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THE GENETIC DIVERSITY OF SMALL MAMMALS OF THE BALE MOUNTAINS, ETHIOPIA

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ABSTRACT: Cytogenetic and allozyme analyses of small mammals (Insectivora and Rodentia) of the Bale Mountains National Park were carried out. Karyotypes and electrophoretic analysis of protein variations of endemic species (*Crocidura lucina, C. glassi, C. harenna, C. bottegoides, Tachyoryctes macrocephalus, Dendromus lovati, Arvicanthis blicki, Stenocephalemys albocaudata, S. griseicauda, Praomys albipes, Mus mahomet* and *Lophuromys melanonyx*) are presented and discussed. New cryptic species in the genera *Crocidura, Lophuromys, Stenocephalemys* and *Otomys* were found. The most interesting finding was a rodent new to science - *Lophuromys* sp.A. This species may be endemic to relic Harenna Forest. High level of genetic isolation between different populations of some endemic species was noted. Importance of genetic approach for conservation of endemic small mammals is emphasized.

Key words/phrases: allozymes, Bale Mountains National Park, cytogenetic analysis, genetic diversity, small mammals

INTRODUCTION

The Bale Mountains National Park (BMNP) encompasses an area of 2,200 km^2 in the Bale Massif. It encloses a great variety of distinctive habitats and can be divided into three regions: the northern woodlands, extending from 3,000 to 3,500 m altitude; the central Sanetti Plateau, from 3,500 to 4,400 m altitude; and the relic Harenna Forest from 1,500 to 3,250 m altitude. The Harenna Forest is a dense tropical forest, which covers the southern slopes of the Sanetti Plateau. Separated from other similar forest blocks by the Rift Valley to the west, the Sanetti Plateau to the north, and the lowlying, arid habitats on the

other sides, Harenna is one of the few large forests in Ethiopia that is relatively intact. This area, together with the neighbouring Sanetti Plateau, represents a continuous range of little affected natural vegetation (Hillman, 1986).

Until recently, the fauna of the small mammals of the Bale Mountains has been unexplored. *Lophuromys melanonyx* and *Megadendromus nikolausi* were described only in 1972 and 1978, respectively (Petter, 1972; Dieterlen and Rupp, 1978). The latter, being the sole representative of the genus, occupies its own unique place in the system of the Muridae family. A rodent new to Ethiopia (*Mus triton*) and two shrews new to science (*Crocidura harrena* and *Crocidura bottegoides*) were collected by the Harenna Forest Expedition in August 1986 (Yalden, 1988a, 1988b; Hutterer and Yalden, 1990). Five species of endemic rodents and three species of endemic shrews are known from the Bale Massif. Some of these species are known only from two or three localities. The data on their biology and ecology are either scanty and fragmentary or totally absent. Excepting a few data (Corti *et al.*, 1995), chromosomal sets and allozyme variations of the majority of these species are unknown. It is possible that other still undiscovered small mammals (including sibling species) occur in the Bale Mountains region.

At present, there is an intensive agricultural activities taking place in the Eastern Highlands. The territories inhabited by the species under consideration are significantly affected by these activities. Further, the indigenous forest species are being replaced by *Eucalyptus* (Stuart and Adams, 1990). Such agricultural activities will eventually lead to a decline of the populations of the endemic species, making them more vulnerable to chance extinctions and to a loss of their genetic diversity. The present study provides allozyme and cytogenetic information on small mammals of the Bale Mountains to describe some of the genetic diversity that exists.

MATERIALS AND METHODS

Specimens were captured in nine localities in the Bale Mountains National Park (Fig. 1). The following localities were explored:

1. *Podocarpus* belt of the Harenna Forest (1,780 m (above sea level) asl, 6°31′N 39°44′E).

2. *Aningeria* belt of the Harenna Forest (1,935 m asl, 6°38′N 39°44′E).
3. *Schefflera-Hagenia* belt of the Harenna Forest in the Katcha area (2,400 m asl, 6°42′N 39°44′E).
4. Mosaic grassland/forest habitats in the Dinsho area (3,170 m asl, 7°06′N 39°47′E).
5. Ericaceous belt of southern slope of the Sanetti Plateau (3,700 m asl, 6°46′N 39°46′E).
6. Ericaceous belt of northern slope of the Sanetti Plateau (3,750 m asl, 6°54′N 39°55′E).
7. Afroalpine belt with sparse and short vegetation in Konteh Area (4,050 m asl, 6°51′N 39°53′E).
8. Ericaceous belt in Chorchora area (3,500 m asl, 6°56′N 39°56′E).
9. Swamp shore areas in Kotera (3,500 m asl, 7°00′N 39°41′E).

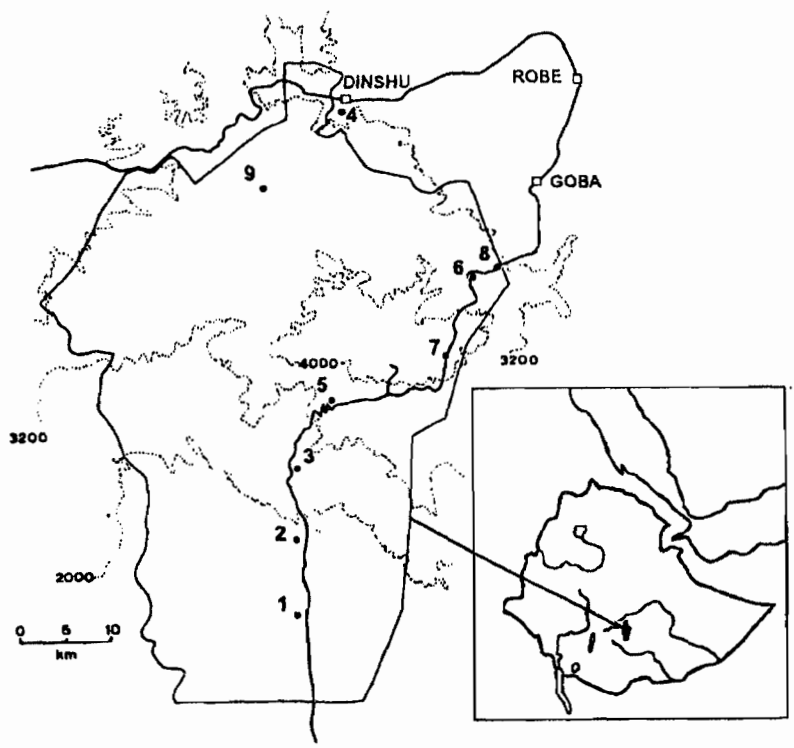

Fig. 1. A map of the Bale Mountains National Park showing trapping sites. See text for abbreviations of localities.

Trapping

All trapping was done with live-traps of three sizes: Sherman traps, Shchipanov's traps (Shchipanov, 1986) and smaller mouse traps. Molerats, *Tachyoryctes splendens* and *T. macrocephalus* were caught by hunting snap-traps (No. 0, 1) in burrows. Field work was carried out within the framework of the Joint Ethio-Russian Biological Expedition (JERBE) between January and April 1995.

Chromosome analysis

Somatic metaphase plates were obtained from bone marrow preparations following the usual air-drying procedure (Ford and Hamerton, 1956). A standard staining was carried out using 4% Giemsa in phosphate buffer at pH 7.

Electrophoretic analysis of proteins

Homogenates for electrophoresis were obtained from portions of blood and kidney tissue crushed in double volume of Protector-E solution (16% saccharose, 0.2% dithiothreitol, 1% phenoxiethanol, 0.2% NADP, 1% $MgCl_26H_2O$, 1% cysteamine-hydrochloride). Standard horizontal starch gel electrophoresis and standard protein staining techniques (Selander *et al.*, 1971; Harris and Hopkinson, 1978) were used to assay twenty nine enzymatic and non-enzymatic proteins from blood and kidney tissues (Table 1).

Table 1. List of proteins examined.

No.	Abbreviation	Name of protein
1	G-6pd	glucose-6-phosphate dehydrogenase
2	Me-1	malic-enzyme-citoplazmatic
3	Me-2	malic-enzyme-mitochondrial
4	Mdh-1	malate dehydrogenase-1
5	Mdh-2	malate dehydrogenase-2
6	Dia-1	diaphorase-1
7	Dia-2	diaphorase-2
8	Hbb	haemoglobin
9	Alb	albumin
10	Adh	alcohol dehydrogenase

Table 1. (Contd).

No.	Abbreviation	Name of protein
11	Sdh	sorbitol dehydrogenase
12	Gdc	glicerophosphate dehydrogenase
13	Idh-1	isocitrate dehydrogenase-1
14	Idh-2	isocitrate dehydrogenase-2
15	Got-1	glutamate-oxaloacetate transaminase-1
16	Got-2	glutamate-oxaloacetate transaminase-2
17	Sod-1	superoxide dismutase-1
18	Sod-2	superoxide dismutase-2
19	Lap-1	leucyl aminopeptidase-1
20	Lap-2	leucyl aminopeptidase-2
21	Ldh-A	lactate dehydrogenase-A
22	Ldh-B	lactate dehydrogenase-B
23	Es-1	esterase-1
24	Es-2	esterase-2
25	Es-3	esterase-3
26	Es-4	esterase-4
27	Es-5	esterase-5
28	Es-7	esterase-7
29	Pabb	prealbumin

RESULTS AND DISCUSSION

A total of 352 small mammals were trapped during the field work (Table 2). In total, all species of small mammals, which were known for the region under study (Yalden, 1988a) were caught. The only exception was the endemic rodent *Megadendromus nikolausi*, described from the Ericaceous belt, 10 km south of Goba (Dieterlen and Rupp, 1978). Study of the type locality showed heavy destruction of the main habitat of this unique species by fire and livestock grazing. It is possible that, *Megadendromus nikolausi* is extinct in this area

now. The most interesting finding was a rodent new to science - *Lophuromys* sp.A. This new form is a sibling-species of *Lophuromys flavopunctatus* and differs from the latter by its soft skin, bright coloration of ventral fur, long tail, small auditory bulla, chromosomal and allozyme characteristics. *Lophuromys* sp.A is a true forest species. It was found in *Podocarpus*, *Aningeria* and *Schefflera* - *Hagenia* belts of the Harenna Forest only. In the last habitat this species coexists with widespread sibling-species *Lophuromys flavopunctatus* **sensu stricto**. We assume that *Lophuromys* sp.A is endemic to the Harenna Forest. A full description of this new species will be made after multivariate analysis of cranial morphology.

Table 2. Small mammals trapped in different sites of the Bale Mountains.

Species	Total caught	Chrom. anal.	Electro-phor. anal.	Trapping sites
Crocidura olivieri	7	3	-	2,3
C. bottegoides	1	1	-	3
C. harenna	8	3	-	3
C. glassi	35	18	23	4,9
C. lucina	31	5	7	6,7,8,9
Mus triton	10	7	6	3
M. mahomet	3	2	2	4
Arvicanthis blicki	1	1	1	7
Praomys albipes	41	6	21	1,2,3,4
Stenocephalemys griseicauda	9	5	8	3,4,5,8,9
S. albocaudata	30	7	15	5,6,7,8,9
Lophuromys flavopunctatus	94	21	70	3,4,6,8,9
Lophuromys sp.A	27	7	14	1,2,3
L. melanonyx	27	8	24	7,9
Otomys sp.A	1	1	1	4
Otomys sp.B	7	6	6	4,7,8,9
Dendromus lovati	2	1	2	4
Dendromus mystacalis	1	-	-	6
Tachyoryctes splendens	12	9	11	3,4
T. macrocephalus	5	3	4	7

Cytogenetic Study

A total of chromosomal sets of 119 small mammals, belonging to 19 species were analyzed using modern cytogenetic techniques (Table 3 and Figs 2–14).

Table 3. Chromosomal data for the studied small mammals.

Species	2n	NFa	X	Y
Insectivora				
Soricidae				
Crocidura bottegoides *	36	48	m	-
C. harenna *	36	50	m	st
C. lucina *	36	50	m	st
Crocidura sp.A*	36	52	m	-
C. glassi *	36	52	m	st
C. olivieri	50	62	m	a
Rodentia				
Muridae				
Mus mahomet	36	34	a	a
M. triton *	34	32	a	a
Praomys albipes	46	58–59	sm	m
Arvicanthis blicki	48	64	sm	m
Stenocephalemys griseicauda A *	54	58	m	-
S. griseicauda B *	54	58	sm	-
S. albocaudata	54	62	m-sm	m
Lophuromys flavopunctatus	68	78	st	a
L. melanonyx	60	90	m	a
Lophuromys sp.A *	54	60	a	a
Dendromus lovati *	44	82	sm	a
Otomys sp. A *	56	54	a	a
Otomys sp. B *	57–58	58	a	a
Rhizomyidae				
Tachyoryctes splendens	48	68–86	m	m
T. macrocephalus *	50	62	m	-

* first description.

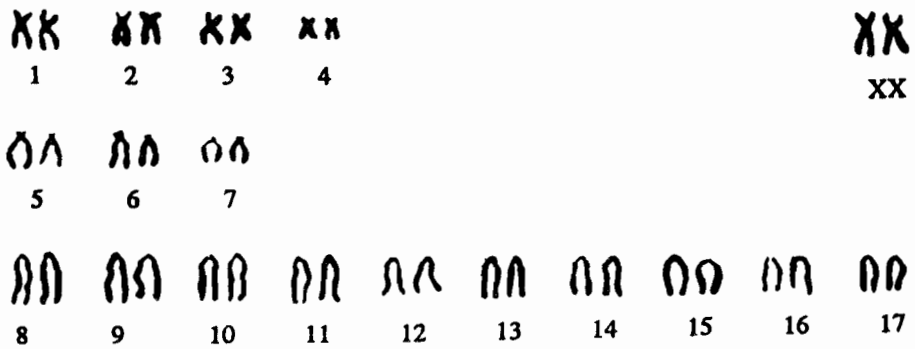

Fig. 2. Karyotype of *Crocidura bottegoides*. Female.

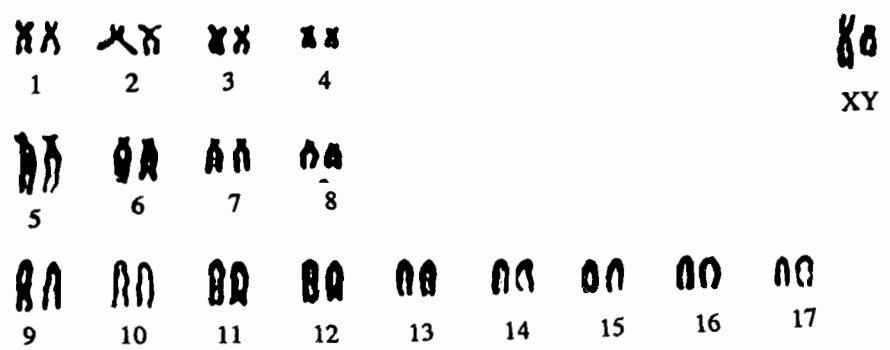

Fig. 3. Karyotype of *Crocidura harenna*. Male.

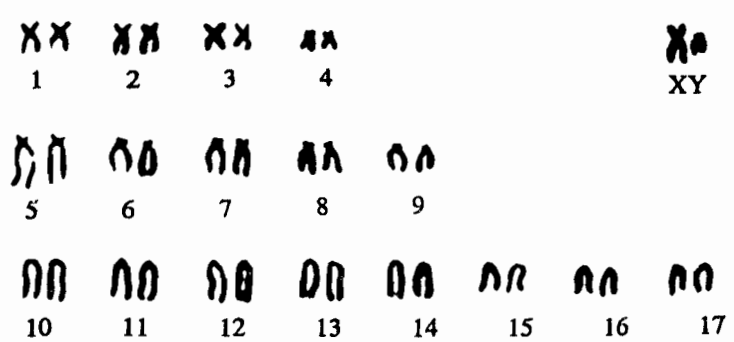

Fig. 4. Karyotype of *Crocidura glassi*. Male.

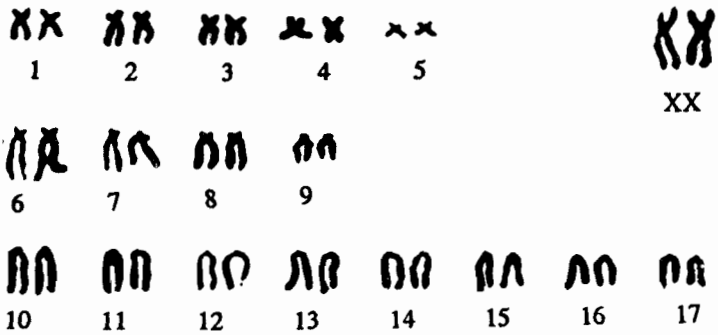

Fig. 5. Karyotype of *Crocidura* sp. A. Female.

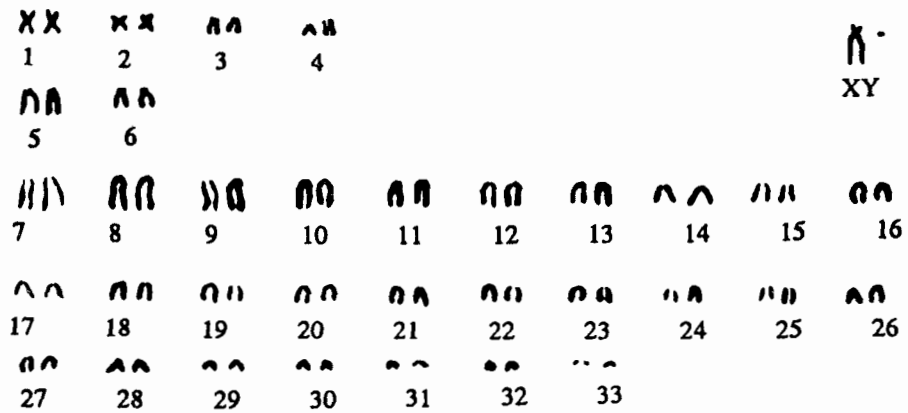

Fig. 6. Karyotype of *Lophuromys flavopunctatus*. Male.

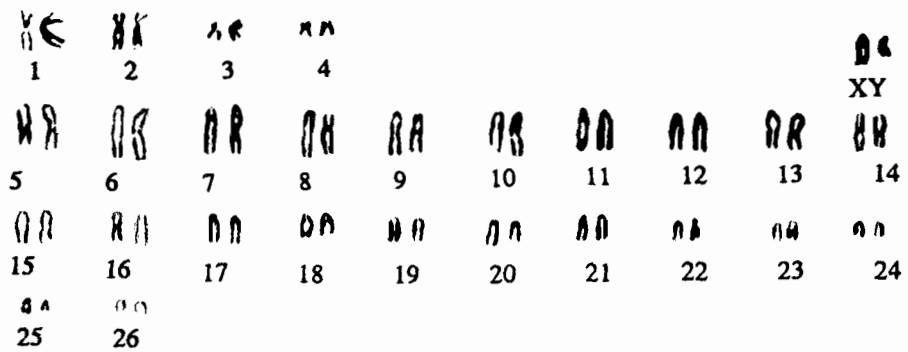

Fig. 7. Karyotype of *Lophuromys* sp. A. Male.

The karyotypes of all *Crocidura* species (excluding *Crocidura olivieri*) consist 36 chromosomes (Figs 2, 3 and 4). The new form *Crocidura* sp.A, with bright reddish dorsal fur, is characterized by the largest metacentric X-chromosome (Fig. 5). There is significant difference between the diploid chromosome numbers of *Lophuromys flavopunctatus* (2n=68, NFa=78) (Fig. 6) and *Lophuromys* sp.A (2n=54, NFa=60) (Fig. 7), which supports species rank of the latter form. The third species of this genus, inhabiting an area of BMNP, exhibits specific karyotype (2n=60, NFa=90) (Fig. 8). Structural characters of the latter strongly differ from that of the other two species. This probably reflects a long evolutionary history of *Lophuromys melanonyx* in connection with the formation of Afroalpine habitat during the Pleistocene period.

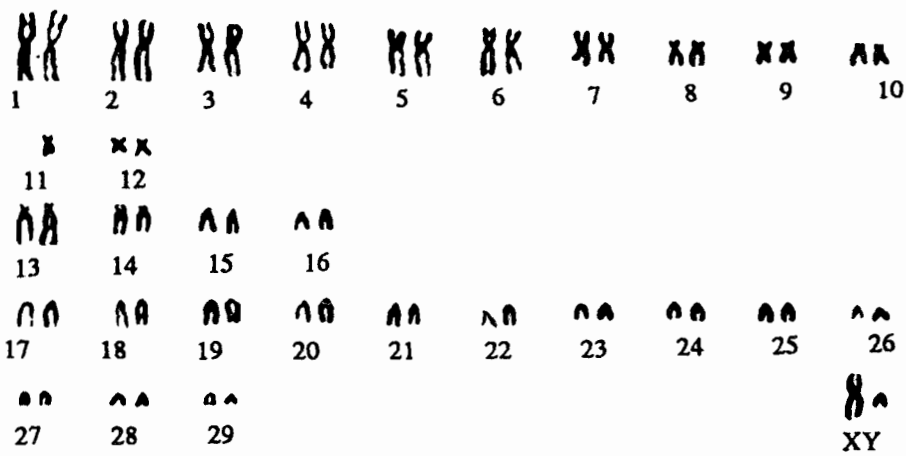

Fig. 8. Karyotype of *Lophuromys melanonyx*. Male.

Similarly, the other high-altitude specialist which is endemic to the Bale Mountains, *Tachyoryctes macrocephalus* (2n=50, NFa=62) (Fig. 9), differs from its close relative, *Tachyoryctes splendens* (2n=48, NFa=68–86) (Fig. 10), in diploid chromosome number. The cytogenetic approach shows coexistence of two chromosomal forms of *Otomys typus* in the region under study. *Otomys* sp.A (2n=56, NFa=54) (Fig. 11) occurs in Dinsho area only, whereas *Otomys*

sp.B (2n=57–58, NFa=58) (Fig. 12) is widespread (Table 2). They coexist in Dinsho area, but hybrids between the two karyological forms have not yet been found. This supports the assumption about species rank of these forms. Two *Stenocephalemys* species, *S. griseicauda* and *S. albocaudata*, have diploid number of 2n=54. On the other hand *S. griseicauda* and *S. albocaudata* are characterized by different fundamental numbers, i.e., NFa=58 and NFa=62, respectively, suggesting that karyotype rearrangements accompanied the differentiation of the genus. Further, two karyomorphs of *S. griseicauda* were encountered, one characterized by metacentric X-chromosome (*S. griseicauda* A) (Fig. 13), the other by submetacentric X-chromosome (*S. griseicauda* B) (Fig. 14).

Allozyme study

A total of 215 specimens of small mammals belonging to 16 species were examined with the use of electrophoretic analysis of proteins (Table 2).

The G-6pd, Dia-2, Hbb and Alb were found to be effective for discrimination between *Lophuromys flavopunctatus* **sensu stricto** and *Lophuromys* sp.A; the Adh, Sdh, Idh-2 and Ldh-B - between *L. flavopunctatus* **sensu lato** and *L. melanonyx* (Table 4). This result supports the rank of "good" species for *Lophuromys* sp.A.

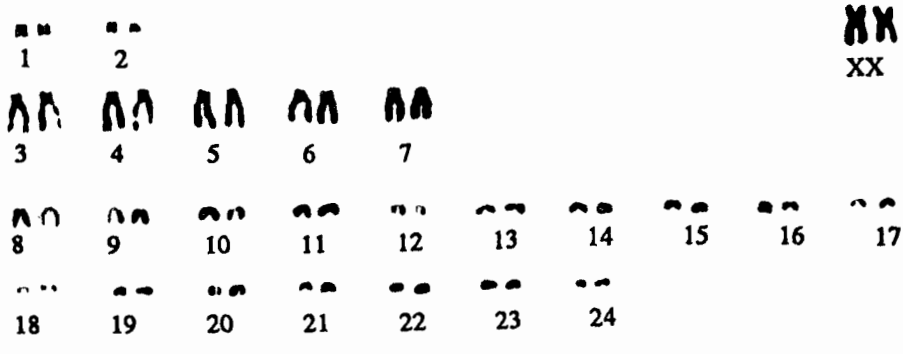

Fig. 9. Karyotype of *Tachyoryctes macrocephalus*. Female.

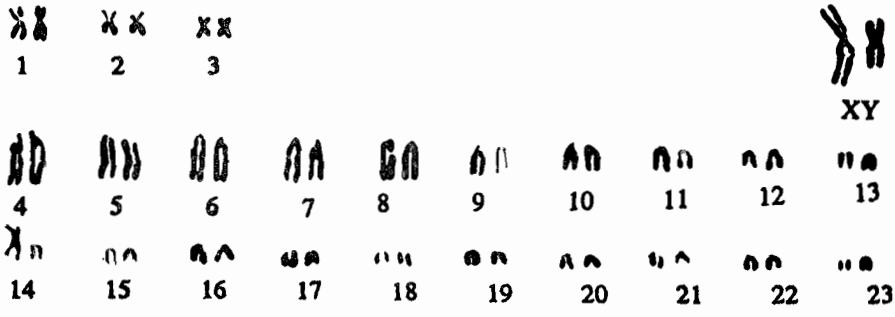

Fig. 10. Karyotype of *Tachyoryctes splendens*. Male.

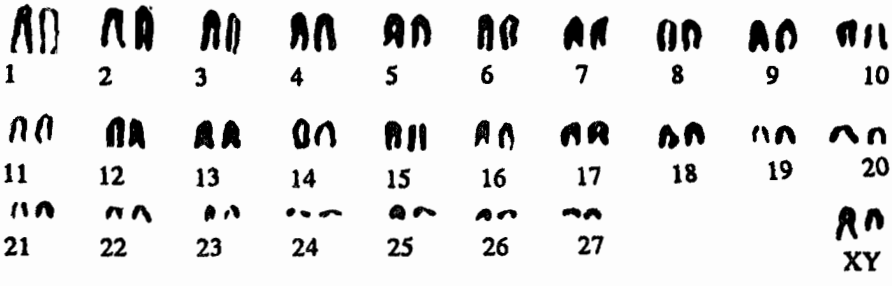

Fig. 11. Karyotype of *Otomys* sp.A. Male.

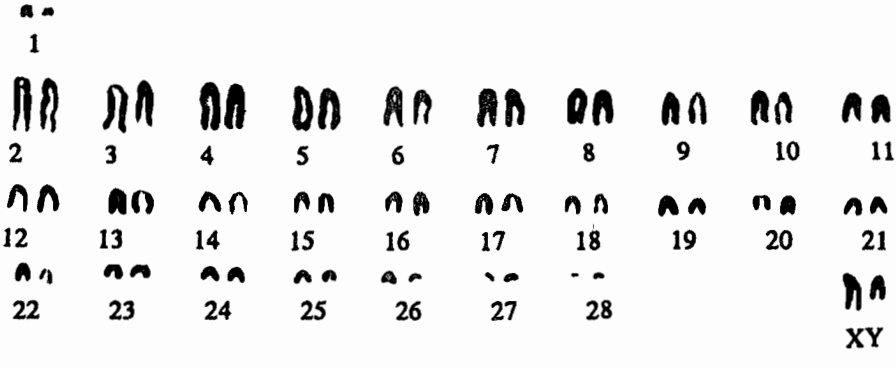

Fig. 12. Karyotype of *Otomys* sp.B. Male.

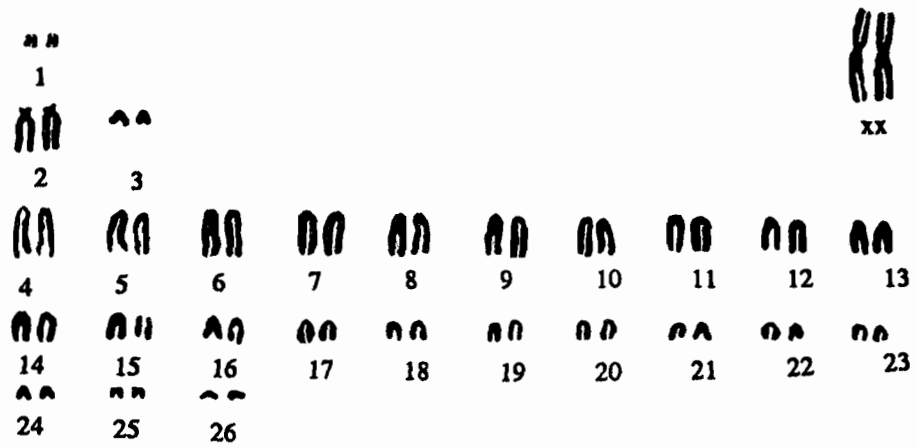

Fig. 13. Karyotype of *Stenocephalemys griseicauda* A. Female.

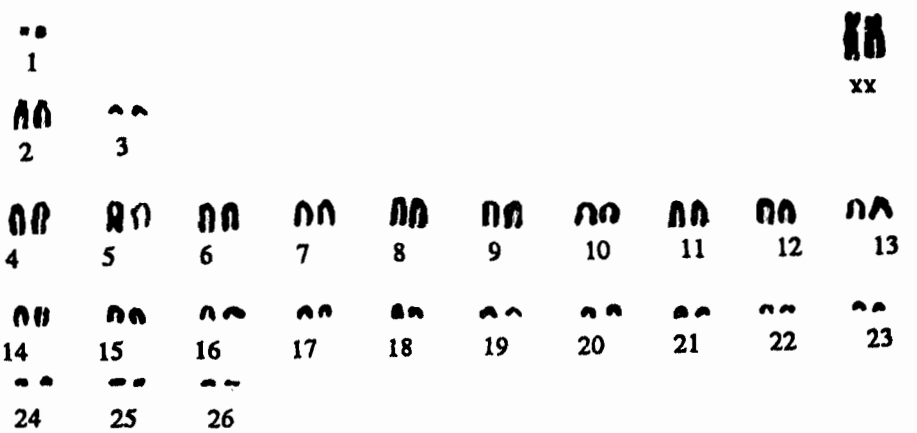

Fig. 14. Karyotype of *Stenocephalemys griseicauda* B. Female.

Further, the significant intraspecific variability on locus Idh-1 was found for different local populations of *L. flavopunctatus* sensu stricto and *L. melanonyx* (Table 4).

Table 4. Genetic loci with fixed diagnostic alleles for Lophuromys species.

Species	L.sp.	L.f.	L.f.	L.f.	L.f.	L.m.	L.m.
Sites	1,2,3	4	3	6,8	9	7	9
N	12	33	2	19	15	21	3
Locus							
G-6pd	b	a	a	a	a	a	-
Dia-2	b	a	a	a	a	a	a
Hbb	a	b	b	-	b	b	-
Alb	a	b	b	b	b	b	-
Adh	b	b	b	b	b	a	a
Sdh	a	a	a	a	a	b	b
Idh-1	b	b,c	b	a,b,c	c	a,b	c
Idh-2	a	a	a	a	a	b	-
Ldh-B	a	a	a	a	a	b	b

Abbreviations: L.sp., *Lophuromys* sp.A; L.f., *L. flavopunctatus*; L.m., *L. melanonyx*.

Allozyme data on *Mus* species show a surprising result. *Mus triton* and *Mus mahomet*, which traditionally belong to subgenus *Nannomys*, differ in 14 out of the 29 loci examined (Table 5). This number reflects distinction on a "good" genus level.

The electrophoretic approach corroborates coexistence of two *Otomys* cryptic species in the region under study. The sole studied specimen *Otomys* sp.A (2n=56) differs from syntopic *Otomys* sp.B (2n=57-58) in three genetic loci (G-6pd, Dia-2, Alb, Got-2). Furthermore the latter form is characterized by the third upper molar possessing seven laminae (5 skulls) and eight laminae (1 skull), whereas the single specimen of *Otomys* sp.A shows six laminae. Yalden and Largen (1992) assumed that Ethiopian *Otomys typus* may be a complex of two or three species, one or more of which may be endemic. There is an obvious genetic intraspecific variability between different local populations of *Otomys* sp.B (Table 6).

Table 5. Genetic loci with fixed diagnostic alleles for *Mus* species.

Species	*M. triton*	*M. mahomet*
Sites	3	4
N	7	2
Locus		
Hbb-2	b	a
Dia-1	b	a
Alb	a	b
Adh	b	a
Sdh	a	b
Idh	b	a,c
Got-1	a	b
Sod-1	a,b	c
Sod-2	b	a
Lap-1	a	b
Ldh-A	a	b
Es-2	a	b
Es-3	a	b
Es-7	a,b	c

A high level of genetic isolation was found between different populations of *Stenocephalemys albocaudata*. Both cytogenetic studies and allozyme analysis support the approach that *S. griseicauda* can be divided into two forms: middle-altitude *S. griseicauda* B (2,400–3,170 m asl, sites 3, 4) and high-altitude *S. griseicauda* A (3,500 m asl, sites 8, 9). The Hbb-2, Me-1, Dia-1 and Sdh were found as diagnostic loci for these groups (Table 7). The problem on taxonomical rank of the two forms will be solved after further multivariate morphological analysis.

Table 6. Genetic loci with fixed diagnostic alleles for *Otomys* forms/populations.

Form	A	B	B	B	B	B	B
2n	56	58	58	57	58	58	58
No.	132	152	232	299	193	281	338
M3/(laminae)	6	7	7	7	8	7	7
Site	4	4	4	4	7	8	9
Locus							
G-6pd	c	b	b	b	b	a	-
Dia-1	b	b	b	b	ab	c	c
Dia-2	c	b	b	b	a	b	b
Alb	b	a	a	-	a	a	-
Gdc	b	b	b	b	b	c	c
Got-1	a	a	-	a	b	c	a
Got-2	a	b	b	b	b	b	b
Ldh-A	a	b	b	b	b	a	-
Ldh-B	a	b	b	b	b	a	-

Table 7. Genetic loci with fixed diagnostic alleles for *Stenocephalemys* species and forms.

Species	S.g.B	S.a	S.a.	S.g.A	S.g.A	S.a.
Sites	3,4	5,7	8	8	9	9
Alt.r.	2,400–3,170	3,700–4,050	3,500	3,500	3,500	3,500
N	6	9	2	1	1	3
Locus						
Hbb-2	c	a	a	a	a	-
Me-1	d,b	a	a	c	c	d
Dia-1	a	b	b	b	b	b
Sdh	b	b	a	a	a	c
Gdc	c	c	c	a	c	c
Idh-1	a	a	a	ab	b	a
Got-1	a	a	c	a	a	a
Ldh-B	b	b	a	b	b	b

Abbreviations: S.g., *Stenocephalemys griseicauda*; S.a., *S. albocaudata*; Alt.r., Altitudinal range (m asl).

The G-6pd, Mdh-2, Alb, Pabl, Idh-1, Got-1, Got-2 and Lap-1 were found to be effective for discrimination between *Tachyoryctes splendens* and *T. macrocephalus* (Table 8). The significant genetic differences reflect an early divergence (probably during Pleistocene) between the two species and an early ecological specialization by *T. macrocephalus* as it started to inhabit the Afroalpine region. The population of *T. splendens* from Katcha area differs from populations studied from the higher altitudes in fixed allele in the Alb locus. This distinction might be connected to adaptation to the different temperature regimes.

Table 8. Genetic loci with fixed diagnostic alleles for *Tachyoryctes* species and populations.

Species	T.s.	T.s.	T.s.	T.m.
Site	4	3	8	7
Alt.r.	3,170	2,400	3,500	4,050
N	4	3	4	4
Locus				
G-6pd	a	a	a	b
Mdh-2	b	b	b	a
Alb	a	b	a	c
Palb	a	a	a	b
Idh-1	a	a	-	b
Got-1	a	a	-	b,c
Got-2	a	a	-	c
Lap-1	b	b	-	a

Abbreviations: T.s., *Tachyoryctes splendens*; T.m., *T. macrocephalus;* Alt.r., Altitudinal Range (m asl).

The Hbb-1, Hbb-2, Me-1, Got-1 and Lap-1 were found as genetic markers for discrimination between *Crocidura glassi* and *C. lucina* (Table 9). Each of the two species is further divided into two syntopic biochemical types. Two biochemical forms of *C. glassi* from Dinsho area differ in the Hbb-1, Me-1, Got-1, Lap-1 and Lap-2. The absence of hybrids between these forms in the area of coexistence supports their species rank. Similar phenomenon was found

for two biochemical and karyotypic forms (*C. lucina* and *Crocidura* sp.A) in the Sanetti Plateau. They differ in the Lap-2 and Es-4 loci. Obviously, the taxonomy of this group is yet an unsolved problem.

Table 9. Genetic loci with fixed diagnostic alleles for some *Crocidura* species and forms.

Species	C.g.	C.g.	C.A.	C.l.
Site	4	4	7	7
N	1	11	1	1
Locus				
Hbb-1	a	b	c	c
Hbb-2	c	c	b	b
Me-1	a	c	b	b
Got-1	b	a	c	c
Lap-1	c	a	b	b
Lap-2	c	a	b	a
Es-4	a	a	b	a

Abbreviations: C.g., *Crocidura glassi*; C.l., *C. lucina*; C.A., *Crocidura* sp.A.

CONCLUSION

The Ethiopian endemic shrew species (*Crocidura glassi, C. harenna, C. bottegoides, C. lucina* and *Crocidura* sp.A) share common diploid number of 36, which was unknown for African Soricidae up to now (Bulatova *et al.*, 1995). Thus, our karyological results show that both forest and montane endemic species of *Crocidura* from the Bale Massif belong to a single phylogenetic cluster despite the high level of morphological diversity. We suppose that the region under study is an ancient centre of speciation for this group and that the Bale Mountains belong to African refuge areas of high diversity and endemism of Soricidae such as Albertine Rift and Mount Cameroon (Hutterer *et al.*, 1987; Nicoll and Rathbun, 1990).

The Bale Mountains support a high diversity of micromammalia. The small mammal species composition of this region is more complex than it has been assumed so far (Yalden, 1988a). The genera *Lophuromys*, *Otomys*, *Stenocephalemys* and *Crocidura* include sibling-species, chromosomal forms and biochemical types inhabiting the region under study. The majority of these new forms are endemics to Bale Mountains. There is an altitudinal zonation of the mammal community (Yalden, 1988a). Cryptic species belonged to superspecies complexes *Lophuromys flavopunctatus* **sensu lato**, *Stenocephalemys griseicauda* **sensu lato** and *Otomys typus* **sensu lato** were found in the different altitudinal belts in the Bale Massif. Further investigation of the distribution and the abundance of endemic sibling-species is indispensable for local conservation activities.

Richness of landscapes, altitudinal zonation and mosaic type of habitats play a major role in determining the intraspecific structure of some species. We found good genetic markers for local populations of some species (*Lophuromys flavopunctatus* **sensu sturcto**, *L. melanonyx*, *Otomys* sp.B, *Stenocephalemys albocaudata*, *Tachyoryctes splendens*) reflecting a strong isolation from other conspecific populations and, probably adaptations to native environments. Thus, the problem of delimitation of conservation units (Vogler and DeSalle, 1994) is very urgent. It is necessary to elaborate a conservation strategy in order to maximally preserve diversity of endemic small mammals in this region.

The most endangered habitats for small mammals in the BMNP are the valleys of streams in Katcha area of the Harenna Forest. These are inhabited by endemic and rare species (*Crocidura bottegoides*, *C. harenna*, *Mus triton* and *Lophuromys* sp.A); and the erica bush in Chorchora area where the unique endemic rodent *Megadendromus nikolausi* probably remains still. In view of the rapid rate of destruction of these habitats by fire, tree felling and heavy livestock grazing, urgent conservation actions are needed.

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