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

Leonid A. Lavrenchenko¹* and Afework Bekele²

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.

¹ Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr., 33, Moscow, 119071 Russia. E-mail: llavrenchenko@gmail.com
² Department of Zoological Sciences, Addis Ababa University, P.O. Box 1176, Addis Ababa, Ethiopia. E-mail: afeworksimegn@gmail.com
*Author to whom all correspondence should be addressed
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, Dhati-Welel National Park,
Babille 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 endemicity

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
(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 Afrolpine 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.

<table>
<thead>
<tr>
<th>No.</th>
<th>Species</th>
<th>Altitudinal range (m a.s.l.)</th>
<th>Habitat</th>
<th>Distribution</th>
<th>Conservation status</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td><em>Cercopithecus djamdjamensis</em> Neumann, 1902</td>
<td>1900–3000</td>
<td>Forest</td>
<td>E</td>
<td>VU B1ab(iii)</td>
</tr>
<tr>
<td>2</td>
<td><em>Theropithecus gelada</em> (Rüppell, 1835)</td>
<td>2350–4600</td>
<td>Highland</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>3</td>
<td><em>Tachyoryctes macrocephalus</em> (Rüppell, 1842)</td>
<td>3000–4150</td>
<td>Highland</td>
<td>W + E</td>
<td>EN B1ab(iii)</td>
</tr>
<tr>
<td>4</td>
<td><em>Dendromuslovati</em> De Winton, 1899</td>
<td>2500–3550</td>
<td>Highland</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>5</td>
<td><em>Dendromus nikolausi</em> Dieterlen, Rüpp, 1978</td>
<td>3000–3300</td>
<td>Highland</td>
<td>E</td>
<td>DD</td>
</tr>
<tr>
<td>6</td>
<td><em>Lophuromys flavopunctatus</em> Thomas, 1888</td>
<td>2600–3000</td>
<td>Forest</td>
<td>W</td>
<td>LC</td>
</tr>
<tr>
<td>7</td>
<td><em>Lophuromys brunneus</em> Thomas, 1906</td>
<td>2000–2800</td>
<td>Forest</td>
<td>W</td>
<td>NE</td>
</tr>
<tr>
<td>8</td>
<td><em>Lophuromys simensis</em> Osgood, 1936</td>
<td>1800–3800</td>
<td>Forest, Highland</td>
<td>W</td>
<td>LC</td>
</tr>
<tr>
<td>9</td>
<td><em>Lophuromys brevicaudus</em> Osgood, 1936</td>
<td>2400–3750</td>
<td>Highland</td>
<td>W + E</td>
<td>NT</td>
</tr>
<tr>
<td>10</td>
<td><em>Lophuromys chrysopus</em> Osgood, 1936</td>
<td>1200–2760</td>
<td>Forest</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>11</td>
<td><em>Lophuromys melanonyx</em> Petter, 1972</td>
<td>3100–4050</td>
<td>Highland</td>
<td>W + E</td>
<td>VU B1ab(iii)</td>
</tr>
<tr>
<td>12</td>
<td><em>Lophuromys menageshae</em> Lavrenchenko <em>et al.</em>, 2007</td>
<td>2100–2600</td>
<td>Forest</td>
<td>W</td>
<td>DD</td>
</tr>
<tr>
<td>14</td>
<td><em>Lophuromys pseudosikapusi</em> Lavrenchenko <em>et al.</em>, 2007</td>
<td>1930</td>
<td>Forest</td>
<td>W</td>
<td>EN B1ab(iii)</td>
</tr>
<tr>
<td>15</td>
<td><em>Mus proconodon</em> Rhoads, 1896</td>
<td>1000–1750</td>
<td>Savanna</td>
<td>NE</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td><em>Mus mahomet</em> Rhoads, 1896</td>
<td>1200–3200</td>
<td>Forest</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>17</td>
<td><em>Mus sp.1</em> (<em>M. cf. triton</em> (Thomas, 1909))</td>
<td>1950–2920</td>
<td>Forest</td>
<td>E</td>
<td>NE</td>
</tr>
<tr>
<td>18</td>
<td><em>Mus imberbis</em> Rüppell, 1842</td>
<td>1900–3400</td>
<td>Highland</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>No.</td>
<td>Species</td>
<td>Altitudinal range (m a.s.l.)</td>
<td>Habitat</td>
<td>Distribution</td>
<td>Conservation status</td>
</tr>
<tr>
<td>-----</td>
<td>---------</td>
<td>-----------------------------</td>
<td>---------</td>
<td>--------------</td>
<td>---------------------</td>
</tr>
<tr>
<td>19</td>
<td><em>Mastomys awashensis</em> Lavrenchenko et al., 1998</td>
<td>950–1650</td>
<td>Savanna</td>
<td>LC</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td><em>Stenocephalemys albipes</em> (Rüppell, 1842)</td>
<td>820–3800</td>
<td>Forest</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>21</td>
<td><em>Stenocephalemys ruppi</em> (Van der Straaten and Dieterlen, 1983)</td>
<td>2800–3200</td>
<td>Forest, Highland</td>
<td>W</td>
<td>DD</td>
</tr>
<tr>
<td>22</td>
<td><em>Stenocephalemys albocaudata</em> Frick, 1914</td>
<td>3000–4100</td>
<td>Highland</td>
<td>E + W</td>
<td>LC</td>
</tr>
<tr>
<td>23</td>
<td><em>Stenocephalemys griseicauda</em> Petter, 1972</td>
<td>2400–4000</td>
<td>Highland</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>24</td>
<td><em>Stenocephalemys sp.A</em></td>
<td>3800</td>
<td>Highland</td>
<td>W</td>
<td>NE</td>
</tr>
<tr>
<td>25</td>
<td><em>Nilopegamyos plumbeus</em> Osgood, 1928</td>
<td>2600</td>
<td>Intrasional</td>
<td>W</td>
<td>CR B2ab(iii)</td>
</tr>
<tr>
<td>26</td>
<td><em>Grammomys minnae</em> Hutterer, Dieterlen, 1984</td>
<td>1400–1800</td>
<td>Forest</td>
<td>W + E</td>
<td>VU B2ab(iii)</td>
</tr>
<tr>
<td>27</td>
<td><em>Dasymys griseifrons</em> (Osgood, 1936)</td>
<td>1800–1900</td>
<td>Intrasional</td>
<td>W</td>
<td>NE</td>
</tr>
<tr>
<td>28</td>
<td><em>Arvicanthis abyssinicus</em> (Rüppell, 1842)</td>
<td>1300–3800</td>
<td>Highland</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>29</td>
<td><em>Arvicanthis blicki</em> Frick, 1914</td>
<td>2750–4100</td>
<td>Highland</td>
<td>E</td>
<td>NT</td>
</tr>
<tr>
<td>30</td>
<td><em>Myomys rex</em> Thomas, 1906</td>
<td>1800</td>
<td>Forest</td>
<td>W</td>
<td>DD</td>
</tr>
<tr>
<td>31</td>
<td><em>Desmomys harringtoni</em> (Thomas, 1903)</td>
<td>1350–3250</td>
<td>Forest</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>32</td>
<td><em>Desmomys yaldeni</em> Lavrenchenko, 2003</td>
<td>1800–1930</td>
<td>Forest</td>
<td>W</td>
<td>VU B1ab(iii)</td>
</tr>
<tr>
<td>33</td>
<td><em>Otomys typus</em> (Heuglin, 1877)</td>
<td>3800</td>
<td>Highland</td>
<td>W</td>
<td>LC</td>
</tr>
<tr>
<td>34</td>
<td><em>Otomys fortior</em> Thomas, 1906</td>
<td>1700–2350</td>
<td>Forest</td>
<td>W</td>
<td>NE</td>
</tr>
<tr>
<td>35</td>
<td><em>Otomys helleri</em> Frick, 1914</td>
<td>3170–4100</td>
<td>Highland</td>
<td>E</td>
<td>NE</td>
</tr>
<tr>
<td>36</td>
<td><em>Otomys cheesmani</em> Taylor et al., 2011</td>
<td>2000–2500</td>
<td>Intrasional</td>
<td>W</td>
<td>NE</td>
</tr>
<tr>
<td>37</td>
<td><em>Otomys yaldeni</em> Taylor et al., 2011</td>
<td>3100–3170</td>
<td>Highland</td>
<td>E</td>
<td>NE</td>
</tr>
<tr>
<td>38</td>
<td><em>Otomys simiensis</em> Taylor et al., 2011</td>
<td>3250</td>
<td>Highland</td>
<td>W</td>
<td>NE</td>
</tr>
<tr>
<td>39</td>
<td><em>Lepus starcki</em> Petter, 1963</td>
<td>2140–4380</td>
<td>Highland</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>40</td>
<td><em>Crocidura thalia</em> Dippenaar, 1980</td>
<td>1935–3300</td>
<td>Forest</td>
<td>W + E</td>
<td>LC</td>
</tr>
<tr>
<td>41</td>
<td><em>Crocidura grissi</em> Heim de Balsac, 1966</td>
<td>2700–4050</td>
<td>Highland</td>
<td>E</td>
<td>NT</td>
</tr>
<tr>
<td>42</td>
<td><em>Crocidura macmillani</em> Dollman, 1915</td>
<td>1220–1930</td>
<td>Forest</td>
<td>W</td>
<td>NT</td>
</tr>
<tr>
<td>43</td>
<td><em>Crocidura baileyi</em> Osgood, 1936</td>
<td>2700–3800</td>
<td>Highland</td>
<td>W</td>
<td>LC</td>
</tr>
<tr>
<td>44</td>
<td><em>Crocidura lucina</em> Dippenaar, 1980</td>
<td>3000–4050</td>
<td>Highland</td>
<td>E</td>
<td>VU D2</td>
</tr>
<tr>
<td>45</td>
<td><em>Crocidura bottegoides</em> Hutterer and Yalden, 1990</td>
<td>2400–3280</td>
<td>Forest</td>
<td>E</td>
<td>EN B2ab(ii,iii)</td>
</tr>
<tr>
<td>46</td>
<td><em>Crocidura harenna</em> Hutterer and Yalden, 1990</td>
<td>2400–2630</td>
<td>Forest</td>
<td>E</td>
<td>CR B1ab(ii,iii) +2ab(ii,iii)</td>
</tr>
<tr>
<td>47</td>
<td><em>Crocidura phaeura</em> Osgood, 1936</td>
<td>1100–2400</td>
<td>Forest</td>
<td>W + E</td>
<td>EN B1ab(iii)</td>
</tr>
<tr>
<td>48</td>
<td><em>Crocidura afeworkbekelei</em> Lavrenchenko et al., 2016</td>
<td>4050</td>
<td>Highland</td>
<td>E</td>
<td>NE</td>
</tr>
<tr>
<td>49</td>
<td><em>Crocidura yaldeni</em> Lavrenchenko et al., 2016</td>
<td>1900</td>
<td>Forest</td>
<td>W</td>
<td>NE</td>
</tr>
<tr>
<td>50</td>
<td><em>Myotis scotti</em> Thomas, 1927</td>
<td>1300–2500</td>
<td>Forest</td>
<td>W + E</td>
<td>VU B2ab(iii)</td>
</tr>
</tbody>
</table>
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 Harenna 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 *Nilopegamus*. The hypothesis of a Palaearctic 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 Palaearctic 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 Palaearctic 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 Palaearctic 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 Palaearctic 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 ruppi*) 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.
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 Largen, 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. harenna 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 djamdjamensis, 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 Réunion (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.
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 Largen, 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 Bebeka 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 km\(^2\)), 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 Babille 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 Rüpp, 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. harenna*). Three mammalian species (*Crocidura harenna*, *Cercopithecus djamdjamensis*, and *Mus* sp.1 = *Mus* cf. *triton*) are known to be endemic to such a relatively small geographic area as the Harenna 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).
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 Harenna 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.

ACKNOWLEDGEMENTS

We are indebted to our Project Coordinators, Dr. Andrei Darkov (Joint Ethio-Russian Biological Expedition, Fourth Phase - JERBE IV) and Ato Woubishet Tafesse (Ethiopian Ministry of Science and Technology) for management of the expedition in the field and in Addis Ababa. We are also indebted to Ato Chemere Zewdie Ejeta (Oromia Forest and Wildlife Enterprise - OFWE) for permanent support of our work. The Department of Zoological Sciences, AAU and the Ethiopian Wildlife Conservation Authority are thanked for their logistic support. We thank our drivers, Mr.
Vladimir Belekhov and Mr. Alexander Myasnikov for their invaluable assistance during all stages of the expedition. Mrs. A.A. Warshavsky, Mohammed Kasso, D.S. Kostin, A.R. Gromov, A.A. Martynov, Ziyad Jemal and Mohammednur Jemal, Drs. Gurja Belay, Yu.F. Ivlev, S.V. Kruskop, D.Yu. Alexandrov, O.O. Grigoryeva, T.A. Mironova, Sewnet Mengistu, K.A. Rogovin, D.A. Vasenkov and A.V. Bochkov provided extensive help in the field and assisted in collecting small mammals for this study. Drs. N.Sh. Bulatova and R.S. Nadjafova made an inestimable contribution to the karyological part of this research. We acknowledge the work of Dr. S.G. Potapov in the molecular laboratory of the Severtsov Institute of Ecology and Evolution. We express thanks to Drs. Josef Bryja (Institute of Vertebrate Biology, Brno) and Radim Šumbera (University of South Bohemia, České Budějovice) for helpful discussions. This research was supported by the Russian Foundation for Basic Research (project no. 15-04-03801-a) during the stage of laboratory research.

REFERENCES


Corti, M., Castiglia, R., Colangelo, P., Capanna, E., Beolchini, F., Afework Bekele, Oguge,


April 2015).


