

DIVERSITY AND CONSERVATION OF ETHIOPIAN MAMMALS: WHAT HAVE WE LEARNED IN 30 YEARS?

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ABSTRACT: For over thirty years, the Mammal Research Group of Joint Ethio-Russian Biological Expedition (JERBE) studied diversity and evolution of Ethiopian mammals. The goal of the present paper is to review the most interesting results of the study and to summarize the present-day knowledge of the highly endemic mammalian fauna of Ethiopia. The obtained data revealed that the species diversity and the level of endemism of the Ethiopian small mammals could be far higher than was suspected before. One order, one family, four genera and 10 species were detected for the first time. Species rank of seven rodent taxa previously held in taxonomic synonymy was confirmed, all these newly recognized species were re-described. Eleven new endemic species were described *de novo*. In addition, 20 species of small mammals, belonging to 11 genera, were identified as new to science and await formal description. Totally, according to our obviously incomplete list, the Ethiopian mammal fauna consists of 311 species, and 55 of them are at present considered to be endemic to the country. The level of mammalian endemism in Ethiopia is much higher than in other African countries. Many of the endemic small mammals are potentially threatened because of their extremely limited distribution ranges and habitat destruction through agricultural expansion. In view of the fast habitat destruction in the country, taxonomic and evolutionary studies on Ethiopian small mammals are especially important and urgent. There is a high risk that some unknown endemic species will become extinct before they can be described and studied.

Key words/phrases: Conservation, Diversity, Endemism, Mammals, New species.

INTRODUCTION

Human actions are causing a biodiversity crisis, with species extinction rates up to 1000 times higher than what normally used to be (Wilson, 2003). Moreover, the processes of driving extinction are eroding the environmental services on which humanity depends. People care most about what is close to them, so most responses to this crisis will be local or national. The conservation of biodiversity is an urgent priority for every African nation.

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Regions of the world with exceptionally high species richness and evidence of threat are recorded as biodiversity hotspots (including Ethiopia), and extra conservation resources are focused on conservation in those areas. Taxonomy and biodiversity conservation go together. We cannot necessarily expect to conserve organisms that we cannot identify, and our attempts to understand the consequences of environmental changes and degradation are compromised fatally if we cannot recognize and describe the interacting components of natural ecosystems (Mace, 2004). Taxonomy reflects our understanding of evolution and ecology, and therefore is critical to developing sound conservation practices and priorities. Faunal surveys of some selected areas are considered prime importance as the basis for effective conservation and management of animal populations. We are still far from knowing, even approximately, the number of extant mammal species. The rate at which new mammal species are being described is about 10 times the rate at which new bird species are described (Patterson, 2000). Larger organisms were more quickly apparent to systematists. Most species being described today are small-bodied forms. In the case of large mammals (some of which are flagships of the current conservation projects), species identification is not much difficult. But, small mammals (e.g. rodents, shrews and bats) pose numerous unresolved questions concerning their distribution, ecology and species identification. For every newly discovered mammal species to be trapped or captured in the tropical forests and fields, three more are discovered in the drawers of museum collections or on the benches of molecular biology laboratories (Patterson, 2001). There are many cryptic species of small mammals that would likely not be recognized without data from karyotypes, allozymes and DNA-sequences. According to current assessment, the number of unrecognized cryptic species of small mammals is close to a few thousands (Baker and Bradley, 2006; Reeder *et al.*, 2007). This underestimation significantly affects conclusions on the estimates of biodiversity, designs of conservation initiatives and zoonoses.

As small mammals influence ecosystems in many ways, dynamics of their diversity is a good indicator of habitat disturbances caused by anthropogenic loads and global climate changes. *Vice versa*, the later, e.g. global warming that causes substantial temperature rise and drought in East Africa, themselves greatly affect mammalian fauna and threaten diversity. Thus, practical application of fundamental studies of mammalian diversity has two interrelated approaches. First, the studies of Ethiopian mammal fauna and its evolution allow monitoring and prediction of long-term changes in natural habitats. Second, these researches extended with ecological-physiology

studies provide a tool to reveal what species and/or their particular populations may be affected by climatic changes purely due to their specific physiological features (Boyles *et al.*, 2011). In combining both approaches, i.e., forecasting of general long-term habitat changes and projecting onto them ecological-physiology profiles of particular species provide a quantitative scientific background (Parmesan, 2006) for development of wildlife management strategies, which is becoming an important issue in modern Ethiopia.

One of the most serious problems facing developing countries is food security (Gebissa Ejeta, 2010). In Africa, cereals are important staple foods. Although much is produced, large portions are lost through pest destruction or contamination at planting, growth, pre-harvest, and storage. Rodents are known to attack crops at each of these stages. In Ethiopia, it has been estimated that rodents consume or destroy up to 20% of the cereal crop in non-outbreak years (Goodyear, 1976; Afework Bekele and Leirs, 1997). Moreover, several species of rodents show irregular population explosions and damage up to 80–100% during outbreak years (Leirs, 1995). Integrated rodent pest management should include habitat management, measures to decrease fertility of the pest species (reproduction-aimed control, e.g. immunocontraception) and use of repellents and rodenticides (anticoagulants and acute poisons). Important rodent pests in Ethiopia include species of *Mastomys*, *Arvicanthis*, *Lemniscomys* and *Tatera*. Our long-term research demonstrated that each of these rodents represents taxonomically difficult complex of sibling species that would likely not be recognized without molecular and cytogenetic data. Each species is unique in its physiology, behavior, and environmental relationship to other species. Therefore, these cryptic species can significantly differ from each other in their population dynamics and sensitivity to chemical poisons. Thus, information on taxonomic composition of the selected rodent species-complexes, geographical distribution of the relevant cryptic species and their life history parameters can provide a real basis for the elaboration of successful rodent pest management in Ethiopia.

For over thirty years, the Mammal Research Group of JERBE studied diversity and evolution of Ethiopian mammals with the application of modern techniques such as multivariate analysis of cranial morphology, cytogenetic and allozyme analyses, sequencing of mitochondrial and nuclear genes. The aims of these studies were to assess systematic position and species composition of some complex groups and reconstruction of phylogeny of some model organisms in the context of the history of the

main ecosystems in Ethiopia. Besides, a set of faunistic surveys was made to document distributions of Ethiopian mammals. Complete mammalian species lists were compiled for Gambela National Park, Awash National Park, Bale Mountains National Park, Simien Mountains National Park, Arsi Mountains National Park, Alatish National Park, Dharti-Welel National Park, Babilie Elephant Sanctuary and Belleta-Gera Regional Forest. The goal of the presented paper is to review the most interesting results of these studies and to summarize the present-day knowledge of the highly endemic mammalian fauna of Ethiopia.

Species composition, diversity and endemism

The number of mammal taxa recorded for Ethiopia has increased significantly. Order Pholidota, family Manidae, four new genera (*Manis*, *Myonycteris*, *Uranomys*, *Aethomys*) and ten species (*Myonycteris torquata*, *Hipposideros abae*, *Pipistrellus aero*, *Pipistrellus nanulus*, *Neoromicia zuluensis*, *Manis temminckii*, *Aethomys hindei*, *Uranomys ruddi*, *Mastomys erythroleucus* and *Crocidura luna*) were detected for the first time within the boundaries of Ethiopia (Lavrenchenko *et al.*, 1992; Lavrenchenko, 1993; Lavrenchenko *et al.*, 1997; 2004a; 2010; Kruskop *et al.*, 2016). Species rank of seven rodent taxa (*Otomys fortior*, *O. helleri*, *Mus proconodon*, *Lophuromys brunneus*, *L. simensis*, *L. brevicaudus*, *L. chrysopus*) previously held in taxonomic synonymy was confirmed. These newly recognized species had already been described as distinct species (or subspecies) during the Splitter's period in systematics but treated as synonyms later. All these species were re-described (Lavrenchenko *et al.*, 1998b; 2007; Taylor *et al.*, 2011). Eleven new endemic species (*Plecotus balensis*, *Mastomys awashensis*, *Desmomys yaldeni*, *Otomys cheesmani*, *O. simiensis*, *O. yaldeni*, *Lophuromys menageshae*, *L. chercherensis*, *L. pseudosikapusi*, *Crocidura afeworkbekelei* and *C. yaldeni*) were described *de novo* (Lavrenchenko *et al.*, 1998a; Kruskop and Lavrenchenko, 2000; Lavrenchenko, 2003; Lavrenchenko *et al.*, 2007; 2016; Taylor *et al.*, 2011). The results are partly included in the 6-volume book set "Mammals of Africa" published in February 2013 by Bloomsbury Publishing, London (Kingdon *et al.*, 2013). In addition, 20 species of small mammals (belonging to the genera *Crocidura*, *Rhinolophus*, *Neoromicia*, *Miniopterus*, *Gerbilliscus*, *Mus*, *Stenocephalemys*, *Acomys*, *Arvicanthis*, *Dasymys* and *Tachyoryctes*) were identified as new to science and await formal description (Baskevich and Lavrenchenko, 2000; Lavrenchenko, 2000; Lavrenchenko and Verheyen, 2006; Kruskop and Lavrenchenko, 2008; Lavrenchenko *et al.*, 2010; Bryja *et al.*, 2014; Lavrenchenko *et al.*, 2014;

2016). Most of these are cryptic species that can be recognized only with application of such modern techniques as sequencing of mitochondrial genes, chromosomal analysis and multivariate analysis of cranial morphology.

According to our data, the Ethiopian mammal fauna consists of 311 species belonging to 144 genera, 43 families and 14 orders. 55 mammalian species (17.7% of the total) are at present considered to be endemic to Ethiopia. Among them are 36 rodents, 10 shrews, 3 bats, 2 primates, 2 artiodactyls, 1 carnivore and 1 hare (Table 1).

Table 1. Updated list of the endemic mammals of Ethiopia. Habitat: Highland = *Erica* bush and Afro-alpine moorland. Distribution is given for forest, highland and intrazonal species: W = western plateau, E = eastern plateau. Conservation status is assessed by the World Conservation Union (IUCN). The IUCN threat categories (based on version 3.1): CR = Critically Endangered; EN = Endangered; VU = Vulnerable; NT = Near Threatened; LC = Least Concern; DD = Data Deficient; NE = Not Evaluated.

No.	Species	Altitudinal range (m a.s.l.)	Habitat	Distribution	Conservation status
1	<i>Cercopithecus djamdjamensis</i> Neumann, 1902	1900–3000	Forest	E	VU B1ab(iii)
2	<i>Theropithecus gelada</i> (Rüppell, 1835)	2350–4600	Highland	W + E	LC
3	<i>Tachyoryctes macrocephalus</i> (Rüppell, 1842)	3000–4150	Highland	W + E	EN B1ab(iii)
4	<i>Dendromus lovati</i> De Winton, 1899	2500–3550	Highland	W + E	LC
5	<i>Dendromus nikolausi</i> Dieterlen, Rüpp, 1978	3000–3300	Highland	E	DD
6	<i>Lophuromys flavopunctatus</i> Thomas, 1888	2600–3000	Forest	W	LC
7	<i>Lophuromys brunneus</i> Thomas, 1906	2000–2800	Forest	W	NE
8	<i>Lophuromys simensis</i> Osgood, 1936	1800–3800	Forest, Highland	W	LC
9	<i>Lophuromys brevicaudus</i> Osgood, 1936	2400–3750	Highland	W + E	NT
10	<i>Lophuromys chrysopus</i> Osgood, 1936	1200–2760	Forest	W + E	LC
11	<i>Lophuromys melanonyx</i> Petter, 1972	3100–4050	Highland	W + E	VU B1ab(iii)
12	<i>Lophuromys menageshae</i> Lavrenchenko <i>et al.</i> , 2007	2100–2600	Forest	W	DD
13	<i>Lophuromys chercherensis</i> Lavrenchenko <i>et al.</i> , 2007	2000–2700	Forest	E	EN B2ab(iii)
14	<i>Lophuromys pseudosikapusi</i> Lavrenchenko <i>et al.</i> , 2007	1930	Forest	W	EN B1ab(iii)
15	<i>Mus proconodon</i> Rhoads, 1896	1000–1750	Savanna		NE
16	<i>Mus mahomet</i> Rhoads, 1896	1200–3200	Forest	W + E	LC
17	<i>Mus</i> sp.1 (<i>M. cf. triton</i> (Thomas, 1909))	1950–2920	Forest	E	NE
18	<i>Mus imberbis</i> Rüppell, 1842	1900–3400	Highland	W + E	LC

No.	Species	Altitudinal range (m a.s.l.)	Habitat	Distribution	Conservation status
19	<i>Mastomys awashensis</i> Lavrenchenko <i>et al.</i> , 1998	950–1650	Savanna		LC
20	<i>Stenocephalemys albipes</i> (Rüppell, 1842)	820–3800	Forest	W + E	LC
21	<i>Stenocephalemys ruppi</i> (Van der Straeten and Dieterlen, 1983)	2800–3200	Forest, Highland	W	DD
22	<i>Stenocephalemys albocaudata</i> Frick, 1914	3000–4100	Highland	E + W	LC
23	<i>Stenocephalemys griseicauda</i> Petter, 1972	2400–4000	Highland	W + E	LC
24	<i>Stenocephalemys</i> sp.A	3800	Highland	W	NE
25	<i>Nilopegamys plumbeus</i> Osgood, 1928	2600	Intrazonal	W	CR B2ab(iii)
26	<i>Grammomys minnae</i> Hutterer, Dieterlen, 1984	1400–1800	Forest	W + E	VU B2ab(iii)
27	<i>Dasymys griseifrons</i> (Osgood, 1936)	1800–1900	Intrazonal	W	NE
28	<i>Arvicanthis abyssinicus</i> (Rüppell, 1842)	1300–3800	Highland	W + E	LC
29	<i>Arvicanthis blicki</i> Frick, 1914	2750–4100	Highland	E	NT
30	<i>Mylomys rex</i> Thomas, 1906	1800	Forest	W	DD
31	<i>Desmomys harringtoni</i> (Thomas, 1903)	1350–3250	Forest	W + E	LC
32	<i>Desmomys yaldeni</i> Lavrenchenko, 2003	1800–1930	Forest	W	VU B1ab(iii)
33	<i>Otomys typus</i> (Heuglin, 1877)	3800	Highland	W	LC
34	<i>Otomys fortior</i> Thomas, 1906	1700–2350	Forest	W	NE
35	<i>Otomys helleri</i> Frick, 1914	3170–4100	Highland	E	NE
36	<i>Otomys cheesmani</i> Taylor <i>et al.</i> , 2011	2000–2500	Intrazonal	W	NE
37	<i>Otomys yaldeni</i> Taylor <i>et al.</i> , 2011	3100–3170	Highland	E	NE
38	<i>Otomys simiensis</i> Taylor <i>et al.</i> , 2011	3250	Highland	W	NE
39	<i>Lepus starcki</i> Petter, 1963	2140–4380	Highland	W + E	LC
40	<i>Crocidura thalia</i> Dippenaar, 1980	1935–3300	Forest	W + E	LC
41	<i>Crocidura glassi</i> Heim de Balsac, 1966	2700–4050	Highland	E	NT
42	<i>Crocidura macmillani</i> Dollman, 1915	1220–1930	Forest	W	NT
43	<i>Crocidura baileyi</i> Osgood, 1936	2700–3800	Highland	W	LC
44	<i>Crocidura lucina</i> Dippenaar, 1980	3000–4050	Highland	E	VU D2
45	<i>Crocidura bottegoides</i> Hutterer and Yalden, 1990	2400–3280	Forest	E	EN B2ab(ii,iii)
46	<i>Crocidura harena</i> Hutterer and Yalden, 1990	2400–2630	Forest	E	CR B1ab(ii,iii) +2ab(ii,iii)
47	<i>Crocidura phaeura</i> Osgood, 1936	1100–2400	Forest	W + E	EN B1ab(iii)
48	<i>Crocidura afeworkbekelei</i> Lavrenchenko <i>et al.</i> , 2016	4050	Highland	E	NE
49	<i>Crocidura yaldeni</i> Lavrenchenko <i>et al.</i> , 2016	1900	Forest	W	NE
50	<i>Myotis scotti</i> Thomas, 1927	1300–2500	Forest	W + E	VU B2ab(iii)

No.	Species	Altitudinal range (m a.s.l.)	Habitat	Distribution	Conservation status
51	<i>Plecotus balensis</i> Kruskop and Lavrenchenko, 2000	1950–3300	Forest	W + E	DD
52	<i>Scotophilus ejetai</i> Brooks, Bickham, 2014	1390–2100	Forest	W	NE
53	<i>Canis simensis</i> Rüppell, 1840	3000–4100	Highland	W + E	EN B1ab(iii,v); C1+2a(i); D
54	<i>Tragelaphus buxtoni</i> (Lydekker, 1910)	1800–3800	Forest, Highland	E	EN C1
55	<i>Capra walie</i> Rüppell, 1835	2600–3900	Highland	W	EN B1ab(iii); D

This list of endemic species is surely far from complete. Our molecular genetic analysis reveals genetic subdivision of the Ethiopian *Tachyoryctes splendens* s.l. including at least four allopatric and deeply divergent mitochondrial lineages, restricted to the Simien Mountains and the northern, southern and eastern parts of the Ethiopian Plateau (Lavrenchenko *et al.*, 2014). Three of them possess unique karyotypes while chromosomal characteristics of the eastern lineage remain unknown. These lineages may represent distinct species, some of which may be endemic to Ethiopia. Preliminary results of our molecular genetic analysis based on mitochondrial and nuclear markers suggest the presence of several presumably undescribed yet *Dendromus* species in Ethiopia. It is worth mentioning that one of them represents a sister lineage to endemic *Dendromus lovati* (Lavrenchenko *et al.*, 2017). Moreover, the sole specimen of *Crocidura* cf. *hildegardeae* collected in *Schefflera-Hagenia* belt of the Harena Forest may indicate the presence of a further new species endemic to Ethiopia (Lavrenchenko *et al.*, 2016). The taxonomy of the genus *Arvicanthis* in East Africa is still much in need of comprehensive review and it seems likely that the number of *Arvicanthis* species endemic to Ethiopia will increase in the future.

Most of the endemic mammal species (74.5%) have evolved from Afrotropical ancestors. Although the Murinae has an Asian origin (Lecompte *et al.*, 2008), all Ethiopian endemic rodents of this subfamily clearly belong to the following Afrotropical genera or subgenera: *Mus* (*Nannomys*), *Mastomys*, *Stenocephalemys*, *Grammomys*, *Arvicanthis*, *Mylomys*, *Desmomys*, *Dasymys* and *Nilopegamys*. The hypothesis of a Palaeartic origin of the endemic bat, *Myotis scotti* was supposed (Lavrenchenko *et al.*, 2004a) as it was suggested to be a member of the subgenus *Selysius* (Koopman, 1994) demonstrating strong zoogeographical affinities to the Palaeartic fauna. However, the later phylogenetic analysis of cytochrome b gene sequences revealed the monophyly of the *Myotis* s.

str. group (including *Myotis scotti*), which is mainly Afrotropical in distribution (Stadelmann *et al.*, 2004). Only four species (7.3% of all endemics) are likely to be descendants of Palaeartic parent species. Three of them (*Canis simensis*, *Capra walie* and *Lepus starcki*) are associated with high altitude grassland or moorland and one (*Plecotus balensis*) (Fig. 1) is with montane forest at lower altitudes. It is noteworthy to mention the absence of such species with Palaeartic ancestry among rodents, which form the most numerous group of endemics. All Ethiopian endemic shrews from the genus *Crocidura* (10 species, 18.2% of all endemics) are likely to be representatives of an ancient group that does not exhibit clear zoogeographical affinities to the Afrotropical or Palaeartic fauna. Phylogenetic analysis of cytochrome b gene sequences (Lavrenchenko *et al.*, 2009) confirmed the monophyly of the group of Ethiopian endemics (*C. glassi*, *C. thalia*, *C. macmillani*, *C. baileyi*, *C. lucina*, and *C. yaldeni*), which was phylogenetically remote from the Afrotropical clade. It was suggested that, in spite of their morphological diversity, all *Crocidura* species endemic to Ethiopia have resulted from a relatively recent adaptive radiation of an ancient lineage of *Crocidura* (Lavrenchenko *et al.*, 2009).

The great majority of endemics is confined to the Ethiopian Plateau, where 23 species are most clearly associated with high-altitude grassland or moorland, 24 with montane forest (Table 1), three with both highland and forest (*Tragelaphus buxtoni*, *Lophuromys simensis* and *Stenocephalemys rupp*) and three with various intrazonal habitats in the altitudinal range 1800–2600 m (*Nilopegamys plumbeus*, *Dasymys griseifrons* and *Otomys cheesmani*). Only two endemic species (*Mus proconodon* and *Mastomys awashensis*) are associated with savannas at lower altitudes (950–1750 m).

The Ethiopian Plateau is divided by the Great Ethiopian Rift Valley into a main north-western massif (western plateau) and a smaller south-eastern mountain range (eastern plateau). It would appear that the Rift Valley has served as a major zoogeographic barrier in Ethiopia (Yalden and Largen, 1992). Twenty montane and forest endemic mammals were found only on western plateau, 13 on eastern plateau, and 20 on both sides of the Rift Valley (Table 1). The separation between western and eastern plateaux caused by the Rift Valley in the early Pliocene created some opportunities for evolutionary diversification of endemic species adapted to high-elevation habitats. Indeed, we can suggest that the split between some high-altitude sister endemic species (e.g., *Crocidura lucina* – *C. baileyi*; *Otomys helleri* – *O. typus* and *Otomys yaldeni* – *O. simiensis*) was caused by the division of Ethiopian highlands by the Rift Valley.



Fig. 1. Picture of *Plecotus balensis* from Debre Sina.

It was supposed that several other endemic species of high altitude grassland or moorland such as *Canis simensis*, *Tachyoryctes macrocephalus* and *Muriculus imberbis* have distinct subspecies on either side of the Rift (Yalden and Lagen, 1992). However, the later phylogeographic analysis revealed the absence of genetic differentiation of *Canis simensis*, which is apparently of rather recent origin (Gottelli *et al.*, 2004). On the other hand, it was shown that more ancient forest and Afro-alpine endemic species (e.g., *Lophuromys chrysopus*; *Theropithecus gelada*) are really represented by genetically distinct forms of presumably subspecies rank on opposite sides of the Rift Valley (Lavrenchenko *et al.*, 2004b; Gurja Belay and Mori, 2006).

The diversity and uniqueness of the Ethiopian fauna can be connected to such specific features of Ethiopian Plateau as pronounced altitudinal zonation, extremely diverse geomorphology and drastic environmental changes in the past. The phylogeny of some selected endemic groups of

rodents and shrews was reconstructed using analysis of molecular data in the context of the history of the main ecosystems in Ethiopia (Lavrenchenko, 2008b). The revealed phylogenetic patterns suggest that the evolutionary history of the Ethiopian small mammals was featured by both intensive local speciation and accumulation of survived evolutionary lineages. Such processes could explain the high level of endemism found in the country. Ethiopia occupies the fourth place among continental countries (after Mexico, Brazil and U.S.A.) for the level of mammalian endemism and the first place in the Eastern Hemisphere. This level (17.7%) is much higher than in other African continental countries (Republic of South Africa – 10.3%, D.R. Congo – 6.1%, Egypt – 5.9%, Libya – 5.8%, Kenya – 5.4%, Somalia – 5.0%, Cameroon – 4.7%, Tanzania – 4.3%, Sudan – 4.0%). Local endemism may also be rather high for example, of the seven shrew species known from the Bale Massif, six (*Crocidura thalia*, *C. glassi*, *C. lucina*, *C. bottegoides*, *C. haremma* and *C. afeworkbekelei*) are endemic (Lavrenchenko *et al.*, 2016). Species which are endemic to just one country add a particular interest to its fauna, and represent a special conservation requirement and concern (Yalden and Largen, 1992).

Vulnerability and conservation

Currently, the IUCN Red List includes 32 Ethiopian threatened (i.e., falling into one of the three categories of Critically Endangered, Endangered and Vulnerable) mammalian species. Among them, 19 are larger mammals and only 13 are small mammals (rodents, shrews and bats). Nevertheless, there is a significant difference between these two lists. The first list includes mainly very popular and charismatic larger mammals, which are flagships of numerous conservation projects (*Loxodonta africana*, *Acinonyx jubatus*, *Panthera leo*, *Equus grevyi*, *Diceros bicornis*, *Hippopotamus amphibius*, etc.). Most of them are relatively widespread. Only four species (*Cercopithecus djamdamensis*, *Canis simensis*, *Tragelaphus buxtoni* and *Capra walie*) are endemic to Ethiopia (Table 1). But, the threatened small mammals of Ethiopia are poorly known species with extremely limited distribution ranges. With the sole exception of *Mormopterus acetabulosus* (Vulnerable D2), all these species are endemic to Ethiopia (Table 1); the latter species is probably not a member of the Ethiopian fauna. It is now considered most likely that specimens of the species taken outside of the Mascarene Islands (including Ethiopia) were vagrants, and that the taxon (recently divided into two close species, *M. acetabulosus* and *M. francoismoutoui*) should be considered endemic to Mauritius and R union (Skinner and Chimimba, 2005; Goodman *et al.*, 2008).

The list of Ethiopian threatened small mammals is obviously incomplete as the conservation status of some new species described and re-described recently by JERBE (*Crocidura afeworkbekelei*, *C. yaldeni*, *Otomys fortior*, *O. helleri*, *O. cheesmani*, *O. yaldeni* and *O. simiensis*) or awaiting formal description (*Mus* sp.1, *Stenocephalemys* sp.A) was not yet assessed under IUCN Red List guidelines.

At least one species from the list, *Nilopegamys plumbeus*, may now be extinct. This species represents a monotypic genus and possesses unique adaptations to life in water. It is a sole swimming rodent in Africa. This species is known from a single specimen collected from near the source of the Little Abbay River in 1927. Repeated attempts were made to recollect this species, but without any success. Other possibly extinct endemic rodents are even not listed as threatened in the IUCN Red List. They are so poorly known that they can only be placed in the category of Data Deficient (Table 1). One of them, *Mylomys rex* is known from a type specimen collected by Peter Zaphiro in 1905 from Charada Forest. During our surveys of the type locality in 1998, we found only greatly destructed natural habitats (primary *Podocarpus* forest has practically disappeared there) and failed to collect additional specimen of this species (Lavrenchenko, 2003). The forest species *Stenocephalemys ruppi* is known only from the type series collected by Hans Rüpp in 1974 from near Bonke at Mt. Gughe (Van der Straeten and Dieterlen, 1983). In 2011, during our surveys of the type locality of the species, we found only agricultural fields in this area, which completely replaced natural habitats. During our studies, several old local people showed us the precise place of Rüpp's trapping line, which was completely forested at that time. Now the place is unfavorable for any forest species and we failed to trap any *Stenocephalemys* from that locality. This shows there is a high risk that some unknown endemic species of Ethiopian small mammals will become extinct before they can be described.



Fig. 2. Picture of *Mastomys awashensis* from Babilie Elephant Sanctuary.

In contrast, the known distribution ranges of some other little-known small mammals increased significantly as revealed from field surveys. For example, two endemic shrews, *Crocidura macmillani* and *C. phaeura* were known only from their type localities (Koteke and Mt. Garumba, respectively) (Hutterer and Yalden, 1990; Yalden and Lagen, 1992). Later, the former species was collected from the Middle Godjeb Valley and Sheko Forest (Lavrenchenko, 2008a), and the latter in the Nachisar National Park (Duckworth *et al.*, 1993). *Crocidura parvipes*, reported for the first time from Ethiopia by Hutterer and Yalden (1990) on the evidence of a single specimen from Bulcha Forest, is currently found to be rather numerous in the Middle Godjeb Valley and near Koi River (37 km SW of the Bebeke Coffee Farm) (Lavrenchenko *et al.*, 2016). The multimammate rat, *Mastomys awashensis*, was initially described by Lavrenchenko *et al.* (1998a) based on samples from two localities of the middle Awash Valley.

Later, Corti *et al.* (2005) found *M. awashensis* in another adjacent locality near Zeway Lake. Because of the restricted distribution area (15000 km²), the species was classified as Vulnerable B1ab(iii) in the IUCN Red List (Lavrenchenko and Corti, 2008). However, during further trapping sessions, this species was recorded in two additional localities; one near Mekelle (Colangelo *et al.*, 2010) and another in the south-eastern side of Tana Lake far to the north (our unpubl. data). Combined with our recent finding of *M. awashensis* (Fig. 2) in the Babile Elephant Sanctuary (Lavrenchenko *et al.*, 2010) and the Dhati-Welel National Park (our unpubl. data), its range extends well beyond the Ethiopian Rift Valley to regions in the north, east and west of the country. Currently, the IUCN threatened category status of *M. awashensis* is re-evaluated and classified as Least Concern (Kennerley and Lavrenchenko, 2016).

All but one (*Theropithecus* Geoffroy, 1841) of the six mammalian genera endemic to Ethiopia are rodents: *Stenocephalemys* Frick, 1914, *Desmomys* Thomas, 1910, *Megadendromus* Dieterlen and Rupp, 1978, *Muriculus* Thomas, 1902, and *Nilopegamys* Osgood, 1928. While taxonomy and phylogeny of the two first rodent genera have been intensively studied (Lavrenchenko *et al.*, 1999; Lavrenchenko, 2003; Bulatova and Lavrenchenko, 2005; Lavrenchenko and Verheyen, 2005; 2006), the rest three genera are monotypic and poorly known. It was demonstrated that *Muriculus imberbis* (Rüppell, 1842) does not belong to a distinct monotypic genus, but to the genus *Mus* Linnaeus, 1758, as the ancient lineage of the African subgenus *Nannomys* Peters, 1876 (Yonas Meheretu *et al.*, 2015). Our later phylogenetic analysis based on mitochondrial (cytochrome b) and nuclear (*IRBP*) gene sequences revealed that another very distinctive Ethiopian endemic, *Megadendromus nikolausi*, placed previously in the monotypic genus *Megadendromus*, occupies an internal position within the genus *Dendromus* (Lavrenchenko *et al.*, 2017). These recent studies demonstrate that two remarkable Ethiopian endemic genera (*Muriculus*, *Megadendromus*) are, in fact, internal lineages of widespread African genera (*Mus* and *Dendromus*), which have evolved into morphologically very distinct phenotypes due to extremely rapid morphological evolution associated with extreme selective pressure in the Ethiopian mountains. Strategies for the conservation of rodent diversity must rely mainly on higher taxon approach (Amori and Gippoliti, 2003). Particularly, threatened monotypic genera require special conservation attention because of the danger of losing a considerable amount of phylogenetic diversity. Although *Megadendromus nikolausi* and *Muriculus*

imberbis were formerly placed in monotypic genera, they should be treated as species of the genera *Dendromus* and *Mus*, respectively. Conservation of these unique and presumably stenobiotic rodents with a restricted distribution is important.

Some of the Ethiopian endemic mammals possess extremely limited distribution ranges. This characteristic is common for high-altitude species inhabiting the upper belts of isolated mountains (e.g., *Tachyoryctes macrocephalus*, *Stenocephalemys albocaudata*, *Lophuromys melanonyx*). However, we found the same distribution pattern for some Ethiopian forest endemics. We can recognize at least two centers of local endemism for small mammals of the Ethiopian Plateau (Lavrenchenko, 2008b). The first is situated at the southern slopes of the Bale Mountains, where rich local shrew fauna is dominated by species which represent relatively recent radiation of 36-chromosomal *Crocidura* lineage (*Crocidura thalia*, *C. glassi*, *C. bottegoides* and *C. harennna*). Three mammalian species (*Crocidura harennna*, *Cercopithecus djamdjamensis*, and *Mus* sp.1 = *Mus* cf. *triton*) are known to be endemic to such a relatively small geographic area as the Harennna Forest. The second “hotspot” of local endemism can be located in the forests of south-western Ethiopia, where extremely small distribution ranges of two rodent species, *Desmomys yaldeni* (Fig. 3) and *Lophuromys pseudosikapusi* are coincided. It was proposed that both these centers of local endemism are associated with montane forested areas characterized by ecoclimatic stability because of persistent orographic rain or mist (Lavrenchenko, 2008b).



Fig. 3. Picture of *Desmomys yaldeni* from Sheko Forest.

Agriculture has been the main human activity in Ethiopia during the past four millennia, and, through time, this has resulted in the massive destruction of natural habitats. Forests and woodlands have been cleared for settlement and cultivation of crops and the recent human population explosion has led to annihilation of indigenous vegetation over most of Ethiopia. The dense forest, once estimated to encompass 40% of the country, has reduced in size to less than 4% (Afework Bekele and Corti, 1997). As a result, there is a possibility that some small forest mammals in Ethiopia may be facing extinction due to habitat destruction even before

their existence in this country has been recognized. Fortunately, the endemics of the Harena Forest are currently protected within the Bale Mountains National Park. On the other hand, the humid evergreen forests of south-western Ethiopia are currently receiving no sufficient form of protection. Two remarkable endemic rodents (*Desmomys yaldeni* and *Lophuromys pseudosikapusi*) with their tiny distribution area are at risk of extinction from habitat loss. These two sylvicolous species are restricted to the forests between Mizan Teferi and Gore, which are currently heavily degraded by cutting, clearing and overgrazing.

CONCLUSIONS

1. The obtained data revealed that the species diversity and level of endemism of the Ethiopian small mammals could be far higher than was suspected before.
2. The mammal fauna of Ethiopia is unique, not only because of high level of endemism, but also as a basis for novel evolutionary models. The local endemics are the most promising for future studies of the role of past climate and geomorphology in evolution of Ethiopian biodiversity in various high-altitude ecosystems.
3. Many of the endemic small mammals are potentially threatened because of their extremely limited distribution ranges and habitat destruction through agricultural expansion. This reinforces the need for effective protection of the remaining montane forests constituting key environment of the narrow endemic species as some of them may become extinct in a short time after their discovery.
4. In view of the fast habitat destruction in the country, taxonomic and evolutionary studies on Ethiopian small mammals are important and urgent. There is a high risk that some unknown endemic species will become extinct before they can be located, described and studied.

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REFERENCES

- Afework Bekele and Corti, M. (1997). Forest blocks and altitude as indicators of *Myomys albipes* (Rüppell 1842) (Mammalia Rodentia) distribution in Ethiopia. *Trop. Zool.* **10**: 287–293.
- Afework Bekele and Leirs, H. (1997). Population ecology of rodents of maize fields and grassland in Central Ethiopia. *Belg. J. Zool.* **127**(suppl.): 39–48.
- Amori, G. and Gippoliti, S. (2003). A higher-taxon approach to rodent conservation priorities for the 21st century. *Anim. Biodivers. Conserv.* **26**: 1–18.
- Baker, R.J. and Bradley, R.D. (2006). Speciation in mammals and the genetic species concept. *J. Mammal.* **87**: 643–662.
- Baskevich, M.I. and Lavrenchenko, L.A. (2000). Review of karyological studies and the problems of systematics of Ethiopian *Arvicanthis* Lesson, 1842 (Rodentia: Muridae). *Bonn. Zool. Monogr.* **46**: 209–216.
- Boyles, J.G., Seebacher, F., Smit, B. and McKechnie, A.E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integr. Comp. Biol.* **51**: 676–690.
- Bryja, J., Mikula, O., Šumbera, R., Yonas Meheretu, Aghová, T., Lavrenchenko, L.A., Mazoch, V., Oguge, N., Mbau, J.S., Welegerima, K., Amundala, N., Colyn, M., Leirs, H. and Verheyen E. (2014). Pan-African phylogeny of *Mus* (subgenus *Nannomys*) reveals one of the most successful mammal radiations in Africa. *BMC Evol. Biol.* **14**: 256.
- Bulatova, N.Sh. and Lavrenchenko, L.A. (2005). Possible karyological affinities of small mammals from North of the Ethiopian Plateau. In: **African Biodiversity: Molecules, Organisms, Ecosystems**, pp. 315–319 (Huber, B.A., Sinclair, B.J. and Lampe, K.H., eds.). Springer, New York.
- Colangelo, P., Leirs, H., Castiglia, R., D’aes, M., Yonas Meheretu and Verheyen, E. (2010). New data on the distribution and phylogenetic position of *Mastomys awashensis* (Rodentia, Muridae). *Mamm. Biol.* **75**: 459–462.
- Corti, M., Castiglia, R., Colangelo, P., Capanna, E., Beolchini, F., Afework Bekele, Oguge,

- N.O., Makundi, R.H., Sichilima, A.M., Leirs, H., Verheyen, W. and Verhagen, R. (2005). Cytotaxonomy of rodent species from Ethiopia, Kenya, Tanzania and Zambia. *Belg. J. Zool.* **135**(suppl.): 197–216.
- Duckworth, J.W., Harrison, D.L. and Timmins, R.J. (1993). Notes on a collection of small mammals from the Ethiopian Rift Valley. *Mammalia* **57**: 278–282.
- Gebissa Ejeta (2010). African green revolution needn't be a mirage. *Science* **327**: 831–832.
- Goodman, S.M., van Vuuren, B.J., Ratrimomanarivo, F., Probst, J.-M. and Bowie, R.C.K. (2008). Specific status of populations in the Mascarene Islands referred to *Mormopterus acetabulosus* (Chiroptera; Molossidae), with description of a new species. *J. Mammal.* **89**: 1316–1327.
- Goodyear, J.J. (1976). **Population Fluctuation of the Rat-like Rodents of Importance in Agricultural Fields in Kaffa Province, Ethiopia**. M.A. dissertation. University of Bowling Green, USA.
- Gottelli, D., Marino, J., Sillero-Zubiri, C. and Funk, S.M. (2004). The effect of the last glacial age on speciation and population genetic structure of the endangered Ethiopian wolf (*Canis simensis*). *Mol. Ecol.* **13**: 2275–2286.
- Gurja Belay and Mori, A. (2006). Intraspecific phylogeographic mitochondrial DNA (D-loop) variation of Gelada baboon, *Theropithecus gelada*, in Ethiopia. *Biochem. Syst. Ecol.* **34**: 554–561.
- Hutterer, R. and Yalden, D.W. (1990). Two new species of shrews from a relic forest in the Bale Mountains, Ethiopia. In: **Vertebrates in Tropics**, pp. 63–72 (Peters, G. and Hutterer, R., eds.). Museum Alexander Koenig, Bonn.
- Kennerley, R. and Lavrenchenko, L.A. (2016). *Mastomys awashensis*. The IUCN Red List of Threatened Species 2016: e.T45060A22425623. <http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T45060A22425623.en>. Downloaded on 08 March 2017.
- Kingdon, J., Happold, D., Butynski, T., Hoffmann, M., Happold, M. and Kalina, J. (eds.). (2013). **Mammals of Africa** (6 vols). Bloomsbury Publishing, London.
- Koopman, K.F. (1994). Chiroptera: Systematics. In: **Handbuch der Zoologie**, V. VII, pp. 100–109 (Niethammer, J., Schliemann, H. and Starck, D., eds.). Walter de Gruyter, Berlin.
- Kruskop, S.V., Benda, P., Vasenkov, D.A. and Lavrenchenko, L.A. (2016). First records of bats from the Alatish National Park, north-western Ethiopia. *Lynx, n. s. (Praha)*. **47**: 35–53.
- Kruskop, S.V. and Lavrenchenko, L.A. (2000). A new species of long-eared bat (*Plecotus*; Vespertilionidae, Mammalia) from Ethiopia. *Myotis* **38**: 5–17.
- Kruskop, S.V. and Lavrenchenko, L.A. (2008). Primary results of a bat survey in south-western Ethiopia, with a new Ethiopian record of *Kerivoula lanosa* (Chiroptera: Vespertilionidae). *Russ. J. Theriol.* **7**: 71–76.
- Lavrenchenko, L.A. (1993). *Uranomys ruddi* Dollman, 1909 (Rodentia, Muridae) – a new genus and species in the fauna of Ethiopia. *Zool. Zh.* **72**: 133–137.
- Lavrenchenko, L.A. (2000). The mammals of the isolated Harena Forest (southern Ethiopia): structure and history of the fauna. *Bonn. Zool. Monogr.* **46**: 223–231.
- Lavrenchenko, L.A. (2003). A contribution to the systematics of *Desmomys* Thomas, 1910 (Rodentia, Muridae) with the description of a new species. *Bonn. Zool. Beitr.* **50**: 313–327.
- Lavrenchenko, L.A. (2008a). *Crociodura macmillani*. The IUCN Red List of Threatened Species. Version 2014.3. Available from: <http://www.iucnredlist.org> (accessed 11

- April 2015).
- Lavrenchenko, L.A. (2008b). The Ethiopian mammals: a model for research in evolutionary biology. In: **Ecological and Faunistic Studies in Ethiopia**, pp. 114–139 (Pavlov, D.S., Dgebuadze, Y.Y., Darkov, A.A., Golubtsov, A.S. and Mina, M.V., eds.). KMK, Moscow.
- Lavrenchenko, L.A., Bannikova, A.A. and Lebedev, V.S. (2009). Shrews (*Crocidura* spp.) endemic to Ethiopia: recent adaptive radiation of an ancient lineage. *Dokl. Biol. Sci.* **424**: 57–60.
- Lavrenchenko, L.A. and Corti, M. (2008). *Mastomys awashensis*. In: IUCN 2010. IUCN Red List of Threatened Species. Version 2010.4.
- Lavrenchenko, L.A., Kruskop, S.V., Afework Bekele, Gurja Belay, Morozov, P.N., Ivlev, Y.F. and Warshavsky, A.A. (2010). Mammals of the Babilie Elephant Sanctuary (Eastern Ethiopia). *Russ. J. Theriol.* **9**: 47–60.
- Lavrenchenko, L.A., Kruskop, S.V. and Morozov, P.N. (2004a). Notes on the bats (Chiroptera) collected by the Joint Ethiopian-Russian Biological Expedition, with remarks on their systematics, distribution, and ecology. *Bonn. Zool. Beitr.* **52**: 127–147.
- Lavrenchenko, L.A., Likhnova, O.P., Baskevich, M.I. and Afework Bekele (1998a). Systematics and distribution of *Mastomys* (Muridae, Rodentia) from Ethiopia, with the description of a new species. *Mamm. Biol.* **63**: 37–51.
- Lavrenchenko, L.A., Likhnova, O.P. and Orlov, V.N. (1992). Hemoglobin patterns: a possible implication in systematics of multimammate rats *Mastomys* (Muridae, Rodentia). *Zool. Zh.* **71**: 85–93.
- Lavrenchenko, L.A., Milishnikov, A.N., Aniskin, V.M. and Warshavsky, A.A. (1999). Systematics and phylogeny of the genus *Stenocephalemys* Frick, 1914 (Rodentia, Muridae): a multidisciplinary approach. *Mammalia* **63**: 475–494.
- Lavrenchenko, L.A., Nadjafova, R.S., Afework Bekele, Mironova, T.A. and Bryja, J. (2017). Phylogenetic position of a monotypic Ethiopian endemic rodent genus *Megadendromus* (Rodentia, Nesomyidae). *Mammalia* **81**: 71–82.
- Lavrenchenko, L.A., Orlov, V.N. and Milishnikov, A.N. (1997). A checklist of the mammals of the Baro-Akobo interfluve. In: **Ecological and Faunistic Studies in Ethiopia**. Part 1. Fauna, ecology and systematics of vertebrates, pp. 24–44, Addis Ababa.
- Lavrenchenko, L.A., Sewnet Mengistu, Bulatova, N.Sh., Afework Bekele, Potapov, S.G., Nadjafova, R.S. and Gurja Belay (2014). Genetic and cytogenetic variation of African root-rats *Tachyoryctes splendens* (Mammalia: Rodentia) from Ethiopia. *Russ. J. Theriol.* **13**: 109–118.
- Lavrenchenko, L.A. and Verheyen, E. (2005). An assessment of the systematics of the genus *Desmomys* Thomas, 1910 (Rodentia: Muridae) using mitochondrial DNA sequences. In: **African Biodiversity: Molecules, Organisms, Ecosystems**, pp. 363–369 (Huber, B.A., Sinclair, B.J. and Lampe, K.H., eds.). Springer, New York.
- Lavrenchenko, L.A. and Verheyen, E. (2006). Evolutionary relationships among narrow-headed rats (Genus *Stenocephalemys*, Muridae, Rodentia) inferred from complete cytochrome b gene sequences. *Russ. J. Genet.* **42**: 439–446.
- Lavrenchenko, L.A., Verheyen, W.N. and Hulselmans, J. (1998b). Systematic and distributional notes on the *Lophuromys flavopunctatus* Thomas, 1888 species-complex in Ethiopia (Muridae-Rodentia). *Bull. Inst. Roy. Sci. Nat. Belg. Biol.* **68**: 199–214.

- Lavrenchenko, L.A., Verheyen, W.N., Verheyen, E., Hulselmans, J. and Leirs, H. (2007). Morphometric and genetic study of Ethiopian *Lophuromys flavopunctatus* Thomas, 1888 species complex with description of three new 70-chromosomal species (Muridae - Rodentia). *Bull. Inst. Roy. Sci. Nat. Belg. Biol.* **77**: 77–117.
- Lavrenchenko, L.A., Verheyen, E., Potapov, S.G., Lebedev, V.S., Bulatova, N.Sh., Aniskin, V.M., Verheyen, W.N. and Ryskov, A.P. (2004b). Divergent and reticulate processes in evolution of Ethiopian *Lophuromys flavopunctatus* species complex: evidence from mitochondrial and nuclear DNA differentiation patterns. *Biol. J. Linn. Soc.* **83**: 301–316.
- Lavrenchenko, L.A., Voyta, L.L. and Hutterer, R. (2016). Diversity of shrews in Ethiopia, with the description of two new species of *Crocidura* (Mammalia: Lipotyphla: Soricidae). *Zootaxa* **4196**: 38–60.
- Lecompte, E., Aplin, K., Denys, C., Catzeflis, F., Chades, M. and Chevret, P. (2008). Phylogeny and biogeography of African Murinae based on mitochondrial and nuclear gene sequences, with a new tribal classification of the subfamily. *BMC Evol. Biol.* **8**: 1–21.
- Leirs, H. (1995). Population ecology of *Mastomys natalensis* (Smith, 1834). Implications for rodent control in Africa. Belgian Administration for Development Cooperation. Agricultural edition, No. 35.
- Mace, G.M. (2004). The role of taxonomy in species conservation. *Philos. T. R. Soc. Lon. B.* **359**: 711–719.
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* **37**: 637–669.
- Patterson, B.D. (2000). Patterns and trends in the discovery of new Neotropical mammals. *Divers. Distrib.* **6**: 145–151.
- Patterson, B.D. (2001). Fathoming tropical biodiversity: the continuing discovery of Neotropical mammals. *Divers. Distrib.* **7**: 191–196.
- Reeder, D.M., Helgen, K.M. and Wilson, D.E. (2007). Global trends and biases in new mammal species discoveries. *Occ. Pap. Mus. Tex. Tech Univ.* **269**: 1–36.
- Skinner, J.D. and Chimimba, C.T. (2005). **The Mammals of the Southern African Subregion**. 3rd edn. Cambridge University Press, Cambridge.
- Stadelmann, B., Jacobs, D.S., Schoeman, C. and Ruedi, M. (2004). Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome *b* sequences. *Acta Chiropterol.* **6**: 177–192.
- Taylor, P.J., Lavrenchenko, L.A., Carleton, M.D., Verheyen, E., Bennett, N.C., Oosthuizen, C.J. and Maree, S. (2011). Specific limits and emerging diversity patterns in East African populations of laminate-toothed rats, genus *Otomys* (Muridae: Murinae: Otomyini): Revision of the *Otomys typus* complex. *Zootaxa* **3024**: 1–66.
- Van der Straeten, E. and Dieterlen, F. (1983). Description de *Praomys ruppi*, une nouvelle espece de Muridae d’Ethiopie. *Ann. Mus. Roy. Afr. Centr. (Tervuren) Ser. 8. Sci. Zool.* **237**: 121–128.
- Wilson, E.O. (2003). What is nature worth for? Woodrow Wilson International Center for Scholars, Washington.
- Yalden, D.W. and Lagen, M.J. (1992). The endemic mammals of Ethiopia. *Mammal Rev.* **22**: 115–150.
- Yonas Meheretu, Šumbera, R. and Bryja, J. (2015). Enigmatic Ethiopian endemic rodent *Muriculus imberbis* (Rüppell 1842) represents a separate lineage within genus *Mus*. *Mammalia* **79**: 15–23.