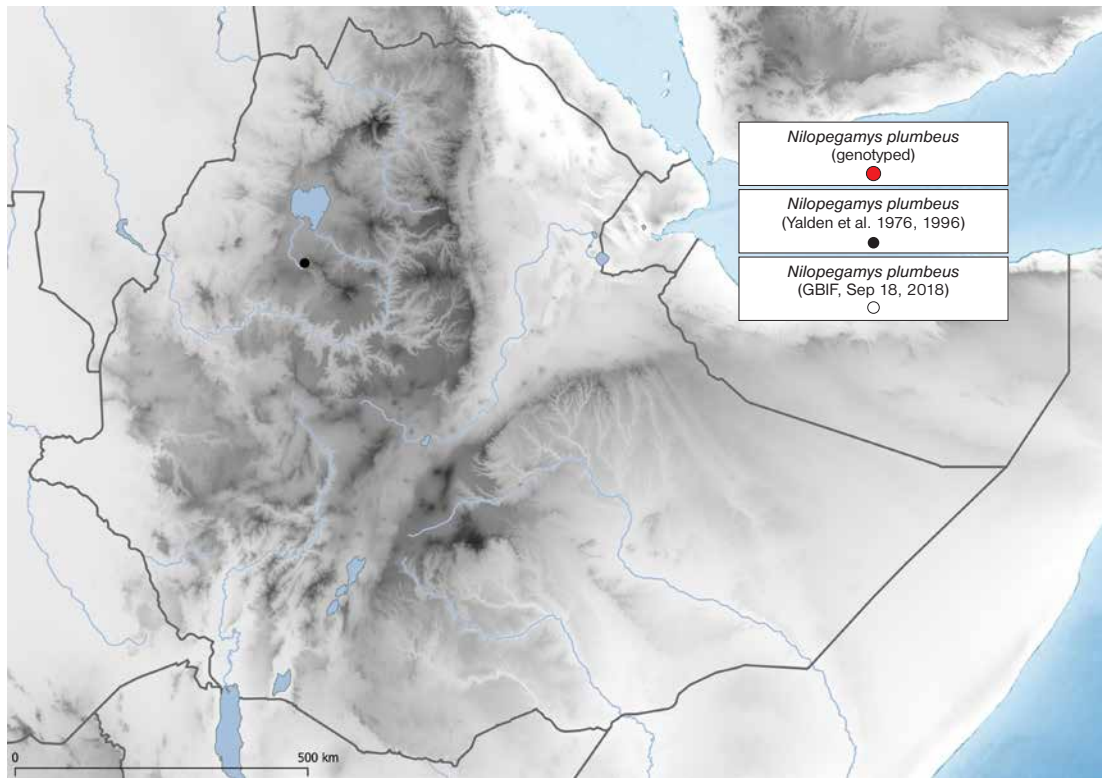


Fig. 61. Distribution of *Niopegamys plumbeus*. The species is known only from the type locality, where the holotype was collected in 1927.

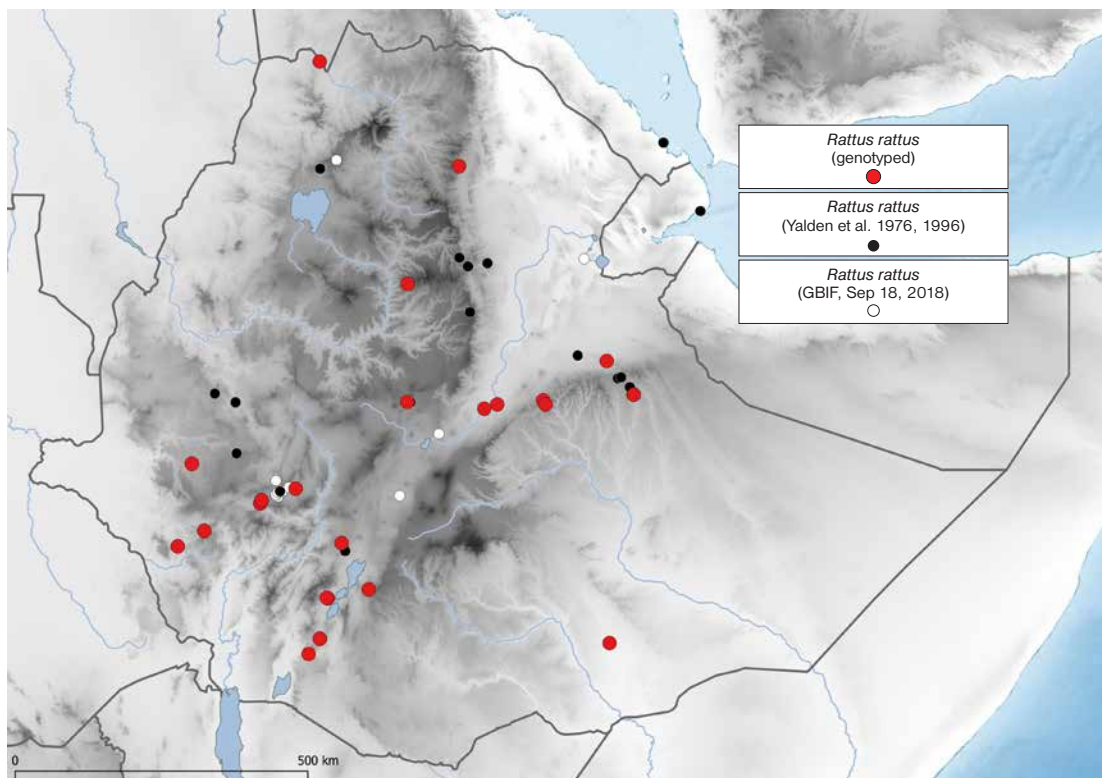


Fig. 62. Distribution of *Rattus rattus*. This commensal species is widespread, but it seems to avoid elevations above 2500 m a.s.l. Its absence in some regions probably reflects the lack of sampling in towns and villages.

is a very high cryptic diversity and many species cannot be easily distinguished using morphological characters due to significant intraspecific variability and generalized morphology. There were repeated attempts for systematic classification using morphological characters (Ellerman 1941, Chevret et al. 1993) and chromosomes (Matthey 1968, Setzer 1975), but the estimation of the total number and delimitation of extant *Acomys* species still requires verification using integrative taxonomy.

Ethiopian material of this genus has been characterized as highly variable, but Yalden et al. (1976, 1996) considered only two species with high intraspecific variability, *A. cahirinus* and *A. wilsoni*. New genetic and karyological data provide evidence that the taxonomic situation is more complicated. The study of Aghová et al. (2019) showed wide genetic variability with 10 genetic groups reported from Ethiopia, where up to three morphologically and genetically clearly distinct species may co-occur at the same locality. Because it is not clear to which taxon the material from Yalden et al. (1976, 1996) belongs, we do not show these localities on the distribution maps (and for the same reason we do not show any GBIF records). All species of *Acomys* avoid moist habitats in highland areas and the genus is distributed in semi-arid regions in Afar, Somali region, and other peripheral parts of Ethiopia. Even though some of *Acomys* taxa in Aghová et al. (2019) are currently known only from Ethiopia, it is likely that they occur in poorly sampled neighbouring countries (especially Sudan, South Sudan and Somalia) and we do not consider them endemic to Ethiopia (see also Lavrenchenko & Bekele 2017).

Acomys cahirinus (É. Geoffroy Saint-Hilaire, 1803)
The species was described from Cairo (Egypt) and Yalden et al. (1976) reported numerous localities across Ethiopia inhabited by this taxon. Phylogenetic analysis of Aghová et al. (2019) showed that the taxon described from Cairo (i.e. *A. cahirinus* = Cah9 in their paper) is distributed in the eastern Mediterranean and the Saharan mountains. Aghová et al. (2019) also discovered a closely related lineage Cah10 from several localities in northernmost Ethiopia. This lineage is closely related not only to Cah9 (*A. cahirinus*), but also to Cah11 (*A. chudeaui*) from Sahel and the southern part of Sahara. We keep it here under the name *A. cahirinus*, but its conspecificity with *A. chudeaui* remains to be tested.

Acomys sp. “Cah7” (sensu Aghová et al. 2019)
Ivlev et al. (2011) and Lavrenchenko et al. (2011) called this lineage *Acomys* sp. “B”. It is sympatric

with *Acomys* sp. “Cah8”, but the two lineages differ significantly in karyotypes (*Acomys* sp. “Cah7” has $2n = 40$, $NF = 68$; Lavrenchenko et al. 2011), physiological and behavioural traits (Ivlev et al. 2011), and likely represent different biological species. The conspecificity of both taxa with *A. cahirinus*, *A. chudeaui*, and *A. sp.* “Cah10” should be further explored – they all belong to the “cahirinus-dimidiatus” clade (sensu Aghová et al. 2019) and are generally distributed on the border of Sahara desert (see Aghová et al. 2019).

Acomys sp. “Cah8” (sensu Aghová et al. 2019)
Ivlev et al. (2011) and Lavrenchenko et al. (2011) called this lineage *A. sp.* “A”. It differs from the sympatric taxon *A. sp.* “B” (= *A. sp.* “Cah7” here) in a number of biological traits (Ivlev et al. 2011), and they likely represent different biological species. It is also the most abundant rodent species in the neighbouring Dinder NP in Sudan (J. Bryja et al., unpublished genetic data). The karyotype of *A. sp.* “Cah8” is $2n = 52$, $NF = 68$ (Lavrenchenko et al. 2011). The taxonomic revision of all genetic lineages from the “cahirinus-dimidiatus” clade (sensu Aghová et al. 2019) occurring in northern Ethiopia is necessary and more intensive sampling, including in Sudan, would be very helpful.

Acomys mullah Thomas, 1904

Awaiting more detailed taxonomic revision, Aghová et al. (2019) assigned the name *A. mullah* to their lineage Cah6 distributed at the border of the Afar triangle in Ethiopia (e.g. it is the most abundant rodent in the Awash NP; our observation). This species is considered a member of the “cahirinus-dimidiatus” complex (Yalden et al. 1976, Wilson et al. 2017), which was confirmed by genetic data (Aghová et al. 2019). This species was found sympatric with *A. louisae* in the Dire Dawa region, from which it also clearly differs in skull morphology (C. Denys, unpublished data). It should also be noted that the type locality of *A. mullah* (Harar) is very close to the only known locality of *A. sp.* “Ign1” and is separated from the Afar lowland by the Chercher Mts. Comparison of *A. sp.* “Ign1” and *A. mullah* (= Cah6) with the type material of *A. mullah* is necessary.

Acomys louisae Thomas, 1896

This species has previously been placed in a separate subgenus *Peracomys* based on dental characters (Denys et al. 1994). Aghová et al. (2019) did not analyse the skull morphology of *A. louisae* (= Dji

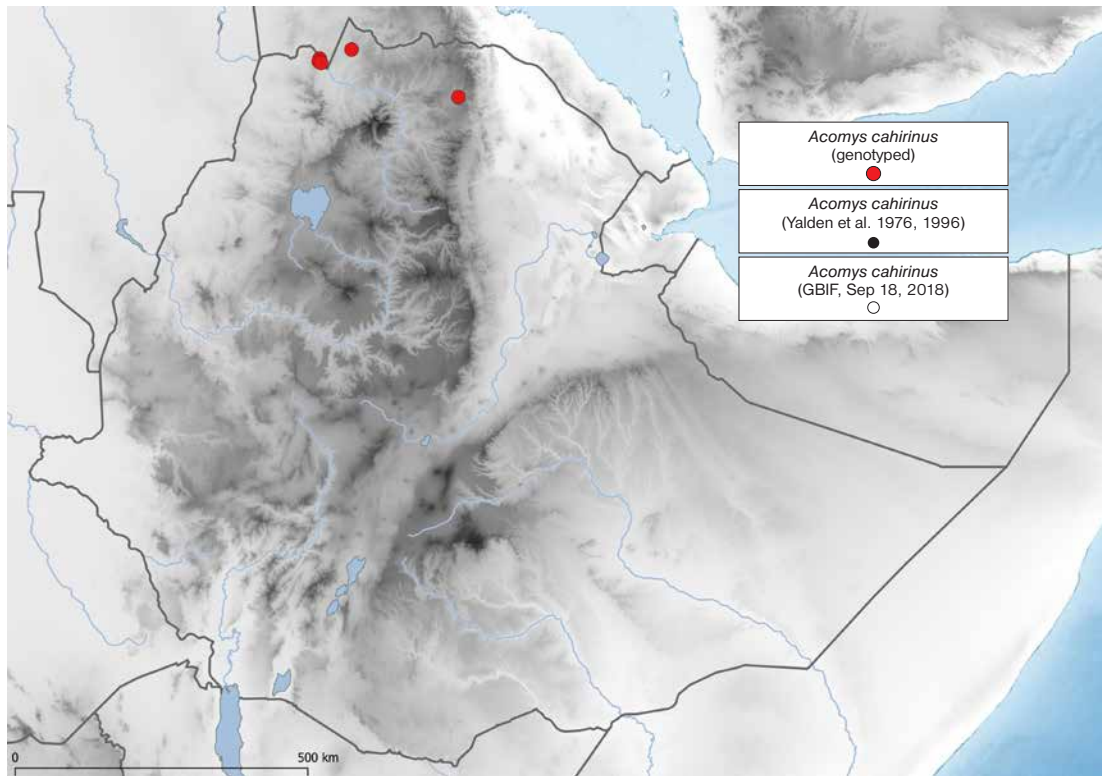


Fig. 63. Distribution of *Acomys cahirinus*. We keep this name for the clade “Cah10” (sensu Aghová et al. 2019), but its conspecificity with *A. cahirinus* described from Cairo (Egypt) has yet to be confirmed.

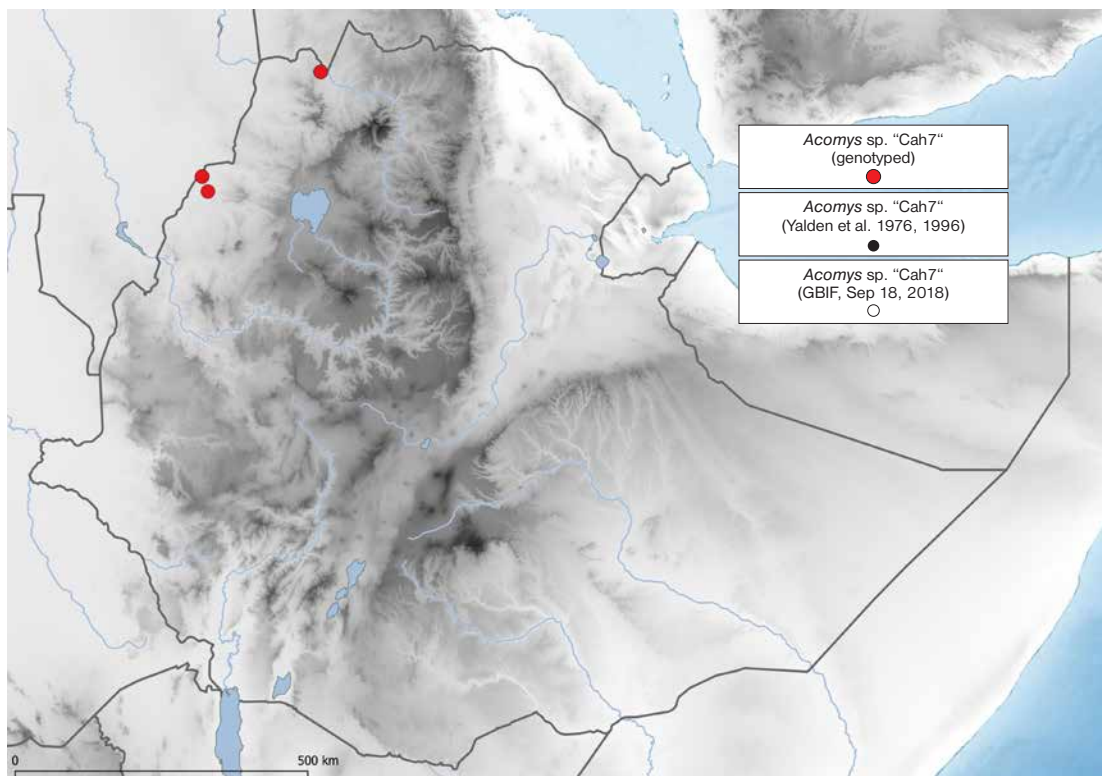


Fig. 64. Distribution of *Acomys* sp. “Cah7”. The species is sympatric with *A. sp.* “Cah8” in the Alatish NP, but differs in karyotype and other biological traits.

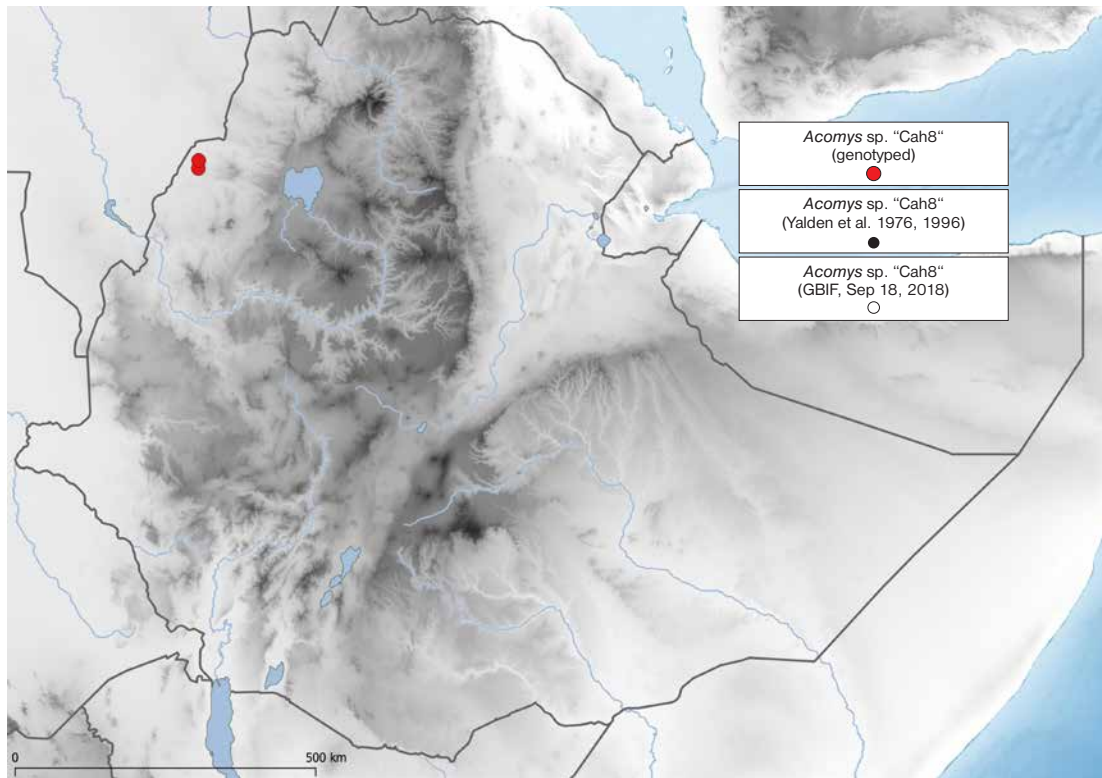


Fig. 65. Distribution of *Acomys* sp. "Cah8". This is the most abundant rodent species in the Dinder NP in Sudan (not shown). In Alatish NP in Ethiopia this species is sympatric with *A.* sp. "Cah7" (Lavrenchenko et al. 2011).

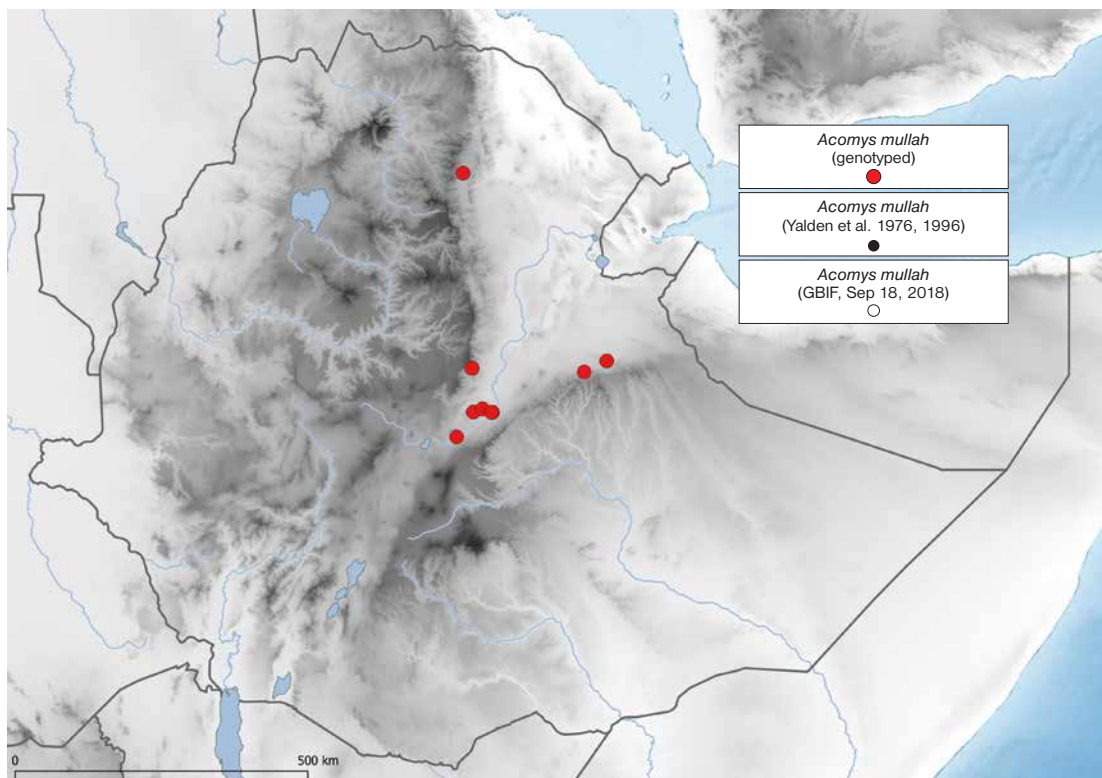


Fig. 66. Distribution of *Acomys mullah*. The species was also recorded from Somaliland (Monadjem et al. 2015), but comparison with type material (from Harar in eastern Ethiopia) is required.

lineage in their study), but the recently collected animals from eastern Ethiopia (Dire Dawa region) assigned to *A. lousiae* by morphological characters (C. Denys, unpublished data) clustered with Dji lineage at mitochondrial sequences (Aghová et al. 2019). According to Petter (1983), however, *A. lousiae* cannot be distinguished from the “cahirinus-dimidiatus complex” (sensu Volobouev et al. 2007) on the basis of skull and external characteristics. This species can be sympatric with *A. mullah* in the Afar triangle (the latter being larger, HB > 100 mm with grey or greyish-brown dorsal pelage). *Acomys lousiae* has a bright rufous or brown dorsal pelage and relatively very long tail (> 100 % of HB; Monadjem et al. 2015). In their analysis, Aghová et al. (2019) were not able to find significant external size differences between individuals of these two species, but detailed morphological investigation based on larger sample size is needed. The specimens from the north-eastern shore of Lake Koka and the Dera National Park have karyotype 2n = 68 and NF = 68 (Sokolov et al. 1993, our unpublished data). It was the only *Acomys* species collected by a recent expedition from the Smithsonian Institute (Washington, D.C.) in Djibuti (Aghová et al. 2019).

Acomys kemp Dollman, 1911

This species was previously listed as a subspecies of *A. ignitus* (Hollister 1919) or *A. cahirinus* (Setzer 1975), but rehabilitated as a clearly distinct species by Janecek (1991). Aghová et al. (2019) reported this species as lineage Ign4, belonging to the *ignitus* clade within the *cahirinus* group. This is the most abundant species of arid areas in central and northern Kenya (east of the Rift Valley), often sympatric with *A. percivali* (the same holds true in southern Ethiopia). The two species can be easily distinguished, e.g. by coat colouration (*A. kemp* has orange-brown pelage and a pure white belly, while *A. percivali* is usually greyish and darker). It is possible that two other Ethiopian lineages from the *ignitus* clade (*A. sp.* “Ign1” and *A. sp.* “Ign2”) are conspecific with *A. kemp*, but their taxonomic analysis is required and we keep them here as separate species (following Aghová et al. 2019).

Acomys sp. “Ign1” (sensu Aghová et al. 2019)

This presumably new species was mentioned for the first time as a genetically and cytogenetically very divergent lineage (*A. sp.* “C”) by Lavrenchenko et al. (2010) from the Babile Elephant Sanctuary in Eastern Ethiopia. This is currently the only known

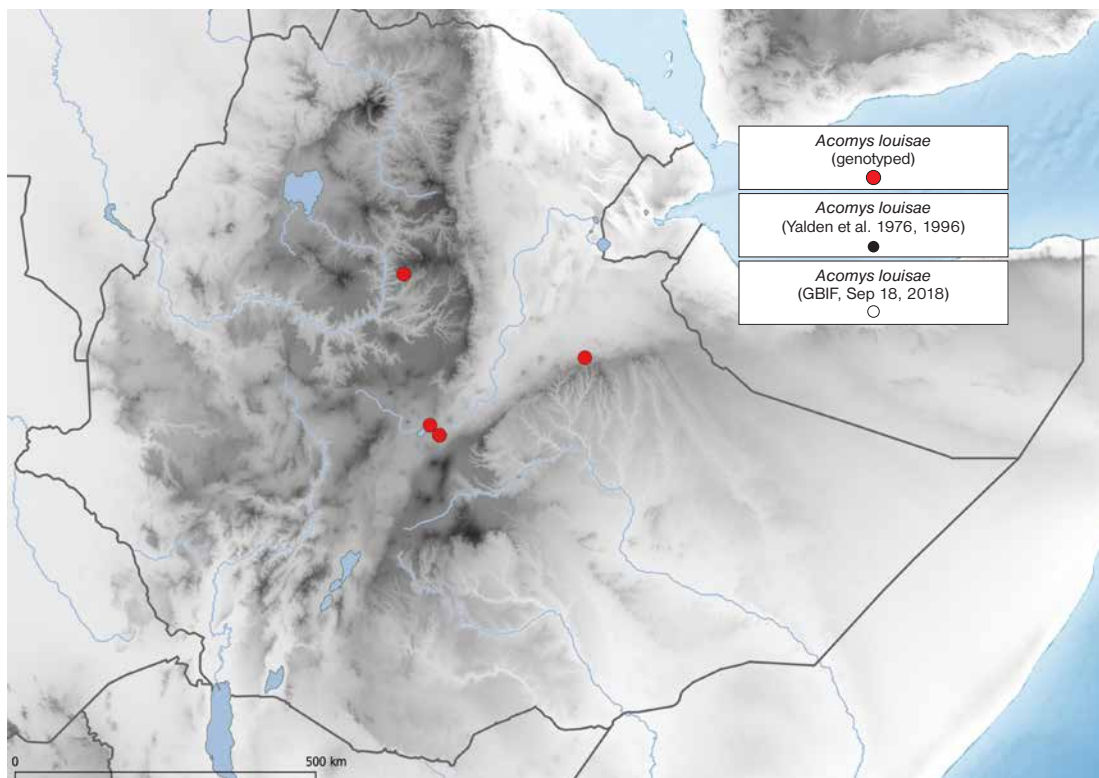


Fig. 67. Distribution of *Acomys lousiae*. Recent records from Djibuti (coll. Smithsonian Institution) are not shown, but they suggest that the species is probably more widespread in the Afar region. Our recent (2018) record from Mekane Selam (northernmost point on the map) suggests that the species enters larger valleys in the Highlands.

locality of this species, but it is very abundant there (our unpublished data). However, we suspect that it may have a wider distribution in poorly sampled regions of south-eastern Ethiopia and Somalia (see similar pattern in gerbils; Aghová et al. 2017). The conspecificity with other genetic lineages of the *ignitus* clade (sensu Aghová et al. 2019), especially its sister lineage *A. kempi*, should be further explored. The comparison with the type material of *A. mullah*, described from nearby town Harar, is necessary. The karyotype of specimens from Babile is $2n = 44$, $NF = 68$ (Lavrenchenko et al. 2010, 2011).

Acomys sp. “Ign2” (sensu Aghová et al. 2019)

This lineage was reported for the first time in Aghová et al. (2019). It is known only from two localities in the south-eastern slope of the Ethiopian Highlands (Sof Omar caves and Imi; each locality has very distinct mitochondrial haplotypes). It might be more widespread in the poorly sampled Somali region of Ethiopia, and in Somalia. Its sister lineage Ign3 (= *A. ignitus*) is geographically distant as the nearest localities are found in southern Kenya (Aghová et al. 2019), but the conspecificity with other lineages of the *ignitus* clade in Ethiopia should be tested by further taxonomic work.

Acomys percivali Dollman, 1911

This is phylogenetically the most distinct genetic taxon in the *wilsoni* group (sensu Aghová et al. 2019), which is represented in Ethiopia by two clearly distinct species (*A. percivali* and *A. wilsoni*). Both species were found sympatric at several localities in southern Ethiopia (e.g. Konso or Mago NP), where they can be distinguished by external morphology (especially colouration; our unpublished data) and karyotypes (Denys et al. 2017a). The karyotype of *A. percivali* is $2n = 36$ and $NF = 68$ (Matthey 1968).

Acomys wilsoni Thomas, 1892

Verheyen et al. (2011) suggested that *A. wilsoni* is probably a species complex. There is considerable genetic diversity in the *wilsoni* group at the Kenya/Tanzania border and species in this group should be delimited by detailed taxonomic work (see Mgode 2006 and Aghová et al. 2019 for some suggestions). All specimens of the *wilsoni* group in Ethiopia (except *A. percivali*, see above) belong to the lineage Wil4, which is widely distributed in the Somali-Masai savanna from northern Tanzania to southern Ethiopia, east of the Rift Valley (Aghová et al. 2019). Because this lineage was found also near the type locality of *A. wilsoni* (Mombasa, Kenya), we use this name for

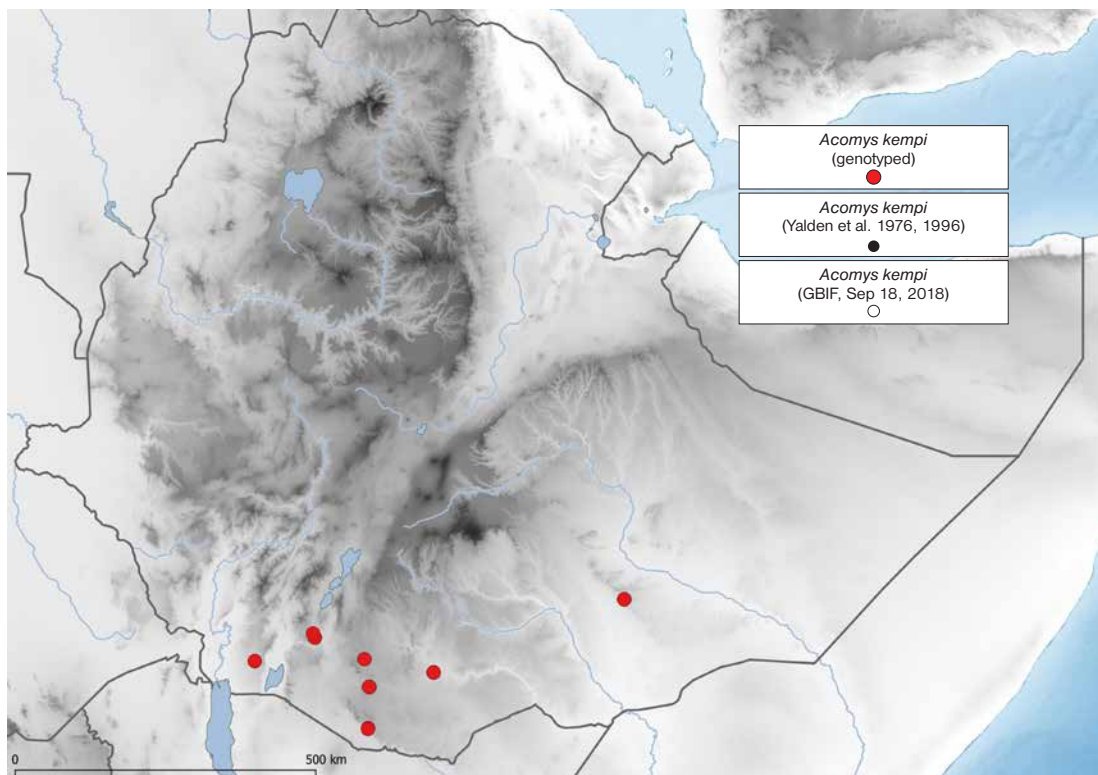


Fig. 68. Distribution of *Acomys kempi*. Genetically related clades Ign1 (from Babile) and Ign2 (Sof Omar + Imi) are considered here as separate species (following Aghová et al. 2019), but await further taxonomic analysis on material from the Somali region.

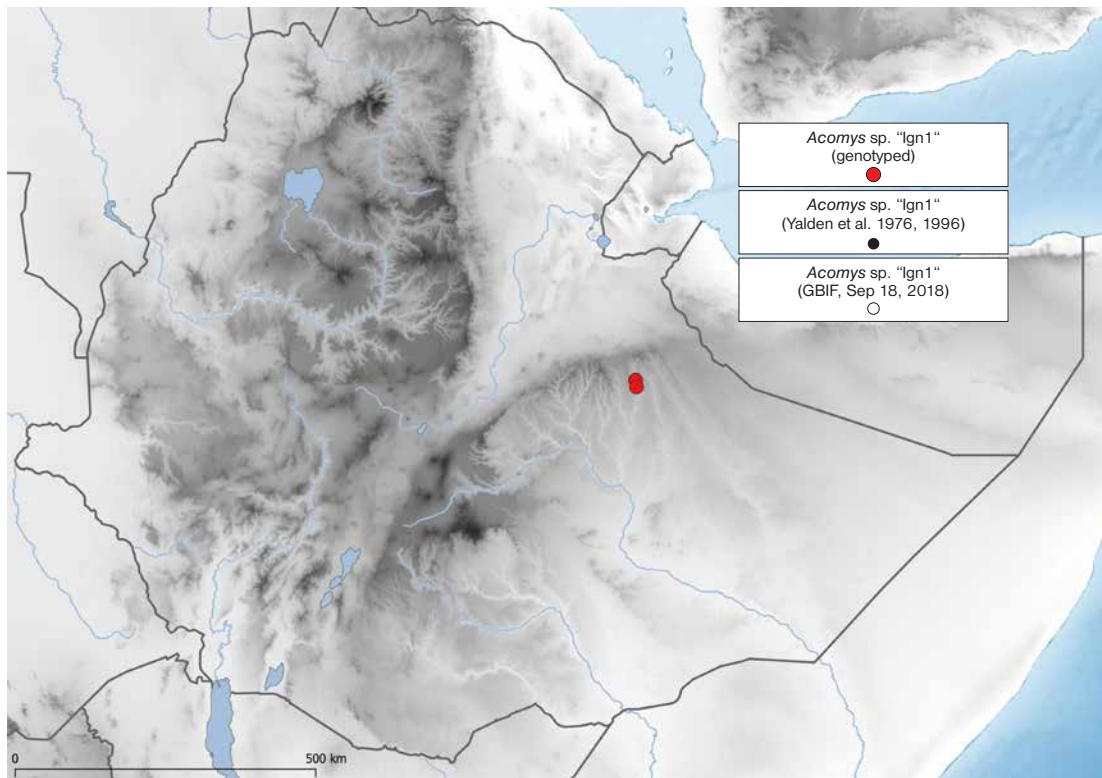


Fig. 69. Distribution of *Acomys* sp. "Ign1". The species may be more widespread in the Somali region of Ethiopia and in Somalia. Its relationships with other taxa from the *ignitus* clade (sensu Aghová et al. 2019) should be further investigated. It is possible that it represents a genetically separate population of *A. kempi*.

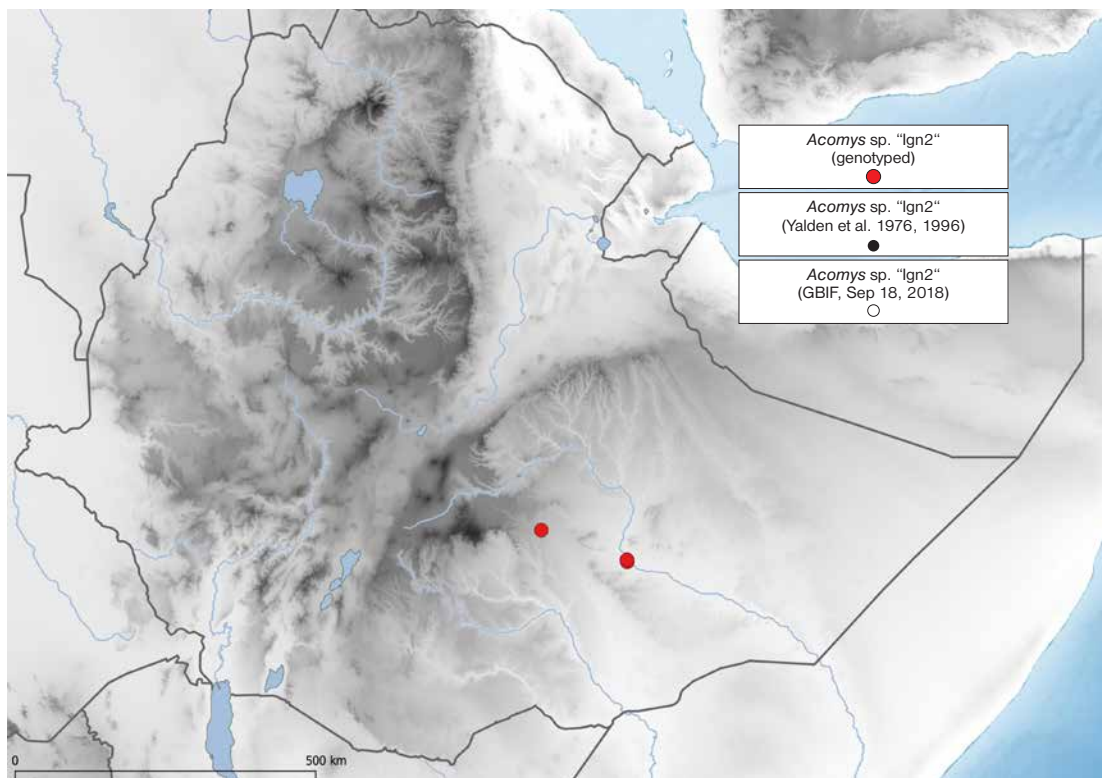


Fig. 70. Distribution of *Acomys* sp. "Ign2". The two Ethiopian populations have distinct mitochondrial haplotypes. The genetically closest are populations of *A. ignitus* in southern Kenya, but the relationships with two other Ethiopian lineages of the *ignitus* clade (sensu Aghová et al. 2019), i.e. *A. kempi* and *A. sp. "Ign1"*, should be further analysed.

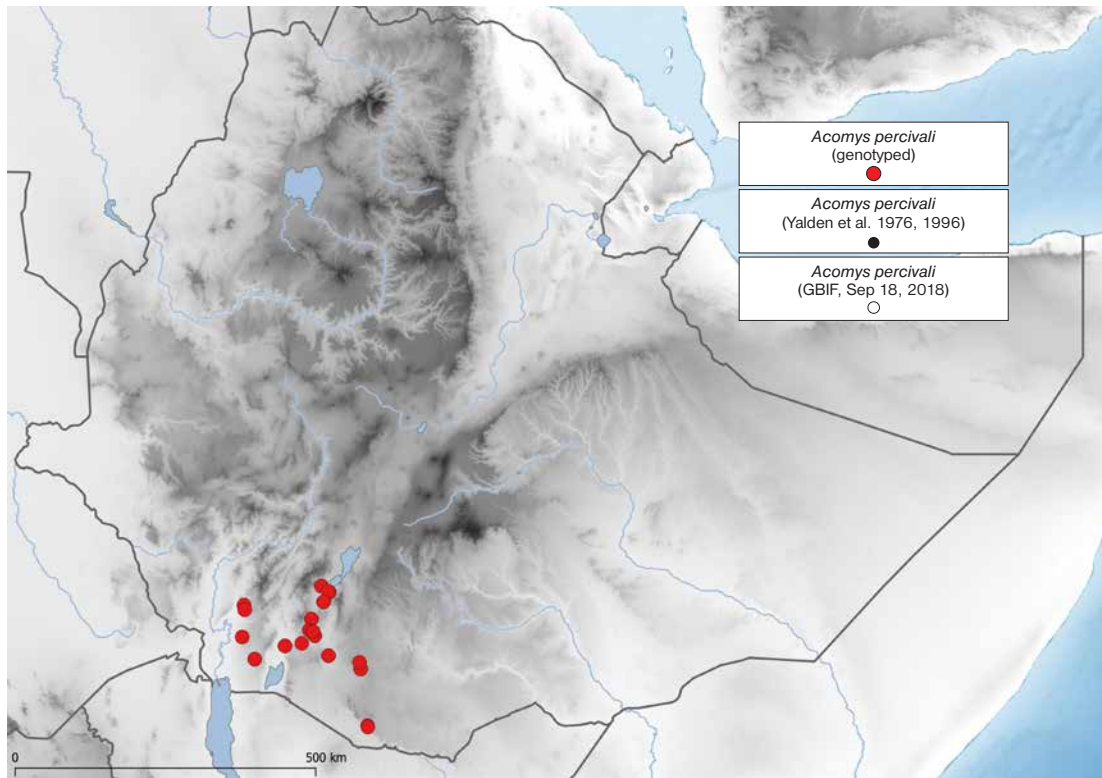


Fig. 71. Distribution of *Acomys percivali*. Outside Ethiopia, the species is abundant in north-western Kenya.

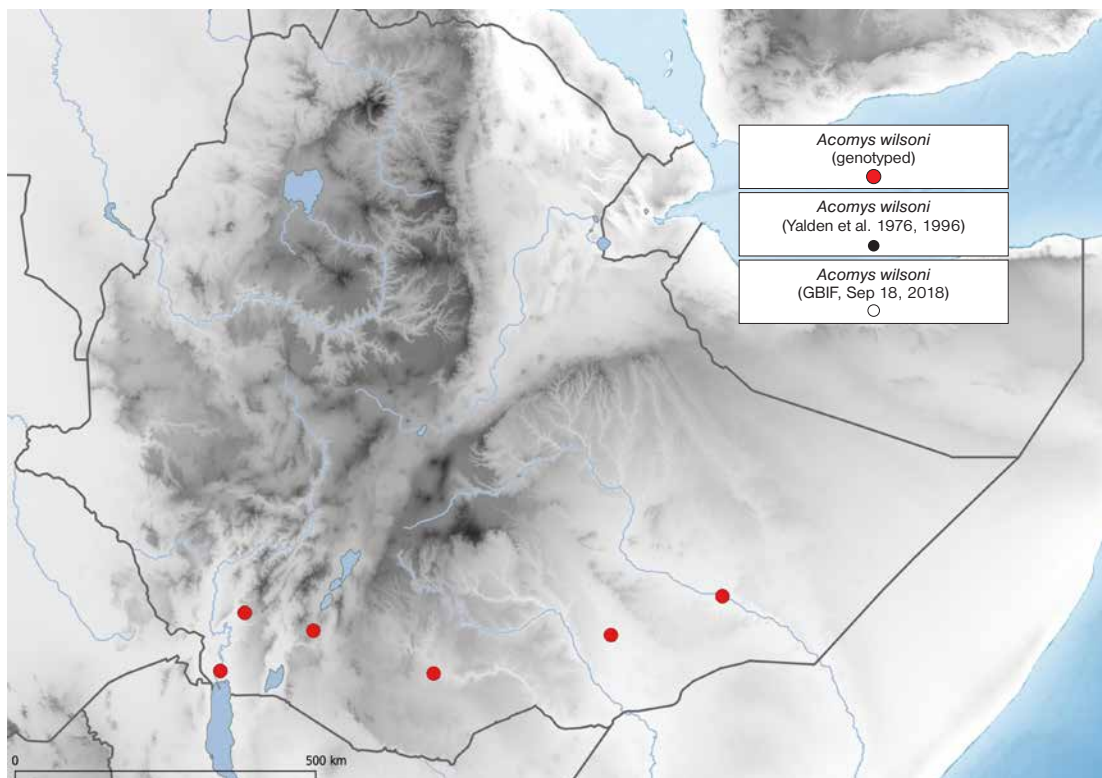


Fig. 72. Distribution of *Acomys wilsoni*. Genetically similar populations have wide distributions in Somali-Masai savanna east of the Rift Valley with their southern limit in central Tanzania (see Wil4 in Aghová et al. 2019).

the Ethiopian populations. Specimens from northern Tanzania and southern Kenya have karyotype $2n = 60-62$ and $NF = 76$ (Fadda et al. 2001b, Corti et al. 2005, Mgone 2006).

Genus *Lophuromys* Peters, 1874

The brush-furred rats (*Lophuromys*) are among the most abundant rodents across the Ethiopian Highlands. They all belong to the monophyletic “*L. flavopunctatus* group” and previous papers considered them as two species, strikingly different by their morphology – the widespread and highly variable *L. flavopunctatus* and the Afroalpine specialist *L. melanonyx* (Yalden et al. 1976, 1996). Morphological (multivariate craniometry) and genetic analyses performed by Lavrenchenko et al. (2001, 2004, 2007) clarified the species limits, distribution and relationships among Ethiopian taxa. Various types of data provided independent support for the presence of both recent and ancient reticulate processes among Ethiopian *Lophuromys* (at least among some of them; Kostin et al. 2019, Komarova et al., in lit.), which seems to be a common, but still unique, evolutionary phenomenon in Ethiopian rodents (see e.g. Bryja et al. 2018a). As a consequence, mtDNA should be used only with caution for species identification of this group. The current diversity of the genus is explained by intensive local speciation, accumulation of survived evolutionary lineages and occasional hybridization within the Ethiopian Plateau (Lavrenchenko et al. 2007). Ethiopia can be considered as a cradle for the *L. flavopunctatus* clade, from where at least two southward dispersal events led to the colonization of other mountains in Eastern Africa (Albertine Rift, Kenyan Highlands, Eastern Arc Mountains, Southern Rift Mountains, etc.), where allopatric speciation has created high levels of *Lophuromys* diversity (Verheyen et al. 2002, 2007, Denys et al. 2017a, Sabuni et al. 2018, our unpublished data). Nine species are currently recognized in Ethiopia (Lavrenchenko et al. 2007, Komarova et al., in lit.), all of them are endemic to the country. Some of them are closely associated with montane forests and heathlands. Because Yalden et al. (1976, 1996) did not recognize particular species within the *L. flavopunctatus* group, and it clearly represents a mix of multiple taxa, we do not show their records in the maps below. The distribution maps are based on the combination of nuclear (RAPD, ddRADseq, nuclear genes) and mitochondrial markers (red points; Lavrenchenko et al. 2004, 2007, Kostin et al. 2019, Komarova et al., in lit.) and cranial morphometry (black points; Lavrenchenko et al. 2007).

Lophuromys chrysopus Osgood, 1936

This is genetically the most distinct species, sister to all other taxa at mitochondrial and nuclear markers (Lavrenchenko et al. 2004, Komarova et al., in lit.) and it also has a unique karyotype ($2N = 54$). It occurs widely in forests in the southern Highlands of Ethiopia, generally at elevations of 1200-2500 m a.s.l., and can be syntopic with *L. brunneus* and/or *L. pseudosikapusi* in south-western Ethiopia (e.g. all three species co-occur in forests around Mizan Teferi; Komarova et al., in lit.). In the Bale and Arsi Mts., it is usually parapatric with *L. brevicaudus*, with *L. chrysopus* living in lower-elevation montane forests (e.g. it is the most abundant rodent in the Harena forest), while *L. brevicaudus* occurs in the *Erica* bush above 2600 m a.s.l. (Lavrenchenko et al. 2007, Kostin et al. 2019, Komarova et al., in lit.). It has a well-pronounced phylogeographic structure with distinct genetic (both nuclear and mitochondrial) populations on both sides of the Rift Valley (Komarova et al., in lit.). Surprisingly, *L. chrysopus* from the Arsi Mts. seems to be more similar to populations from the Beletta and Sheko forests west of the Rift Valley than to those from the geographically neighbouring Bale Mts., at least in mtDNA (Kostin et al. 2019).

Lophuromys melanonyx Petter, 1972

This Afroalpine specialist was already recognized as a separate species in Yalden et al.’s work (1976, 1996). It is substantially larger than other Ethiopian taxon from the *L. flavopunctatus* group and also differs in colour, being a speckled grey-brown dorsally and having characteristic black claws (Yalden et al. 1976). It was documented in the Arsi Mts. that the species shares its habitat (and even burrows) with *Arvicanthis blicki* which it superficially resembles (Yalden et al. 1976, Kostin et al. 2019). Its karyotype is $2N = 60$. There are two very distinct mitochondrial lineages occurring in this species in the Arsi Mts. (but the population is homogenous at nuclear markers; Komarova et al., in lit.), suggesting past introgressive hybridization with *L. menageshae*, followed by partial mtDNA replacement (see more details in Kostin et al. 2019 and Komarova et al., in lit.). The record from Debre Sina, west of the Rift Valley (Yalden et al. 1976), needs to be confirmed genetically.

Lophuromys flavopunctatus Thomas, 1888

There are two currently recognized species with $2N = 68$ in the western part of the Ethiopian plateau, *L. flavopunctatus* and *L. brunneus* (Lavrenchenko et al. 2007, Komarova et al., in lit.). Based on genetic and morphological data, Lavrenchenko et al. (2007) assumed contemporary gene flow among

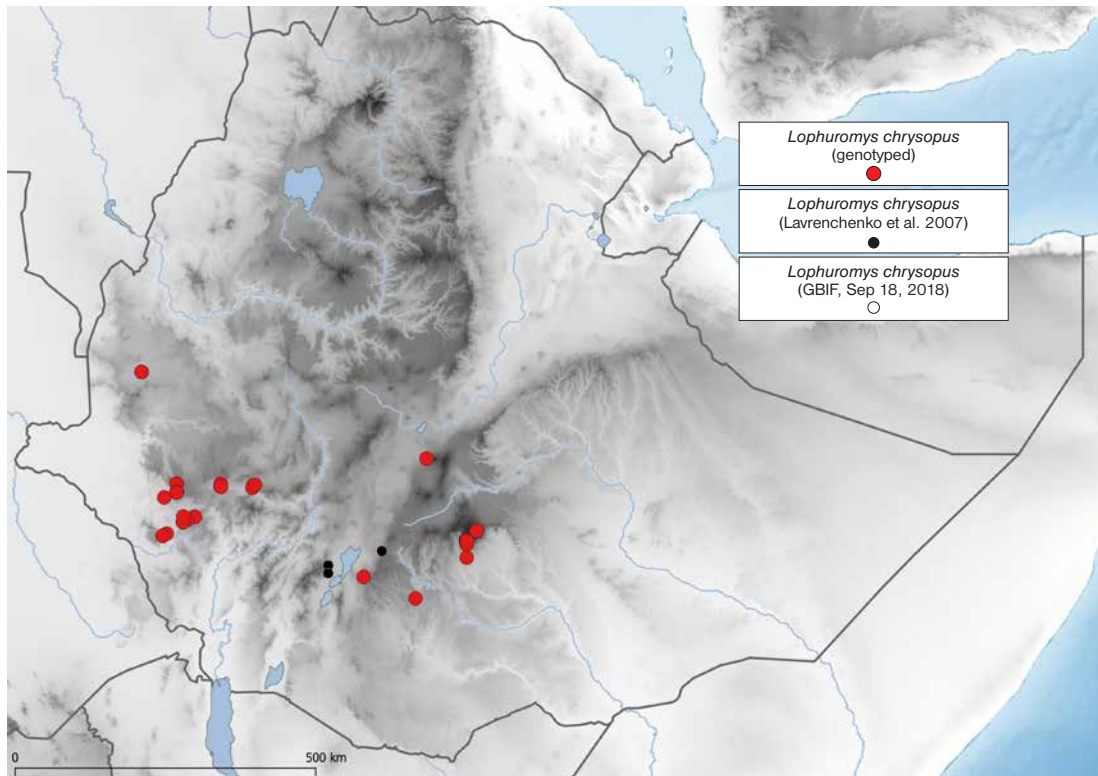


Fig. 73. Distribution of *Lophuromys chrysopus*. Numerous records reported by Yalden et al. (1976) from forests in southern Ethiopia (not shown) probably belong to this species.

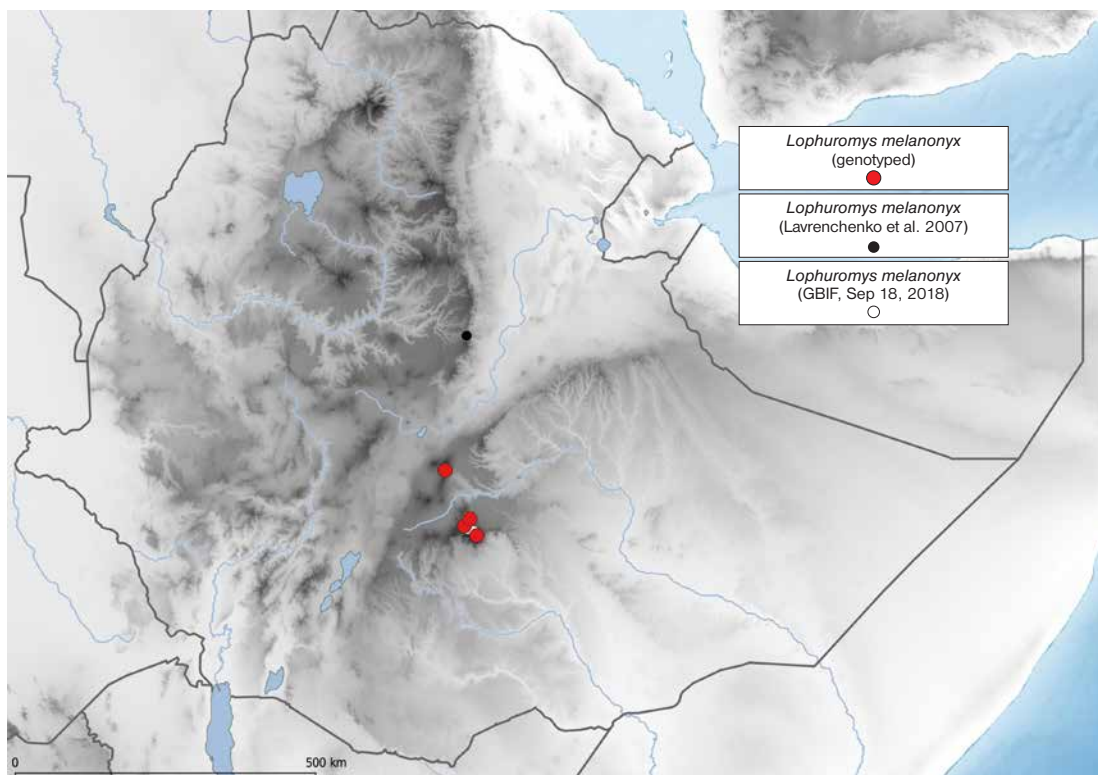


Fig. 74. Distribution of *Lophuromys melanonyx*. The localities from Yalden et al. (1976) in Bale NP are not shown, but they are generally identical with localities from which we confirmed the species genetically; i.e. Afroalpine habitats. The record from Debre Sina west of the Rift Valley (Yalden et al. 1976) is based only on morphological analysis of skulls from BMNH in London (Lavrenchenko et al. 2007) and should be confirmed genetically.

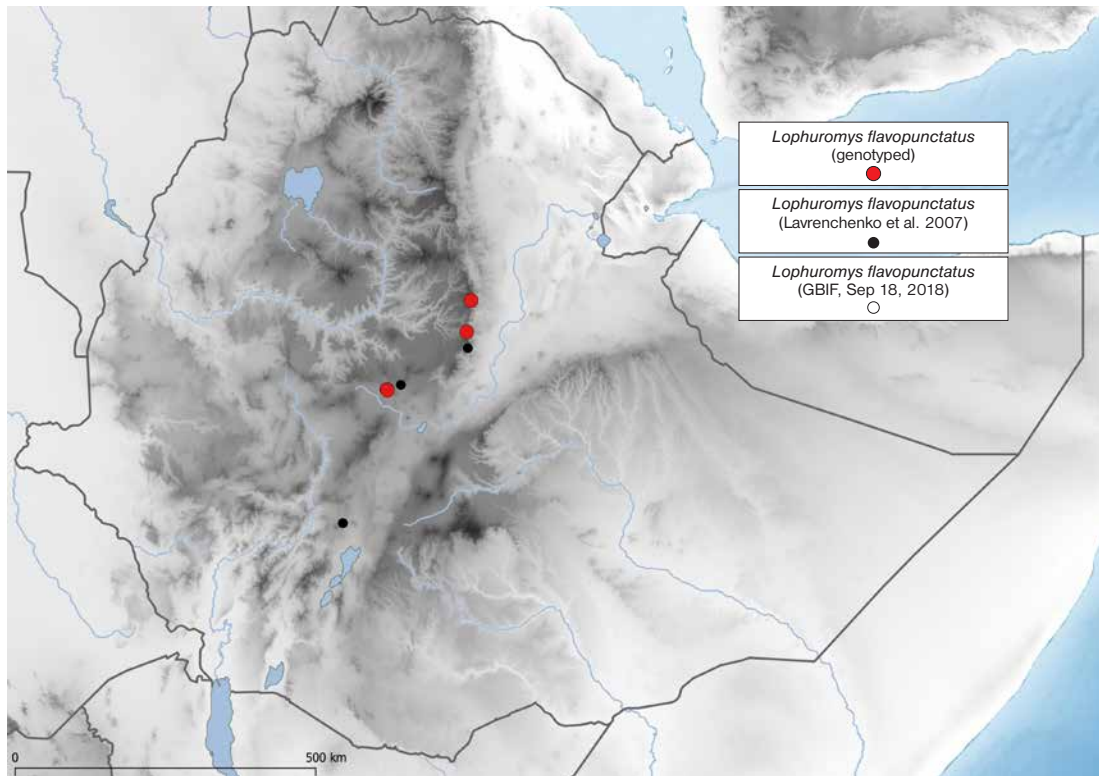


Fig. 75. Distribution of *Lophuromys flavopunctatus*. Most records reported by Yalden et al. (1976) under this name belong to other taxa. The distributional limits and possible hybridization with *L. brunneus* in their contact zone in south-western Ethiopia needs to be identified by new sampling and genomic analysis. The southernmost record is based on cranial morphometry and should be confirmed genetically.

them (“parapatry with hybridization”). The exact distribution ranges of the two forms as well as precise location of the contact zone between them remain unclear and require further investigation. The species can co-occur with *L. menageshae*, as documented e.g. in Menagesha forest, close to Addis Ababa (Lavrenchenko et al. 2007, Komarova et al., in lit.).

Lophuromys brunneus Thomas, 1906

This is an abundant species in forest margins in south-western Ethiopia (e.g. Beletta or Chingawa forests), where it can be also found in various crop cultivations (e.g. we collected many individuals in the bean fields in Wushwush). Genetically confirmed records are from 1500-2500 m a.s.l. It is often sympatric with *L. chrysopus* (generally smaller) and at one locality near Mizan Teferi also with *L. pseudosikapusi* (differing by pelage colouration; see Lavrenchenko et al. 2007). It has an identical karyotype ($2N = 68$) to *L. flavopunctatus* and their hybridization was suspected by Lavrenchenko et al. (2007), because some populations of *L. brunneus* have very similar mtDNA to *L. flavopunctatus* (despite being different at nuclear markers; Komarova et al., in lit.).

Lophuromys brevicaudus Osgood, 1936

This species is the only *Lophuromys* with the karyotype of $2N = 68$ in the eastern part of the Ethiopian plateau. It is restricted to Afroalpine heathlands above 2600 m a.s.l., mainly in the Bale and Arsi Mts. The highest records are from the top of the Galama ridge in the Arsi Mts. (Badda area; 3800 m a.s.l.), where the mosaic habitat with elements of both Afroalpine (*Alchemilla*, *Helichrysum*, *Lobelia*) and ericaceous (*Erica arborea*) vegetation allows the co-existence of both Afroalpine and heathland specialists; in *Lophuromys* it concerns *L. melanonyx* and *L. brevicaudus*, respectively (Kostin et al. 2019). In the Bale Mts. the separation of different elevation zones is more pronounced and three species of *Lophuromys* live in elevational parapatry (*L. chrysopus* in forest, *L. brevicaudus* in heathland, *L. melanonyx* in Afroalpine meadows). The isolated record from Bonke in southern Ethiopia is based on discrimination by cranial morphometry (Lavrenchenko et al. 2007) and needs to be confirmed genetically.

Lophuromys simensis Osgood, 1836

This is one of four Ethiopian *Lophuromys* with $2N = 70$ karyotype. While it is monophyletic at nuclear markers

(e.g. Lavrenchenko et al. 2004, Komarova et al., in lit.), it can have mtDNAs belonging to three very distinct clades. Lavrenchenko et al. (2004) described two mitochondrial haplogroups, North I and North II, which are probably the results of past introgressive hybridization with *L. menageshae* (see similar situation in *L. melanonyx*; Kostin et al. 2019). The genetic difference between *L. simensis* and *L. menageshae* is rather small and the extent of their hybridization should be further explored. For example recent data from Borena Saynt NP showed that the highland populations of *Lophuromys* are *L. simensis* (based on nuclear data), but they have recently introgressed mtDNA of *L. menageshae* (Komarova et al., in lit.). Most records of this species originate from above 3000 m a.s.l. in northern Ethiopia, but Lavrenchenko et al. (2004) also confirmed this taxon at both nuclear and mitochondrial markers from Vanzaye (1800 m a.s.l.) and Debre Tabor (2550 m a.s.l.). In the Semien Mts. it was captured between 2900 and 3600 m a.s.l. (most abundant at 3250 m a.s.l.), but it was absent in 4000 m a.s.l. (Craig et al., in lit.).

Lophuromys menageshae Lavrenchenko et al., 2007
 This is one of three relatively recently described species with $2N = 70$ (Lavrenchenko et al. 2007). It

co-occurs with *L. flavopunctatus* in the Menagesha forest, i.e. the type locality of *L. menageshae* and the only one from where it was genetically characterized and clearly delimited by nuclear genetic markers (Komarova et al., in lit.; Mikula et al., in lit.). Because, the mitochondrial DNA of this species is very similar to that of some populations of *L. simensis* (“North-II”) and *L. melanonyx* (“Melanonyx-II”), Kostin et al. (2019) proposed an ancient hybridization among these taxa. More recent hybridization with *L. simensis* is documented by introgression of *L. menageshae* mtDNA in the Borena Saynt NP (Komarova et al., in lit.).

Lophuromys chercherensis Lavrenchenko et al., 2007
 The species (with $2N = 70$) was described by Lavrenchenko et al. (2007) on the basis of genetic (both mitochondrial and nuclear) data and skull morphology. It lives in allopatry and it is the only *Lophuromys* species inhabiting the Chercher Mts. in eastern Ethiopia, where it lives in forest margins in 2000-2800 m a.s.l. It may be threatened because of its relatively limited distribution and intensive human exploitation of remaining suitable habitats in this part of Oromia. Genetically (using nuclear markers) it is a

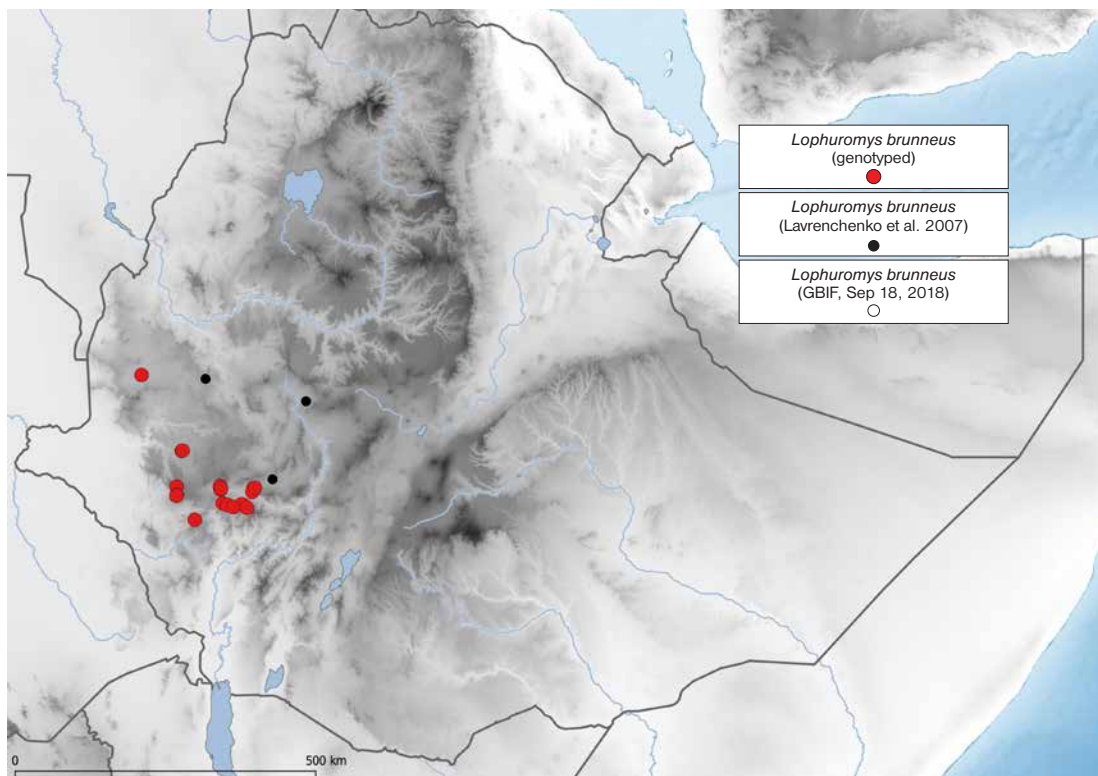


Fig. 76. Distribution of *Lophuromys brunneus*. Northern limits of its distribution and possible hybrid zone with *L. flavopunctatus* are not known. North-eastern populations were analysed only by cranial morphometry and genetic confirmation is required.

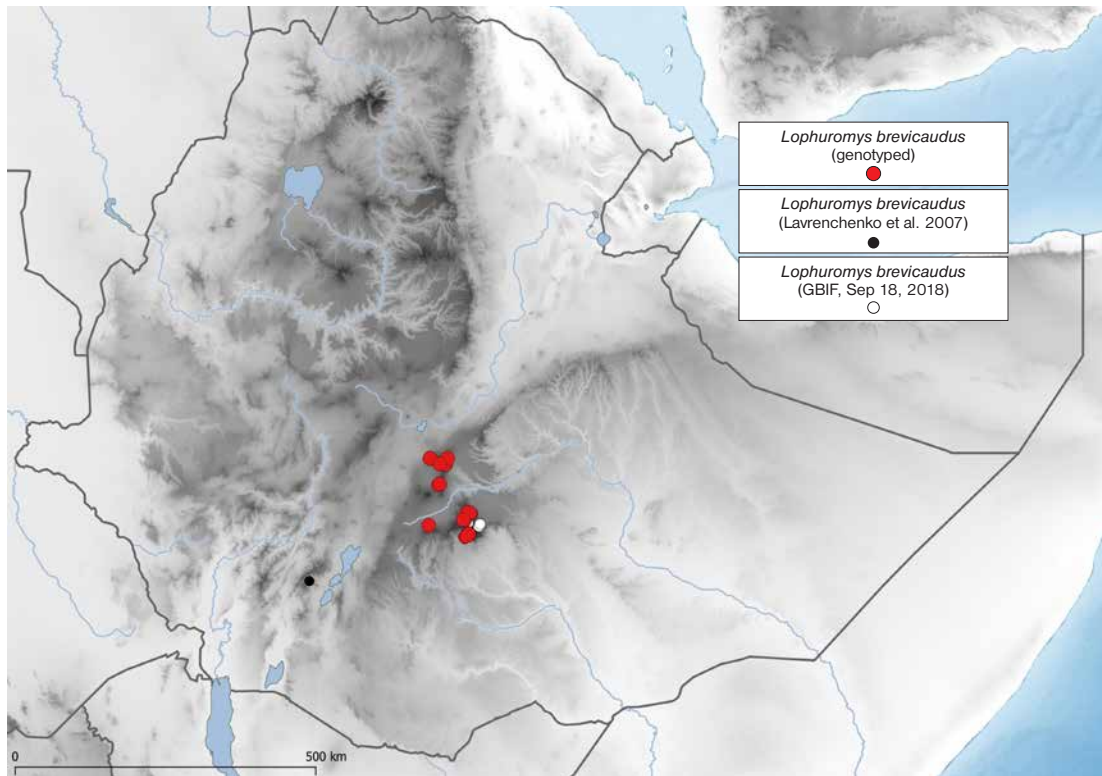


Fig. 77. Distribution of *Lophuromys brevicaudus*. The isolated record from Bonke in southern Ethiopia is based on discrimination by cranial morphometry (Lavrenchenko et al. 2007) and needs to be confirmed genetically.

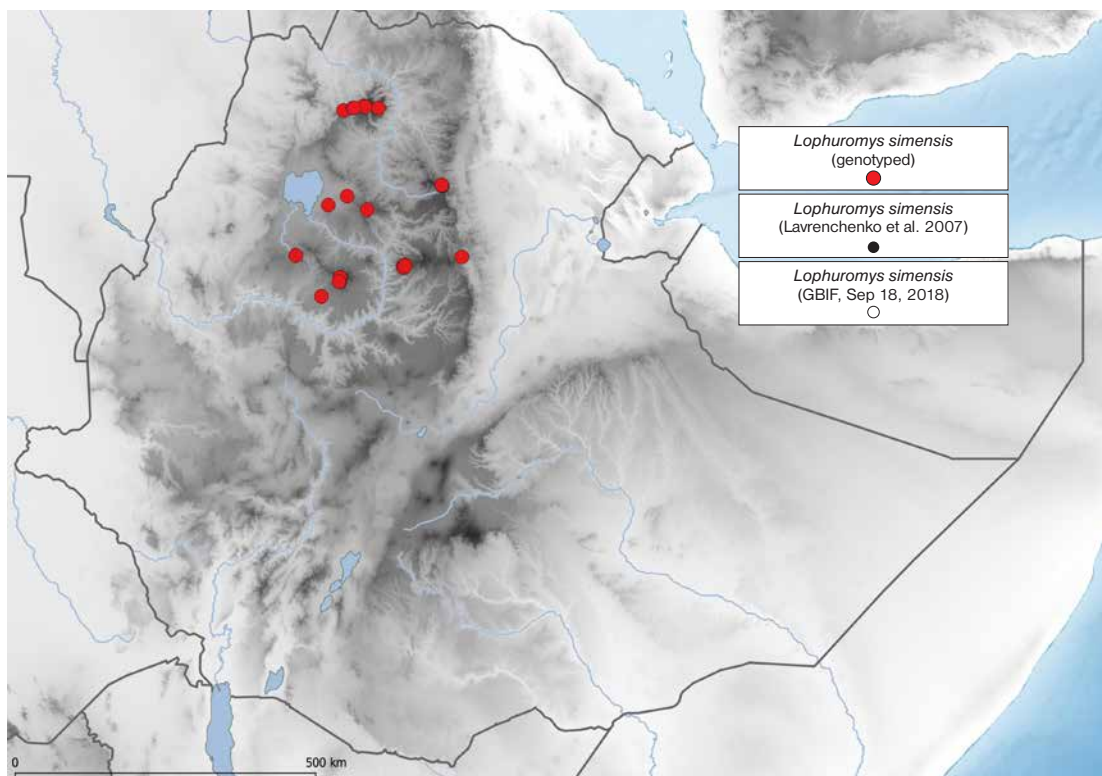


Fig. 78. Distribution of *Lophuromys simensis*. This distribution includes all individuals identified by nuclear DNA markers as *L. simensis*. Some populations have mtDNA called "North-II", which is probably the result of an old introgressive hybridization with *L. menageshae*, while the population of *L. simensis* in the Borena Saynt NP and Kombolcha is characterized by recently introgressed mtDNA of *L. menageshae*.

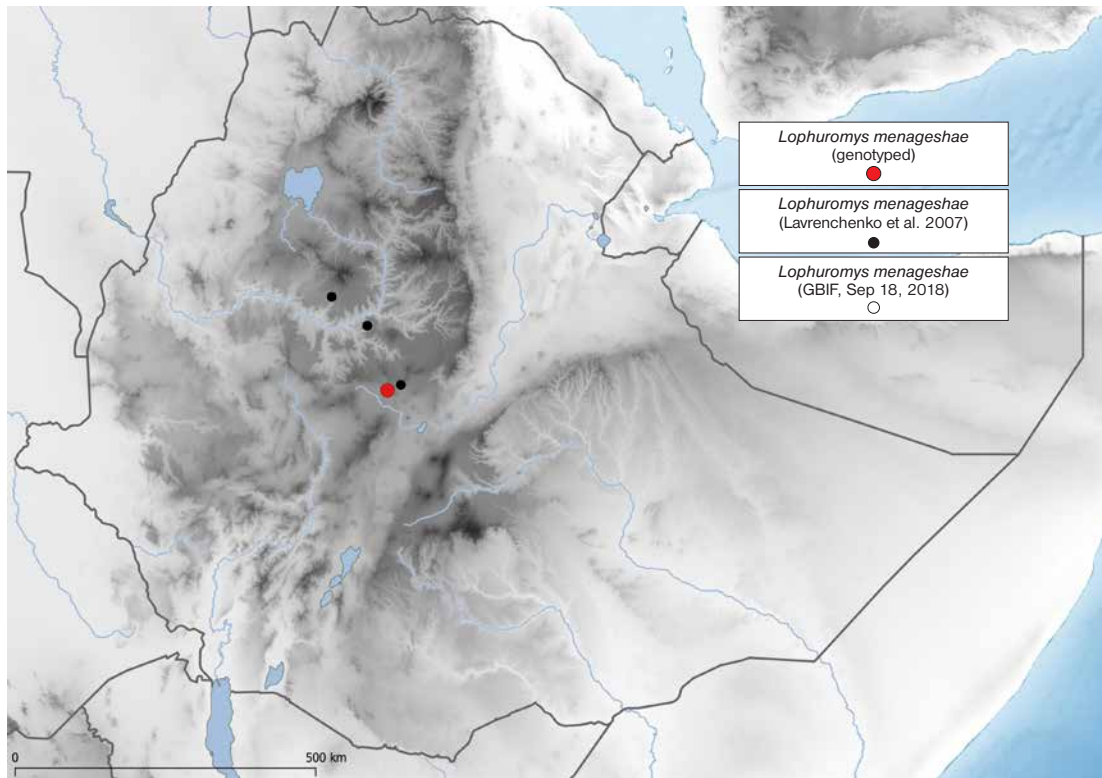


Fig. 79. Distribution of *Lophuromys menageshae*. The distributional limits in central Ethiopia and the extent of hybridization with *L. simensis* needs to be investigated with transects across elevations and nuclear genetic markers. The only genetically confirmed record of the species is from its type locality in the Menagesha forest.

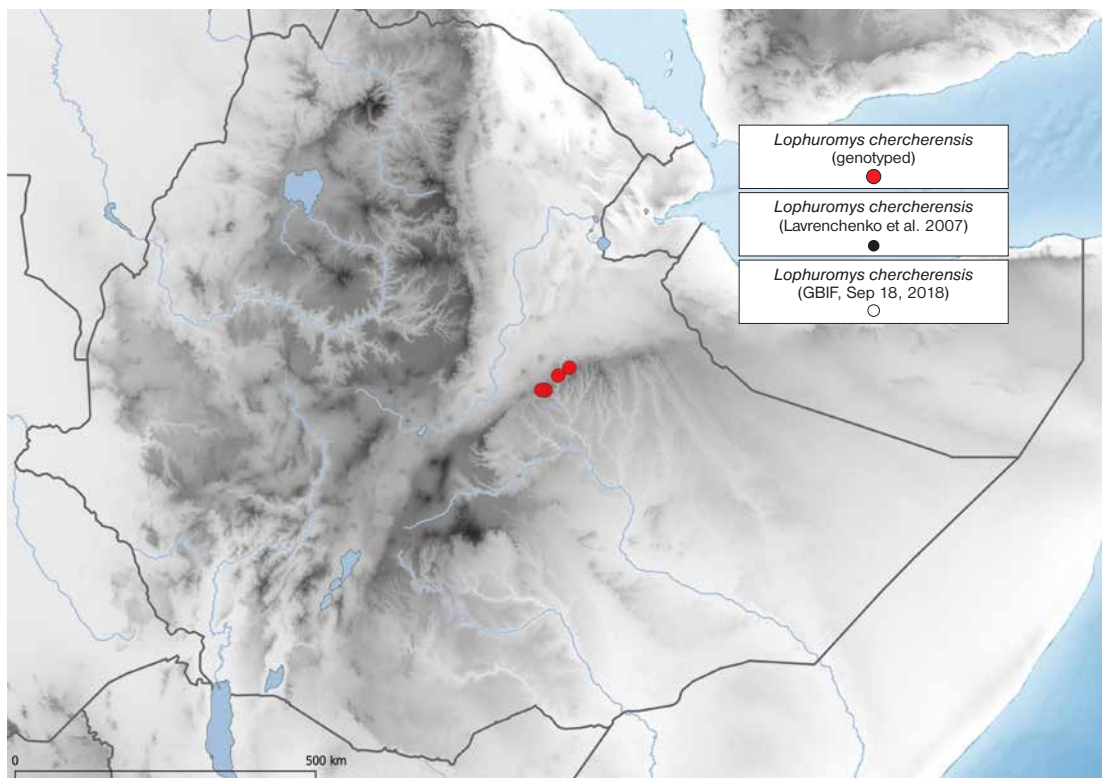


Fig. 80. Distribution of *Lophuromys chercherensis*. The distribution is limited to the Chercher Mts., whose easternmost areas have yet to be satisfactorily explored.

sister clade to other species with $2N = 70$ karyotype (i.e. *L. simensis*, *L. menageshae*, *L. pseudosikapusi*) (Komarova et al., in lit.).

Lophuromys pseudosikapusi Lavrenchenko et al., 2007

This species (with the karyotype $2N = 70$) was described by Lavrenchenko et al. (2007) based on two individuals captured in the disturbed moist Sheko forest in south-western Ethiopia (1930 m a.s.l.). Its distribution is extremely limited, but we found it recently at two additional localities, Mizan Teferi (1980 m a.s.l.) and the village Koji (= Magenteya 1440 m a.s.l.). It is a large-sized representative of the genus with a relatively long tail, large ears and flattened skull. It differs from all other members of the *L. flavopunctatus* group by its “unspckled” pelage (Lavrenchenko et al. 2007). At all known localities it lives in syntopy with *L. chrysopus*, and in Mizan Teferi even with *L. brunneus*. It seems to be a forest specialist (in rather low elevations), potentially endangered by intensive exploitation of forests in south-western Ethiopia.

Genus *Uranomys* Dollman, 1909

The genus lives in various types of savanna habitats, but the amount of available information is limited, because of its rarity or difficulty of capture. Despite some chromosomal variability, *Uranomys* is still considered monotypic and only one widespread species is recognized (Denys et al. 2017a). There is no genetic study of the genus, but this is required for taxonomic evaluation across its very large and discontinuous distribution in sub-Saharan Africa.

Uranomys ruddi Dollman, 1909

The only recognized species of the genus has a wide distribution in savanna zones from Senegal to Zimbabwe and Mozambique, with a presumably isolated population in W Ethiopia (Denys et al. 2017a). Most information about the biology of the species originates from W Africa, where it is probably more abundant (Denys et al. 2017a). In Ethiopia, it was reported by Lavrenchenko et al. (1989) and Lavrenchenko (1993) from the River Alvero, 30 km W of Abobo at altitude of 440 m a.s.l. Recently, five additional individuals were captured in the Dhati-Welel NP in W Ethiopia at an elevation of 1400 m a.s.l. (L. Lavrenchenko et al., unpublished data). More sampling from South Sudan is required for the assessment of the geographic isolation of Ethiopian population.

Subfamily Gerbillinae

Gerbils are typically inhabitants of arid environments. Four genera were recorded in Ethiopia, all of them in the lowlands. The knowledge of rodents in arid Ethiopian ecosystems, especially in the Somali and Afar regions, is limited and more detailed surveys should be performed. Additional species of gerbils (especially from genera *Gerbillus*) have been reported from neighbouring countries (South Sudan, Sudan, Somalia; see Monadjem et al. 2015) and it is likely that they occur in Ethiopia as well. Other than the genus *Gerbilliscus*, which has been well studied (Aghová et al. 2017), genetic details are missing for Ethiopian gerbils and future taxonomic studies are required.

Tribe Taterillini

Genus *Gerbilliscus* Thomas, 1897

Gerbils of this genus (with former name *Tatera*, which is now reserved only for one Asian species, *T. indica*) are widely distributed in savannas of sub-Saharan Africa. They evolved into four major clades, one of them includes the morphologically very distinct former genus *Gerbillurus* from South Africa (Colangelo et al. 2007, Granjon et al. 2012). The four clades have broadly parapatric distributions (e.g. Granjon et al. 2012). The evolutionary history and distribution of the eastern (= *robustus*) clade, including numerous Ethiopian material, was recently reviewed by Aghová et al. (2017). One species from the western clade and four taxa from the eastern clade have been reported in Ethiopia. As widespread savanna species, none of them is endemic to the country.

Gerbilliscus giffardi (Wroughton, 1906)

It is a widespread species of the Sudanian savanna belt, belonging to the so-called “western” African clade of the genus (Granjon et al. 2012), while other Ethiopian species are members of the “eastern clade”. Eastern Ethiopia is probably the north-western margin of its distribution, but at the same time it is likely to be the origin of the species as two most basal genetic lineages of the species are found in this country. The southern lineage (in Gambella and River Koi region) is distributed even more to the south (up to north-western Tanzania), while the northern lineage was found only in Alatish NP and River Didessa region (T. Aghová et al., unpublished data). In agreement with the analysis of cranial morphology of the type material (Granjon et al. 2012), we call this taxon *G. giffardi* (Wroughton, 1906). However this was probably overlooked in recent compendia (e.g. Monadjem et al. 2015 and Denys et al. 2017a), where this widely

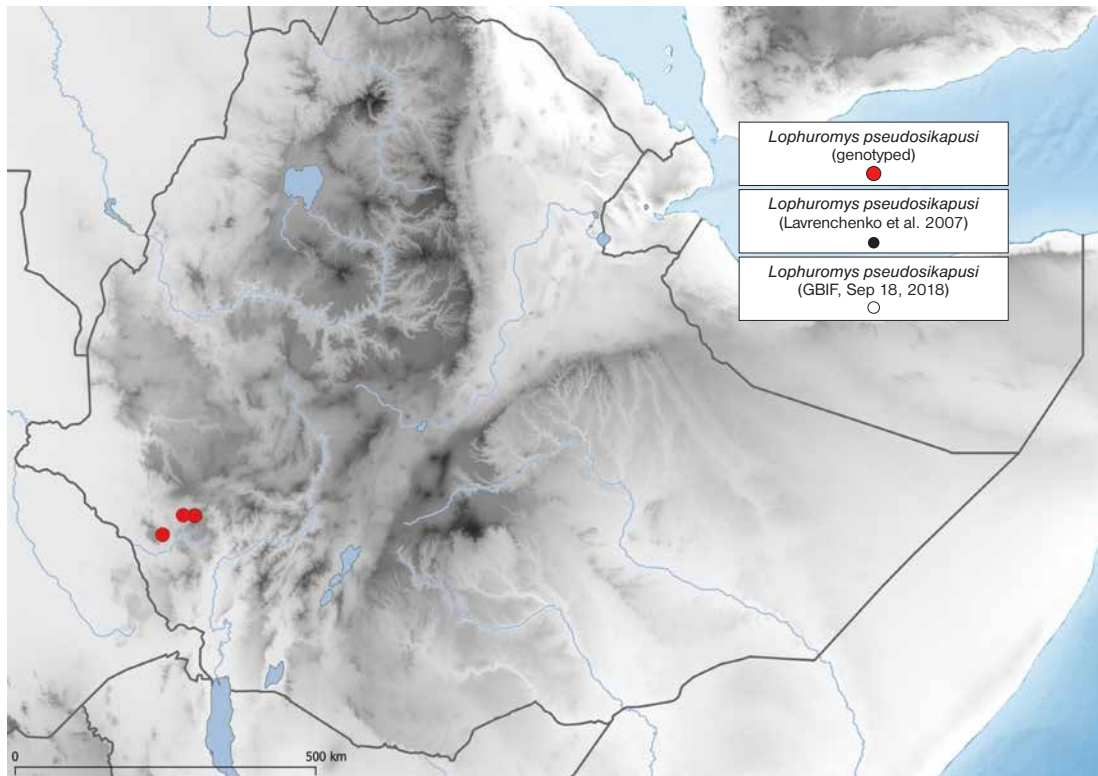


Fig. 81. Distribution of *Lophuromys pseudosikapusi*. This clearly distinct species was genetically confirmed only from three localities south of Mizan Teferi and may be threatened by intensive human exploitation of forests in this area.

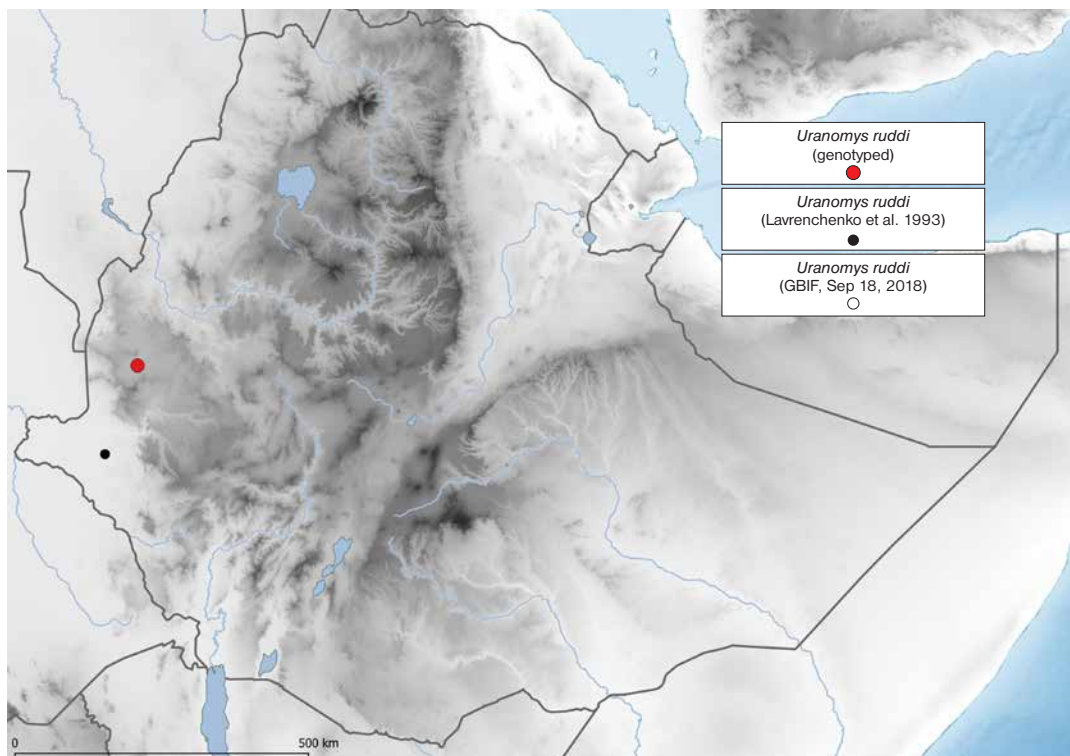


Fig. 82. Distribution of *Uranomys ruddi*. The species may be more widespread in Sudanian savanna in western Ethiopia; e.g. in the Gambella region.

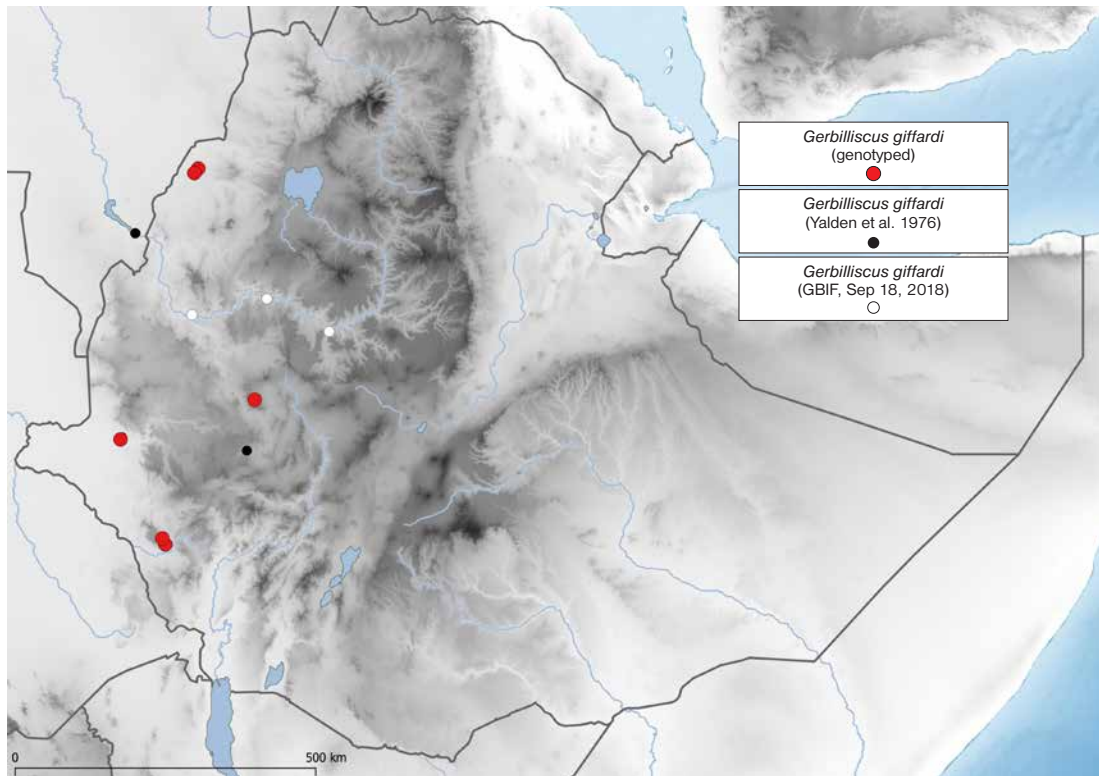


Fig. 83. Distribution of *Gerbilliscus giffardi*. Yalden et al. (1976) reported this species under the name *Tatera valida*, GBIF records are named *G. validus*.

distributed taxon is still called *G. kempfi* (Wroughton, 1906).

Gerbilliscus robustus (Cretzschmar, 1826)

Beside the Rift Valley in Ethiopia, the species is distributed in Sudan and Chad (Monadjem et al. 2015, Aghová et al. 2017). Ethiopian populations form a relatively separated genetic cluster (Aghová et al. 2017). Many previous records of *G. robustus* (reported by Yalden et al. 1976 as *Tatera robusta*; see also distributional map in Monadjem et al. 2015) probably represent other taxa, especially *G. sp.* “Babile” and *G. phillipsi*. Morphological differences between *G. robustus* and its sister taxon *G. sp.* “Babile” remain to be investigated.

Gerbilliscus sp. “Babile” (sensu Aghová et al. 2017)

Gerbilliscus sp. “Babile” was first reported as a genetically distinct lineage (12.5-17.6 % genetic distance at *cyt b* gene from other species in the eastern clade; see Aghová et al. 2017) from the Babile Elephant Sanctuary in eastern Ethiopia (Lavrenchenko et al. 2010). Aghová et al. (2017) genotyped additional individuals of this species from the same site, but also museum specimens from additional localities in

Ethiopia and Somalia. A coalescence-based species tree demonstrated that *G. sp. n.* (Babile) is a sister lineage to *G. robustus*, from which it seems to be separated by a mountain ridge in the eastern Ethiopian Highlands. Present records of *G. sp.* “Babile” suggest its occurrence is associated with transitional semi-evergreen bushland, which is localized only in the narrow belt along mountain chains in Ethiopia (Van Breugel et al. 2016). This taxon may be more widespread in south-eastern Ethiopia and part of Somalia, and museum records of *G. robustus* or *G. phillipsi* from Somalia (Monadjem et al. 2015) may in fact represent this species (M.M. McDonough et al., unpublished data). The same may be true for some records reported by Yalden et al. (1976) under the name *Tatera robusta*, especially for those south of the Harar massif.

Gerbilliscus phillipsi (de Winton, 1898)

This species was previously listed as a subspecies of *G. robustus* but elevated to species status on morphological grounds by Bates (1988). The two species also significantly differ genetically (Granjon et al. 2012, Aghová et al. 2017). Localities from southern Ethiopia mentioned by Yalden et al. (1976)

under the name *Tatera robusta* probably represent this species. Genetically confirmed records of this taxon are all from the bottom of the Rift Valley in southern Ethiopia and Kenya (Aghová et al. 2017). However, the type locality of *G. phillipsi* is in Somaliland, and it is therefore possible that the name *phillipsi* should belong rather to *G. sp.* “Babile”. Detailed analysis of Somali material (including the holotype of *G. phillipsi*) is necessary to solve this taxonomic problem.

Gerbilliscus nigricaudus (Peters, 1878)

The species is distributed in Somali-Masai savanna from northern Tanzania to southern Ethiopia. It differs from other taxa by the colouration of the tail, which is dark both above and below (Yalden et al. 1976) and it is also larger than sympatric *G. phillipsi*. In Ethiopia, it was confirmed from several localities in the Rift Valley in the southern part of the country, e.g. Nechisar NP, Mago NP and Turmi (Aghová et al. 2017). In Kenya it occurs only east of the Rift Valley, while the area west of the Rift Valley is inhabited by its sister taxon, *G. cf. bayeri* (Aghová et al. 2017), which can also occur in dry savannas in south-western Ethiopia, west of the River Omo.

Genus *Taterillus* Thomas, 1910

The genus contains middle-sized gerbils with a long tail, distributed in numerous species mainly in Sudanian savanna. The genus is characterized by very intense karyotype evolution (e.g. Dobigny et al. 2005). All East African populations are now considered to be monotypic, but there are no genetic data available and taxonomic revision is pending.

Taterillus emini (Thomas, 1892)

This is the only species of the genus reported from eastern Africa, from CAR to Somalia. Previous studies (e.g. Robbins 1977, Yalden et al. 1996) considered also *T. harringtoni* (Thomas, 1906) with smaller body size, but this taxon has the same karyotype as *T. emini* and they can both occur in sympatry in southern Ethiopia (Yalden et al. 1996), so they were put in synonymy by Happold (2013) and Monadjem et al. (2015). More genetic data on eastern African *Taterillus* are needed to solve their taxonomy and relations to other members of the genus. In Ethiopia, the species was reported from arid Somali-Masai savanna in lowlands at 200-2000 m a.s.l.

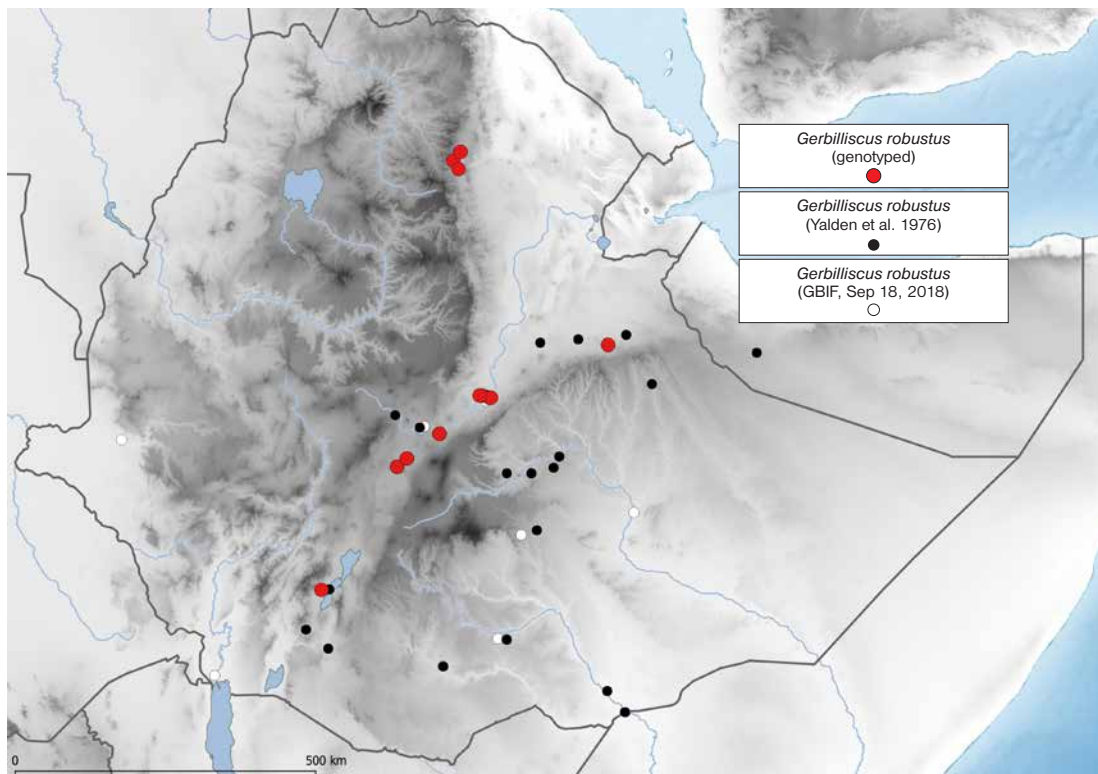


Fig. 84. Distribution of *Gerbilliscus robustus*. Part of localities from GBIF and those reported by Yalden et al. (1976) under the name *Tatera robusta* likely represent *G. sp.* “Babile” (south of the Harar massif) and *G. phillipsi* (southern Ethiopia). The southernmost genotyped record from Arba Minch is based on a short sequence obtained from an old museum specimen collected by H. Rupp and should be confirmed by genetic analysis of new material. The GBIF record from the Gambella region needs to be confirmed.

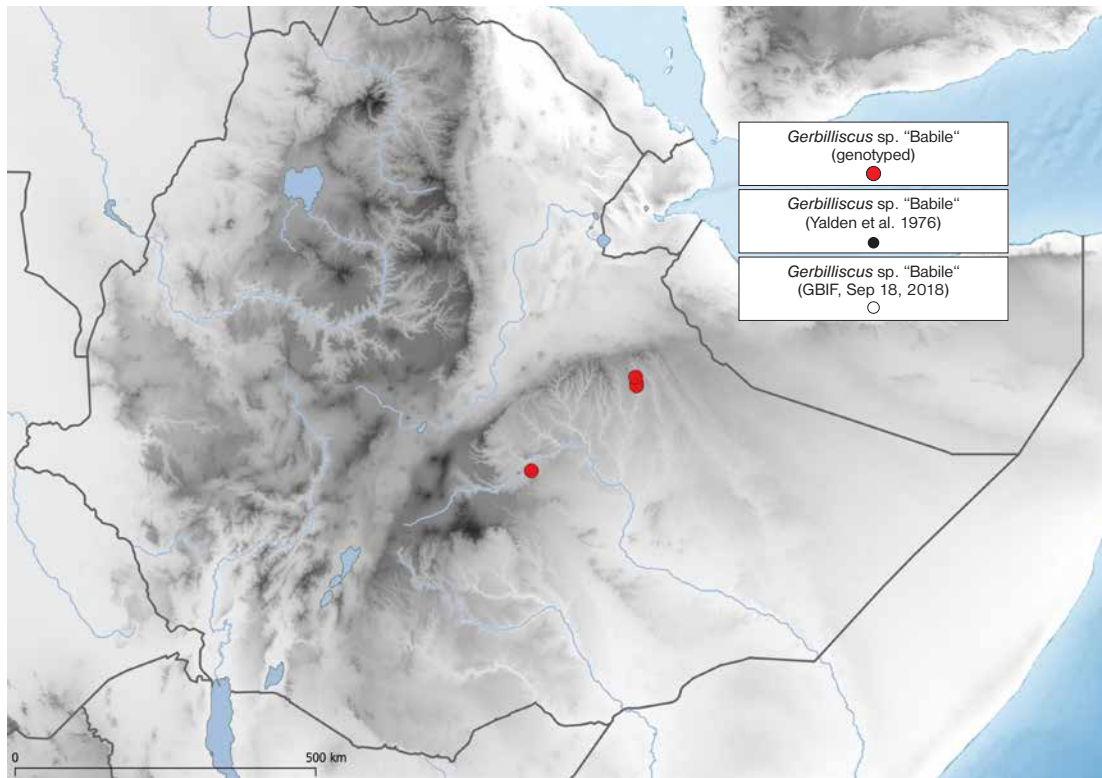


Fig. 85. Distribution of *Gerbilliscus* sp. "Babile". Some localities reported by Yalden et al. (1976) under the name *Tatera robusta* may represent this taxon.

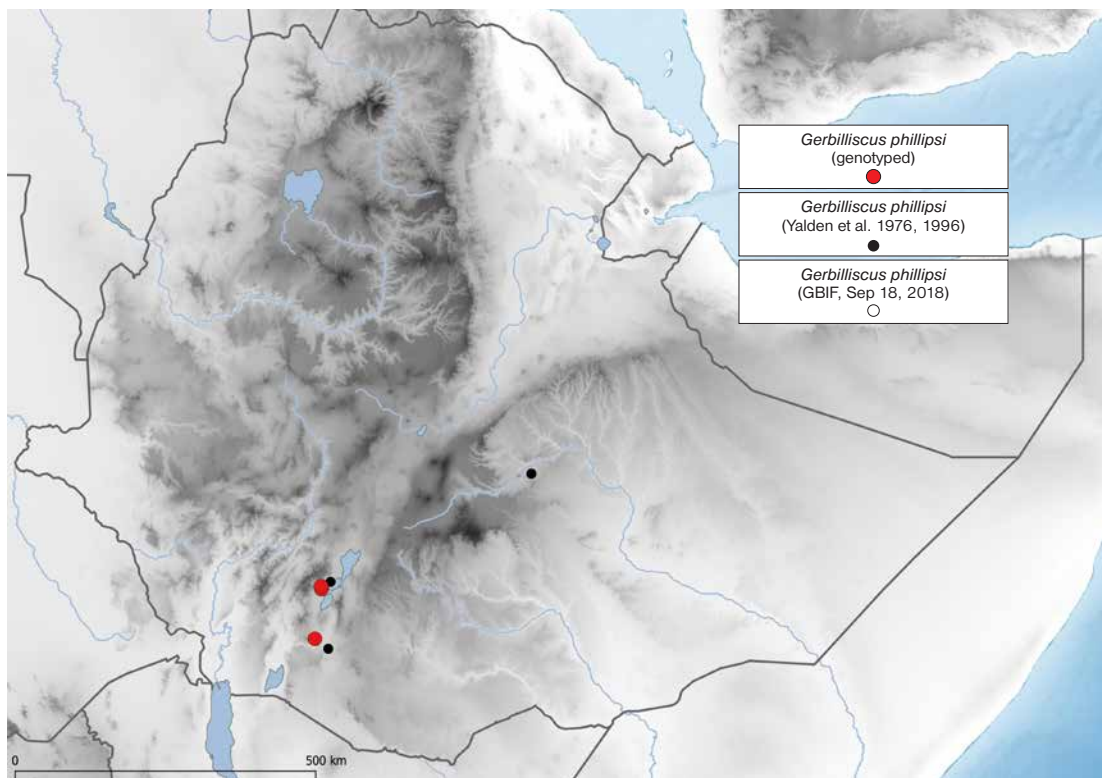


Fig. 86. Distribution of *Gerbilliscus phillipsi*. The northernmost locality reported by Yalden et al. (1976), Sheikh Hussein (the same in GBIF database), probably represents *G.* sp. "Babile" and should be confirmed genetically.

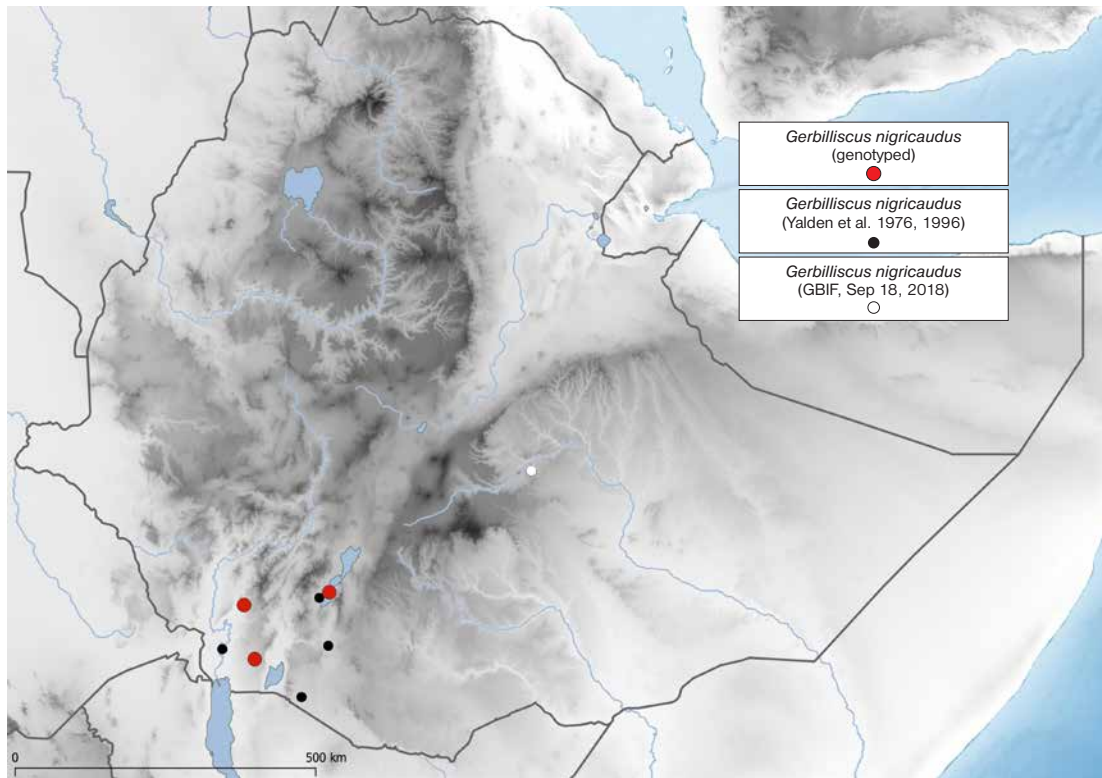


Fig. 87. Distribution of *Gerbilliscus nigricaudus*. The species is widespread in Kenya and northern Tanzania, east of the Rift Valley (Aghová et al. 2017).

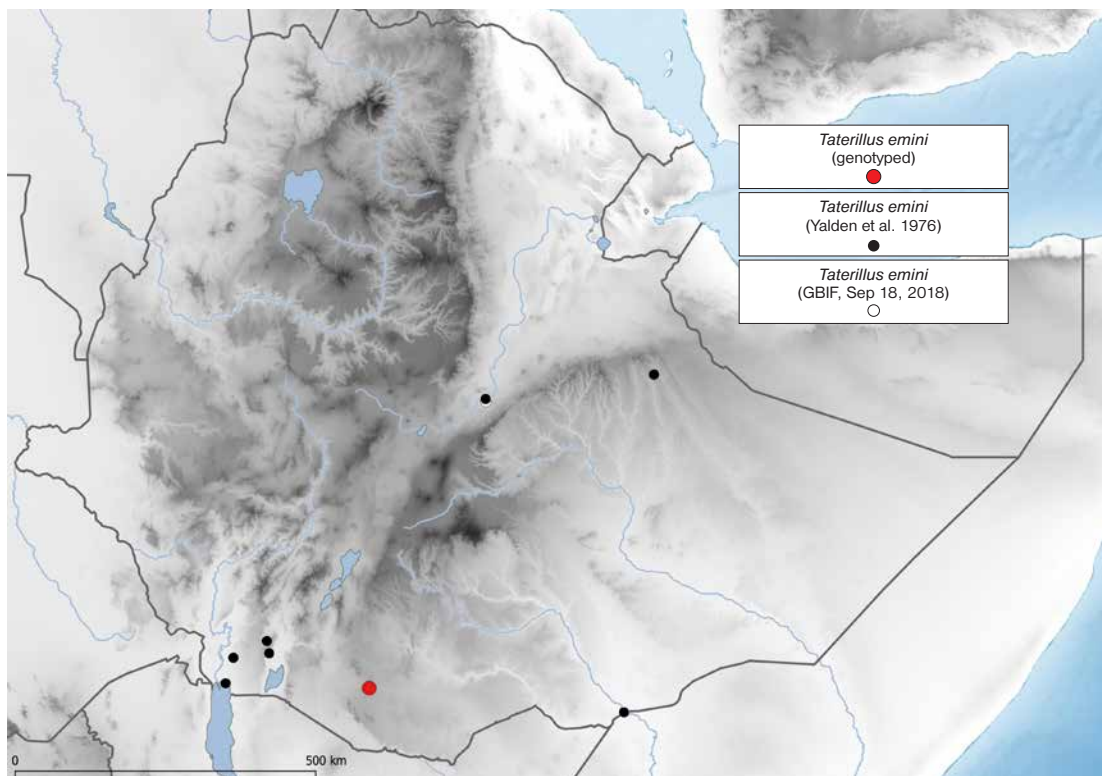


Fig. 88. Distribution of *Taterillus emini*. Eastern Ethiopian records may represent a separate species *T. harringtoni* (Yalden et al. 1996), which is currently considered as a synonym of *T. emini*.

Genus *Ammodillus* Thomas, 1904

This is a monotypic genus. Pavlinov (1987) suggested it to be distinct enough to warrant its own tribe, Ammodillini. Cladistic analysis of craniodental characters indicates that this genus is a basal lineage of Gerbillinae, but its relationships with other tribes and genera of gerbils is uncertain (Pavlinov 2008). No genetic data are available and the genus was missing in all previous phylogenetic analyses of the subfamily based on DNA sequences (Alhajeri et al. 2015 and references therein).

Ammodillus imbellis (de Winton, 1898)

This species is restricted to the Horn of Africa where it is known from just a few localities in Somalia and eastern Ethiopia (Monadjem et al. 2015). The karyotype described from Somalia is $2N = 18$ (Capanna & Merani 1981). There is only a single old record of this species from Ethiopia, at locality Gerlogobi at 700 m a.s.l. (Thomas 1904), but it can be more widespread in arid habitats of the understudied Somali region.

Genus *Gerbillus* Desmarest, 1804

This genus is the most species-rich group of the subfamily Gerbillinae, with 48 species listed in the

most recent mammal compendium (Wilson et al. 2017). They are distributed mainly in northern parts of Africa and the Middle East, with more or less isolated populations in Eastern Africa (e.g. Masai steppe in Tanzania). The taxonomy is only partly resolved. Recent molecular phylogenies (e.g. Ndiaye et al. 2016) recognize four genetic clades (= subgenera) within this group, also differing by cytogenetics, external and skull morphology: *Dipodillus*, *Gerbillus*, *Hendecapleura*, *Monodia*. Species limits within these groups are relatively well defined in western Africa and the Sahara (e.g. Ndiaye et al. 2013, 2014, 2016), while genetic data from eastern Africa are virtually missing. Based on Yalden et al. (1976, 1996) we include three species in the Ethiopian list, but the diversity of the genus *Gerbillus* in Ethiopia must be carefully re-evaluated. The following species are reported from neighbouring regions (see Wilson et al. 2017) and there is no biogeographic reason why they should be absent in the understudied arid parts of Ethiopia: *G. bottai* (Sudan), *G. campestris* (Sudan), *G. gerbillus* (Djibouti; see also Yalden et al. 1976, 1996), *G. henleyi* (Sudan, Djibouti; see Pearch et al. 2001), *G. watersi* (Sudan, Djibouti, Somalia), *G. agag* (South Sudan, Kenya), *G. nancillus* (Sudan), *G. pyramidum* (Sudan), *G. stigmonyx* (Sudan), *G. acticola* (northern

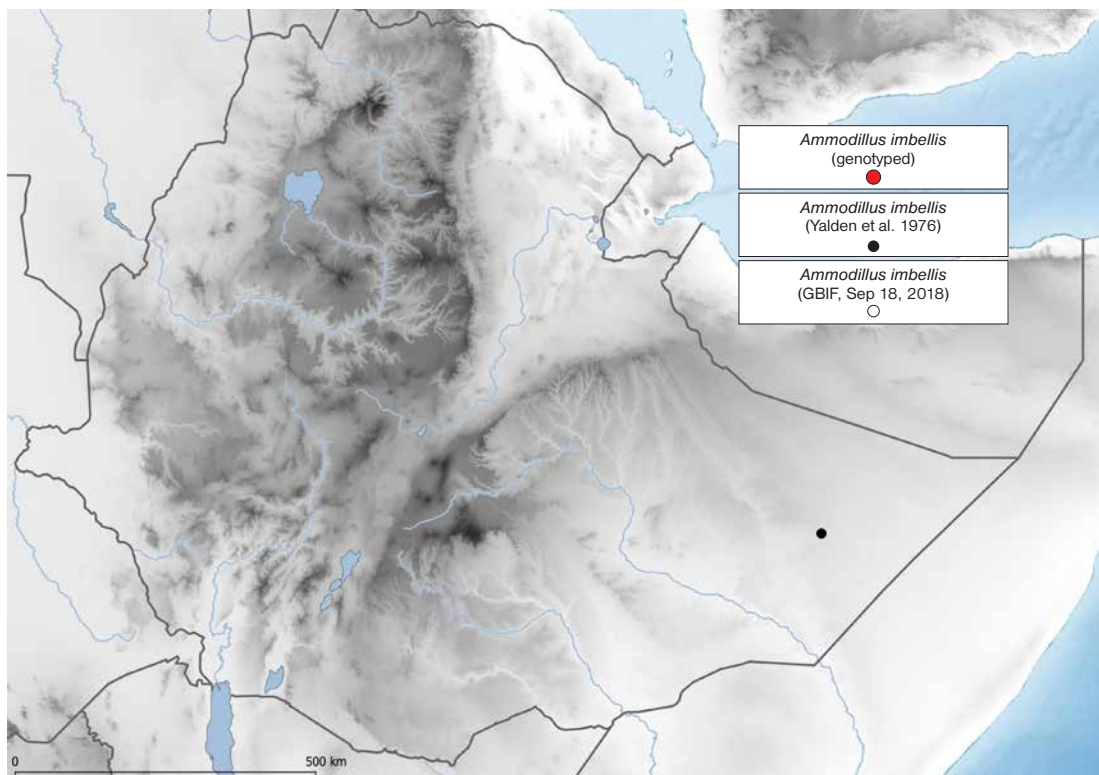


Fig. 89. Distribution of *Ammodillus imbellis*. The species has not been reported from Ethiopia for over 110 years, but we suspect that it may be widespread in the under-sampled Somali region.

Somalia), *G. brockmani* (northern Somalia), *G. mackilligini* (Sudan), *G. rosalinda* (Sudan, Somalia), and *G. somalicus* (Djibouti, northern Somalia). Because of taxonomic uncertainty we do not show the GBIF records for this genus.

Gerbillus dunni Thomas, 1904

The species was described from Gerlogobi in the Somali region in East Ethiopia (Happold 2013). Some authors considered it a form of *G. pyramidum* (e.g. Yalden et al. 1976) or *G. latastei*, but it can be distinguished by its morphological and chromosomal characters (Denys et al. 2017a), with $2N = 74$ (Capanna & Merani 1981). It is assumed to be distributed in the Horn of Africa, including the Afar triangle, but genetic data are completely missing. It is possible that records from the lower Omo valley reported as *G. pyramidum* by Yalden et al. (1976) in fact represent *G. pulvinatus*.

Gerbillus pulvinatus Rhoads, 1896

Yalden et al. (1976) treated this taxon as a synonym of *G. pyramidum*, but recent compendia (Happold 2013, Monadjem et al. 2015, Wilson et al. 2017) consider it valid. It was described from the lower Omo region, but the extent of its distribution is not known. The

karyotype in southern Ethiopia is $2N = 62$ (Hubert 1978b). Conspecificity with material reported from Djibouti (Pearch et al. 2001) needs to be further explored.

Gerbillus pusillus Peters, 1878

The taxonomic status of this group is not clear and it may include other taxa like *G. ruberrimus*, *G. diminutus* or *G. percivali* (Denys et al. 2017a). The species in the current taxonomic treatment seems to be widespread in Somali-Masai savanna from the Afar triangle to central Tanzania, but more data are required. All records of naked-soled gerbils (reported as *G. ruberrimus* by Yalden et al. 1976 and as *G. pusillus* by Yalden et al. 1996) are included here in this species. Four genotyped specimens from Metahara cluster with those from Kenya and Tanzania (our unpublished data).

Genus *Microdillus* Thomas, 1910

Very rare gerbils from the Horn of Africa with only few records. One record is now also reported from Ethiopia (Monadjem et al. 2015), but the genus was not included in previous checklist of Ethiopian mammals (Yalden et al. 1996).

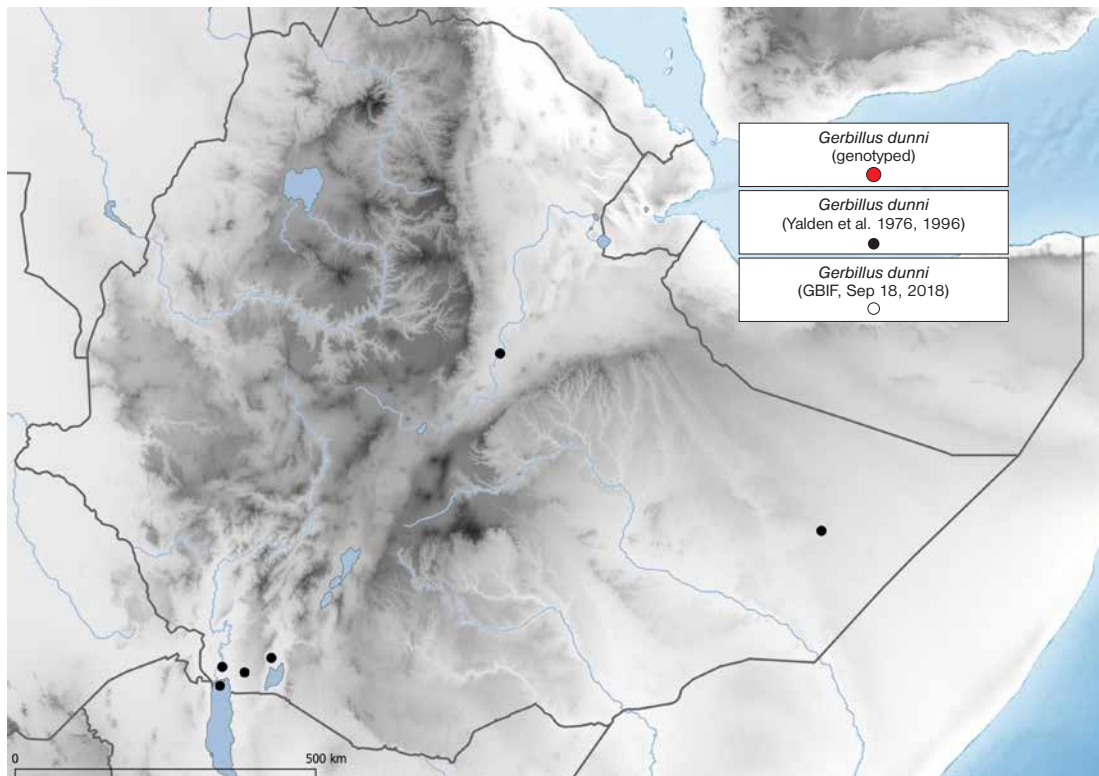


Fig. 90. Distribution of *Gerbillus dunni*. We show all records reported as *G. pyramidum* by Yalden et al. (1976), because it is not clear which of them represent *G. dunni*. The easternmost point is Gerlogobi, the type locality of the species.

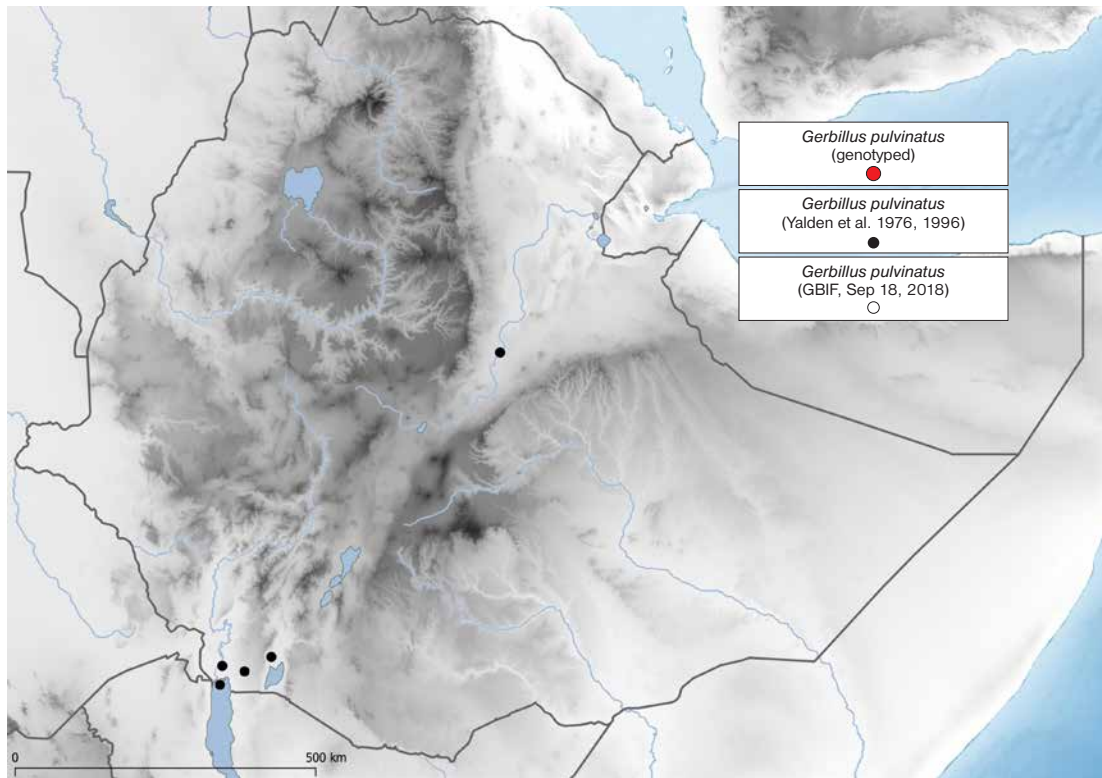


Fig. 91. Distribution of *Gerbillus pulvinatus*. We show all records reported as *G. pyramidum* by Yalden et al. (1976) (except Gerlogobi, the type locality of *G. dunni*), because it is not clear which of them represent *G. pulvinatus*. Especially the record from the Awash valley (locality Bilen) needs to be confirmed.

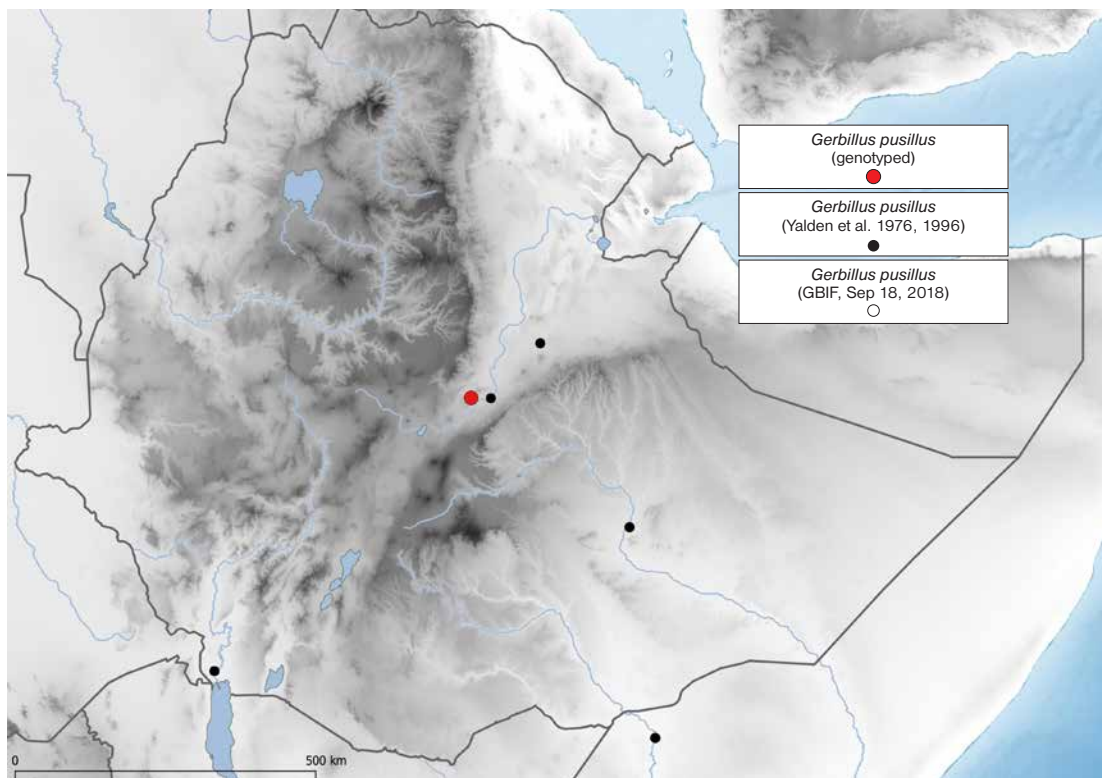


Fig. 92. Distribution of *Gerbillus pusillus*. This species was reported as *G. ruberrimus* in Yalden et al. (1976).

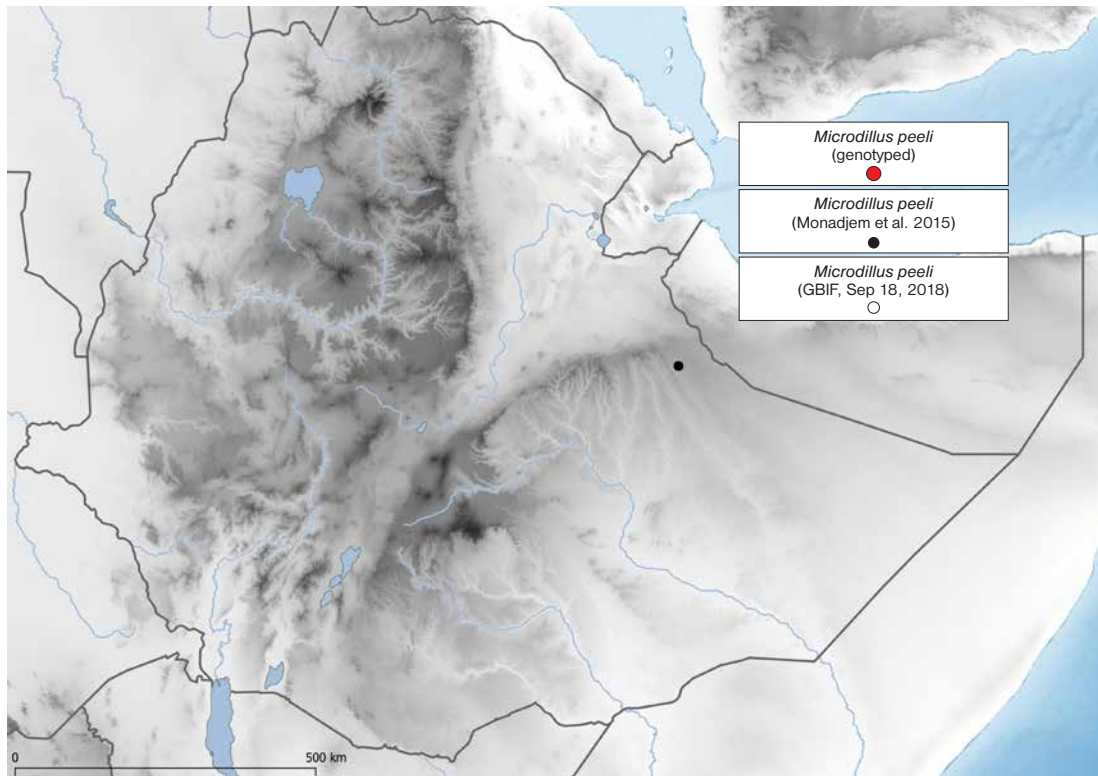


Fig. 93. Distribution of *Microdillus peeli*. The only record (close to Jijiga) is based on two specimens preserved in MNHN in Paris.

Microdillus peeli (de Winton, 1898)

In the characteristics of the genus, Monadjem et al. (2015) write that the genus is distributed in “the extreme western parts of Ethiopia”, while in the description of the species they mention that it is known from “northern Ethiopia”. Their distribution map shows the majority of localities in Somalia, but there is also one locality in eastern Ethiopia (close to Harar), which is probably based on two individuals in the collection of MNHN in Paris (from locality Jijiga, 9 km route de Dagehbur = Ogaden = Degeh Bur). It may be more widespread, but more research in the arid habitats of Somali region is required. It is a small gerbil (< 15 g), with short tail (Monadjem et al. 2015).

Subfamily Lophiomyinae

Monotypic subfamily, belonging to the family Muridae based on multilocus phylogenetic analyses (Schenk et al. 2013, Aghová et al. 2018).

Genus *Lophiomys* Milne-Edwards, 1867

The only genus in the subfamily, patchily distributed in forests and woodlands from western Tanzania to Eritrea.

Lophiomys imhausi Milne-Edwards, 1867

It is a large species (600-800 g) with unmistakable morphology and colouration. Yalden et al. (1976)

summarized previous records of this species and showed that it is widely distributed from sea level (in Eritrea) to 3300 m a.s.l. in the Bale Mts. It is tolerant of a wide range of habitats and not confined to forested localities. The records mentioned by Yalden et al. (1976), however, are at least 50 years old and there is very little updated information about its distribution and population status. In fact, there are only two well documented more recent findings. One specimen was collected in Harena forest in the Bale Moutains and is preserved as skin and skull in the Zoological Museum of Moscow University (ZMMU). The most recent record is from the camera traps in the Belete-Gera montane rainforest in south-western Ethiopia, which expands the known Ethiopian range of this elusive species westwards (De Beenhouwer et al. 2015).

Family Sciuridae (squirrels)

Small to medium-sized mammals with long bushy tails. They are widespread in various ecosystems on all continents except Australia. All African squirrels belong to the subfamily Xerinae (together with Holarctic ground squirrels) and are divided into ground (tribe Xerini) and tree (tribe Protoxerini) squirrels. Two genera of ground (*Xerus*, *Euxerus*) and two of tree squirrels (*Heliosciurus* and *Paraxerus*) have been recorded in Ethiopia.

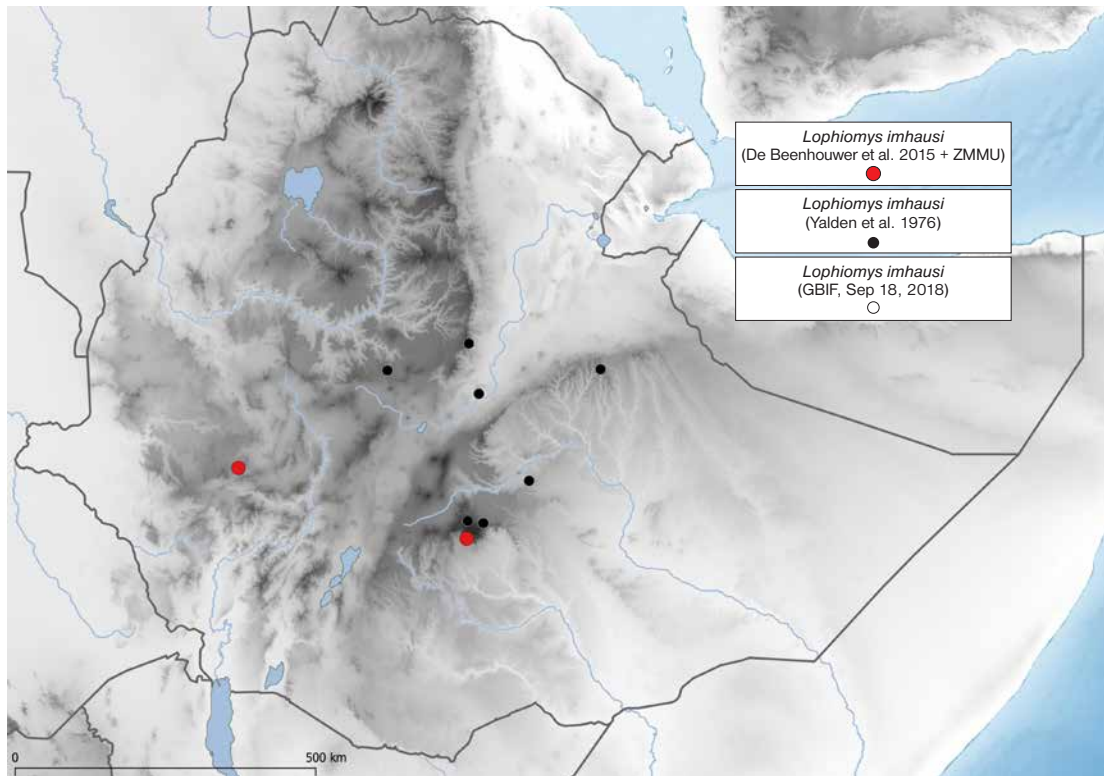


Fig. 94. Distribution of *Lophiomys imhausi*. Numerous additional records were reported by Yalden et al. (1976) from Eritrea, where it was even found at sea level.

Subfamily Xerinae

Tribe Xerini (African ground squirrels)

This tribe includes one Asian and four African genera of ground squirrels (Koprowski et al. 2016). African members of this tribe are typically associated with drier conditions than other African squirrels. They occur in the Kalahari and Namib Deserts of southern Africa, the deserts and arid savannas of the Horn of Africa and neighbouring Kenya-Tanzania, and the arid Sahel. They are terrestrial, and do not climb trees, resting up in burrows at the base of trees, in termite mounds, piles of rocks or in the ground (Happold 2013, Monadjem et al. 2015). Two monotypic genera (sometimes considered as a single genus *Xerus*) live in Ethiopia (from sea level to 2000 m a.s.l.; Yalden et al. 1976), and partially overlap in the southern part of the country; one is primarily the genus of Sudanian savanna, while the other of Somali-Masai savanna.

Genus *Xerus* Hemprich & Ehrenberg, 1832

Xerus rutilus (Cretzschmar, 1828)

The unstriped ground squirrel is widely distributed in the arid Somali-Masai zone of East Africa, commonly also in disturbed habitats and cultivated agricultural lands (Koprowski et al. 2016). In Ethiopia it is

widespread in the south-eastern part of the country as well as in some parts of the Afar triangle.

Genus *Euxerus* Thomas, 1909

Euxerus erythropus (E. Geoffroy, 1803)

The striped ground squirrel is widely distributed in the belt of Sudanian savanna from Senegal to Ethiopia and western Kenya, overlapping marginally with *X. rutilus* in Kenya, Ethiopia and Eritrea. They can readily be distinguished by the presence of a white flank stripe in *E. erythropus* (*X. rutilus* has no flank stripe). In Ethiopia it is distributed in the western parts of the country and southern part of the Rift Valley. The record from Dire Dawa region (Joyeux et al. 1936; see Yalden et al. 1976) very likely represents misidentification with *X. rutilus* and is not shown on the map.

Tribe Protoxerini (African tree squirrels)

Genus *Heliosciurus* Trouessart, 1880

Species in this genus are medium-sized (150-390 g) arboreal squirrels widely distributed in sub-Saharan Africa. Their habitats are very variable (from woodland savanna to primary montane and lowland forests) and differ between species. Six species are currently recognised in this genus, but species limits

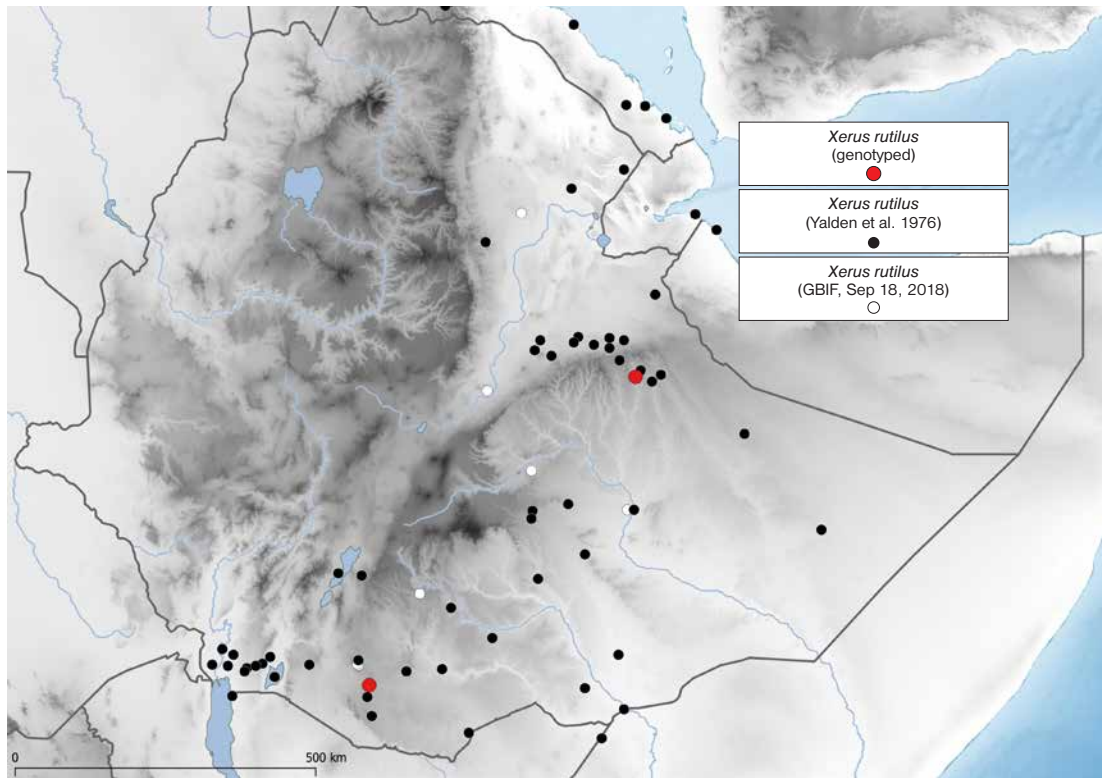


Fig. 95. Distribution of *Xerus rutilus*. This is a typical species of Somali-Masai savanna, distributed from northern Tanzania to Ethiopia. In the southern part of the Ethiopian Rift Valley it overlaps with *E. erythropus*.

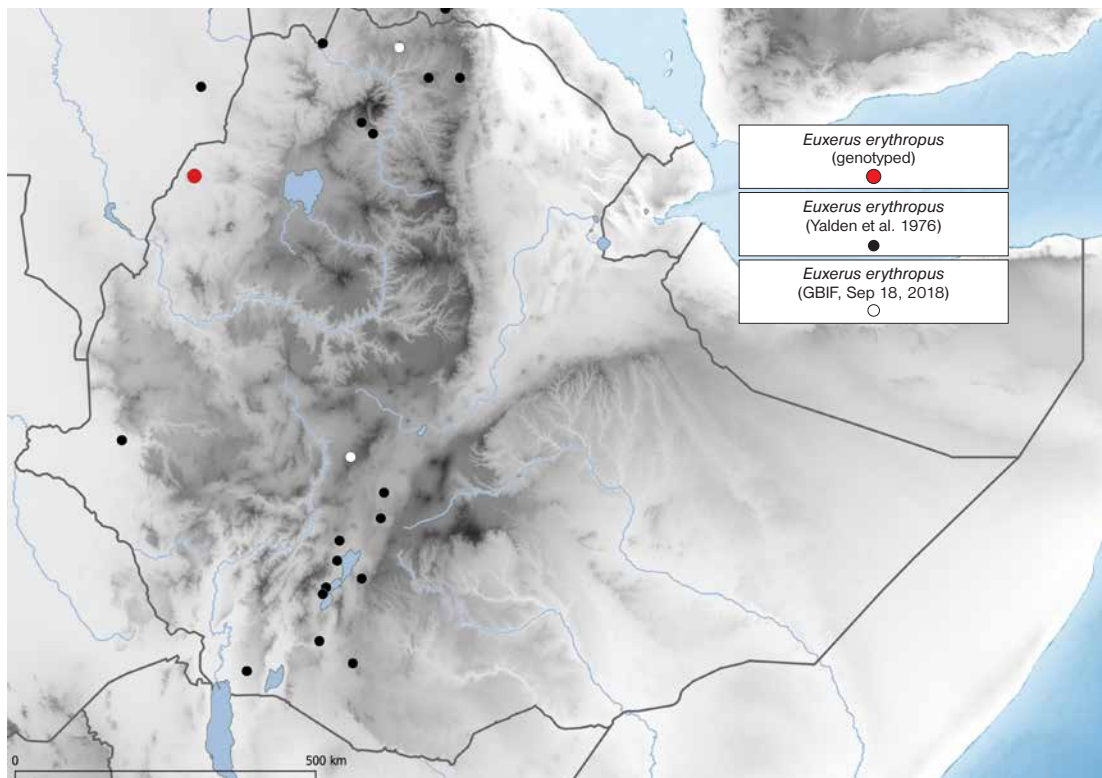


Fig. 96. Distribution of *Euxerus erythropus*. The species is widespread in Sudanian savanna from Senegal to western Kenya. The easternmost record from the Dire Dawa region (Yalden et al. 1976) is not shown as we consider it more likely to be misidentified *X. rutilus*.

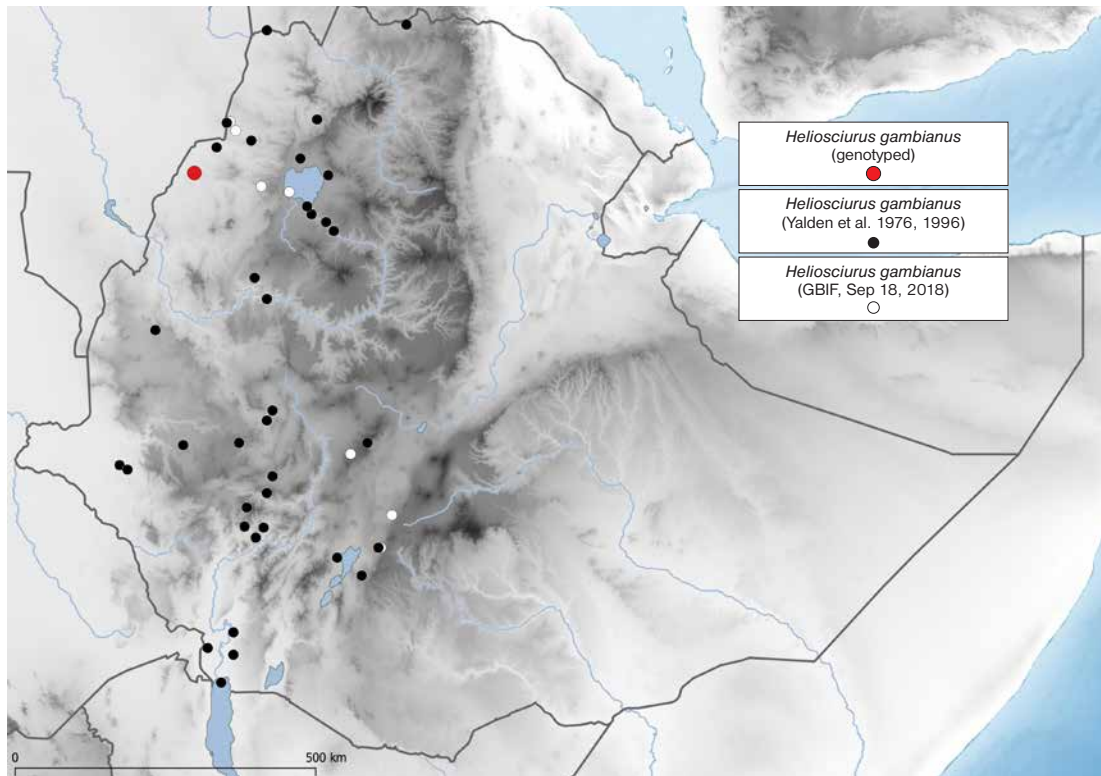


Fig. 97. Distribution of *Heliosciurus gambianus*. The species is widespread in woodlands and forests in the western part of the country.

are still not fully resolved. A molecular phylogeny of the genus is urgently required (Monadjem et al. 2015).

Heliosciurus gambianus (Ogilby, 1835)

This species exhibits significant geographical variation in pelage characteristics and at least four subspecies are currently recognised (Happold 2013), at least some of which may be shown to be valid species. It is widely distributed in the moister savannas of tropical Africa from Senegal through Ethiopia and eastern Africa to Angola, avoiding rainforest and arid regions (Monadjem et al. 2015). In Ethiopia it is confined to the western half of the country and extends to about 2000 m a.s.l. It seems tolerant of conditions ranging from true tropical forest to arid scrub (Yalden et al. 1976).

Genus *Paraxerus* Forsyth Major, 1893

The genus has a wide distribution across Sub-Saharan Africa, mostly confined to tropical latitudes. It occurs from Sierra Leone and Guinea in the west to Ethiopia and Somalia in the east, and south to Namibia, Botswana and South Africa. The centre of diversity for this genus is in East Africa. They occur in a variety of different wooded habitats such as

rainforest, coastal and riparian forest, montane forest, and dry savanna and woodland. The forest species are typically arboreal, but the savanna species regularly descend to the ground to move between trees as well as for foraging (Monadjem et al. 2015). One species has its distributional limit in southern Ethiopia.

Paraxerus ochraceus (Huet, 1880)

This species is widely distributed in East African savanna from southernmost Tanzania to southern Ethiopia, where it reaches the extreme northern limit of its distribution. The last published record of this species in Ethiopia is by De Beaux (1922), almost 100 years ago, but the lack of contemporary records is probably caused by the absence of recent surveys in the Somali region.

Family Gliridae (dormice)

Dormice are small- to medium sized nocturnal rodents, with large eyes and moderately long tails, often scantily haired. They all live in the Old World.

Subfamily Graphiurinae (African dormice)

This subfamily with the only genus *Graphiurus* contains more than half of all known species of dormice in the world.

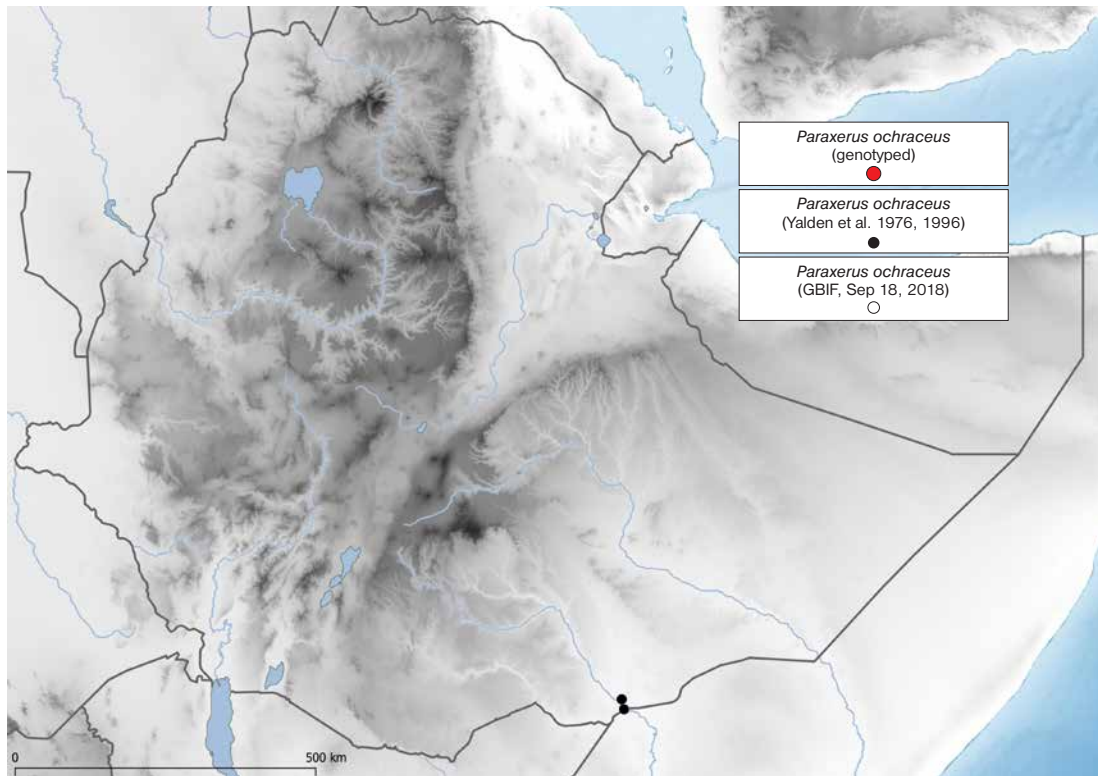


Fig. 98. Distribution of *Paraxerus ochraceus*. The species may be more widespread in south-eastern Ethiopia, but there is significant lack of data from the Somali region.

Genus *Graphiurus* Smuts, 1832

This is the only genus of dormice in sub-Saharan Africa, where up to 16 species were described on the basis of morphological traits. Integrative taxonomic revision employing genetic data is missing, but urgently required. Based on morphological analyses of skulls and middle ear, three subgenera were proposed (see review in Holden-Musser et al. 2016). Two species from the subgenus *Graphiurus*, *G. murinus* (Desmarest, 1822) and *G. parvus* (True, 1893) were reported from Ethiopia (Yalden et al. 1996), supposedly differing in body size. Our preliminary genetic data showed the presence of three highly differentiated clades in Ethiopia, but they are completely overlapping in all external measurements and new distinguishing traits must be defined. Awaiting taxonomic revision, including comparison with the type material, we call these clades as *G. sp. "A"*, *G. sp. "B"*, and *G. sp. "C"*. The three species also seem to differ in the preferred habitat type.

Graphiurus sp. "A"

Preliminary genetic data (Bendová et al., in lit.) show that two Ethiopian species belong to a large clade of *Graphiurus* with several very distinct species, distributed

mainly in western Africa and Ethiopia. One of its subclades consists of three lineages that differ geographically and ecologically and we consider them as separate species. Lineage 1 (= *G. sp. "A"*) from the Sudanian savanna in Alatish NP and Dhati-Welel NP in Ethiopia is sister to two remaining lineages, i.e. Lineage 2 (= *G. sp. "B"*) from the Ethiopian Highlands on both sides of the Rift Valley) and Lineage 3 (southern Niger, called *G. kelleni* by Fabre et al. 2013). It seems likely that *G. sp. "A"* will be more widely distributed in understudied eastern part of Sudanian savanna, but for now we can only confirm its presence at two localities in Ethiopia.

Graphiurus sp. "B"

This taxon, endemic to Ethiopia, seems widespread across the Ethiopian Highlands on both sides of the Rift Valley up to ca. 3200 m a.s.l. In the southern part of its distribution it occurs at the lowest elevation of 1945 m a.s.l. (Bulcha forest). Preliminary mitochondrial phylogeny indicated that *G. cf. kelleni* from southern Niger is its sister taxon (Bendová et al., in lit.). Part of the material summarized by Yalden et al. (1976, 1996) very probably belongs to this species, especially from the localities in the Ethiopian Highlands and potentially also some from the Rift Valley.

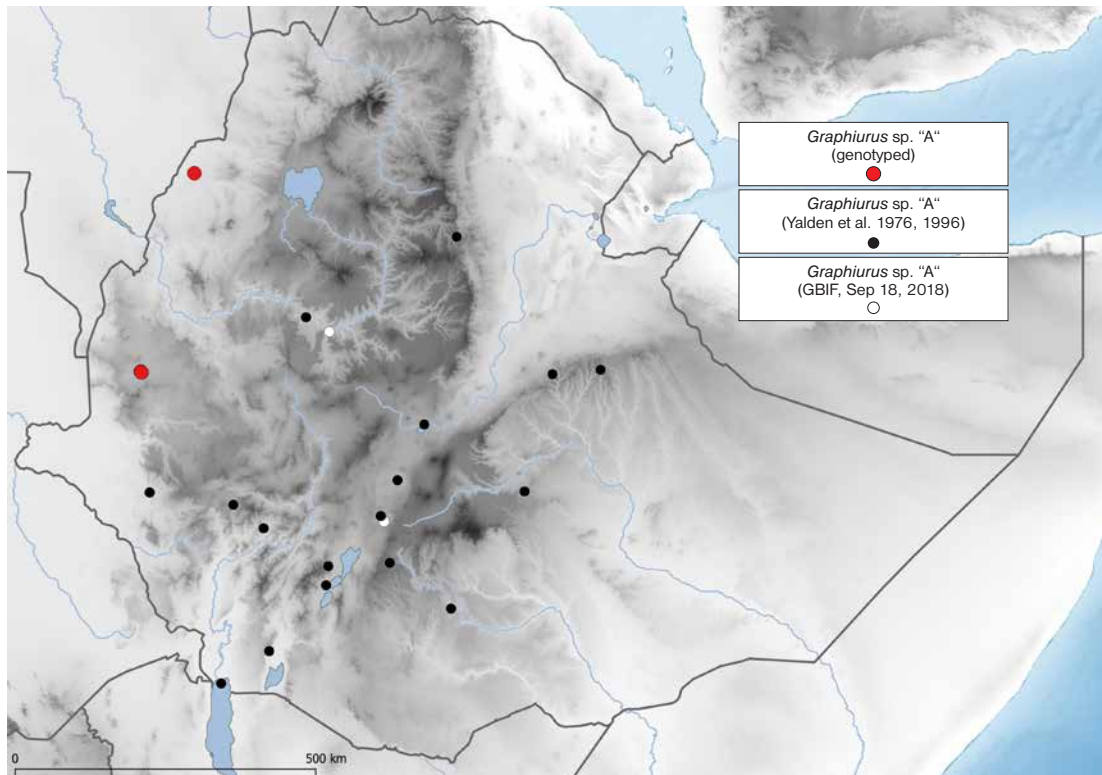


Fig. 99. Distribution of *Graphiurus* sp. "A". This species lives in Sudanian savanna. Most of localities reported by Yalden et al. (1976, 1996) and GBIF likely belong to other species (see below). Taxonomic revision of the genus is urgently required.

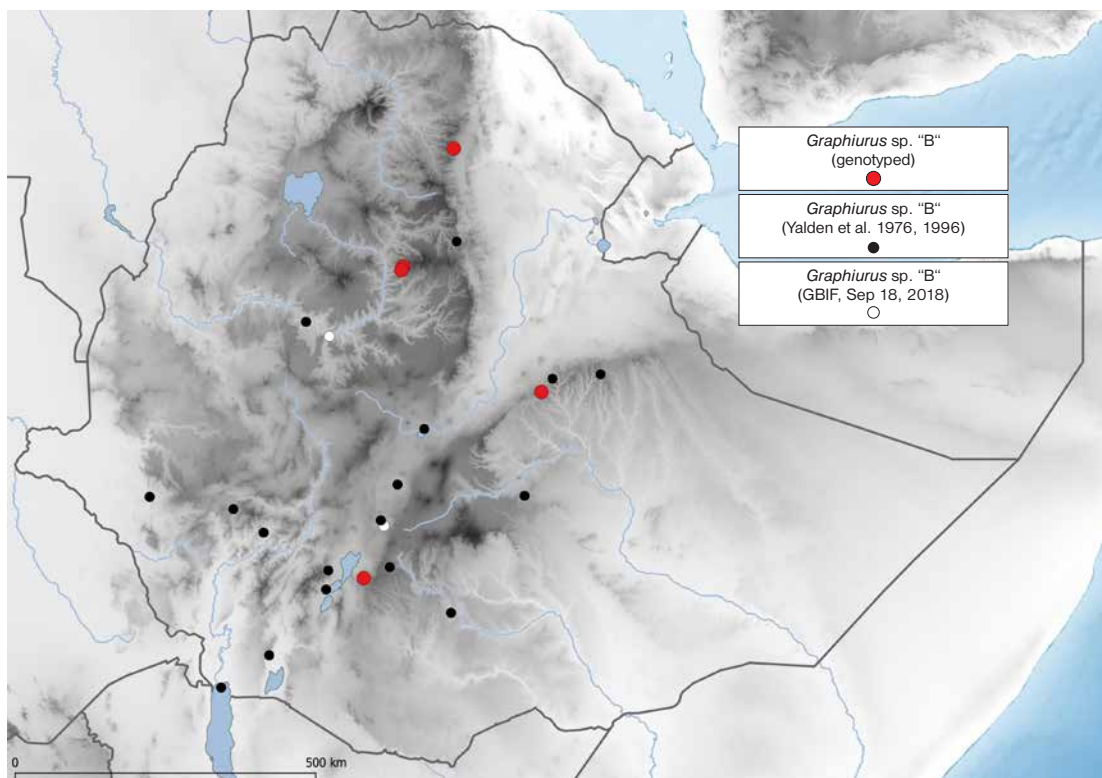


Fig. 100. Distribution of *Graphiurus* sp. "B". Part of localities reported by Yalden et al. (1976, 1996) and GBIF probably belong to this taxon, especially those at higher elevations of the Ethiopian Highlands and central Rift Valley (while those from south-eastern Ethiopia are more likely *G.* sp. "C").

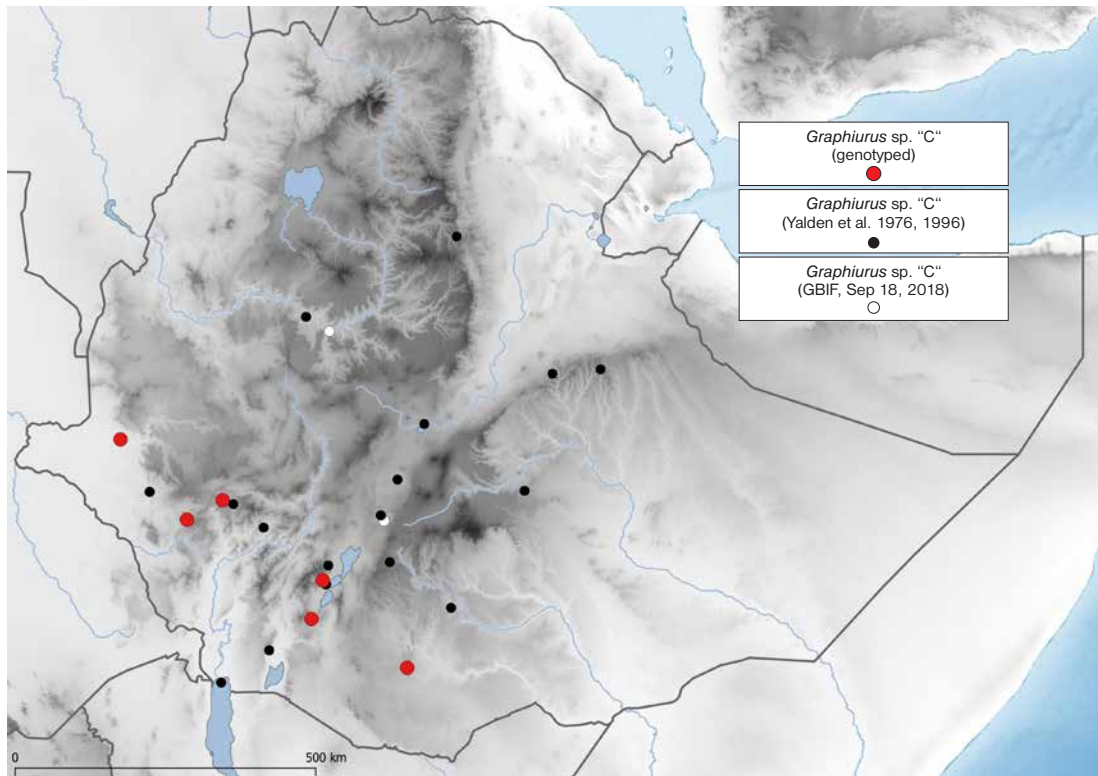


Fig. 101. Distribution of *Graphiurus* sp. “C”. This species is a typical inhabitant of forest-savanna mosaic in southern Ethiopia and genetically identical populations are also known from the Kenyan Highlands. Some records reported by Yalden et al. (1976, 1996) from southern Ethiopia probably represent this taxon.

Graphiurus sp. “C”

The second major clade of dormice living in Ethiopia is called here *G.* sp. “C”. It was found only in the forests and woodlands of south-western Ethiopia. Genetically very similar populations are widely distributed across the highlands of eastern Africa, through the Kenyan Highlands and Eastern Arc Mountains to southern Tanzania (Bendová et al., in lit.). Integrative taxonomic revision is required, but Ethiopian material is surely conspecific at least with populations from the northern Kenyan Highlands along the Rift Valley, e.g. Nassalot, Marsabit and Maralal. Part of the material summarized by Yalden et al. (1976, 1996) very probably belongs to this taxon, especially that from localities in south-western Ethiopia.

Family Dipodidae (jerboas)

This family is widely distributed in the arid regions of northern Africa and especially in central Asia, where its diversity is high. Many taxa have specific adaptations to live in extremely dry and hot environments.

Genus *Jaculus* Erxleben, 1777

The only African genus of the family widely distributed in the Saharo-Sahelian region.

Jaculus hirtipes (Lichtenstein, 1823)

This species can only be differentiated from *J. jaculus* (Linnaeus, 1758) on molecular grounds; morphologically and karyotypically the two species are indistinguishable (Ben Faleh et al. 2010, 2012, Boratyński et al. 2012, 2014). Here we follow Michaux & Shenbrot (2017) and assign the Ethiopian material to *J. hirtipes*, which was synonymized with *J. deserti* (Loche, 1867). However, see opposite opinion in Monadjem et al. (2015), who considered the taxon from eastern Africa belonging to *J. jaculus*. Genetic analysis of new material from arid regions in Ethiopia (especially the Afar region) is required to resolve the taxonomy of Ethiopian jerboas. The only Ethiopian locality reported by Yalden et al. (1976) is located between Zeila and Jildessa, based on Neumann (1902). The species may be more widespread in the Afar region, but there are no recent data.

Family Spalacidae (muroid mole rats)

This family represents an old lineage of muroid rodents. It includes small to medium sized rodents with different adaptations to subterranean life. Species performing regular above ground activity have ear pinnae, remarkable tails and eyes, whereas others belong to the most fossorial mammals with

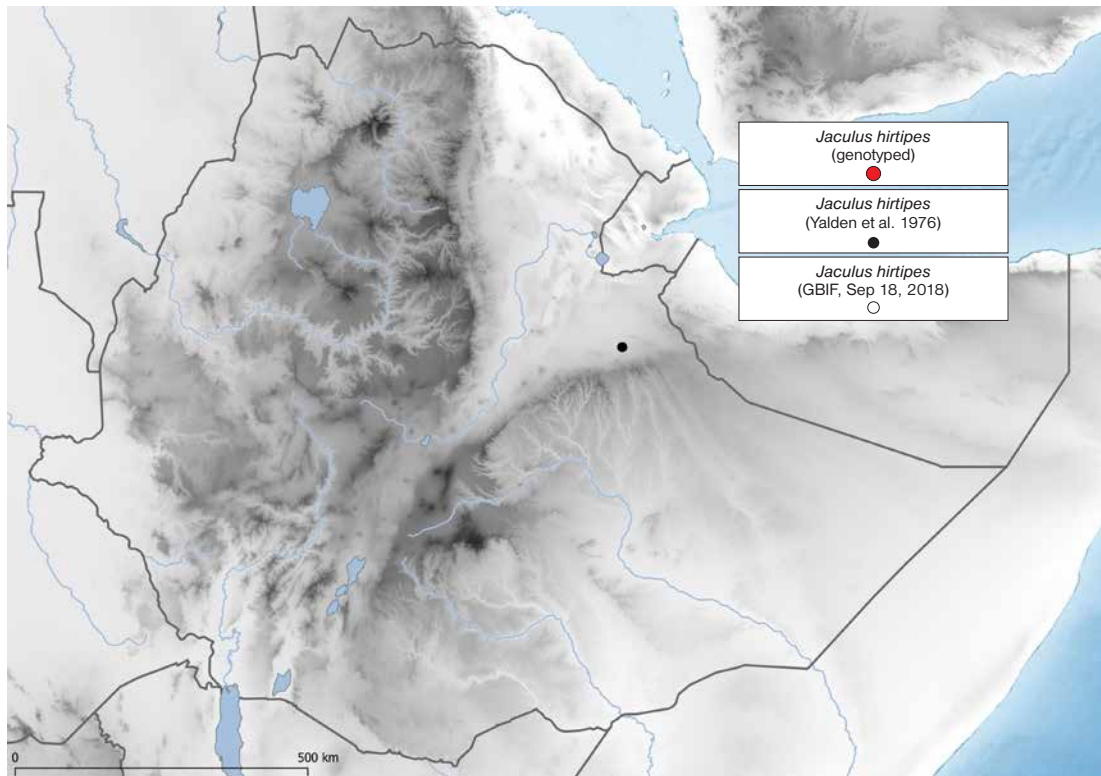


Fig. 102. Distribution of *Jaculus hirtipes*. All other localities summarized by Yalden et al. (1976) are from coastal Eritrea.

reduced body extremities and eyes covered by skin. The family has an Asian origin with at least two immigrations into Africa (*Spalax* and *Tachyoryctes*). In Africa, *Spalax* lives in the eastern Mediterranean coastal region in North Africa, whereas the root-rats (*Tachyoryctes*) occur at higher altitudes usually above 1200 m a.s.l. in north-eastern parts of the continent.

Subfamily Rhizomyinae

Tribe Tachyoryctini

Genus *Tachyoryctes* Rüppel, 1835

This genus is the only representative of the tribe Tachyoryctini and includes only African species. The oldest *Tachyoryctes* in Africa is known from middle Pliocene from Ethiopia (Sabatier 1978). The genus is distributed in Ethiopia, Somalia, Kenya, Tanzania, Uganda, East DR Congo, Burundi and Rwanda in areas of higher rainfall usually above 500 mm per year. The northern part of its distribution (mainly Ethiopia) is separated from the southern part by a wide belt of dry lowland in northern Kenya. Root rats are not strictly subterranean as indicated by visible eyes, pinnae and relatively long tails. There are two morphological forms – one has a large body and regular surface activity (*Tachyoryctes macrocephalus*), while the other is smaller and more fossorial (the complex of *Tachyoryctes*

splendens; see below). These two forms were recognised as only two root-rat species (Beolchini & Corti 2004, Kingdon et al. 2013, Wilson et al. 2017), but some authors split *T. splendens* into more than 10 species (Ellerman 1941, Musser & Carleton 2005, Monadjem et al. 2015). Recently, Lavrenchenko et al. (2014) found high mitochondrial diversity in *T. splendens* in Ethiopia. Later, Šumbera et al. (2018) extended the geographic sampling and number of genetic markers from the preceding study. By using two mitochondrial and three nuclear genes, the authors found six lineages (putative species) of *Tachyoryctes* across the genus distribution; all but one of them occurring in Ethiopia. The most recent common ancestor of extant *Tachyoryctes* occurred in 2.1 Mya (95 % highest posterior density = 1.4-2.9 Mya) and their diversification was very likely related to the Pleistocene climate oscillations. Verification of the number of root-rat species requires detailed integrative taxonomy.

Tachyoryctes splendens (Rüppel, 1835)

Recent multilocus phylogenetic analysis identified five gene pools within *T. splendens* sensu lato, possibly representing separate species, four of them endemic to Ethiopia (Šumbera et al. 2018). Below we provide more details on the four Ethiopian lineages with this phenotype, but the integrative taxonomic revision and their formal description are still needed. All of them are

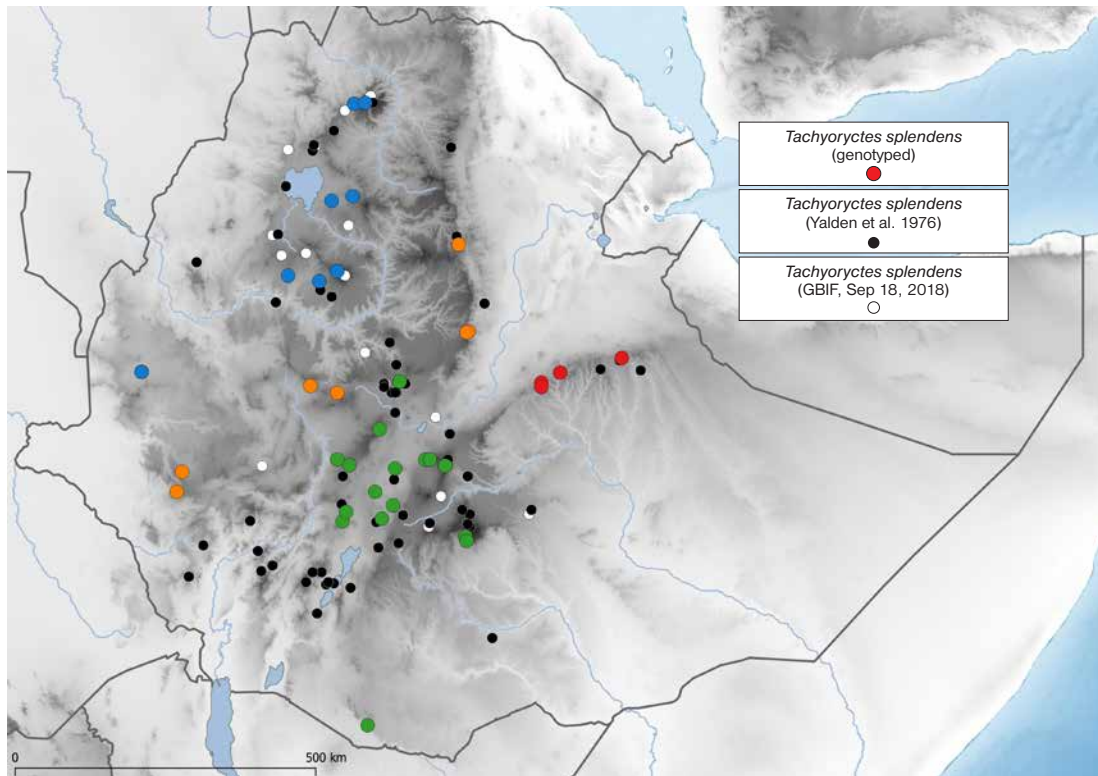


Fig. 103. Distribution of *Tachyoryctes splendens* sensu lato. Four putative species (sensu Šumbera et al. 2018) are denoted by different colours: *T. splendens* species 1 (red = *T. somalicus*), *T. splendens* species 2 (blue = *T. splendens* s. str.), *T. splendens* species 3 (yellow) and *T. splendens* species 4 (green). The southernmost record was recently genetically confirmed from the Gamadu area of the Megadu block of the Borena NP (L. Lavrenchenko, unpublished data).

robust rodents with short limbs weighting usually up to 330 g (Wilson et al. 2017). They are variable in colour from light ginger, cinnamon brown up to black. They live in well-drained soils in open habitats at elevation from 1200 to 4000 m.

Tachyoryctes splendens species 1 (sensu Šumbera et al. 2018)

This taxon lives in the easternmost part of the Ethiopian Highlands in the Chercher Mountains and root-rats from northern Somalia are probably conspecific. This eastern *Tachyoryctes* has already been described as subspecies *T. s. somalicus* (Rahm, 1980), so it could bear the name *T. somalicus*, if its separate species status could be confirmed.

Tachyoryctes splendens species 2 (sensu Šumbera et al. 2018)

This taxon is distributed in the north-western part of the Ethiopian Highlands mainly north of the River Blue Nile. It has four subclades with allopatric distribution (Šumbera et al. 2018). The type locality of *T. splendens* is in the area of this taxon, so it should bear the name *T. splendens* (sensu stricto). Members

of this species may be very large, because some individuals captured on Mt. Choqa weighted more than 500 g (our own unpublished data). Interestingly, root-rats from Mt. Choqa were documented to feed in a similar way to *T. macrocephalus*, i.e. foraging on the surface while having their hind legs still in the burrow (L. Lavrenchenko, unpublished data). There are two distinct karyotypes $2n = 48$, $FN = 58$; $2n = 50$, $FN = 58$ (Lavrenchenko et al. 2014).

Tachyoryctes splendens species 3 (sensu Šumbera et al. 2018)

This taxon is distributed in the north-western Ethiopian Highlands, south and east of the River Blue Nile. Root-rats in Debre Sina have karyotype $2n = 48$, $FN = 58$ (Lavrenchenko et al. 2014).

Tachyoryctes splendens species 4 (sensu Šumbera et al. 2018)

This taxon lives on both sides of the Rift Valley and its bottom in southern Ethiopia. It has five mitochondrial subclades; two of which live on the slopes of the Bale Mountains. It thus occurs in the same mountain block as *T. macrocephalus*, but usually at lower altitudes.

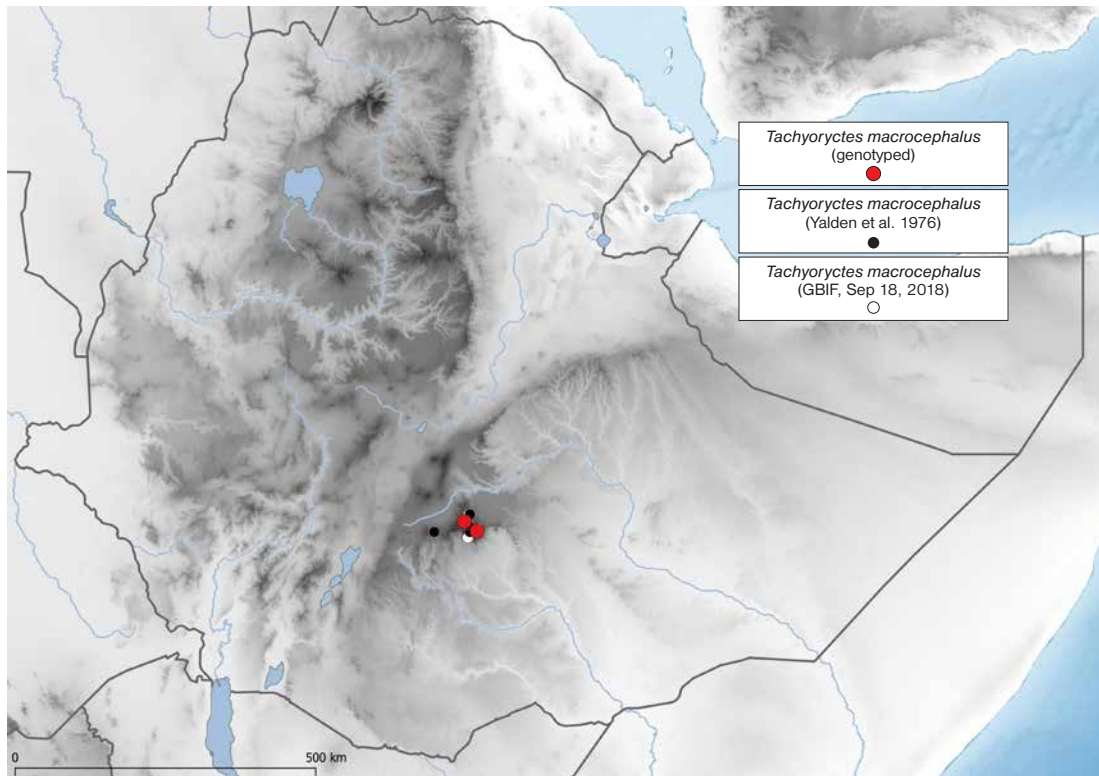


Fig. 104. Distribution of *Tachyoryctes macrocephalus*. The species is currently endemic to the Bale Mts. However, it was described from Wollo or Shoa Provinces north-west of the Rift Valley – either the type locality was incorrect or the species is extinct at Shoa.

Some records are from high elevation, e.g. at 3900 m a.s.l. (Urgana Valley) and even 4150 m a.s.l. from Mt. Batu. However, they originated from owl pellets, which could have been brought up by owls from lower elevations (see Yalden et al. 1996).

Tachyoryctes macrocephalus (Rüppel, 1842)

This species is currently endemic to the Bale Mountains, where it lives at altitudes from 3200 to 4150 m a.s.l. It is one of the most peculiar rodents in the world. It is easily recognised from the *T. splendens* sensu lato group by its large body mass (around 1 kg) and eyes on top of the head due to interorbital constriction, considered as an adaptation to detect predators in open Afroalpine habitats. Although it was described originally in Shoa (Shewa) Province in northern Ethiopia, its presence there was found to be dubious, because no other specimen has been recorded north-west of the Rift Valley since that time (see more details about its description and putative type locality in Yalden 1975 and Yalden & Largen 1992). The diploid number is $2n = 50$, $FN = 66$ (Aniskin et al. 1997). Recent phylogenetic analyses placed *T. macrocephalus* as an internal lineage within *T. splendens* sensu lato (Šumbera et al. 2018). The split from its sister clade (*T. splendens* species 1) was estimated to occur 1.3 Mya.

Family Heterocephalidae (naked mole rats)

This monotypic family of small strictly subterranean rodents with small eyes, absent ear pinnae and wrinkled skin belongs to the suborder Hystricomorpha. The single known species is hairless other than a few sensory hairs scattered across its body and occupies arid to semiarid habitats in the Horn of Africa.

Genus *Heterocephalus* Rüppel, 1842

The genus *Heterocephalus* was for a long time included in the African mole rat family (Bathyergidae). Recently, Patterson & Upham (2014) emancipated it to familial status due to differences in cranial, dental, postcranial, and ecological characteristics as well as its ancient split from the bathyergids dated to the early Oligocene (31.2 Mya). This division, however, is not generally accepted and for example Bryja et al. (2018b) found the split of *Heterocephalus* and bathyergid genera much more recent (23 Mya).

Heterocephalus glaber Rüppel, 1842

The naked mole rat (*H. glaber*) is distributed in Djibouti, eastern and south-eastern Ethiopia, Somalia and northern and eastern Kenya. This is a highly social species living in families of several tens or hundreds of individuals where only a single female breeds. In

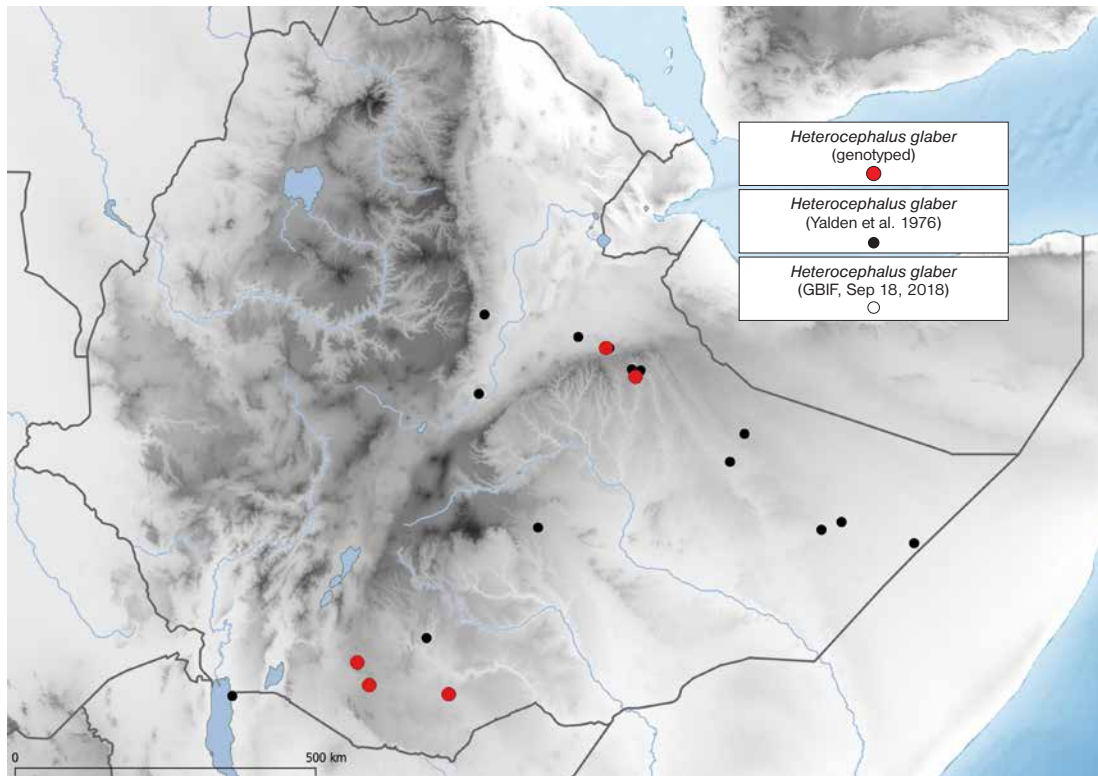


Fig. 105. Distribution of *Heterocephalus glaber*. This is a typical species inhabiting Somali-Masai savanna.

Ethiopia, it occurs in arid lowlands at altitudes of 400-1500 m a.s.l. However it probably avoids the very dry areas of Afar. Because two basal lineages of *H. glaber* were found in Ethiopia, Faulkes et al. (2004) suggested its spread from north to south. The diploid number of animals from Kenya (Mtito Andei) is $2n = 60$, $FN = 120$ (George 1979). Individuals from Somalia (War Mahn and Warshek) have the same number of chromosomes, but differ in fundamental number ($FN = 82$, Capanna & Merani 1980). There are also some morphological and genetic differences between populations from different parts of its distribution. Faulkes et al. (1997) found differences in *cyt b* to be 5.8 % between populations from southern Kenya (Mtito Andei) and southern Ethiopia (Dembalawachu), and Faulkes et al. (2004) found even higher differences 10.3 % and 10.6 % between populations from Dire Dawa (Ethiopia) and Dembalawachu, and Dire Dawa and Mtito Andei, respectively. However, the authors of both studies suggested keeping the monotypic status of the genus. The revision of the genus including more localities in Ethiopia is required.

Family Hystricidae (Old World porcupines)

Porcupines represent a family of large-bodied nocturnal terrestrial rodents belonging to the suborder Hystricomorpha. Long quills cover their bodies and

have an antipredator function. Old World porcupines are distributed in Africa, Asia and Indomalayan regions. In Africa, the family is represented by three species (Wilson et al. 2016).

Genus *Hystrix* Linneaus, 1758

This genus is widely distributed in Africa, the Middle East, India, Southeast Asia and the Indonesian archipelago (Happold et al. 2013). It contains three subgenera (*Thecurus*, *Acantion*, *Hystrix*). Subgenus *Hystrix* is characterised by very long quills on the back, which can be erected to the crest. It occurs in various habitats excluding rainforest. Two species of this subgenus occur in Africa (Wilson et al. 2016).

Hystrix cristata Linneaus, 1758

This species has a wide disjunctive distribution in southern Europe, the Mediterranean region of north Africa and the wide savanna belt from Senegal to Tanzania, with isolated populations in the Sahara. The populations in South Sudan, Ethiopia, Somalia, Djibouti and Eritrea may be isolated from other sub-Saharan populations (Wilson et al. 2016). In Ethiopia, *H. cristata* is widely distributed across the country including even moorlands at 3550 m in the Simien Mountains (Bekele & Yalden 2013). The population in eastern Africa, which has the largest body size,

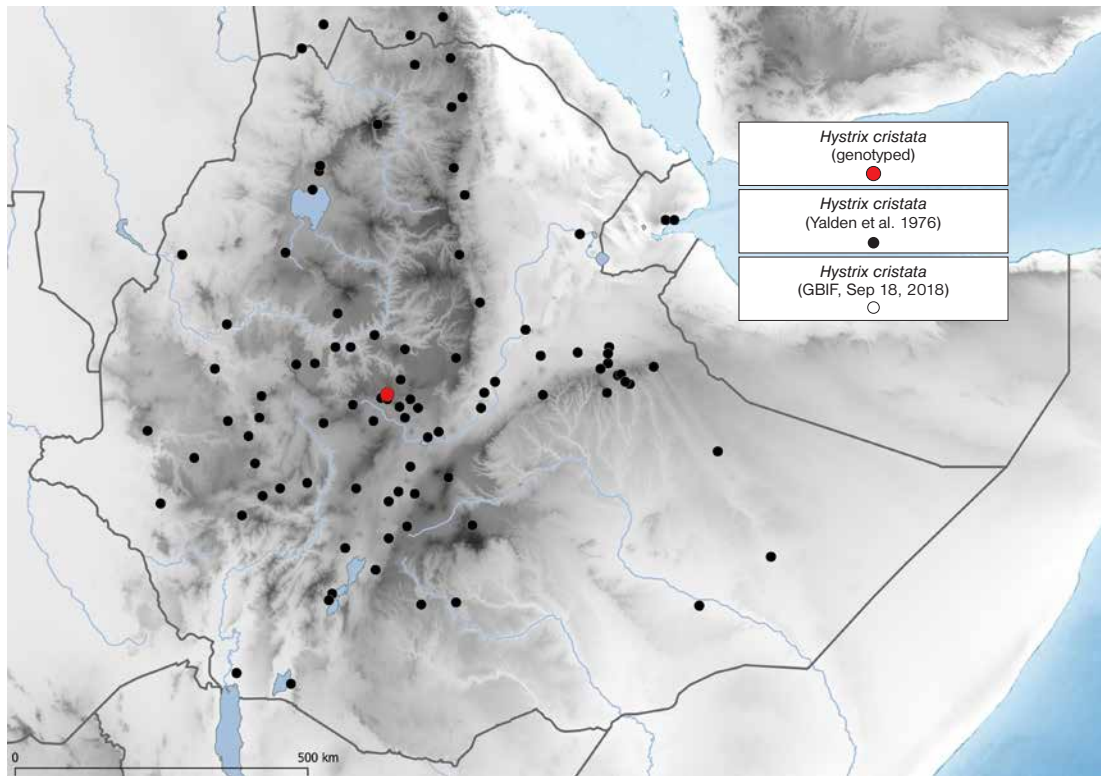


Fig. 106. Distribution of *Hystrix cristata*. The species is widespread across the country, most data coming from questionnaires. Genetic data are from Trucchi et al. (2016).

was known as *H. c. galeata*, but Corbet & Jones (1965) showed that it overlaps in all characters with *H. c. cristata* and the variability is clinal. According to the phylogenomic study of Trucchi et al. (2016), the population in Ethiopia clusters with those in sub-Saharan Africa, not with northern Africa and the Middle East, with the closest relationship with a Tanzanian population (but other east African populations were not sampled).

Family Thryonomyidae (cane rats)

Cane rats are large-sized robust rodents from suborder Hystricomorpha with a relatively short tail, limbs and ears. There are only two extant species in a single genus, but the family underwent a wide expansion during the Miocene and there are numerous extinct taxa. They represent an original African group.

Genus *Thryonomys* Fitzinger, 1867

The two extant cane rat species probably split in the mid Pliocene (Wilson et al. 2017). They are of similar appearance, but differ in body size, inflation of skull, length of tail and position of three grooves on the incisors. Cane rats are nocturnal, strictly herbivorous feeding mainly on grass. They are largely overlapping in geographic distributions in sub-Saharan Africa,

but they inhabit different ecological niches. Whereas *T. swinderianus* prefers semiaquatic habitats as marshes, the more terrestrial *T. gregorianus* occupies moist savanna at higher altitudes (Wilson et al. 2017). Both species avoid the central African forest.

***Thryonomys gregorianus* (Thomas, 1894)**

The lesser cane rat is widely distributed in south-central and eastern Africa, with isolated records from Cameroon (Monadjem et al. 2015). Ethiopian records reported by Yalden et al. (1976) from altitudes of 500-1750 m a.s.l. are assigned to this species. The only genotyped individual (by structural analysis of short retroposon B1; L. Lavrenchenko et al., unpublished data) originates from the Beletta forest. As both known species of the genus significantly overlap in eastern Africa and *T. swinderianus* occurs in Kenya, Uganda and South Sudan, specific status of *Thryonomys* from Ethiopia needs to be confirmed. Based on the distribution maps in Wilson et al. (2016), both species may overlap in southwestern Ethiopia.

Family Ctenodactylidae (gundis)

Gundis are medium sized hystricomorph rodents with short legs, tails, flat ears, large eyes and long whiskers.

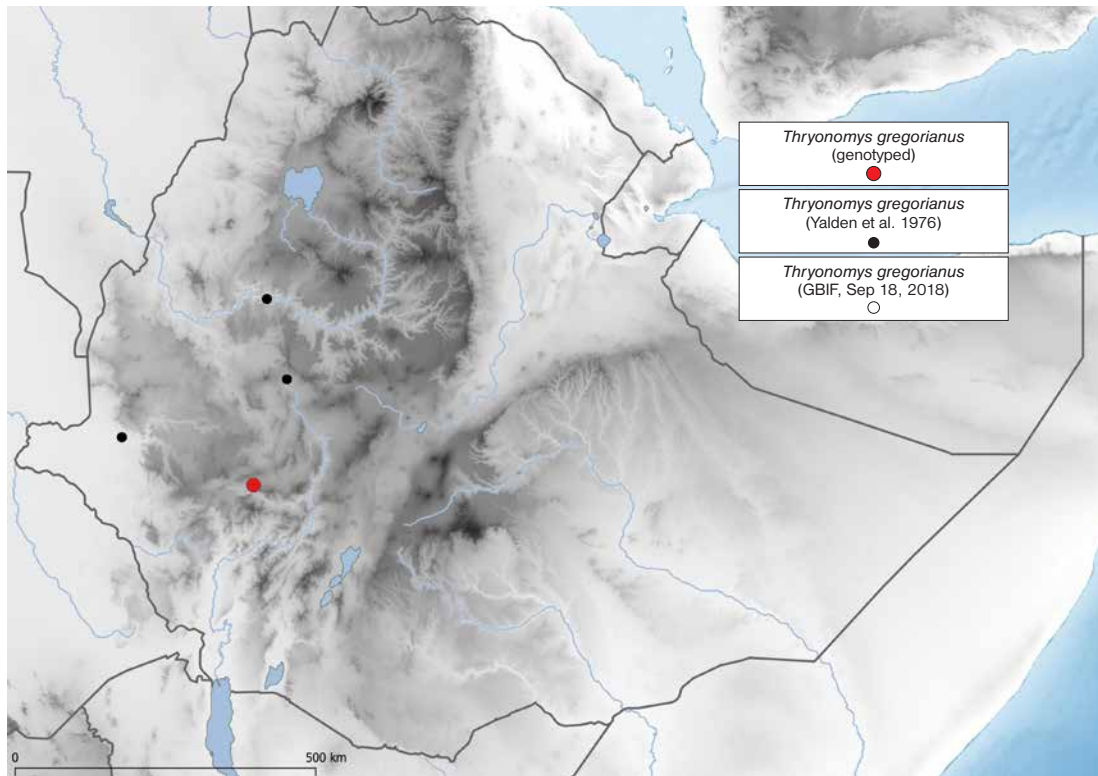


Fig. 107. Distribution of *Thryonomys gregorianus*. The species is likely to be confined in the western part of the country.

There are four extant genera of gundis and all species live in deserts and semi-deserts in north Africa and the Horn of Africa. The current distribution of the family is limited to Africa (Wilson et al. 2016).

Genus *Pectinator* Blyth, 1856

This monotypic genus is endemic to the Horn of Africa and geographically isolated from other genera. Compared to other species, the ears are only partially flattened on top of its head. It conserves numerous archaic dental characteristics of the first ctenodactylids including deciduous premolars (Wilson et al. 2016) and represents the first split within extant species (López-Antoñanzas & Knoll 2011).

Pectinator spekei Blyth, 1856

This is the only species of gundis in Ethiopia. It inhabits rocky (especially limestone) cliffs in desert and semi-desert regions and often occurs with hyraxes. All records reported by Yalden et al. (1976) lie at altitudes between sea level and 1200 m a.s.l. with the exception of that from Sheikh Mahomet, which is considered rather doubtful and is not shown on the map. The species is probably relatively common in Afar and Somali regions, but there is a general lack of data from these arid parts of Ethiopia.

Discussion

Checklist of Ethiopian rodents

In the present study, we provide distributional data for 104 species (40 genera from 10 families) of Ethiopian rodents. This diversity is very high reflecting primarily the diversity of ecosystems in Ethiopia. Based on the recently published checklists in other African countries, the number of species is comparable with Kenya (106 rodent species; Musila et al. 2019), which is another east African country with very diverse geomorphology and natural ecosystems, ranging from deserts to montane tropical forests. Even though it is difficult to compare these studies, especially due to different approaches to species delimitations, the diversity in other African countries of comparable area seems to be much lower: 82 species in Angola (Taylor et al. 2018), 51 species in Mozambique (Neves et al. 2018), or 74 species in the Republic of South Africa, including Swaziland and Lesotho (Child et al. 2016).

Compared to the last checklist of Ethiopian rodents (Yalden et al. 1996), the number of species has significantly increased (Table 1). This is caused primarily by the use of integrative taxonomy, allowing the delimitation of species based on the combined analysis of morphological, genetic and

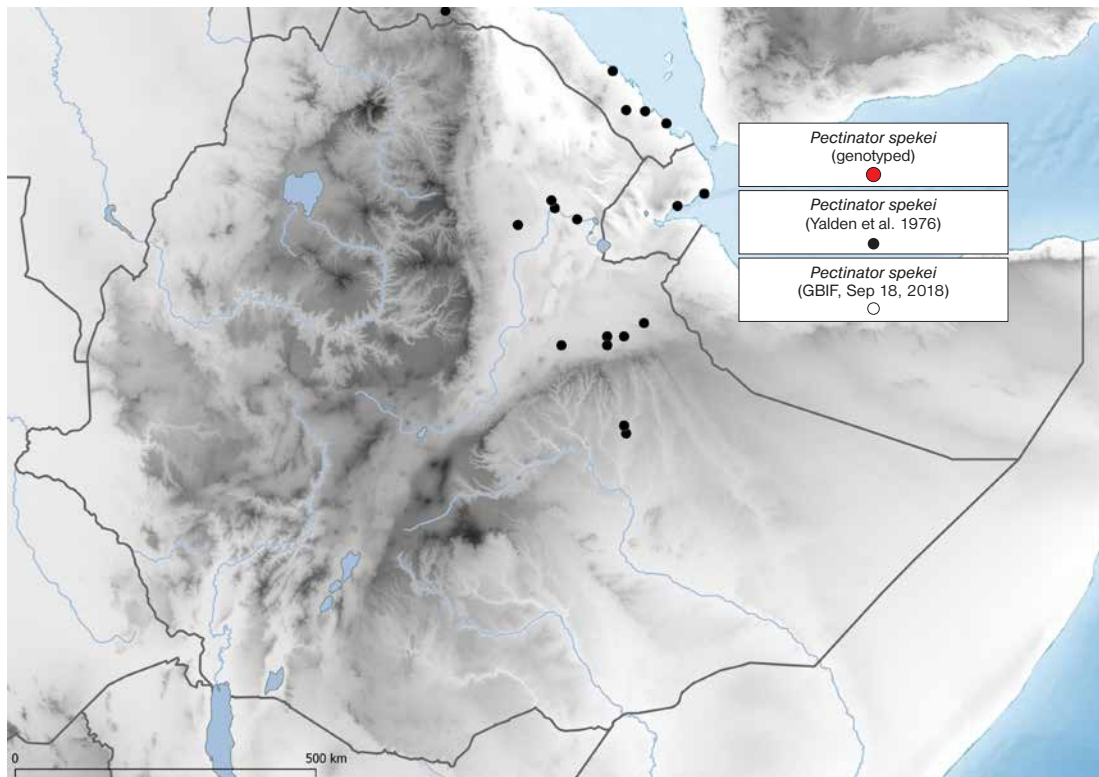


Fig. 108. Distribution of *Pectinator spekei*. The species might be more widespread in the Somali region, but there is currently a lack of data.

ecological traits. Even though we are not proponents of unnecessary splitting of species, recent research has clearly showed important genetic and ecological differences e.g. between individual species in genera *Lophuromys* (Lavrenchenko et al. 2007), *Mus* (Bryja et al. 2014), *Stenocephalemys* (Bryja et al. 2018a), *Arvicanthis* (Bryja et al. 2019) or *Otomys* (Taylor et al. 2011), leading to us to unequivocally accept new species. This significantly increased the number of species, but at the same time it reflects the unique situation in the Ethiopian Highlands, where both geographic barriers and steep elevational gradients in ecological conditions interplay during the process of speciation. We now know that individual taxa (as defined in this study) represent evolutionarily and ecologically distinct units, but formal taxonomic descriptions are still to be done for some genera (e.g. *Acomys*, *Dendromus*, *Graphiurus*, etc.).

On the other hand, we were not able to confirm the presence of 12 species previously listed from Ethiopia (see Table 1), despite intensive field research in the last three decades. Two of these are known only from the holotypes (*Nilopegamys plumbeus* collected in 1927, *Mylomys rex* in 1905) and may now be extinct. Similarly, *Otomys cheesmani*, described by Taylor et al. (2011) based on cranial morphology of museum

vouchers, is known only from the type series and there are no records after 1968. Repeated recent attempts to collect these three species at type localities have failed (see individual species accounts for more details) and their assumed natural habitats are now greatly destroyed. Other poorly known species are probably still extant members of the Ethiopian fauna, but either there is a lack of recent research activity in their natural habitats (e.g. genera *Amodillus*, *Gerbillus*, *Microdillus*, *Paraxerus*, and *Jaculus*, occurring in deserts and semi-deserts of the Afar and Somali regions), and/or they are difficult to capture using routinely employed trapping methods for small mammal research (*Steatomys*, *Thallomys*); hence we have little recent data on these species.

The presented checklist is not definitive and future work will very likely increase the number of Ethiopian species of rodents. We see at least two major domains where taxonomic research will be useful. First, more intensive sampling in arid lowland habitats may reveal the occurrence of species reported from neighbouring countries, e.g. Somalia, Djibouti, Sudan or South Sudan. Second, integrative taxonomic revision of widespread genera may lead to delimitation of new species. We indicated this approach e.g. for *Tachyoryctes splendens* (see that account), but for the

purpose of our biogeographic summary (see Results) we have retained it as a single species. Taxonomic revision at the pan-African scale can be very useful also for some other genera, especially for those where genetic data are almost completely missing (e.g. *Uranomys*, *Oenomys*, *Thallomys*, *Steatomys*).

Evolutionary history of Ethiopian rodents

The recent boom of phylogeographical studies of African rodents allows us to better understand the evolutionary history of taxa living in particular ecosystems. The diversification/speciation processes in Ethiopian rodents were mostly affected by the interplay of complex geomorphology and climatic changes in Plio-Pleistocene. Relatively detailed information is now available for murids (family Muridae), the most diversified group of African rodents. While three murid subfamilies (Deomyinae, Gerbillinae, Lophomyinae) are of African origin, the most speciose subfamily Murinae started to diversify in south-eastern Asia and colonized Africa in several independent waves at the end of the Miocene, probably through the Afro-Arabian land bridge (Aghová et al. 2018). The Ethiopian mountains were thus one of the first biogeographic barriers that these colonizers encountered. Several old murine genetic lineages support this view. For example two genera (*Desmomys* and *Stenocephalemys*) currently live only in the Ethiopian Highlands, and the first split in African *Mus* also happened there (Bryja et al. 2014, Meheretu et al. 2015). The Ethiopian Highlands are also the cradle for multiple taxa outside the Murinae, e.g. the so-called *Lophuromys flavopunctatus* group from subfamily Deomyinae (Lavrenchenko et al. 2007), nesomyid genus *Dendromus* (Lavrenchenko et al. 2017, Voelker et al., in lit.), and root-rats of the genus *Tachyoryctes* (Šumbera et al. 2018). While genera *Desmomys* and *Stenocephalemys* diversified only in Ethiopia (e.g. Bryja et al. 2018a), the remaining groups were able to disperse from their Ethiopian cradle and colonize other mountains south of the Ethiopian Highlands (see e.g. Šumbera et al. 2018 and Krásová et al. 2019 for more details).

The process of speciation in the Ethiopian Highlands is also interesting from a general evolutionary point of view. Even though most diversification events can be explained by a classical allopatric model, there are indications of ecological speciation at elevational gradient (Bryja et al. 2018a) and so-called reticulate evolution (Lavrenchenko et al. 2004). The latter process combines allopatric diversification with hybridization and was caused especially by Pleistocene climatic changes, when elevational shifts

in the distribution of major ecosystem types allowed the contact of previously fragmented and differentiated populations, not yet completely reproductively isolated. As a consequence, we observe frequent cases of partial (e.g. mitochondrial) introgression and simple DNA barcoding is not sufficient for reliable species identification in such cases (e.g. Lavrenchenko et al. 2004, Bryja et al. 2018a, 2019, Komarova et al., in lit.). The data on the evolution of taxa living in open savanna-like habitats are relatively rich, but general patterns are only beginning to emerge. For example, the comparison of phylogeographic histories of species living in the Sudanian savanna belt revealed that the first intraspecific splits occurred in eastern Africa (e.g. *Mastomys erythroleucus* – Brouat et al. 2009, *Arvicanthis niloticus* complex – Dobigny et al. 2013, Bryja et al. 2019, *Gerbilliscus giffardi* – our unpublished data). The region with the highest and most pronounced evolutionary diversity of taxa living in the Sudanian savanna thus lies in eastern Africa (including western Ethiopia), while populations in western Africa represent relatively recent and genetically less variable colonizers. On the contrary, it is not possible to unequivocally identify the centres of evolutionary diversity in the Somalian region (sensu Linder et al. 2012). The currently observed phylogeographic structure of Somali-Masai savanna specialists seems to be the result of allopatric diversification, where the Rift Valley lakes and mountain ranges created major barriers to gene flow in humid Plio-Pleistocene periods, while hyper-arid regions (e.g. the so-called Turkana belt) separated populations of savanna-dwellers during dry periods (Aghová et al. 2017, 2019, Bryja et al. 2019).

Ethiopian endemism and threats to a unique biodiversity

Ethiopia is recognised as one of the most important centres of endemism on Earth. In a synthesis paper by Lavrenchenko & Bekele (2017), 55 mammalian species (17.7 % of the total) are at present considered to be endemic to Ethiopia. Among them are 36 rodents, ten shrews, three bats, two primates, two artiodactyls, one carnivore and one hare. In our annotated checklist we report 44 species living only in the Ethiopian Highlands and virtually all of them can be considered endemic to the country (albeit some of them may be shown to occur in the Eritrean Highlands or even in Somaliland). In fact only five species of rodents living in the Ethiopian Highlands have been recorded outside Ethiopia, and genetic data are only available for three of them, confirming the mitochondrial similarity of Ethiopian populations with those from other east African mountain

ranges (i.e. *Grammomys minnae*, *Grammomys* sp. “m4”, and *Graphiurus* sp. “C”). These data thus suggest extremely high levels of endemism from 41 % (if we consider all rodent species in Ethiopia) to 90 % (if we consider only Afroalpine taxa).

Yet, this unique Ethiopian diversity is highly endangered. The human population in Ethiopia is increasing rapidly (almost doubling in the last 20 years from ca. 60 to 110 million), and there has also been intensive immigration from neighbouring countries affected by various conflicts (e.g. Somalia, South Sudan, Eritrea). This situation has created additional demands on natural resources, as a result of which large areas of pristine habitats are being irreversibly lost. Furthermore, ongoing climate change will have a significant negative effect on mountain species, especially those from the Afroalpine zone which, from an evolutionary perspective, represent the most valuable part of the Ethiopian biota. Numerous species have restricted distributions, relying on specific habitats. This is most obvious for Afroalpine and humid Afroalpine forest specialists. In the current interglacial, the Afroalpine specialists live in fragmented populations in the highest elevations of the Ethiopian Highlands. Some of them are known only from a single mountain range, e.g. *Tachyoryctes macrocephalus* in the Bale Mts. Despite the fact that the value of these unique habitats has been recognized and they are often protected as natural parks (e.g. in the Bale or Semien Mts.), they are still endangered by increased rates of (over-)grazing, agriculture, poaching, and climate change. The situation is even more critical for moist Afroalpine forests, which support a high number of unique species with highly restricted distributions (e.g. *Stenocephalemys ruppi*, *Lophuromys pseudosikapusi*, *Desmomys yaldeni*, or undescribed *Mus* sp. “Harena”). These forest remnants are currently limited to the lower elevations of the Bale Mts. and to fragmented patches in south-western Ethiopia. In contrast to Afroalpine habitats, their protection is minimal and they are rapidly disappearing due to logging and structural changes (e.g. coffee plantations). These two types of ecosystem should

be given priority for nature conservation efforts in Ethiopia, but other types of highland habitats should not be overlooked in the process.

There are several additional species, known currently only from Ethiopia, occurring in lowland open habitats (see e.g. genera *Acomys* or *Arvicanthis*; Aghová et al. 2019, Bryja et al. 2019, respectively). However, we do not consider them endemic to Ethiopia, because they are probably more widespread in neighbouring countries (South Sudan, Somalia, Kenya), where specialist taxonomic research has not yet been performed. In general, research on arid-adapted rodents in the Ethiopian lowlands has been limited, but is worth pursuing, as it may lead to important findings. The Afar region may be especially interesting, because it is effectively separated from other arid regions (e.g. Sahara or Somalia) by mountain ranges. The level to which these barriers has facilitated the evolution of significantly differentiated units (e.g. species) in this region should be investigated in the future.

Acknowledgements

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