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Morphometric and genetic study of Ethiopian *Lophuromys flavopunctatus* THOMAS, 1888 species complex with description of three new 70-chromosomal species (Muridae, Rodentia)

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Abstract

Morphological (multivariate craniometry) and genetic (cytochrome b sequence) analyses combined with available chromosome and RAPD data were performed to clarify species limits, distribution, and relationships in the diverse *Lophuromys flavopunctatus* species complex of Ethiopia. This approach allowed us to evaluate real taxonomic diversity of the group and describe three new species. The revealed level of interspecific morphological diversity in *L. flavopunctatus* s. lat. was significantly higher among Ethiopian taxa compared to non-Ethiopian ones. Moreover, the results of multivariate analyses of craniometric data provide independent support for our earlier supposition about the presence of both recent and ancient reticulate processes among Ethiopian *Lophuromys* species. In general, the results of our study support the recognition of nine distinct species (including newly described ones), all of which are endemic to this country. The current diversity of the group could be explained by intensive local speciation and accumulation of survived evolutionary lineages within the Ethiopian Plateau. Most of the Ethiopian members of this species complex are closely associated with montane forests; some of them have rather limited geographic ranges and seem to be threatened due to habitat destruction.

Key words: Rodentia, Ethiopia, *Lophuromys*, taxonomy, morphometrics, cytochrome b, hybridization, biodiversity.

INTRODUCTION

The "speckled brush furred" rats assigned to the *Lophuromys flavopunctatus* THOMAS, 1888 species complex are widely distributed in moist bush and forest vegetation from North-Eastern Angola through Eastern Congo, Uganda, Kenya, and south through Tanzania, Malawi, Northern Zambia, and Northern Mozambique (DIETERLEN, 1976; MUSSER & CARLETON, 1993; VERHEYEN *et al.*, 2002). Northern (Ethiopian) part of the range of this species complex is separated from its main part by dry lowland uninhabitable for *Lophuromys* (KINGDON, 1974). The isolated position attributes particular interest to Ethiopian *L. flavopunctatus* s. lat. which is presumably evolved in the area under isolation. The taxonomy of the Ethiopian *L. flavopunctatus* s. lat. has had a turbulent history. Seven taxa have been described from Ethiopia, based on the considerable variation in pelage colouration and external and cranial measurements: *L. flavopunctatus* THOMAS, 1888; *L. zaphiri* THOMAS, 1906; *L. aquilus brunneus* THOMAS, 1906; *L. flavopunctatus simensis* OSGOOD, 1936; *L. brevicaudus* OSGOOD, 1936; *L. aquilus chrysopus* OSGOOD, 1936 and *Neanthomys giaquintoi* TOSCHI, 1946 (the last taxon was based upon a *Lophuromys* specimen with lost tail, TOSCHI, 1963). Until recently, all these taxa were lumped under *L. flavopunctatus* (YALDEN, LARGEN & KOCK, 1976; YALDEN *et al.*, 1996; MUSSER & CARLETON, 1993; AFEWORK BEKELE & CORTI, 1994). Furthermore, large *L. melanonyx* PETTER, 1972 is known only from a restricted range in the Bale Mountains and the vicinities of Debre Sina (YALDEN, LARGEN & KOCK, 1976). Although this specialized Afroalpine species is morphologically well differentiated from any other representative of the *Lophuromys flavopunctatus* s. lat., it was supposedly considered to be a part of this species complex as well (LAVRENCHENKO, VERHEYEN & HULSELMANS, 1998). Therefore, only two *Lophuromys* species have been recognised from Ethiopia: *L. flavopunctatus* widespread throughout most of Central and East Africa and endemic *L. melanonyx*. Recent chromosomal, allozyme, RAPD PCR, and morphometric studies revealed the presence of three more distinct species, endemic to Ethiopia: *L. chrysopus* OSGOOD, 1936 (2n=54), *L. brevicaudus* OSGOOD, 1936 (2n=68), and *L. brunneus* THOMAS, 1906 (2n=68) (ANISKIN *et al.*, 1997; LAVRENCHENKO *et al.*, 1998; LAVRENCHENKO *et al.*, 2001).

The latest study based upon on mtDNA, RAPD PCR and chromosomal data (LAVRENCHENKO *et al.*, 2004) of new material collected in south-western, eastern and northern Ethiopia demonstrated that species diversity of Ethiopian *Lophuromys* could be far higher than it was suspected. Species rank was supported for the recently re-described *L. chrysopus* and *L. brevicaudus* (LAVRENCHENKO *et al.*, 1998), while two well-differentiated (at approximately species-rank level) mitochondrial lineages "Flav-Brun" and "Brun-I" (sharing 2n=68) were supposedly associated with two other described taxa, *L. flavopunctatus* and *L. brunneus*. Moreover, the molecular (mtDNA and RAPD) data suggested the existence of three new potential species, corresponding to the following mitochondrial groups: "Chercher", "Menagesha" and "cf. sikapusi". To assess whether or not these "cryptic" forms merit species status requires further detailed morphometrical study. The representatives of these three mtDNA lineages share identical karyotype (2n=70, NFa=84) which was unknown for Ethiopia so far. As followed from RAPD data two further mitochondrial groups from the north of Ethiopia possessing the same 70-chromosomal karyotype ("North-I" and "North-II") might be conspecific and were tentatively attributed to *L. simensis* OSGOOD, 1936. Furthermore, analysis of RAPD data suggested that at least two mtDNA types might have been subject to interspecific transfer due to hybridization. In case of two sympatric haplotypes of *L. brunneus* we assumed that the contemporary pattern of variation between them can be explained by relatively recent hybridization with another distinct species *L. flavopunctatus*. The formation of two groups ("North-I" and "North-II") belonging to distinct mitochondrial lineages within northern populations was associated with more complex processes including ancient hybridization (LAVRENCHENKO *et al.*, 2004). Finally, this analysis demonstrated that all Ethiopian *Lophuromys* (including morphologically substantially divergent *L. melanonyx*) belong to the *L. flavopunctatus* species complex.

During trapping sessions of rodents in the Simien Mountains National Park (Northern Ethiopia) in 2005 the senior author collected sizable topotypical series of *L. simensis*. Together with other important series collected in south-western, eastern and northern Ethiopia between 1998 and 2004 (see above), this *simensis*-material allows us to revise the taxonomy of the Ethiopian members of the *L. flavopunctatus* species complex and to describe three new species. The present systematic reevaluation of this diverse group is mainly based on multivariate morphometrics combined with molecular study (cytochrome b sequence). Because of the evidence of reticulation among Ethiopian *Lophuromys* and restricted size of a few key samples we integrate, where necessary, current data and the results of our previous cytogenetic and RAPD analyses published earlier (LAVRENCHENKO *et al.*, 2004).

MATERIAL AND METHODS

The specimens

This study is largely based on extensive collections that are the result of 11 field trips in Ethiopia, realized between 1995 and 2005 by the Mammal Research Group of the Joint Ethio-Russian Biological Expedition (JERBE). All voucher specimens are housed at the Zoological Museum of the Moscow State University (ZMMU), Russia. Where necessary, our study material was completed with skulls and skins from other museums. In appendix 1 we have grouped the specimens examined and measured per OTU. For each OTU the number of specimens, classified by sex, is provided. For the description of the acronyms that identify the museums and institutions were these specimens are curated, we refer to VERHEYEN *et al.* (1996). Table 1 is an alphabetical listing of the collecting localities, followed by their geographical co-ordinates and the OTU numbers into which the localities are included. Fig.1 visualizes the geographical distribution of the OTU's. Part of this material was included in our previous revision of the *L. flavopunctatus* species complex (VERHEYEN *et al.*, 2002), which, however, was focused particularly on the non-Ethiopian representatives of the group. Moreover, for comparative analyses in the present study we use some of these non-Ethiopian OTU's. Hence, we use the same OTU's numbering as in this paper (see appendix 2 in VERHEYEN *et al.*, 2002). For the relevant data concerning the type specimens of the *L. flavopunctatus* species group (type-localities, geographical co-ordinates etc…) and their skull-measurements see appendices 1.1 and 1.2 in VERHEYEN *et al.* (2002).

Morphometry

We apply the same standardized methodology that we used in our former publications on *Lophuromys* (VERHEYEN *et al.*, 1996, 2000, 2002, LAVRENCHENKO *et al.*, 1998). Here we only recall some of the essentials. All skulls are grouped into age-classes using tooth eruption and tooth-wear patterns as described in

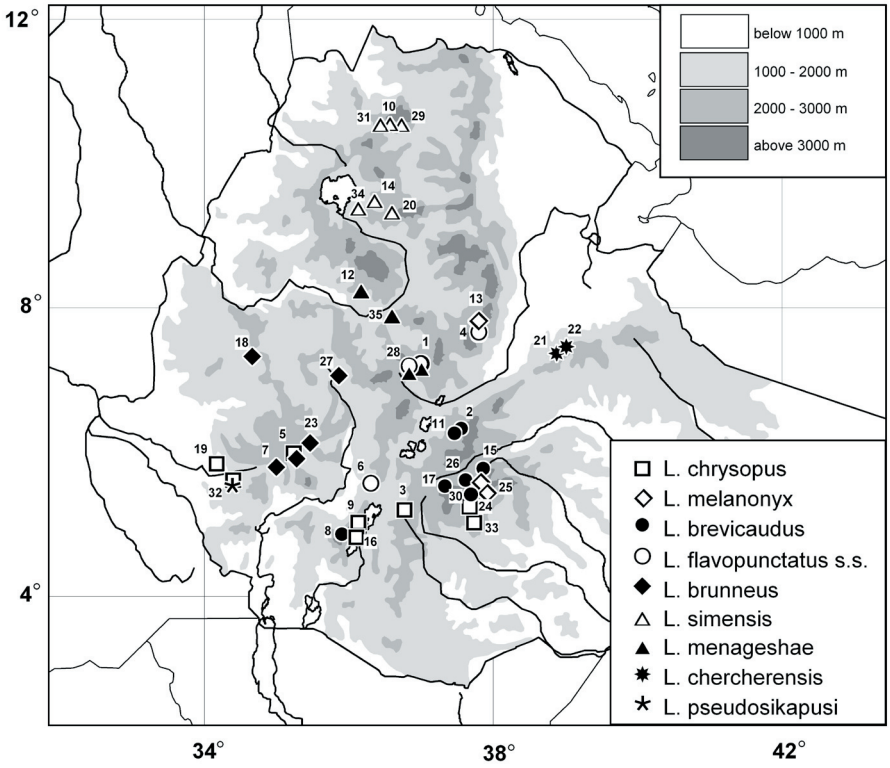


Fig. 1.
Schematic representation of the geographic distribution of the collecting localities of the Ethiopian *Lophuromys*. The numbers of the localities refer to table 1 where co-ordinates and altitudes are mentioned.

REF NR.	LOCALITY	COORDINATES	ALT.	OTU
1	Addis Ababa	09.02N-38.45E	2600	34, 700
2	Albasso Mt. (=Mt. Badda)	07.55N-39.27E	3300	*brevicaudus* – type loc.
3	Allata (Alleta), Sidamo	06.33N-38.28E	2500	*chrysopus* – type loc.
4	Ankober	09.35N-39.45E	3000	34, *flavopunctatus* - type loc.
5	Beletta Forest	07.32N-36.33E	2050	36, 39
6	Bodeli, Walamo	06.58N-37.53E	1900	*zaphiri* – type loc.
7	Bonga	07.15N-36.15E	1900	36
8	Bonke	06.05N-37.23E	3200	-
9	Chencha	06.20N-37.40E	2500	-
10	Chennek, Simien Mts	13.15N-38.13E	3800	40
11	Chilalo Mts	07.50N-39.20E	-	37
12	Debre Markos	10.21N-37.43E	2500	700
13	Debre Sina, 4 km S of	09.50N-39.44E	3300	-
14	Debre Tabor, 10 km W of	11.55N-37.57E	2550	51
15	Dinshu, Bale	07.06N-39.47E	3200	35, 37, *melanonyx* - type loc.
16	Dorsey	06.13N-37.40E	2400	-
17	Gedeb Mts	06.55N-39.10E	-	-
18	Ghimbi, Wollega	09.10N-35.50E	2150	-
19	Godare Forest	07.21N-35.13E	1200	503
20	Guna, Mt.	11.43N-38.15E	3800	51
21	Hhirna	09.13N-41.06E	2000	500
22	Hirna, 22 km NE of	09.20N-41.16E	2700	500
23	Jimma	07.40N-36.50E	1800	36
24	Katcha, Harenna	06.42N-39.44E	2400	37, 38
25	Konteh, Mt.	06.51N-39.53E	4050	35
26	Kotera, Bale	07.00N-39.41E	3500	35, 37
27	Manno	08.50N-37.20E	2800	*brunneus* - type loc.
28	Menegesha	08.57N-38.33E	2600	34, 700
29	Ras Dasham	13.14N-38.25E	3400	*simensis* - type loc.
30	Rira, Harenna	06.45N-39.44E	2760	37, 38
31	Sankaber, Simien Mmts	13.14N-38.03E	3250	40
32	Sheko	07.04N-35.30E	1930	39, 800
33	Shisha River, Harenna	06.27N-39.44E	1680	38
34	Vanzaye	11.47N-37.40E	1800	51
35	Yah Yah	09.55N-38.15E	2100	700

Table 1.
Alphabetical gazetteer of the collecting localities of the Ethiopian *Lophuromys*. The localities are followed by their co-ordinates and approximate altitudes (m). The numbers preceding the localities refer to Fig. 1 illustrating the distribution of the species.

Table 2. A summary of the measurements used in this study. For a full description we refer to Verheyen *et al.* (1996).

NUMBER	ACRONYMS	MORPHOMETRICAL CHARACTERS
	W	weight
	HB	head and body length
	TL	length of tail
	HF(-n)	length of hind-foot (-nail)
	HF (+n)	length of hind-foot (+nail)
	EL	length of ear
M 1	GRLS	greatest length of skull
M 2	PRCO	condylobasal length
M 3	HEBA	henselion-basion
M 4	HEPA	henselion-palation
M 5	PAFL	length of palatal foramen
M 6	DIA1	length of diastema
M 7	DIA2	distance between alveolus M^1 and cutting edge of upper incisor
M 8	INTE	smallest interorbital breadth
M 9	ZYGO	zygomatic breadth
M 10	PALA	smallest palatal breadth
M 11	UPTE	length of upper cheekteeth
M 12	UPDA	breadth of upper dental arch
M 13	M^1BR	greatest breadth of first upper molar
M 14	ZYPL	smallest breadth of zygomatic plate
M 15	BNAS	greatest breadth of nasals
M 16	LNAS	greatest length of nasals
M 17	LOTE	length of mandibular teeth
M 18	CHOB	greatest breadth of choanae
M 19	BULL	length of auditory bulla
M 20	BRCA	greatest breadth of braincase
M 21	DINC	depth of upper incisor
M 22	ROHE	mediosagittal projection of rostrum heigth
M 23	ROBR	greatest rostrum breadth
M 24	PCPA	distance between coronoid and angular processes

VERHEYEN *et al.* (1996); we also use the same cranial and external measurements and the same acronyms (ibid). The cranial measurements were taken with callipers with digital reading graduated to hundreds of millimetres, but were recorded with a precision of 0.05 mm. In addition, standard external dimensions and weight (in grams) were transcribed from skin tags as given by the collector. To facilitate interpretation of our results in the present paper, we include in table 2 the description of these measurements accompanied by their acronyms.

Standard descriptive statistics, Students t-tests and one-way ANOVA were derived for the OTU's. Principal Components were extracted from the variance-covariance or correlation matrix and computed using raw or log-transformed (Log_{10}) metrical data. Multiple Discriminant Analyses (Canonical Analyses) were executed on raw untransformed metrical data. Tree-diagrams were constructed based on the Mahalanobis squared distances between OTU's centroids using the Unweighted Pair Group Arithmetic Average method (UPGMA). This approach accounts for all the relevant axes in the canonical hyperspace. All univariate and multivariate analyses were performed on a PC with statistical package STATISTICA 6.0 (Statsoft, Inc.). . (Statistical analyses were always carried out using the whole set of available data regardless of sex, but excluding data from specimens of age classes 0 and 5. Sometimes missing data are replaced by group means.

DNA METHODS

All tissue samples that were used for this study were collected in the course of the Joint Ethio-Russian Biological Expedition (JERBE) between 1997 and 2005. All tissues were stored in ethanol at 4°C. DNA was extracted from 96% alcohol preserved heart, liver and kidney tissue by the standard phenol-chloroform method (MATHEW, 1984). We amplified and sequenced a 402 bp segment of the cytochrome-b gene (from position 14139 to 14540 on the mitochondrial DNA sequence of *Mus musculus* (BIBB *et al.*, 1981). The primers used to amplify the cytochrome-b segment were L13724 (5'-CGAAGCTTGATATGAAAAACC ATCGTTG-3') and H14139 (5'-AAACTGCAGCCC CTCAGAATGATATTTGTCCTCA-3') (KOCHER *et al.*, 1989) and the PCR reaction was done using the protocols given in KOCHER *et al.* (1989). The PCR-products were cycle-sequenced with the H14139-primer according to the manufacturer's protocol (Amersham Pharmacia Biotech), using 0.8 μM primer, 2.5 units of Taq polymerase and approximately 0.15-0.20 μg of the PCR product. The cycle-sequencing reaction consisted of 30 cycles: 36 s at 94°C, 36 s at 52°C and 80 s at 72°C. Sequences were read and aligned by eye. The obtained nucleotide sequences were imported in Mega 2.1 for analyses (KUMAR *et al.*, 2001).

RESULTS

1. Preliminary craniometric characterization of newly collected samples

Before a regrouping of some newly collected samples which were not included in our previous analyses (LAVRENCHENKO *et al.*, 1998; VERHEYEN *et al.*, 2002) we evaluated their morphometric similarities with other relevant OTU's.

1.1. Craniometric variation within 70-chromosomal Ethiopian *Lophuromys*

The representatives of four new OTUs (51: area between Tana Lake and Mount Guna; 40: Simien Mountains; 500: Chercher Mountains; 700: Menagesha) and two specimens of *Lophuromys* cf. *sikapusi* from the Sheko Forest (OTU 800) share identical karyotype (2n=70, NFa=84) which clearly differentiated them from all other Ethiopian *Lophuromys*. Principal component analysis reveals that scores representing specimens from the Simien and Tana intermingle to form a single cluster slightly overlapping with two other clusters formed by scores of specimens from Chercher and Menagesha (see graph 1). The type of *simensis* clearly falls within the cloud of scores derived from the Simien and Tana samples. Two specimens of *L.* cf. *sikapusi* occupy marginal placement within the Chercher cluster.

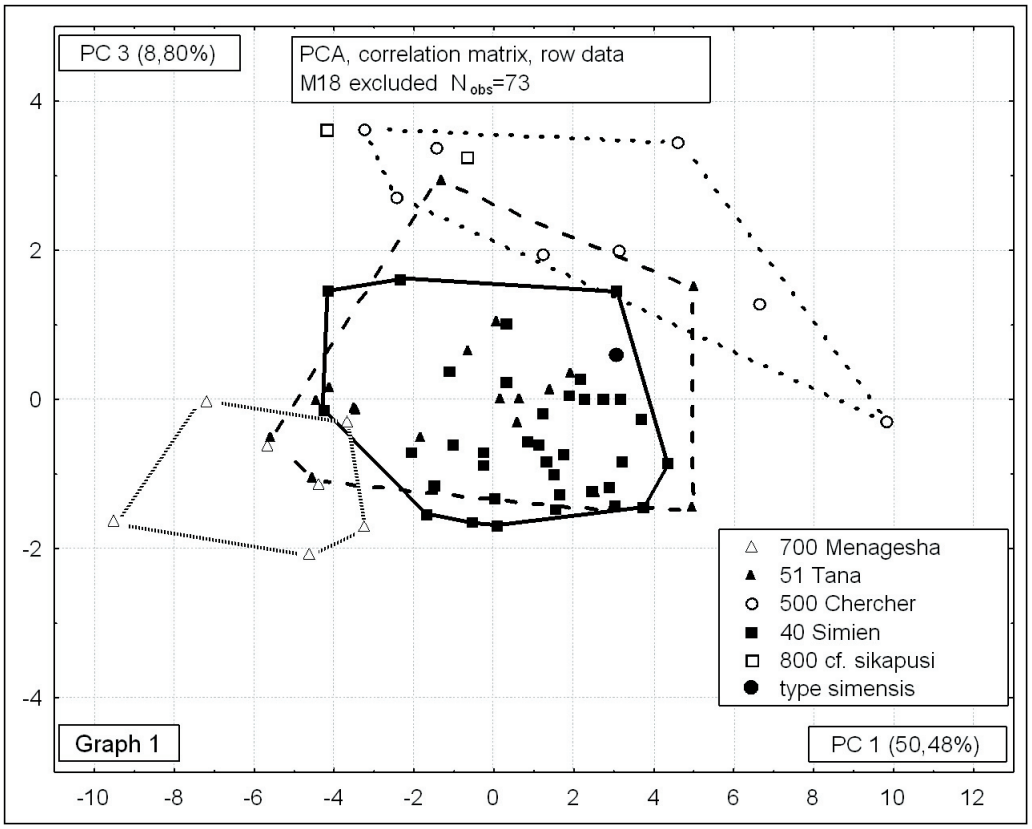
Results of canonical analysis also highlight the same pattern revealed by principal component analysis. We see that OTU 51 (Tana Lake) coincides with topotypical *simensis* (OTU 40) slightly overlapping with OTUs 500 (Chercher) and 700 (Menagesha) which are clearly differentiated from each other (see graph 2). The specimens of *L.* cf. *sikapusi* plot within OTU 500. In view of their craniometrical similarity and genetic identity (see ch. 4) samples from the Simien and Tana can be regrouped in one OTU 40+51 that we assign to *L. simensis*. All other 70-chromosomal forms (OTUs 500, 700 and *L.* cf. *sikapusi*) will be described as new taxa (see ch. 6).

1.2. Craniometric variation within *Lophuromys chrysopus*

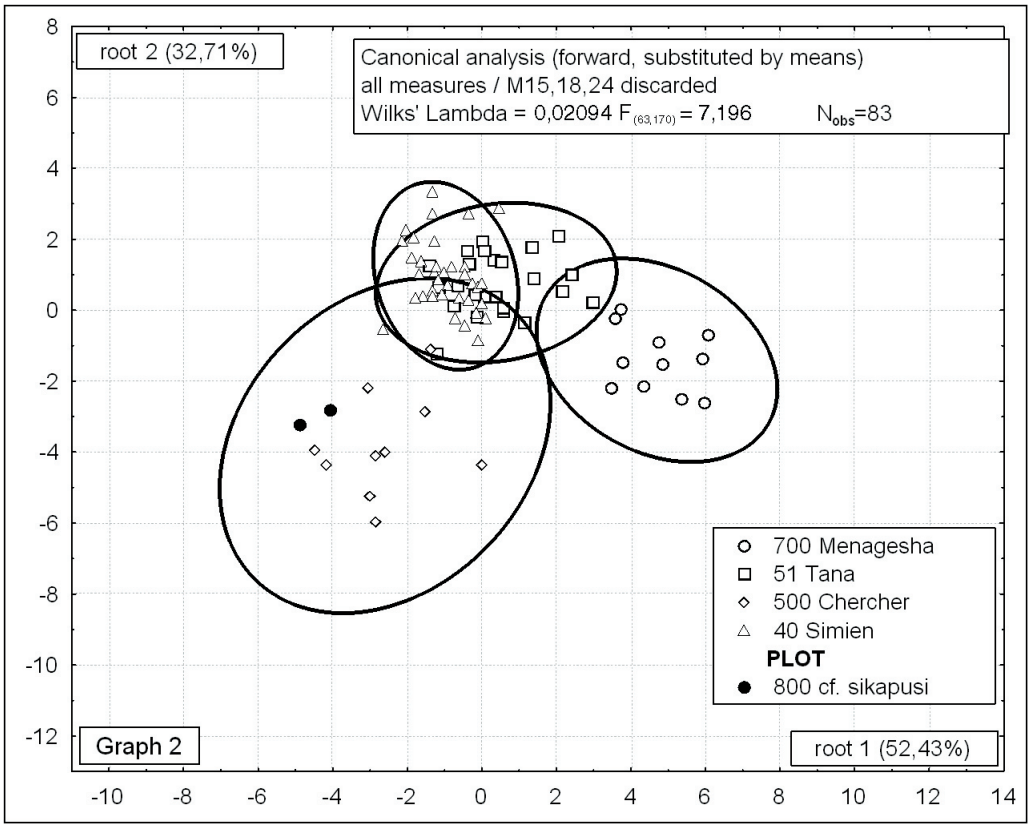
According to cytogenetic and genetic data our newly collected sample from the Godare Forest can be undoubtedly identified as *L. chrysopus* (LAVRENCHENKO *et al.*, 2004). Canonical analysis reveals that samples of this species from eastern (OTU 38) and western (OTU 39) sides of the Ethiopian Rift Valley overlap completely, whereas the new sample from the Godare Forest (OTU 503) is partly differentiated from them along the second axis (see graph 3). This is a rather unexpected result, taking into account significant intraspecific level of genetic divergence between OTU 38 and OTU 39 and genetic identity of the latter with the Godare sample (LAVRENCHENKO *et al.*, 2004). We assume that the slight craniometrical differentiation of the Godare population can be adaptation to its habitat (lowland tropical evergreen rain forest) at lowest altitudinal limit for *L. chrysopus* (1200 m a.s.l.). Nevertheless, in all performed canonical analyses the Godare sample closely clusters with OTUs 38 and 39, being clearly separated from any other Ethiopian OTU. Therefore, for the further analyses we regroup all our samples of this species into one OTU 38+39+503 (*L. chrysopus*).

2. Craniometric differentiation between some Ethiopian *Lophuromys*

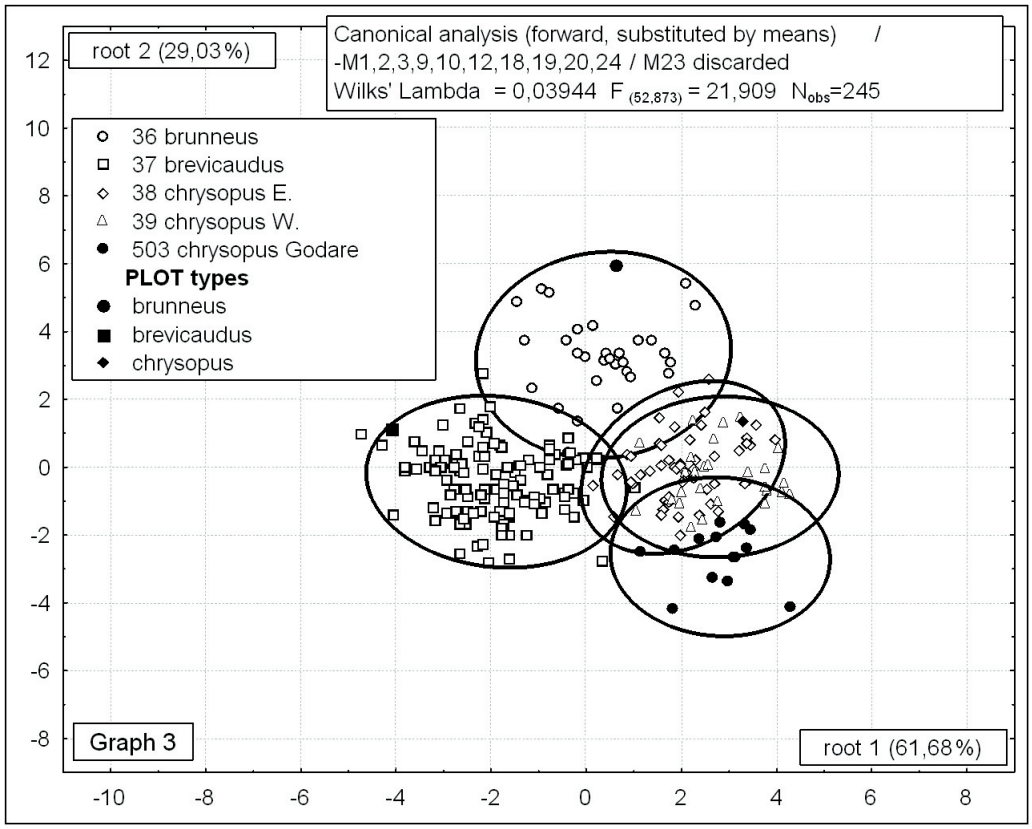
Since *L.* cf. *sikapusi*, recently found in southwestern Ethiopia, possesses "unspeckled" pelage which is very



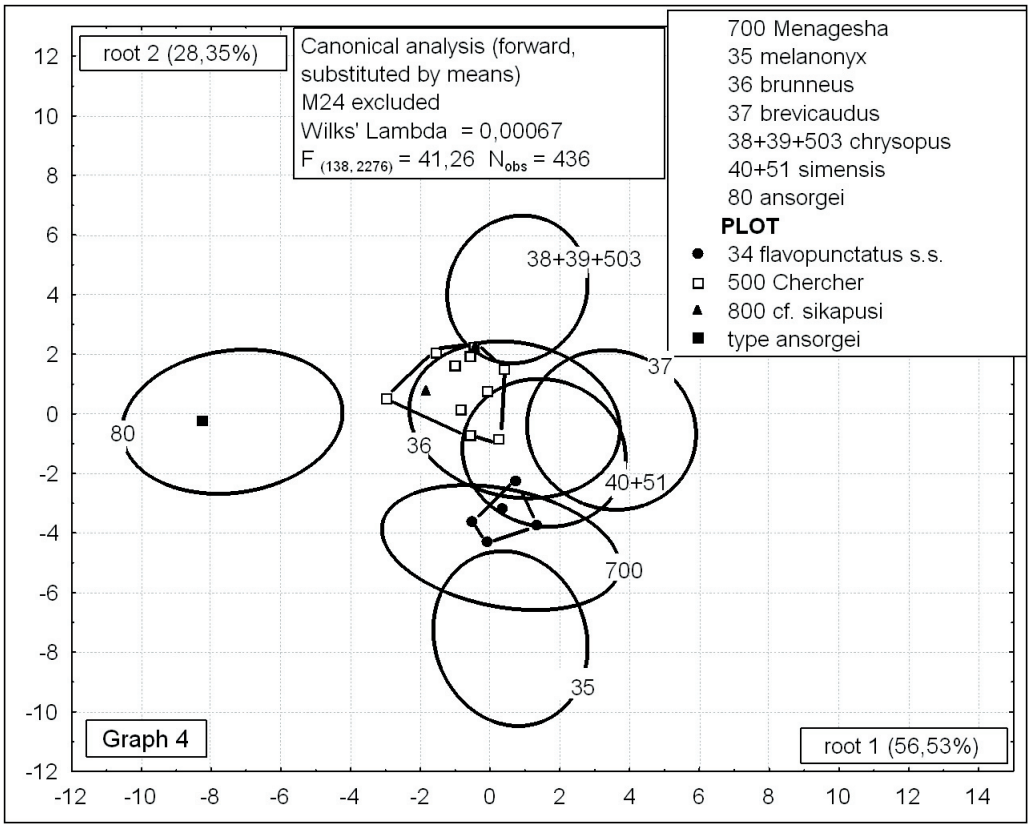
Graph 1.
Graphic representation of a principal component analysis performed on the 70-chromosomal Ethiopian *Lophuromys* OTU's (40, 51, 500, 700, 800) and the type specimen of *L. simensis*.



Graph 2.
Graphic representation of a forward canonical analysis of four 70-chromosomal Ethiopian *Lophuromys* OTU's (40, 51, 500, 700). The two specimens of *L.* cf. *sikapusi* from the Sheko Forest (OTU 800) are plotted.

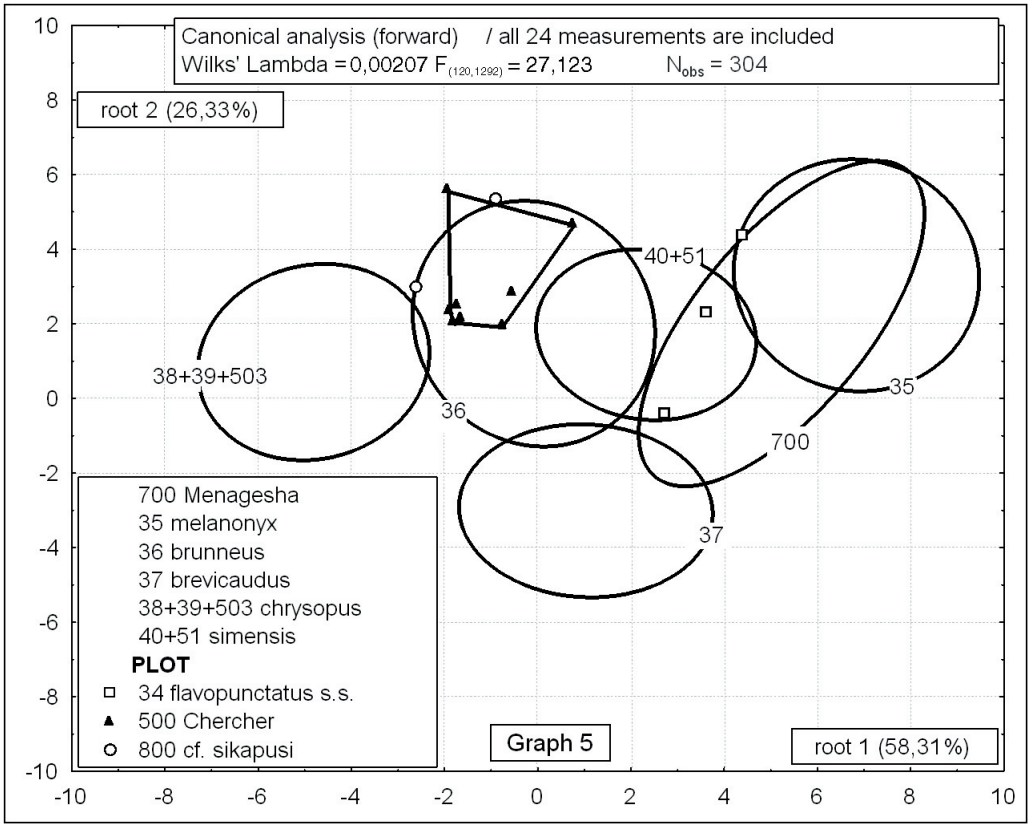


Graph 3.
Graphic representation of a forward canonical analysis of three *L. chrysopus* OTU's (38, 39, 503) compared with *L. brunneus* (OTU 36) and *L. brevicaudus* (OTU 37). The relevant type specimens are plotted.

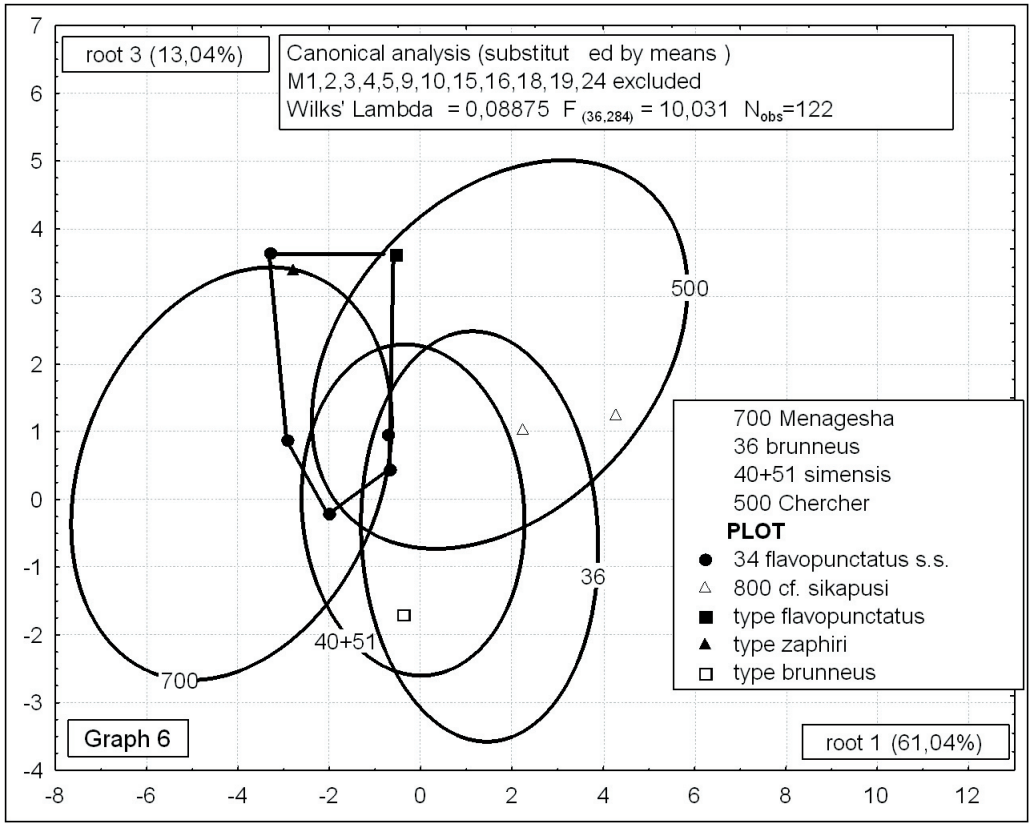


Graph 4.
Graphic representation of a forward canonical analysis performed on the Ethiopian *Lophuromys* OTU's (35, 36, 37, 38+39+503, 40+51, 700) compared with *L. ansorgei* (OTU 80). The samples with n ≤ 10 (OTU's 34, 500, 800) and the type specimen of *L. ansorgei* are plotted.

Graph 5.
Graphic representation of a forward canonical analysis of six Ethiopian *Lophuromys* OTU's (35, 36, 37, 38+39+503, 40+51, 700) providing the background to allocate by plotting the samples with n ≤ 10 (OTU's 34, 500, 800).



Graph 6.
Graphic representation of a forward canonical analysis of four Ethiopian *Lophuromys* OTU's (36, 40+51, 500, 700) providing the background to allocate by plotting the samples with n ≤ 5 (OTU's 34, 800) and the relevant type specimens.



uncommon for *L. flavopunctatus* s.lat. but typical for *L. sikapusi* s.lat., firstly we compared all Ethiopian material with a representative of the latter species complex in East Africa, *L. ansorgei*. The results of a canonical analysis reveal that these two species groups are really separated from each other; two specimens of *L.* cf. *sikapusi* being plotted clearly fall within Ethiopian *L. flavopunctatus* s.lat. Nevertheless, among all Ethiopian forms, *L.* cf. *sikapusi* together with OTU 500 (Chercher) occupies closest position to *L. ansorgei* (see graph 4). As it will be shown below (see ch. 6.3), *Lophuromys* from the Chercher Mountains demonstrates some intermediate stage between "speckled" and "unspeckled" pelage. This is in concordance with the results of our previous molecular phylogenetic analysis suggesting that *L.* cf. *sikapusi* undoubtedly belongs to the Ethiopian *L. flavopunctatus* species group and its superficial similarity with *L. sikapusi* s.lat. can be considered as a result of convergent evolution in a similar environment of evergreen tropical rain forest (Lavrenchenko *et al.*, 2004).

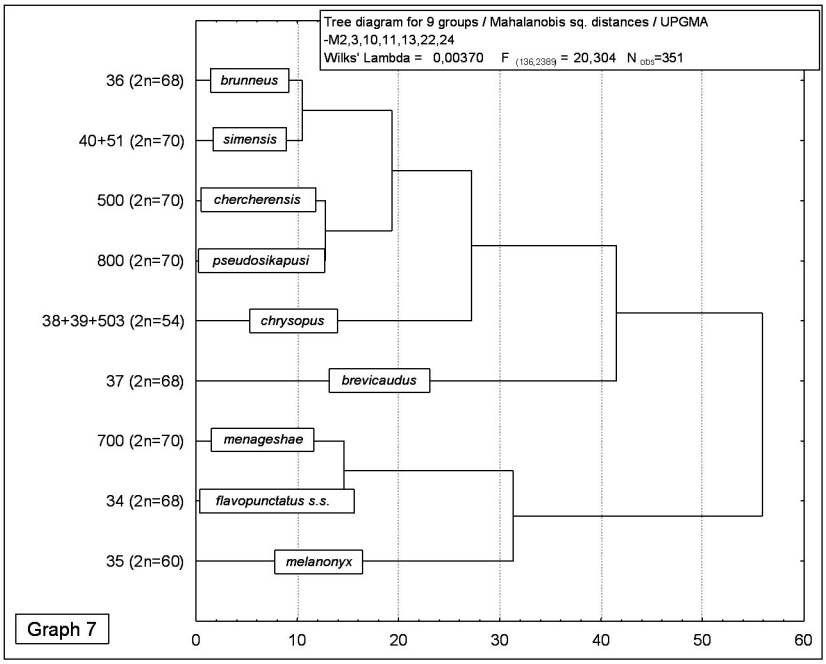
Graph 5 represents the results of a canonical analysis that involves all available Ethiopian OTU's. After plotting specimens from small ($n < 10$) samples we see that they clearly fall outside the 95% equal probability ellipses of the groups sharing the same chromosomal number. Thus, *L.* cf. *sikapusi* and the sample from the Chercher Mountains are undoubtedly distinct from 70-chromosomal *L. simensis* (OTU 40+51) and Menagesha (OTU 700), whereas *L. flavopunctatus* s.str. is distant from 68-chromosomal *L. brunneus* (OTU 36) and *L. brevicaudus* (OTU 37). From the next canonical analysis (graph 6) we excluded some OTU's (OTU 38+39+503: *L. chrysopus*, OTU 35: *L. melanonyx*, OTU 37: *L. brevicaudus*) representing species which are morphometrically clearly distinct from the resting samples (see graph 4, 5). Moreover, *L. chrysopus* and *L. melanonyx* have specific chromosomal sets ($2n = 54$ and 60, respectively) that undoubtedly distinguish them from all other Ethiopian *Lophuromys*, possessing karyotypes of 68 or 70 chromosomes. Besides that some measures were eliminated to involve in the analysis incomplete skulls including some relevant type specimens. Graph 6 shows almost complete overlapping between two groups consisting of 68- and 70-chromosomal forms. Nevertheless, again we see differentiation between two taxa sharing diploid number of 68. Three of the five plotted *L. flavopunctatus* s.str. together with the types of *L. flavopunctatus* and *L. zaphiri* clearly fall outside the range of *L. brunneus*, the two remaining specimens lie in a periphery of its equiprobable ellipse. Synonymy of *flavopunctatus* and *zaphiri* was suggested in our previous paper (Verheyen *et al.*, 2002). In all additional analyses the *zaphiri*-type is found outside the ranges of OTU's 500 and 700 (e.g. see graph 16). This result and a significant distance between the locality of the type (Bodeli-Walamo, E. of upper Omo river) and known distributional areas of the Chercher and Menagesha forms suggest that the name *zaphiri* cannot be attributed to them.

3. Delineating of the craniometric variation within the *Lophuromys flavopunctatus* s. lat. focusing on the Ethiopian representatives of this species complex.

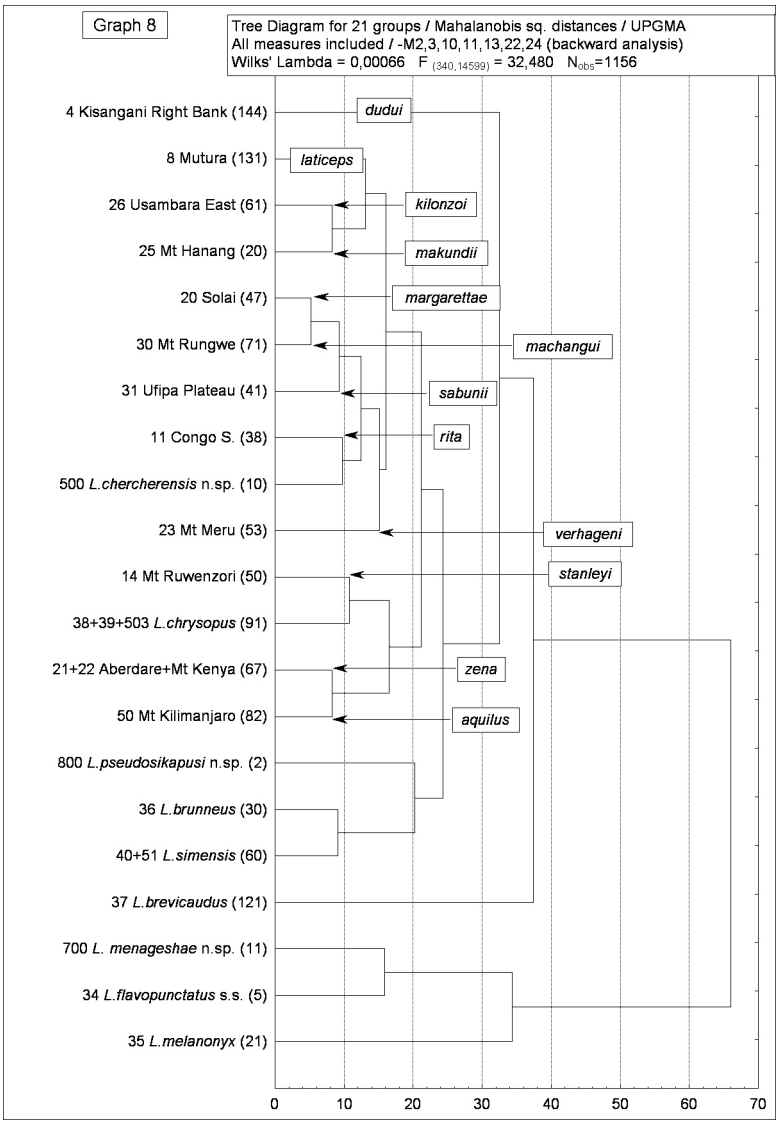
For a definition of craniometric variation in the Ethiopian *L. flavopunctatus* s. lat. and their comparison with non-Ethiopian representatives of this species complex we performed additional canonical analyses. The results were visualized as tree-diagrams (UPGMA) based upon the Mahalanobis squared distances between the obtained centroids. First of all, we want to point out the methodological advantages and limitations of this approach. Using of the generalized (Mahalanobis squared) distance between centroids over all canonical variates derived provides more information than can be seen in score scatter on the first two canonical variates. On the other hand, the UPGMA algorithm (as a cluster-analytic method) forces hierarchical patterns on data that may not, in fact, be hierarchically structured (De Queiroz & Good, 1997). For that reason, the discrete species rather than populations (that can exhibit intraspecific clinal variation) should preferably be used as OTU's for such analysis. Moreover, the reliability of this approach is limited by the size of the OTU's (numbers of skulls) in comparison to the number of cranial variables (measurements) taken per skull. As the size of two of our crucial samples (OTU's 34 and 800) is very small ($n \leq 5$) we performed all analyses in three different ways: 1) the small samples are excluded from analysis; 2) the small sample is *a posteriori* included in analysis using average Mahalanobis squared distances between their specimens and each of the obtained centroids; 3) the small samples are *a priori* included in analysis as real groups. Since the UPGMA-dendrograms resulting from these three procedures are quite comparable in all analyses we can presume that the small size of OTU's 34 and 800 did not affect significantly the tree topology.

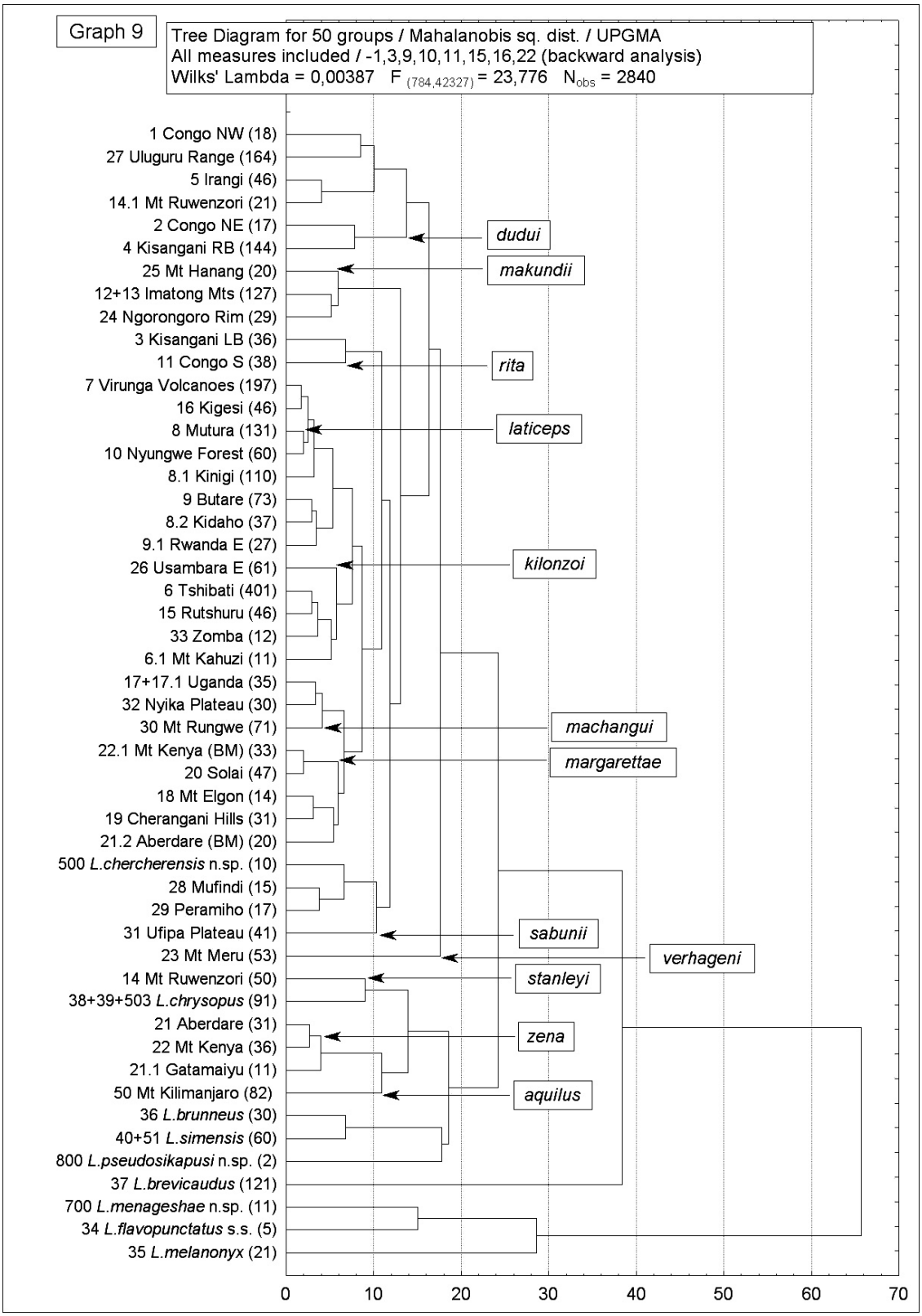
In a first analysis we include only the nine Ethiopian groups that correspond to the known and putative new species (graph 7). In a second step 12 taxonomically most important OTU's representing the described non-Ethiopian taxa are added in the analysis

Graph 7.
UPGMA dendrogram based upon the craniometric comparison of nine Ethiopian *Lophuromys* OTU's representing the known and newly described species. The diploid number of chromosomes is represented between brackets to the right of the corresponding OTU number.



Graph 8.
UPGMA dendrogram based upon the craniometric comparison of 21 taxonomically most important OTUs of the *L. flavopunctatus* species group representing the described Ethiopian and non-Ethiopian taxa.





Graph 9. UPGMA dendrogram based upon a set of 50 OTUs of the *L. flavopunctatus* species group.

(graph 8). Finally, we include as many non-Ethiopian OTU's as possible (n = 41) distributed over the entire geographical range of the species complex (for detailed information concerning these OTU's see Verheyen *et al.*, 2002, 2007) (graph 9). It is noteworthy that similar additional analyses (based upon varying sets of OTU's and/or varying numbers of measures) always give comparable results.

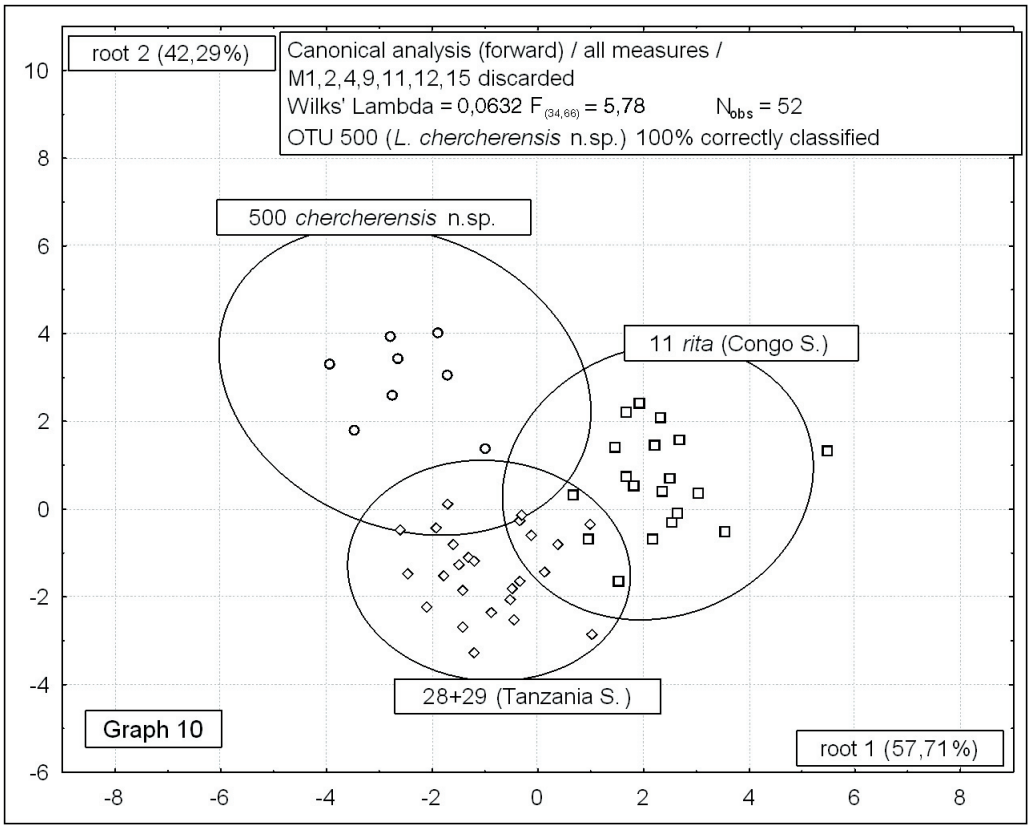
Graph 7 shows absence of correspondence between the clustering pattern of the Ethiopian forms and characteristics of their karyotypes. This corroborates our preceding finding concerning broad overlapping between two Ethiopian groups consisting of 68- and 70-chromosomal forms (graph 6). The pair of taxa, *L. brunneus* and *L. simensis*, represents the most remarkable example of such disparity between chromosomal and craniometric traits. In all dendrograms these species appear always as morphometrically similar (graph 7, 8, 9). Nevertheless, *L. brunneus* and *L. simensis* belong to distinct chromosomal groups (2n=68 and 2n=70, respectively) and their distribution ranges (the South-West and the North of Ethiopia) are clearly separated in the geographical context. We can conclude that morphometrical analyses for taxonomic purpose should preferably be performed separately for 68- and 70-chromosomal Ethiopian *Lophuromys*. Nevertheless, as the chromosomal characteristics for most of the non-Ethiopian OTU's remain unknown, we include all of them for a comparison to the Ethiopian material in the framework of an integrated study (graphs 8, 9).

In all obtained UPGMA-dendrograms four Ethiopian forms, *L. melanonyx*, *L. flavopunctatus* s. str., OTU 700 (Menagesha) and *L. brevicaudus*, being clearly morphometrically separated from all other OTU's demonstrate the same branching order. Both analyses including non-Ethiopian OTU's (graphs 8 and 9) reveal marked morphological similarity between *L. chrysopus* and the newly described species *L. stanleyi* from Mt Ruwenzori. However, as it was shown in our preceding univariate and multivariate analyses these two species are really distinct (VERHEYEN *et al.*, 2007). The pair *chrysopus – stanleyi* joins always with the pair of other non-Ethiopian montane species, *L. aquilus* and *L. zena* (graphs 8, 9). *L.* cf. *sikapusi* from the Sheko Forest (OTU 800) clusters to the Ethiopian pair *brunneus – simensis*. In graph 9 the two clusters mentioned above form the aggregation of both Ethiopian (*L. brunneus*, *L. simensis*, *L. chrysopus* and *L.* cf. *sikapusi*) and East African montane species (*L. aquilus*, *L. zena* and *L. stanleyi*) that correspond generally to the so-called "*aquilus*" group (sensu VERHEYEN *et al.*, 2007). Taking into account its genetic and cytogenetic heterogeneity, this group can be considered only as craniometric entity. OTU 500 (Chercher Mts) appears always within the "*laticeps*" group (sensu VERHEYEN *et al.*, 2007) consisting of non-Ethiopian OTU's. It is closest to OTU 11 (*L. rita*, Congo S.) in graph. 8 and to the cluster of OTU 28 and OTU 29 (Southern Tanzania) in graph. 9. When we try to find out whether these similarities are valid, we find through canonical analysis that OTU 500 is craniometrically well differing from OTU's 11 and 28+29 (see graph 10), and the obtained classification is correct even for 100%. Moreover, the "speckled brush furred" rats from the Chercher Mountains (Ethiopia, OTU 500) and Nakahuga (Southern Tanzania, OTU 29) possess undoubtedly distinct karyotypes (2n = 70, NFa = 84 and 2n = 68, NFa = 90, respectively) (LAVRENCHENKO *et al.*, 2004; CORTI *et al.*, 2004). Therefore, we can conclude that OTU's 500, 700 and 800 are clearly differentiated from all other Ethiopian and non-Ethiopian forms. These results combined with the available RAPD and mtDNA data (see below) suggest that these OTU's can be considered for formal taxonomic recognition.

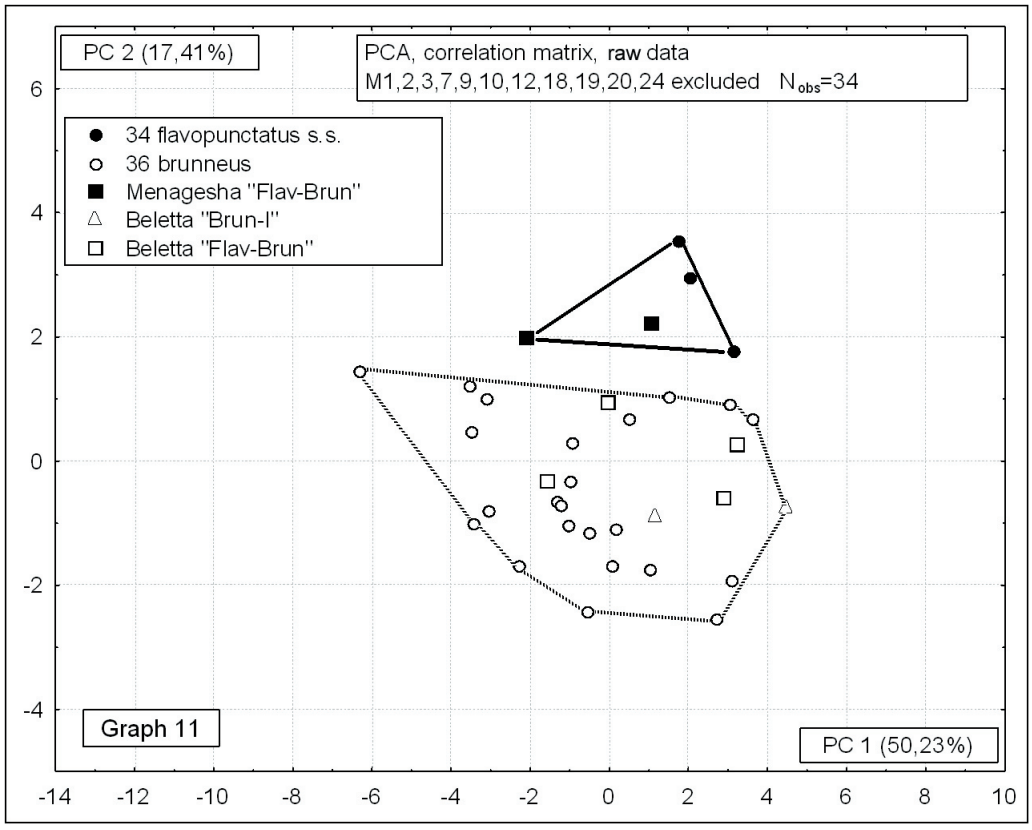
Finally, some remarks concerning a level of interspecific morphological diversity in distinct regions inhabited by *L. flavopunctatus* s. lat. can be noted. All analyzed UPGMA-trees (graphs 8, 9) suggest that such level is significantly higher within the area of the Ethiopian Plateau than within the rest of the much larger distribution range of this entire species complex. The most basal branches of all phenetic trees are always represented by the Ethiopian OTU's 35, 34+700 and 37, whereas the other Ethiopian forms are included in different clusters together with non-Ethiopian OTU's. These relationships can be quantified using the average Mahalanobis squared distance between all species from the area. For the data presented in graph 8 this average distance between Ethiopian species (40.38 ± 4.55 for all species and 31.44 ± 3.25 excluding morphologically most deviant *L. melanonyx*) is considerably larger than between non-Ethiopian species (18.62 ± 0.93).

4. Genetic results

Previous phylogenetic analysis of mtDNA data revealed the presence of 10 main haplotype groups within Ethiopian *Lophuromys* (LAVRENCHENKO *et al.*, 2004). Six of these groups corresponded to distinct OTU's: *L. melanonyx* (OTU 35), *L. brevicaudus* (OTU 37), *L. chrysopus* (OTU's 38+39+503), *L.* cf. *sikapusi* (OTU 800), "Chercher" (OTU 500) and "Menagesha" (OTU 700). On the other hand *L. brunneus* (OTU 36) appeared as paraphyletic, since some individuals of this



Graph 10.
Graphic representation of a forward canonical analysis demonstrating that *L. chercherensis* n.sp. (OTU 500) can easily be differentiated for 100% by craniometry from OTUs 11 (South Congo, *L. rita*) and 28+29 (South Tanzania).



Graph 11.
Graphic representation of a principal component analysis, showing that *L. flavopunctatus* s. str. (OTU 34) and *L. brunneus* (OTU 36) can readily be differentiated by craniometry. Note intermediate position of possible *brunneus* x *flavopunctatus* s. str. hybrids (possessing haplotype "Flav-Brun") between *L. brunneus* bearing haplotype "Brun-I" and *L. flavopunctatus* s. str. from Menagesha.

Table 3. List of the parsimony informative sites of the studied mitochondrial cytochrome b DNA fragment for the Ethiopian *Lophuromys*. Listed are OTU-number, species name, haplotype name, specimen number and locality number (in parentheses). Shown are the 82 of the 84 parsimony informative sites; two sites (15 and 24) that were not readable in some sequences are not shown. See fig. 1 for numbers of sampling localities.

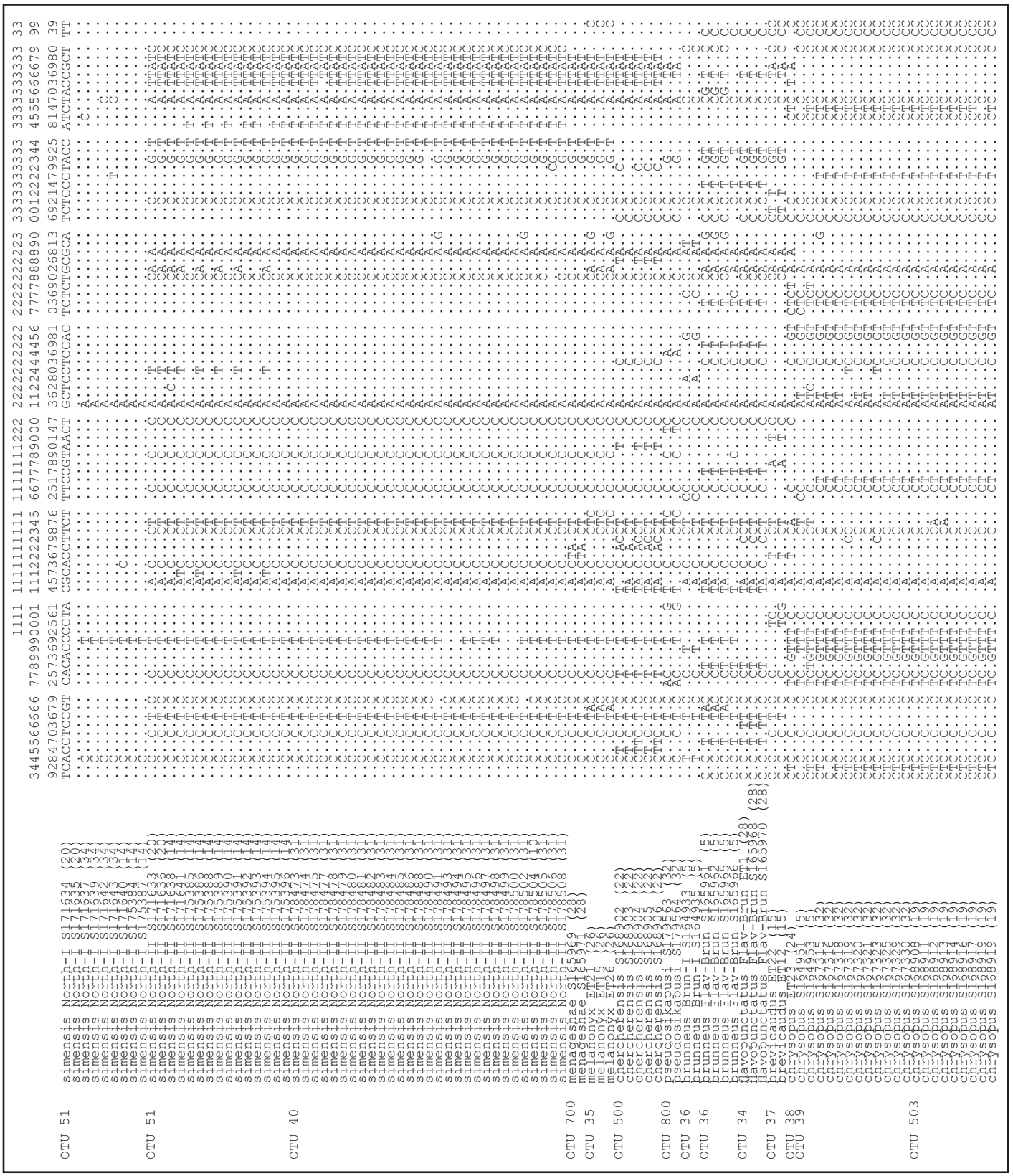


Table 4. Estimates of mean divergence between main lineages of Ethiopian *Lophuromys* for cytochrome *b* given as average uncorrected p-distances (below the diagonal) and standard errors based on 10.000 bootstrap replicates (above the diagonal). Observed values (average uncorrected p-distances followed by standard errors) of within-lineage sequence variation are given along the diagonal.

	1	2	3	4	5	6	7	8	9	10	11
(1) *simensis* North I OTU 51	0.006 (0.002)	0.012	0.012	0.012	0.013	0.012	0.012	0.013	0.014	0.014	0.013
(2) *simensis* North II OTU's 40+51	0.065	0.005 (0.002)	0.005	0.006	0.009	0.009	0.011	0.012	0.013	0.012	0.015
(3) *menageshae* OTU 700	0.067	0.015	0.000 (0.000)	0.007	0.009	0.009	0.012	0.013	0.013	0.013	0.015
(4) *melanonyx* OTU 35	0.071	0.018	0.021	0.002 (0.002)	0.010	0.009	0.012	0.012	0.013	0.013	0.015
(5) *chercherensis* OTU 500	0.074	0.042	0.038	0.048	0.009 (0.003)	0.010	0.013	0.012	0.012	0.014	0.015
(6) *pseudosikapusi* OTU 800	0.067	0.036	0.038	0.037	0.048	0.000 (0.000)	0.012	0.012	0.012	0.013	0.015
(7) *brunneus* Brun I OTU 36	0.059	0.049	0.056	0.061	0.068	0.062	0.000 (0.000)	0.013	0.013	0.014	0.014
(8) *brunneus* Flav-Brun OTU 36	0.084	0.067	0.073	0.066	0.073	0.068	0.069	0.017 (0.005)	0.006	0.012	0.014
(9) *flavopunctatus* Flav-Brun OTU 34	0.084	0.067	0.070	0.069	0.064	0.065	0.067	0.022	0.000 (0.000)	0.012	0.015
(10) *brevicaudus* OTU 37	0.082	0.065	0.067	0.066	0.084	0.070	0.075	0.075	0.067	0.005 (0.004)	0.014
(11) *chrysopus* OTU's 38+39+503	0.083	0.096	0.104	0.098	0.104	0.102	0.080	0.090	0.093	0.091	0.010 (0.002)

taxon arose as separate lineage "Brun-I", whereas the rest of *brunneus* haplotypes together with individuals of *L. flavopunctatus* s.str. (OTU 34) formed the group "Flav-Brun". Furthermore, haplotypes from the area between Tana Lake and Mount Guna (OTU 51) divided into two deeply diverged lineages ("North-I" and "North-II") which were sympatric in two localities (14 and 20). Our recent collecting efforts resulted in extended sample consisting in OTU 51 including both haplotype groups ("North-I", n=9 and "North-II", n=15). Moreover, only "North-II" lineage was found in the newly collected sizeable topotypical series of *L. simensis* (OTU 40, n=36) (Table 3).

The genetic distances between eight main haplotype groups (uncorrected p-distance = 0.036-0.104, see table 4) are lying well within the range typical for close species in muroid rodents (Bradley & Baker, 2001; Jaarola *et al.*, 2004). Four of them correspond to described or putative new species (*L. chrysopus*, *L. brevicaudus*, *L.* cf. *sikapusi* and "Chercher"); two of the rest ("North-I" and "North-II") are coexisting in some populations of *L. simensis* and the last pair ("Flav-Brun" and "Brun-I") occur in *L. brunneus* from Beletta where the former group is shared by a different species *L. flavopunctatus* s. str. Contrariwise, two haplotype groups representing morphologically "good" species (*L. melanonyx* and "Menagesha") are very close both to each other and to the "North-II" (p-distance between them = 0.015-0.021) (Table 4). For the cytochrome b gene, such differences fall within the range of intraspecific genetic variation, usually observed in Muroidea (Patton & Smith, 1992; Bradley & Baker, 2001). The discrepancy between genetic and morphological characterizations of some Ethiopian OTU's can be explained by processes of hybridization and will be discussed in the next chapter.

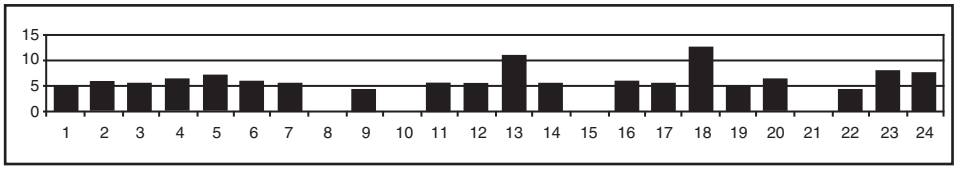
5. Morphometric characterization of the hybridization patterns in Ethiopian *Lophuromys*.

In our earlier publication based mainly on the results of mtDNA and RAPD PCR analyses (Lavrenchenko *et al.*, 2004) we supposed the recent hybridization between *L. flavopunctatus* s. str. and *L. brunneus*, and the successful introgression of the "foreign" mtDNA in some populations of *L. simensis* due to ancient hybridization. Multivariate analysis of cranial morphology can constitute a useful tool for a better characterization of the processes of hybridization in mammals (e.g. see Gaubert *et al.*, 2005). Thus, we conducted a few analyses of relevant Ethiopian *Lophuromys* forms including specimens that were characterized by mitochondrial and nuclear markers (for detailed information see ch. 4 of the current publication and Lavrenchenko *et al.*, 2004).

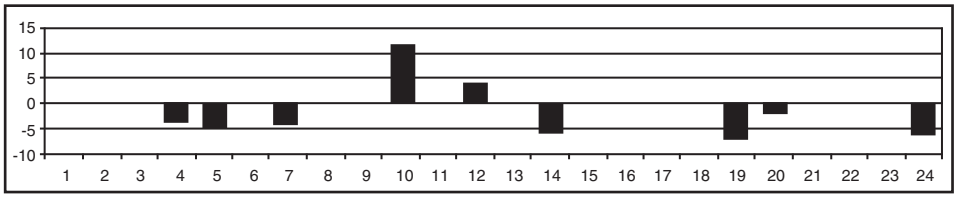
The univariate comparison (Tables 5.2, 7.5, 7.6) shows that the skull of *L. flavopunctatus* s. str. has about the same general size as *L. brunneus*. Nevertheless, it is significantly bigger for the cheekteeth measures (M13 and M17), but smaller for the interorbital breadth M8 (INTE), nasal length M16 (LNAS) and the upper

Table 5. Synoptic representation of the percentage craniometric differences (% diff.) between the means of: (1) *L. simensis* (OTU's 40+51) and some other Ethiopian taxa (table 5.1); (2) *L. flavopunctatus* s. str. (OTU 34), *L. menageshae* n.sp. (OTU 700) and *L. brunneus* (OTU 36) (table 5.2); (3) *L. chercherensis* n.sp. (OTU 500) and *L. menageshae* n.sp. (OTU 700) (table 5.3). Only the statistically significant differences are represented (t-test of STUDENT).

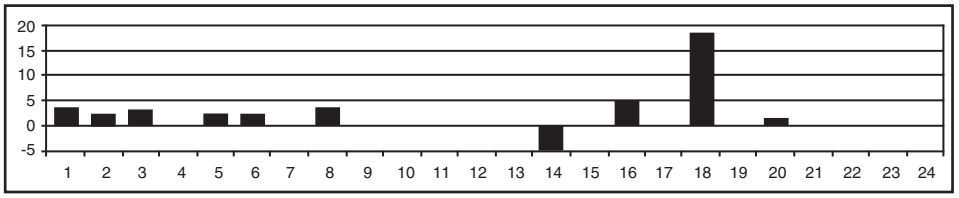
OTU 40 + 51 (*L. simensis*) = 100 % versus... Table 5.1
OTU 700 (*L. menageshae*)



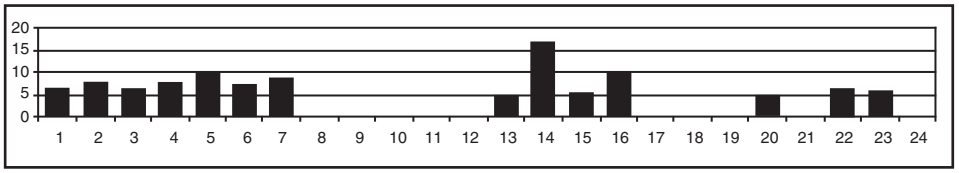
OTU 500 (*L. chercherensis*)



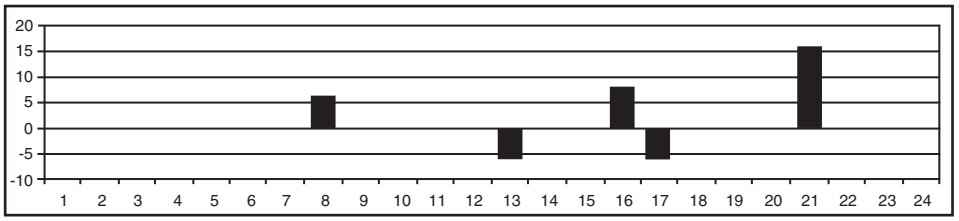
OTU 36 (*L. brunneus*)



OTU 34 (*L. flavopunctatus*) = 100 % versus... Table 5.2
OTU 700 (*L. menageshae*)



OTU 36 (*L. brunneus*)



OTU 500 (*L. chercherensis*) = 100 % versus... Table 5.3
OTU 700 (*L. menageshae*)

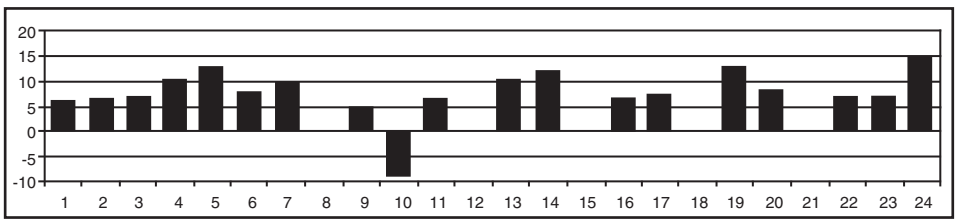
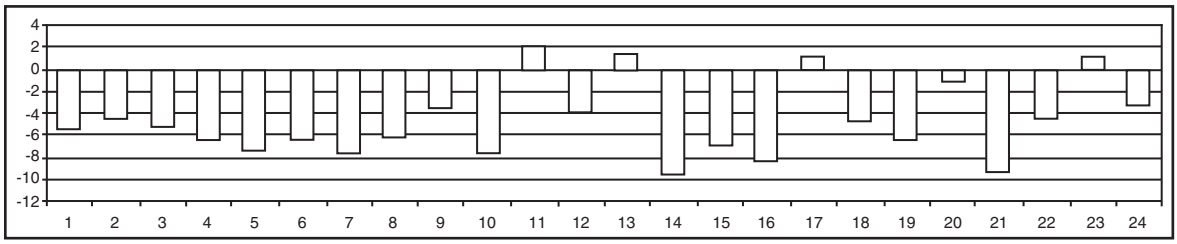


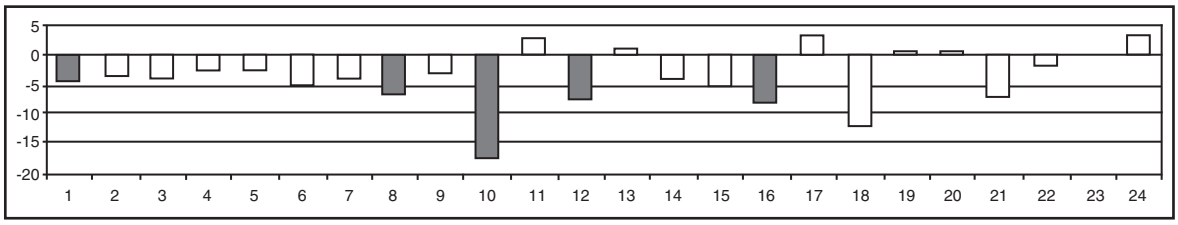
Table 6. Synoptic representation of the percentage craniometric differences (% diff.) between the means of *L. pseudosikapusi* n.sp. (OTU 800) and some of the neighbouring taxa. Statistically significant differences (t-test of STUDENT) are shown as grey bars.

OTU 800 (*L. pseudosikapusi*) = 100 % versus...

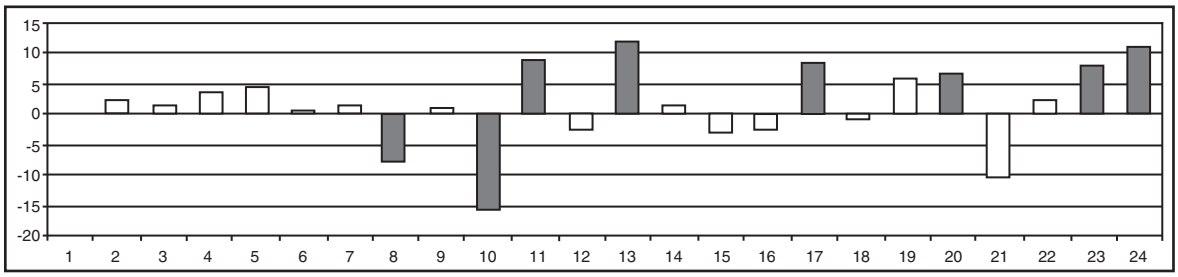
OTU 500 (*L. chercherensis*)



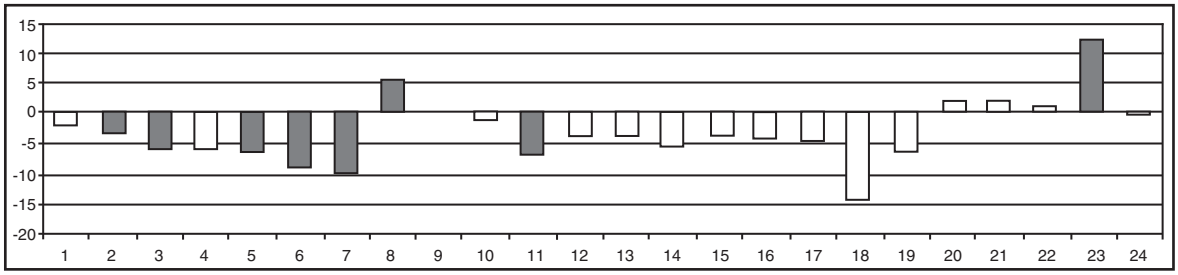
OTU 40 + 51 (*L. simensis*)



OTU 700 (*L. menageshae*)



L. dieterleni



incisor depth M21 (DINC). The principal component analysis reveals that *L. flavopunctatus* s. str. from the Menagesha Forest (OTU 34) and *L. brunneus* from the Beletta Forest (including putative hybrids with the former species - OTU 36) separate clearly along the PC 2 with no overlap between them (graph. 11). PC2 is characterized by positive correlation with the length of upper cheekteeth M11 (UPTE), breadth of first upper molar M13 (M^1BR) and length of lower cheekteeth M17 (LOTE) (loadings > 0.50) contrasted by negative correlation with the upper incisor depth M21 (DINC) (loading = -0.48). Therefore, the difference between the two species along the second axis again reflects slender and shorter molars but heavier upper incisors of *L. brunneus* in comparison with *L. flavopunctatus* s. str.

In our previous study we identified the four Beletta specimens possessing the *flavopunctatus* s. str. mitochondrial haplotype ("Flav-Brun") as possible *brunneus* x *flavopunctatus* s. str. hybrids because of the multidimensional scaling of RAPD data shown

Table 7.1 OTUs 40+51
L. simensis M+F age 1-4

	N	Mean	Min	Max	SD	CV%
M1	58	30,08	28,40	31,70	0,842	2,8
M2	60	29,37	27,45	31,25	0,880	3,0
M3	60	24,97	22,90	26,80	0,781	3,1
M4	60	12,90	11,60	13,75	0,432	3,4
M5	60	6,61	6,00	7,30	0,287	4,3
M6	60	7,97	7,20	8,80	0,337	4,2
M7	60	9,66	8,65	10,65	0,393	4,1
M8	60	5,88	5,55	6,25	0,169	2,9
M9	60	15,07	14,20	16,00	0,423	2,8
M10	60	2,79	2,50	3,25	0,160	5,7
M11	60	5,35	5,00	5,95	0,198	3,7
M12	60	6,68	6,15	7,20	0,228	3,4
M13	60	1,82	1,70	2,05	0,079	4,3
M14	60	3,34	2,85	3,95	0,235	7,0
M15	60	2,89	2,65	3,20	0,132	4,6
M16	58	12,10	10,25	13,40	0,593	4,9
M17	60	4,82	4,40	5,20	0,195	4,1
M18	60	1,24	0,80	1,65	0,157	12,7
M19	60	5,59	5,20	6,20	0,246	4,4
M20	60	12,79	12,25	13,50	0,335	2,6
M21	60	1,35	1,15	1,60	0,098	7,3
M22	60	6,53	5,60	7,45	0,356	5,5
M23	60	4,88	4,35	5,50	0,236	4,8
M24	56	9,23	8,35	10,35	0,480	5,2
W	60	57,13	37,00	74,00	8,884	15,6
HB	60	133,40	114,00	145,00	7,263	5,4
TL	42	71,38	58,00	85,00	5,405	7,6
HF(-n)	60	20,45	18,00	22,50	0,951	4,7
HF(+n)	60	23,05	21,00	25,00	0,959	4,2
EL	60	17,51	15,50	20,00	1,065	6,1
TL/HB %	42	53,53	41,26	65,38	4,612	8,6

Table 7.2 OTU 700
L. menageshae n.sp. M+F age = 2+3

	N	Mean	Min	Max	SD	CV%
M1	10	31,62	31,00	33,15	0,618	2,0
M2	11	31,11	30,45	32,65	0,636	2,0
M3	10	26,39	25,80	27,75	0,568	2,2
M4	11	13,70	13,20	14,40	0,413	3,0
M5	11	7,08	6,60	7,70	0,407	5,7
M6	11	8,44	8,10	8,85	0,238	2,8
M7	11	10,19	9,60	10,90	0,350	3,4
M8	11	5,81	5,45	6,05	0,174	3,0
M9	11	15,72	14,80	16,75	0,524	3,3
M10	11	2,85	2,50	3,15	0,167	5,9
M11	11	5,65	5,30	5,85	0,177	3,1
M12	11	7,05	6,90	7,30	0,115	1,6
M13	11	2,01	1,90	2,10	0,067	3,3
M14	11	3,52	3,20	3,90	0,200	5,7
M15	11	2,96	2,80	3,10	0,095	3,2
M16	11	12,83	12,20	13,65	0,479	3,7
M17	11	5,08	4,85	5,35	0,169	3,3
M18	11	1,39	1,15	1,70	0,185	13,3
M19	11	5,87	5,45	6,15	0,203	3,5
M20	11	13,58	12,85	14,20	0,430	3,2
M21	11	1,30	1,10	1,50	0,123	9,5
M22	11	6,80	6,55	7,25	0,209	3,1
M23	11	5,28	5,05	5,75	0,202	3,8
M24	7	9,92	9,45	10,90	0,492	5,0
W	2	74,50	72,00	77,00	3,536	4,7
HB	6	134,33	129,00	143,00	5,279	3,9
TL	6	67,83	60,00	75,00	5,636	8,3
HF(-n)	2	20,50	20,00	21,00	0,707	3,4
HF(+n)	8	22,63	22,00	24,00	0,744	3,3
EL	9	17,39	15,00	20,00	1,364	7,8
TL/HB %	6	50,52	45,80	57,25	4,173	8,3

Table 7.3 OTU 500
L. chercherensis n.sp. M+F age = 1-4

	N	Mean	Min	Max	SD	CV%
M1	9	29,80	27,85	31,90	1,208	4,1
M2	10	29,13	26,95	30,85	1,296	4,4
M3	10	24,65	22,30	26,00	1,287	5,2
M4	10	12,39	11,15	13,10	0,661	5,3
M5	10	6,27	5,80	6,85	0,362	5,8
M6	10	7,84	7,15	8,40	0,371	4,7
M7	10	9,27	8,35	10,00	0,520	5,6
M8	10	5,91	5,50	6,30	0,254	4,3
M9	9	15,04	13,80	16,25	0,845	5,6
M10	10	3,12	2,55	3,90	0,376	12,0
M11	10	5,30	4,90	5,80	0,277	5,2
M12	10	6,96	6,30	7,35	0,347	5,0
M13	10	1,83	1,75	1,90	0,063	3,5
M14	10	3,15	2,80	3,60	0,224	7,1
M15	10	2,84	2,60	3,20	0,185	6,5
M16	9	12,06	10,50	13,20	0,900	7,5
M17	10	4,73	4,45	5,00	0,178	3,8
M18	10	1,34	1,00	1,70	0,229	17,1
M19	10	5,20	4,85	5,60	0,251	4,8
M20	10	12,55	12,00	13,25	0,391	3,1
M21	10	1,32	1,10	1,55	0,142	10,8
M22	10	6,37	5,55	7,25	0,499	7,8
M23	10	4,93	4,65	5,50	0,272	5,5
M24	10	8,63	7,65	9,50	0,629	7,3
W	9	60,33	36,00	78,00	13,601	22,5
HB	9	128,33	114,00	145,00	9,605	7,5
TL	4	62,50	60,00	65,00	2,887	4,6
HF(-n)	9	20,33	20,00	21,00	0,500	2,5
HF(+n)	9	22,89	22,00	24,00	0,928	4,1
EL	5	17,80	17,00	18,00	0,447	2,5
TL/HB %	4	49,81	47,62	51,18	1,537	3,1

Table 7.4 OTU 800
L. pseudosikapusi n.sp. M+F age = 3+4

	N	Mean	Min	Max	SD	CV%
M1	2	31,50	31,25	31,75	0,354	1,1
M2	2	30,48	30,40	30,55	0,106	0,3
M3	2	26,00	25,90	26,10	0,141	0,5
M4	2	13,23	12,95	13,50	0,389	2,9
M5	2	6,78	6,70	6,85	0,106	1,6
M6	2	8,38	8,20	8,55	0,247	3,0
M7	2	10,03	9,65	10,40	0,530	5,3
M8	2	6,30	6,20	6,40	0,141	2,2
M9	2	15,58	15,35	15,80	0,318	2,0
M10	2	3,38	3,20	3,55	0,247	7,3
M11	2	5,20	5,15	5,25	0,071	1,4
M12	2	7,23	6,95	7,50	0,389	5,4
M13	2	1,80	1,75	1,85	0,071	3,9
M14	2	3,48	3,35	3,60	0,177	5,1
M15	2	3,05	3,00	3,10	0,071	2,3
M16	2	13,15	12,80	13,50	0,495	3,8
M17	2	4,68	4,50	4,85	0,247	5,3
M18	2	1,40	1,35	1,45	0,071	5,1
M19	2	5,55	5,45	5,65	0,141	2,5
M20	2	12,70	12,40	13,00	0,424	3,3
M21	2	1,45	1,40	1,50	0,071	4,9
M22	2	6,65	6,45	6,85	0,283	4,3
M23	2	4,88	4,75	5,00	0,177	3,6
M24	2	8,93	8,90	8,95	0,035	0,4
W	2	60,00	53,00	67,00	9,899	16,5
HB	2	134,00	130,00	138,00	5,657	4,2
TL	2	82,00	78,00	86,00	5,657	6,9
HF(-n)	2	22,00	21,00	23,00	1,414	6,4
HF(+n)	2	24,25	23,50	25,00	1,061	4,4
EL	2	19,75	19,50	20,00	0,354	1,8
TL/HB %	2	61,16	60,00	62,32	1,640	2,7

Table 7. Basic statistics of measurements (mm) and weight (g) of *L. simensis* (table 7.1), *L. menageshae* n.sp. (table 7.2), *L. chercherensis* n.sp. (table 7.3), *L. pseudosikapusi* n.sp. (table 7.4), *L. brunneus* (table 7.5) and *L. flavopunctatus* s. str. (table 7.6). [Tables 7.1, 7.2, 7.3 and 7.4 on opposite page]

Table 7.5 OTU 36

L. brunneus M+F age = 1-4

	N	Mean	Min	Max	SD	CV%
M1	29	31,09	28,75	33,75	1,389	4,5
M2	30	29,96	27,05	32,65	1,422	4,7
M3	30	25,66	23,00	28,10	1,295	5,0
M4	30	13,00	11,60	14,60	0,603	4,6
M5	30	6,77	5,80	7,45	0,389	5,7
M6	30	8,16	7,25	8,85	0,434	5,3
M7	30	9,65	8,55	10,40	0,526	5,5
M8	30	6,07	5,70	6,65	0,222	3,7
M9	30	15,18	14,05	16,85	0,681	4,5
M10	30	2,83	2,40	3,30	0,225	8,0
M11	30	5,37	5,00	5,85	0,220	4,1
M12	30	6,75	6,20	7,50	0,301	4,5
M13	30	1,81	1,65	1,90	0,066	3,6
M14	30	3,19	2,75	3,70	0,260	8,2
M15	30	2,83	2,50	3,25	0,156	5,5
M16	29	12,62	11,05	14,40	0,865	6,9
M17	30	4,78	4,45	5,30	0,200	4,2
M18	30	1,47	0,95	1,85	0,200	13,6
M19	30	5,67	5,10	6,20	0,261	4,6
M20	30	12,96	12,20	13,85	0,358	2,8
M21	30	1,36	1,15	1,55	0,110	8,1
M22	30	6,38	5,55	7,35	0,420	6,6
M23	30	4,93	4,50	5,60	0,241	4,9
M24	30	9,07	7,70	10,70	0,677	7,5
W	31	61,90	38,00	76,00	10,336	16,7
HB	31	124,42	101,00	138,00	8,495	6,8
TL	17	70,21	55,00	84,50	6,757	9,6
HF(-n)	31	21,96	21,00	23,70	0,725	3,3
HF(+n)	31	24,56	22,75	26,70	0,856	3,5
EL	31	18,62	17,00	20,20	0,688	3,7
TL/HB %	17	58,06	50,78	65,00	4,319	7,4

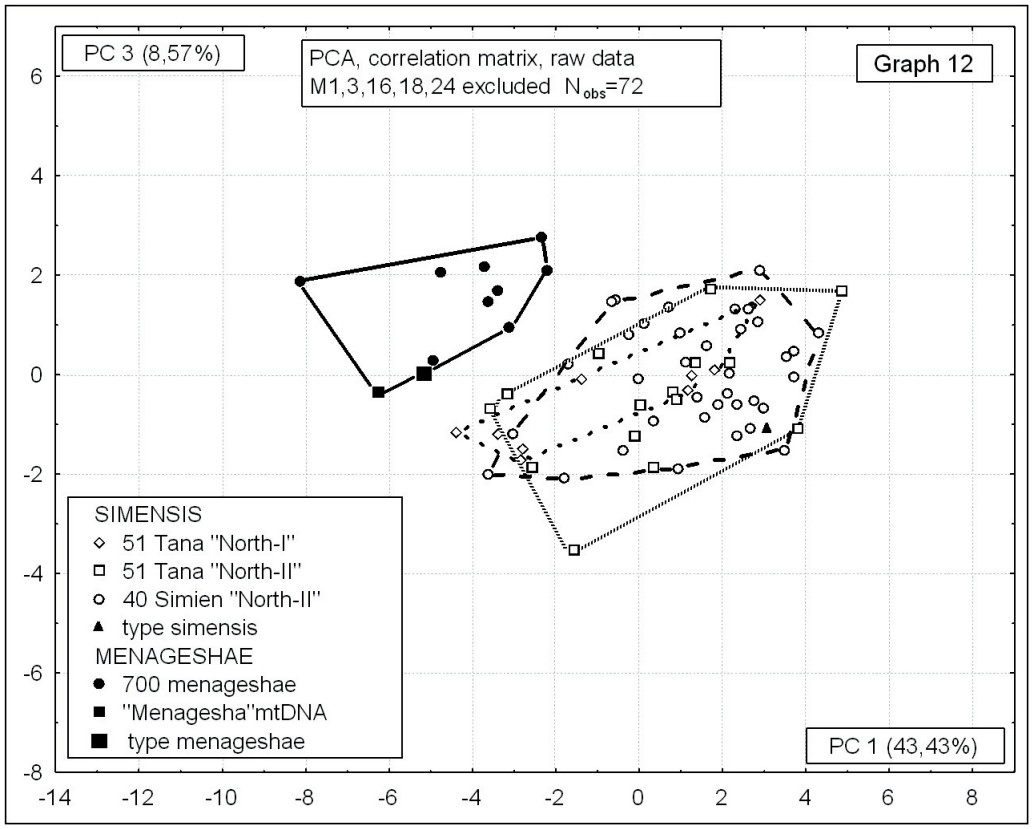
Table 7.6 OTU 34

L. flavopunctatus s.s. M+F age = 1-3

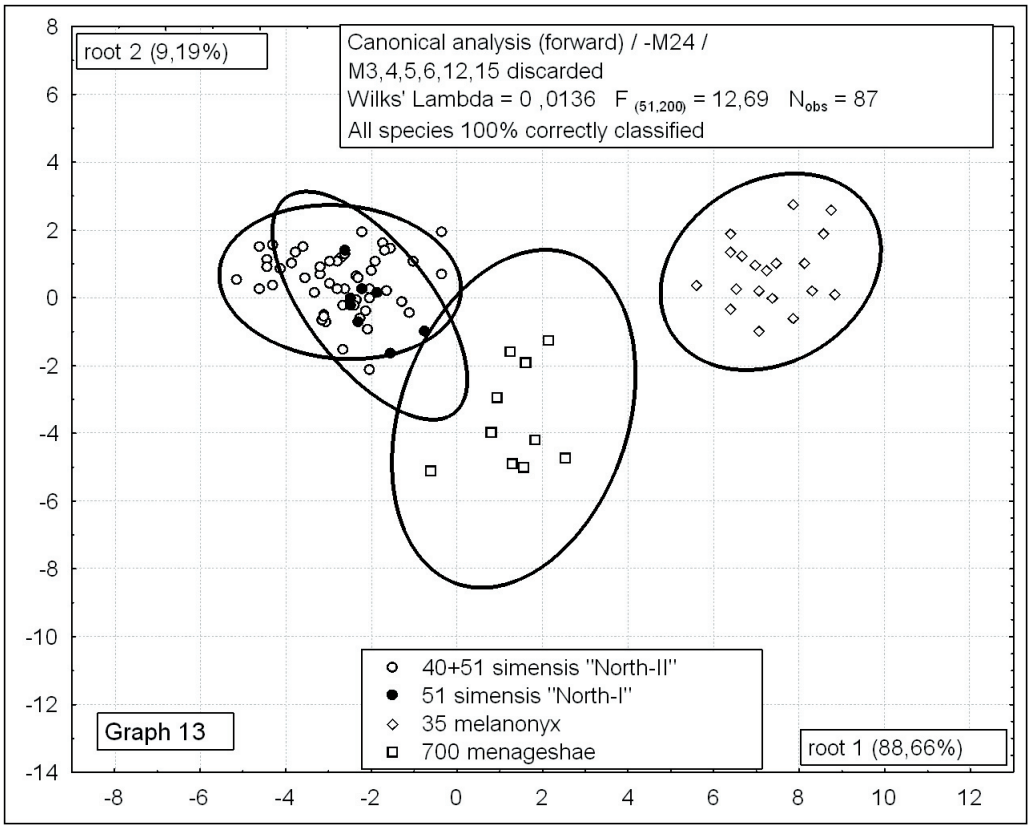
	N	Mean	Min	Max	SD	CV%
M1	5	29,80	28,55	31,40	1,124	3,8
M2	5	28,96	27,60	31,00	1,423	4,9
M3	5	24,82	23,60	26,90	1,325	5,3
M4	5	12,75	12,50	13,40	0,376	2,9
M5	5	6,46	6,20	7,00	0,331	5,1
M6	5	7,87	7,50	8,75	0,544	6,9
M7	5	9,38	8,90	10,40	0,623	6,6
M8	5	5,71	5,35	6,00	0,248	4,4
M9	5	15,10	14,00	16,20	0,809	5,4
M10	5	2,75	2,35	3,20	0,341	12,4
M11	5	5,47	5,25	5,60	0,144	2,6
M12	5	6,84	6,30	7,20	0,352	5,2
M13	5	1,92	1,85	2,00	0,057	3,0
M14	5	3,02	2,50	3,40	0,329	10,9
M15	5	2,81	2,75	2,90	0,082	2,9
M16	5	11,71	11,35	12,50	0,459	3,9
M17	5	5,09	4,95	5,30	0,134	2,6
M18	5	1,46	1,10	1,85	0,363	24,9
M19	5	5,76	5,15	6,45	0,620	10,8
M20	5	12,98	12,75	13,30	0,256	2,0
M21	5	1,17	0,95	1,30	0,148	12,7
M22	5	6,42	6,25	6,55	0,157	2,4
M23	5	5,00	4,80	5,10	0,117	2,3
M24	3	9,27	8,75	9,75	0,501	5,4
W	2	69,00	69,00	69,00	0	0
HB	3	127,00	125,00	129,00	2,000	1,6
TL	3	62,33	58,00	68,00	5,132	8,2
HF(-n)	2	21,90	21,50	22,30	0,566	2,6
HF(+n)	3	24,20	23,00	25,30	1,153	4,8
EL	3	18,00	17,00	19,00	1,000	5,6
TL/HB %	3	49,12	45,67	54,40	4,645	9,5

their intermediate position between the two Beletta specimens bearing the *brunneus* haplotype ("Brun-I") and *L. flavopunctatus* s. str. from Menagesha (see figs 5B, 6A in LAVRENCHENKO *et al.*, 2004). Graph 11 demonstrates that these four putative hybrids can also be characterized by skull morphology somewhat intermediate between "pure" *L. brunneus* and *L. flavopunctatus* s. str.; the pattern remains stable in additional analyses of principal components extracted from the covariance or correlation matrix and computed using both raw and log-transformed metrical data (results not shown). The concordant results of analyses based on such independent data sets as nuclear markers (RAPD PCR) and cranial measures reinforce the supposition about recent hybridization between these two species. Nevertheless, we failed to find any clear separation between specimens possessing distinct mitochondrial haplotypes ("Flav-Brun" and "Brun-I") in all principal component analyses including only OTU 36 which appears always as a rather homogeneous set. This result can be explained by the predominant inherence of *brunneus* type of cranial morphology under hybridization and/or by the assumption that the putative *brunneus* x *flavopunctatus* s. str. hybrids are actually a product of recurrent backcrossing to *L. brunneus*.

Furthermore, the coexistence of two highly diverged mitochondrial lineages ("North-I" and "North-II") and the remarkable similarity in the RAPD band patterns between the specimens bearing these distinct haplotypes were revealed in the populations of *L. simensis* from the area between Tana Lake and Mount Guna (OTU 51, n = 24) (see previous chapter and LAVRENCHENKO *et al.*, 2004). We explained the apparent discordance between nuclear and mitochondrial perspectives by an ancient mtDNA introgression from distinct hypothetical species (that remains unsampled or is even extinct). Only haplotype "North-II" is found in all specimens of *L. simensis* (OTU 40, n = 36) collected recently in the Simien Mountains (see previous chapter). Moreover, rather low level of differences (p-distance = 0.015)



Graph 12.
Graphic representation of a principal component analysis showing that *L. menageshae* n.sp. (OTU 700) and *L. simensis* (OTU's 40 and 51) can readily be differentiated by craniometry. Note complete overlapping between three groups of *L. simensis* (specimens with haplotype "North-II" from OTU's 40 and 51 and specimens with haplotype "North-I" from OTU 51).



Graph 13.
Graphic representation of a forward canonical analysis demonstrating that *L. menageshae* n.sp. (OTU 700), *L. simensis* (OTU's 40, 51) and *L. melanonyx* (OTU 35) can easily be differentiated by craniometry (100% of correct classification). Note complete overlapping between two groups of *L. simensis* belonging to very distinct mitochondrial lineages ("North-I" from OTU 51 and "North-II" from OTU's 40+51).

was observed between this mitochondrial lineage and that of the new 70-chromomal form (OTU 700) from Menagesha (table 4). On the other hand, the significantly different RAPD profiles (see Figs 4, 5B, 6A, 7 in LAVRENCHENKO *et al*., 2004) in *L. simensis* and representative of the OTU 700 can imply their divergence at the species level.

The principal component analysis of cranial measures reveals clear separation between *L. simensis* and the OTU 700 in the plain of the first and third principal components (graph. 12). For detailed discussion of the results of this analysis we refer to chapter 6.2, but we note here that three groups of *L. simensis* (specimens with haplotype "North-II" from OTU's 40 and 51 and specimens with haplotype "North-I" from OTU 51) are widely overlapping without any clear separation between them. The same result is obtained in additional principal components analyses with the OTU 700 excluded (not shown). Moreover, the canonical (forward) analysis demonstrates that three groups of specimens possessing very close mitochondrial haplotypes ("North-II" from OTU's 40+51, OTU 35 (*L. melanonyx*) and OTU 700 - see ch. 4) are clearly differentiated from each other, whereas two groups of *L. simensis* belonging to very distinct lineages ("North-I" from OTU 51 and "North-II" from OTU's 40+51) overlap completely (graph. 13). Thus, we can conclude that despite of the presence of two deeply diverged mitochondrial lineages, the taxon *L. simensis* can be characterized as a rather homogeneous entity in the terms of both nuclear markers and cranial morphology. This finding agrees with the pattern one would expect to see as a product of interspecific transfer of mtDNA due to ancient hybridization. Therefore, the results of multivariate analyses of craniometric data provide independent support for our earlier supposition on existence of both recent and ancient reticulate processes among Ethiopian *Lophuromys* species.

6. Taxonomic results

6.1. Redescription of *Lophuromys simensis* OSGOOD, 1936, new rank

Lophuromys flavopunctatus simensis OSGOOD, 1936, Publs Field Mus. nat. Hist. (Zool.) 20: 238. Type locality: Ras Dashan (Mount Geech).
Lophuromys flavopunctatus (non THOMAS): partim AFEWORK BEKELE & CORTI, 1994, J. Zool., Lond. 232: 677.

DESCRIPTION AND DIAGNOSIS

Lophuromys simensis stat. nov. is a medium-sized representative of the *L. flavopunctatus* species complex. The dorsal pelage is blackish-brownish, the hairs are dark rufous at the base and blackish in distal half with white subterminal bands and black tips which produce the abundant "speckled" appearance (fig. 2D). Ventral pelage is cream-yellowish to pale orange, the hairs are white tipped and yellowish-darkgrey at the base. The dorsal surface of the forefeet is dark, whereas the dorsal surface of the hindfeet is pale yellowish with a central longitudinal darkish band. The black claws are long, especially on the forefeet, whereas on the hindfeet they sharply contrast with whitish toes. The tail is of medium length (ca. 54% of HB), and it appears strictly bicoloured. Relatively long hairs are black on the upper tail surface and white on the lower surface.

The skull is typical of the *L. flavopunctatus* species complex, with relatively slender rostrum and orbital region, narrow choanae and large tympanic bullae (fig. 3.1). The upper cheekteeth rows are relatively rather close to each other. Measurements are given in table 7.1.

The karyotype of *L. simensis* ($2n$ = 70, NFa = 84; 10 m, sm + 6st + 52a + Xsm + Ya) is described by LAVRENCHENKO *et al.* (2004).

GENETIC CHARACTERIZATION

As it was shown above (ch. 4) two highly diverged mitochondrial lineages ("North-I" and "North-II", uncorrected p-distance between them = 0.065) are coexisting in populations of *L. simensis* from the area between Tana Lake and Mount Guna (OTU 51), whereas only one of them ("North-II") was found in the topotypical series from the Simien Mountains (OTU 40). Contrariwise, the results of the RAPD-PCR analysis revealed striking similarity between specimens from the former region belonging to the distinct mitochondrial lineages (LAVRENCHENKO *et al.*, 2004). Besides that, allozyme investigation of 27 enzymatic and non-enzymatic proteins (Adh, Alb, Dia-2, Es-1, Es-2, Es-3, Es-4, Es-6, Hbb, Gdc, Got-1, Got-2, G6pd-1, Gpc, Lap-1, Ldh-A, Ldh-B, Idh-1, Mdh-1, Mdh-2, Me-1, Me-2, Pgd-1, Pgm, Sdh, Sod-1 and Sod-2) revealed no loci discriminating these two groups ("North-I" versus "North-II") within Debre Tabor sample (our unpublished data). The evidence combined with the results of multivariate morphometric analyses (graph. 12, 13) exposes *L. simensis* as a rather uniform species in the terms of both nuclear genes

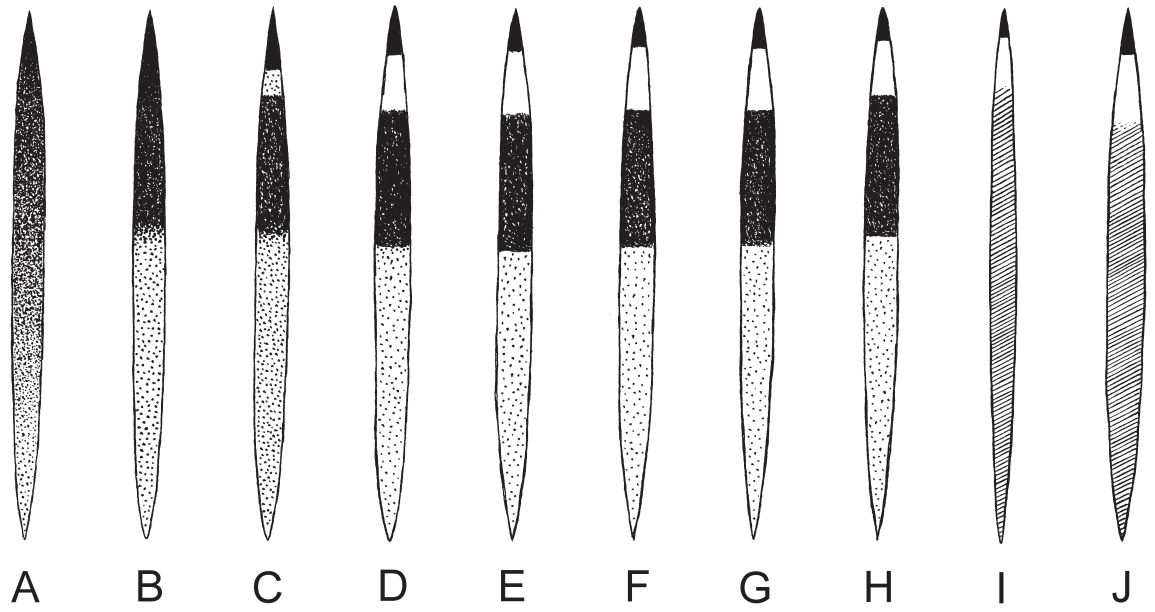


Fig. 2. Schematic representation of the banding of the hairs of *Lophuromys* species. Colour banding was examined on a typical dorsal hair, halfway along the back. Hatch = grey pigmentation, stipple = red pigmentation, hatch/stipple density corresponds to pigmentation intensity. A - *L. ansorgei* (KMMA 16980), B – L. *pseudosikapusi* n.sp. (ZMMU S-179563, holotype), C – *L. chercherensis* n.sp. (ZMMU S-168902, holotype), D – *L. simensis* (ZMMU S-178503), E – *L. menageshae* n.sp. (ZMMU S-165969, holotype), F – *L. flavopunctatus* s.str. (ZMMU S-165970), G – *L. brunneus* (ZMMU S-164940), H – *L. chrysopus* (ZMMU S-164840), I – *L. brevicaudus* (ZMMU S-162503), J – *L. melanonyx* (ZMMU S-162510).

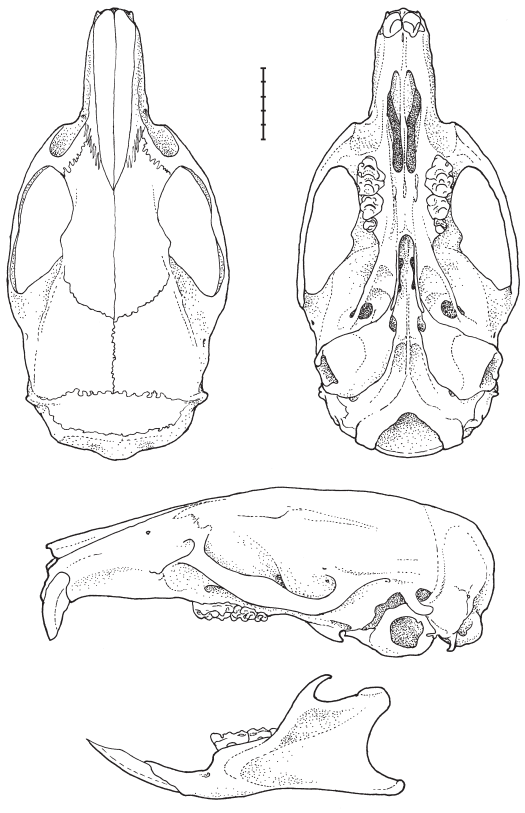


Fig. 3.1. Views of skull and mandible of *Lophuromys simensis* (ZMMU S-178473). Scale bar = 5 mm.

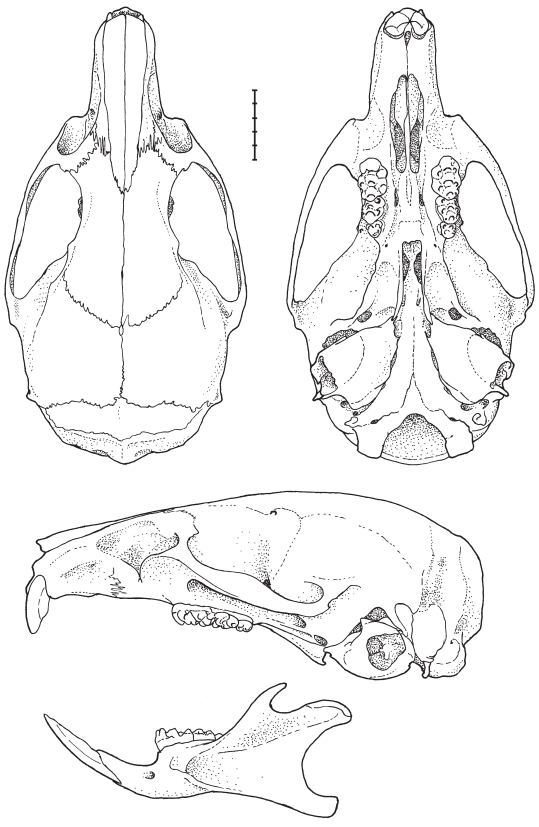


Fig. 3.2. Views of skull and mandible of *Lophuromys menageshae* n.sp. (ZMMU S-165969, holotype). Scale bar = 5 mm.

(RAPD PCR, allozymes) and cranial morphology. The presence of two sympatric mitochondrial lineages in some populations of *L. simensis* can be explained as a result of ancient introgression of the "foreign" mtDNA (see ch. 5).

DISTRIBUTION AND ECOLOGY

The species has been found in two regions of northern Ethiopia: the Simien Mountains and the area between Tana Lake and Mount Guna. Being, apparently, the most ecologically ambivalent species among Ethiopian *L. flavopunctatus* s.lat., *L. simensis* has a wide altitudinal range (1800 - 3800 m ASL). At the lowest limit of the range this species inhabits dry woodlands (Wanzaye, 11°47'N 37°43'E, 1800 m ASL) together with species characteristic of lowland savanna, *Mastomys* sp., *Mus setulosus* PETERS, 1876, and *Arvicanthis dembeensis* RÜPPEL, 1842. On the other hand, *L. simensis* occupies the high-altitude grassland and moorland habitats (Mount Guna, 11°43'N 38°15'E, 3800 m ASL; Simien Mountains, Chennek area, 13°15'N 38°13'E, 3800 m ASL) where it co-exists with such specialized afroalpine form as *Stenocephalemys* sp.

6.2. Description of *Lophuromys menageshae* n.sp.

Lophuromys flavopunctatus (non THOMAS): partim AFEWORK BEKELE & CORTI, 1994, J. Zool., Lond. 232: 677.
Lophuromys flavopunctatus (non THOMAS): partim VERHEYEN *et al.*, 2002, Bull. Inst. R. Sci. Nat. Belg. Biol. 72: 145.

HOLOTYPE

ZMMU S-165969; adult male; dry skin and skull; collected by L.A. LAVRENCHENKO (4 May 1998) in Menagesha Forest, Suba Forest Station (08°57'N 38°33'E, 2600 m ASL), Central Ethiopia; collecting number 868.

PARATYPE

ZMMU S-165971; adult male; skull; collected by L.A. LAVRENCHENKO (3 May 1998) in the same locality; collecting number 873.

ADDITIONAL SPECIMENS

Three specimens from Debre Markos collected by R.E. CHEESMAN (April 1926).
BMNH 28.1.11.118 (ad. male; skull + dry skin; coll. nr 5688)
BMNH 28.1.11.119 (ad. female; skull)
BMNH 28.1.11.120 (ad. female; skull + dry skin; coll. nr 5733)

Five specimens from Addis Ababa collected by E. DEGEN, R.E. CHEESMAN and M. EWEN between 1902 and 1946.
BMNH 2.9.9.31 (ad. male; skull)
BMNH 2.9.9.32 (ad. male; skull + dry skin; coll. nr 36)
BMNH 2.9.9.34 (ad. female; skull + dry skin; coll. nr 24)
BMNH 37.2.24.76 (ad. female; skull + dry skin; coll. nr 160)
BMNH 50.57 (ad. female; skull + dry skin; coll. nr MG-3)

Another specimen from Yah Yah, Shoa, collected by E. DEGEN (18 April 1902)
BMNH 2.9.9.35 (ad. male; skull + dry skin; coll. nr 40)

TYPE LOCALITY

Suba Forest Station, Menagesha Forest, Central Ethiopia (08°57'N 38°33'E, 2600 m ASL).

ETYMOLOGY

The name *menageshae* refers to Menagesha Forest, which is the type locality of this new species.

DIAGNOSIS

A typical large-sized representative of the *L. flavopunctatus* species complex. Differs from all other members of this species group (excluding aberrant *L. melanonyx*) by its bigger skull with relatively narrow orbital and palatal regions.

DESCRIPTION

When we do not consider *L. melanonyx*, *L. menageshae* n.sp. is the largest known representative of this species complex. The dorsal pelage is blackish-brownish, the hairs are reddish at the base and blackish in the distal half with whitish subterminal bands and black tips which produce the "speckled" appearance (fig. 2E). Ventral pelage is greyish-yellow to pale orange, the hairs are white tipped and dark grey or yellow-orange at the base. The dorsal surface of the forefeet and hindfeet is greyish-yellow. The claws are light coloured. The bicoloured tail is relatively short (ca. 50% of HB); the hairs are black on the upper tail surface and nearly white on the lower surface.

The large skull with relatively narrow orbital and palatal regions possesses a broad inflated braincase, relatively large tympanic bullae and wide protruding zygomatic arches (fig. 3.2). Measurements are given in table 7.2 and appendix 2.

The chromosome set of *L. menageshae* n.sp.: 2*n* = 70, NFa = 84; 10 m, sm + 6st + 52a + Xsm + Ya (LAVRENCHENKO *et al.*, 2004).

UNIVARIATE ANALYSIS

A comparison with allopatric *L. simensis* possessing the same karyotype (2n = 70, NFa = 84) shows that *L. menageshae* has a significantly bigger skull, which is expressed by all measures excluding M8, M10, M15 and M21 (table 5.1). When comparing the means of the cranial measurements of the new taxon with sympatric and syntopic 68-chromosomal *L. flavopunctatus* s. str. we notice that the skull of *L. menageshae* is statistically bigger for M1, M2, M3, M4, M5, M6, M7, M13, M14, M15, M16, M20, M22, M23 (table 5.2).

MULTIVARIATE ANALYSIS

The results of a principal component analysis reveal clear separation between specimens of *L. simensis* and *L. menageshae* in the plain of the first and third principal components (graph. 12). All variables have negative loadings on PC1 ranging between -0.28 and -0.90, indicating that this component can be interpreted as a variant of size dimension. PC3 is characterized by positive correlation with the breadth of first upper molar M13 (M^1BR) (loading = 0.46) contrasted by negative correlation with the interorbital breadth M8 (INTE) and the palatal breadth M10 (PALA) (loadings < -0.50). Therefore, the difference between the two species along the first axis reflects larger average size of *L. menageshae* while the third component is associated with changes in skull shape.

The forward canonical analysis demonstrates that *L. menageshae* (OTU 700) can readily be differentiated from *L. simensis* (OTU's 40+51) as well as from *L. melanonyx* (OTU 35) with a percentage of correct classification of 100% (graph. 13). The canonical function includes 17 of the 24 measures available. We can safely conclude that these three OTU's possessing very close mitochondrial haplotypes (ch. 4) are craniometrically sufficiently differentiated to be taxonomically recognized.

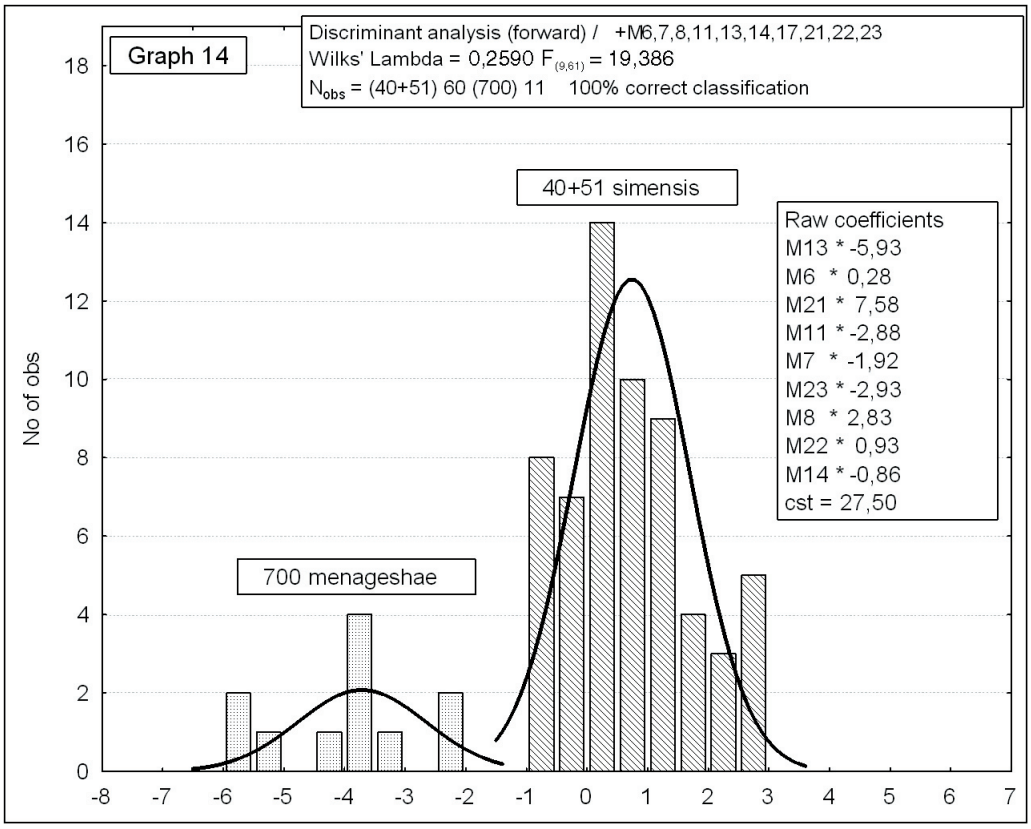
The forward discriminant analysis (graph. 14) characterizing *L. menageshae* versus *L. simensis* allows 100% correct classification and needs only 9 discriminating measures to achieve this goal: M6 (DIA1), M7 (DIA2), M8 (INTE), M11 (UPTE), M13 (M^1BR), M14 (ZYPL), M21 (DINC), M22 (ROHE), M23 (ROBR).

GENETIC CHARACTERIZATION

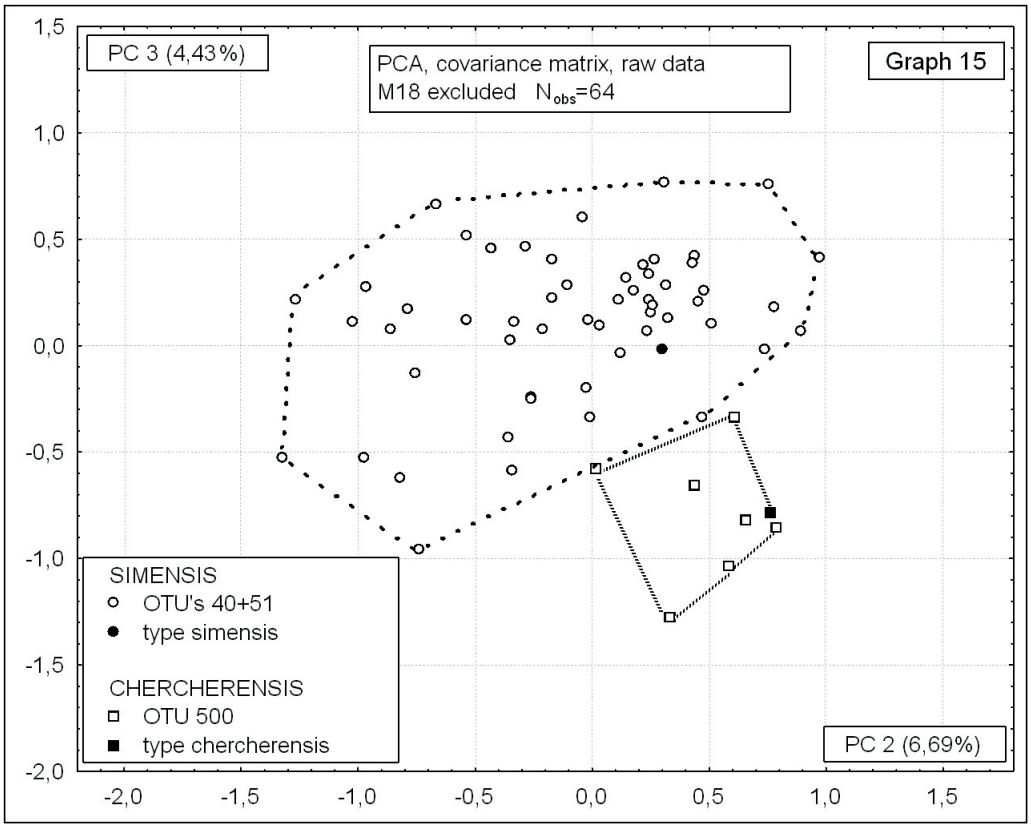
As it was shown above (ch. 4), the exposed mitochondrial haplotype of *L. menageshae* is very close to that of *L. melanonyx* and to one of the two mitochondrial lineages ("North-II") in *L. simensis* (p-distance between them = 0.015-0.021). On the other hand, the karyotype of *L. melanonyx* (2n=60, NFa=90) is clearly distinct from those of *L. menageshae* and *L. simensis* (2n=70, NFa=84). Moreover, the significant differences between *L. menageshae* and *L. simensis* in the specific profiles obtained by RAPD-PCR analysis should probably be situated at the species level (LAVRENCHENKO *et al.*, 2004). Taking into account these genetic data together with the results of multivariate morphometric analyses (graph. 12, 13), the remarkable similarity between mitochondrial haplotypes of *L. menageshae*, *L. simensis* ("North-II") and *L. melanonyx* can be explained as a result of interspecific transfer of mtDNA due to ancient hybridization (see ch. 5). It is worth mentioning that the partial mtDNA cytochrome b sequence of 402 base pairs can be used as barcoding tool to identify even these three taxa. Thus, three sites (positions 126, 127 and 390) distinguish *L. menageshae* from *L. simensis* ("North-II") and six sites (positions 67, 126, 127, 156, 282 and 399) discriminate *L. menageshae* versus *L. melanonyx* (Table 3).

DISTRIBUTION AND ECOLOGY

The species has been found in three regions: the Addis Ababa district (including Menagesha Forest), the south bank of the Blue Nile canyon (Yah Yah) and the vicinities of Debre Markos. All specimens of *L. menageshae* were collected in forested areas between 2100 and 2600 m ASL. The holotype and paratype were captured at the edge of the typical undifferentiated afromontane forest (trees: *Juniperus procera, Podocarpus falcatus, Olea europaea, Pinus radiata, Cupressus lusitanica, Maytenus gracilipes*; shrub: *Solanecio gigas*) with open grassy patches. Five other rodent species were trapped in the same area of the Menagesha Forest: *Tachyoryctes splendens* RÜPPELL, 1835, *Lophuromys flavopunctatus* s. str., *Praomys albipes* (RÜPPELL, 1842), *Mus mahomet* RHOADS, 1896, and *Desmomys harringtoni* (THOMAS, 1903).



Graph 14.
Graphic representation of the discriminant function (forward analysis) differentiating between *L. menageshae* n.sp. (OTU 700) and *L. simensis* (OTU's 40+51). The raw canonical coefficients permitting 100 % correct diagnosis are also listed.



Graph 15.
Graphic representation of a principal component analysis demonstrating that *L. chercherensis* n.sp. (OTU 500) and *L. simensis* (OTU's 40+51) can readily be differentiated by craniometry.

6.3. Description of *Lophuromys chercherensis* n.sp.

HOLOTYPE

ZMMU S-168902; adult male; skull and dry skin; collected by L.A. LAVRENCHENKO (24 September 2000) in montane forest between Hirna and Deder (09°19'43''N 41°15'53''E, 2700 m ASL), Chercher Mountains, Eastern Ethiopia; collecting number 1006.

PARATYPES

Four specimens from the same locality, collected by L.A. LAVRENCHENKO (21 - 23 September 2000).
ZMMU S-168903 (ad. male; skull + dry skin; coll. nr 1007)
ZMMU S-168904 (ad. female; skull + dry skin; coll. nr 1008)
ZMMU S-168905 (ad. female; skull + dry skin; coll. nr 1009)
ZMMU S-168906 (subad. female; skull + dry skin; coll. nr 1011)

ADDITIONAL SPECIMENS

Another specimen from the same locality (SMNS 23415), collected by Hans RUPP in 1974.

Four specimens from the vicinities of Hirna (09°12'58''N 41°05'36''E, 2000 m ASL), Chercher Mountains, collected by G. NICOLAUS between 9 and 10 December 1975.
SMNS 23894 (ad. male; skull + dry skin; coll. nr 217)
SMNS 23895 (ad. female; skull + dry skin; coll. nr 233)
SMNS 23896 (ad. female; skull + dry skin; coll. nr 243)
SMNS 23897 (ad. male; skull + dry skin; coll. nr 248)

TYPE LOCALITY

22 km northeast Hirna (near road Hirna – Deder), Chercher Mountains, Eastern Ethiopia (09°19'43''N 41°15'53''E, 2700 m ASL).

ETYMOLOGY

The name *chercherensis* refers to Chercher Mountains, to which the new species is endemic.

DIAGNOSIS

A medium-sized "speckled" *Lophuromys* with a relatively short tail. Differs from all other "speckled" Ethiopian *Lophuromys* by slighter "speckled" effect and richer reddish shade of the dorsal pelage, and more widely separated upper cheekteeth rows.

DESCRIPTION

L. chercherensis n.sp. is a medium-sized representative of the *L. flavopunctatus* species complex. The dorsal pelage is blackish-brownish with a reddish shade, the hairs are bright reddish at the base and blackish in the distal half with relatively narrow pale yellow subterminal bands and black tips which produce a moderate "speckled" appearance (fig. 2C). Ventral pelage is greyish-yellow to pale rufous, the hairs are white tipped and greyish-yellow or rufous at the base. The dorsal surface of the forefeet is dark brownish, whereas the dorsal surface of the hindfeet is rufous with a central longitudinal brownish band. The light claws are long, especially on the forefeet, very much like in *L. brevicaudus* and *L. simensis*. The tail is relatively short (ca. 50% of HB). The hairs are black on the upper tail surface and dark grey with white tips on the lower surface, however, since they are relative short the tail does not appear bicoloured (as in *L. simensis* and *L. menageshae*).

The skull is similar in size to *L. simensis* but with more widely separated upper cheekteeth rows and somewhat smaller tympanic bullae (fig. 3.3). Measurements are given in table 7.3 and appendix 2.

The karyotype of *L. chercherensis* n.sp. comprises $2n = 70$ chromosomes (NFa = 84; 10 m, sm + 6st + 52a + Xsm + Ya) (LAVRENCHENKO *et al*. 2004).

UNIVARIATE ANALYSIS

The skull of *L. chercherensis* is of comparable size as *L. simensis*, but is also overall somewhat smaller for the henselion-palation length M4 (HEPA), foramen palatal length M5 (PAFL), diastema length M7 (DIA2), zygomatic plate M14 (ZYPL), bullae length M19 (BULL), braincase breadth M20 (BRCA) and ramus-height of mandibula M24 (PCPA). On the other hand *L. chercherensis* has a significantly broader palatal region M10 (PALA) and upper dental arch M12 (UPDA) than *L. simensis* (table 5.1).

A comparison with *L. menageshae* reveals that *L. chercherensis* is statistically smaller for 18 measurements; the difference is most pronounced for M4 (HEPA), M5 (PAFL), M7 (DIA2), M13 (M^1BR), M14 (ZYPL), M19 (BULL), M24 (PCPA). We see however, that in contrast the palatal breadth (M10 - PALA) in *L. chercherensis* is somewhat bigger than in *L. menageshae* (table 5.3).

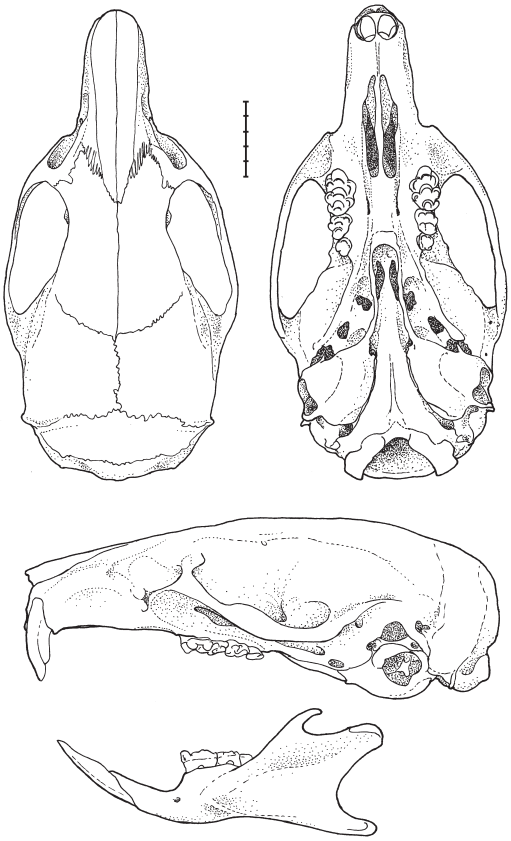


Fig. 3.3. Views of skull and mandible of *Lophuromys chercherensis* n.sp. (ZMMU S-168902, holotype). Scale bar = 5 mm.

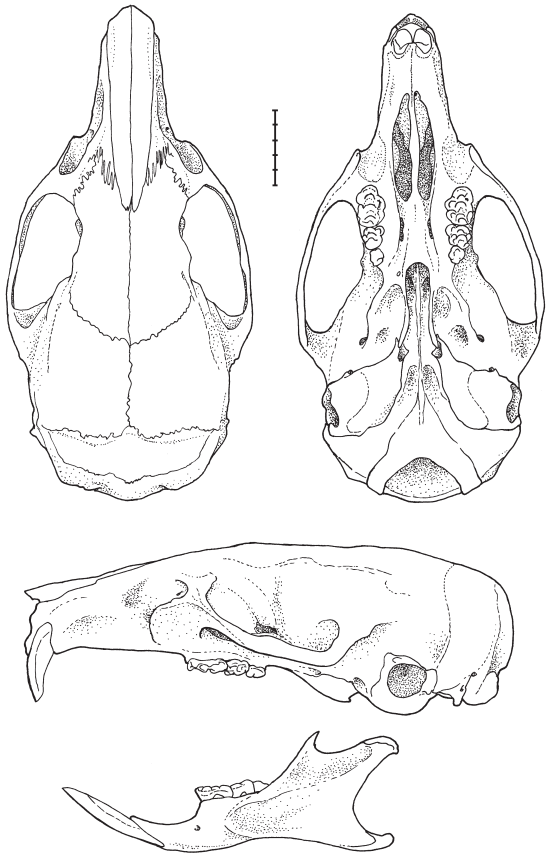


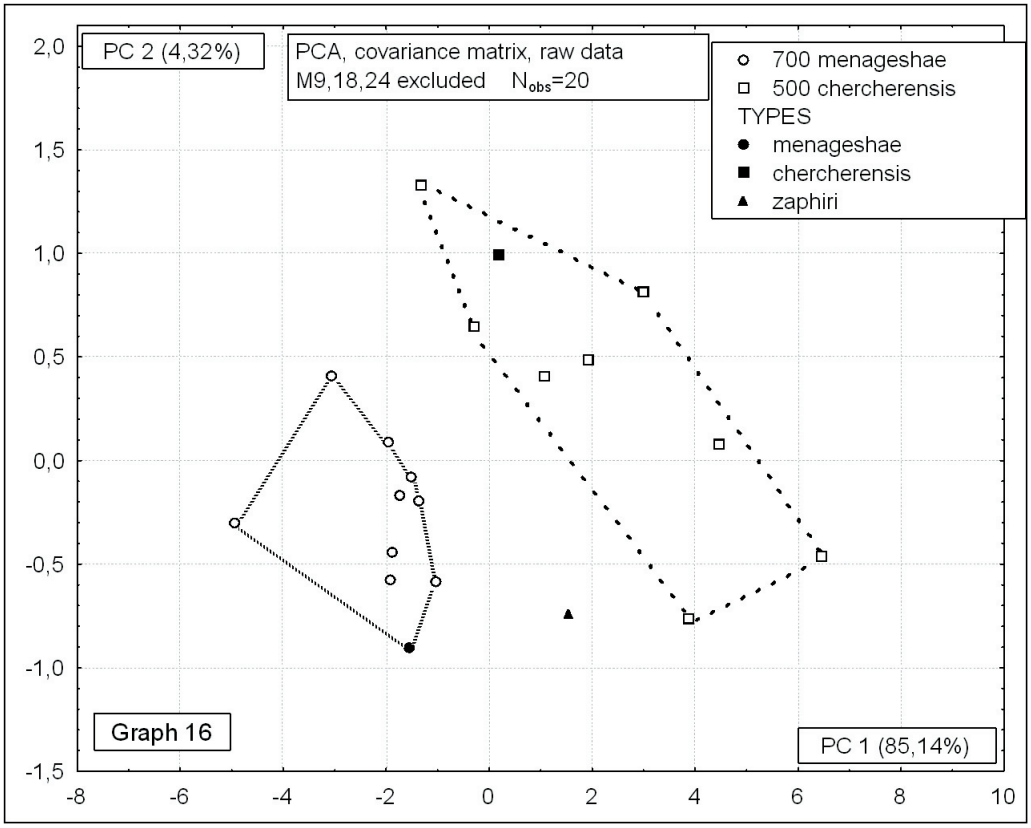
Fig. 3.4. Views of skull and mandible of *Lophuromys pseudosikapusi* n.sp. (ZMMU S-179563, holotype). Scale bar = 5 mm.

Multivariate analysis

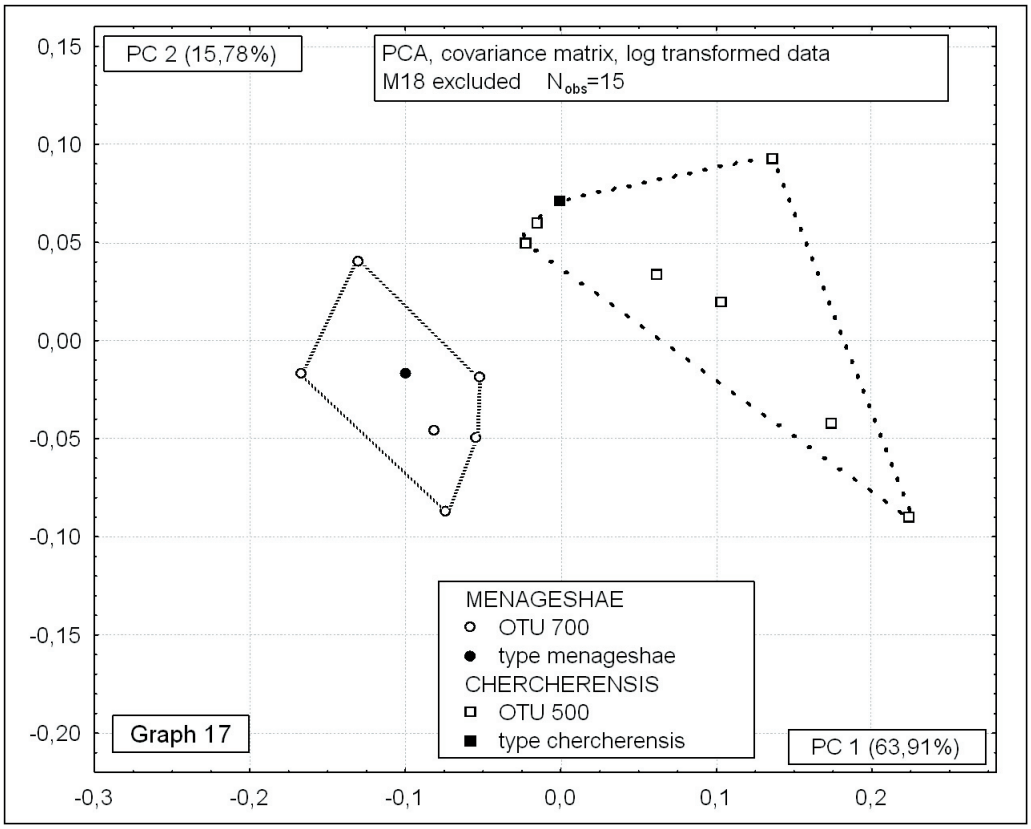
The segregation of *L. chercherensis* from *L. simensis* in the plain of the second and third principal components (graph. 15) reflects differences between these two species in cranial proportions. The loadings indicate that PC 2 represents a contrast between the nasal length M16 (LNAS) (loading = 0.37) on the one hand and the zygomatic breadth M9 (ZYGO), bullae length M19 (BULL), braincase breadth M20 (BRCA) and ramus-height of mandibula M24 (PCPA) (loadings < -0.40) on the other hand. PC 3 is characterized by positive correlation with the henselion-palation length M4 (HEPA) (loading = 0.42) contrasted by negative correlation with the palatal breadth M10 (PALA), dental arch breadth M12 (UPDA) and rostrum breath M23 (ROBR) (loadings < -0.40).

The results of the principal component analyses executed on both raw (untransformed) and log-transformed metrical data (graphs 16 and 17) reveal that *L. chercherensis* and *L. menageshae* separate with no overlap mainly along the PC 1. The coefficients and loadings (data not shown) indicate that PC 1 in both analyses represents a contrast between overall size and the palatal breadth (M10 - PALA). All measurements but the palatal breadth load negatively; thus, specimens with low scores on PC 1 (left portion of graphs 16 and 17) have relatively large values for all measurements except the palatal breadth. In contrast, specimens with high scores (right portion of graphs 16 and 17) hold small values for most measurements, but large ones for the palatal breadth.

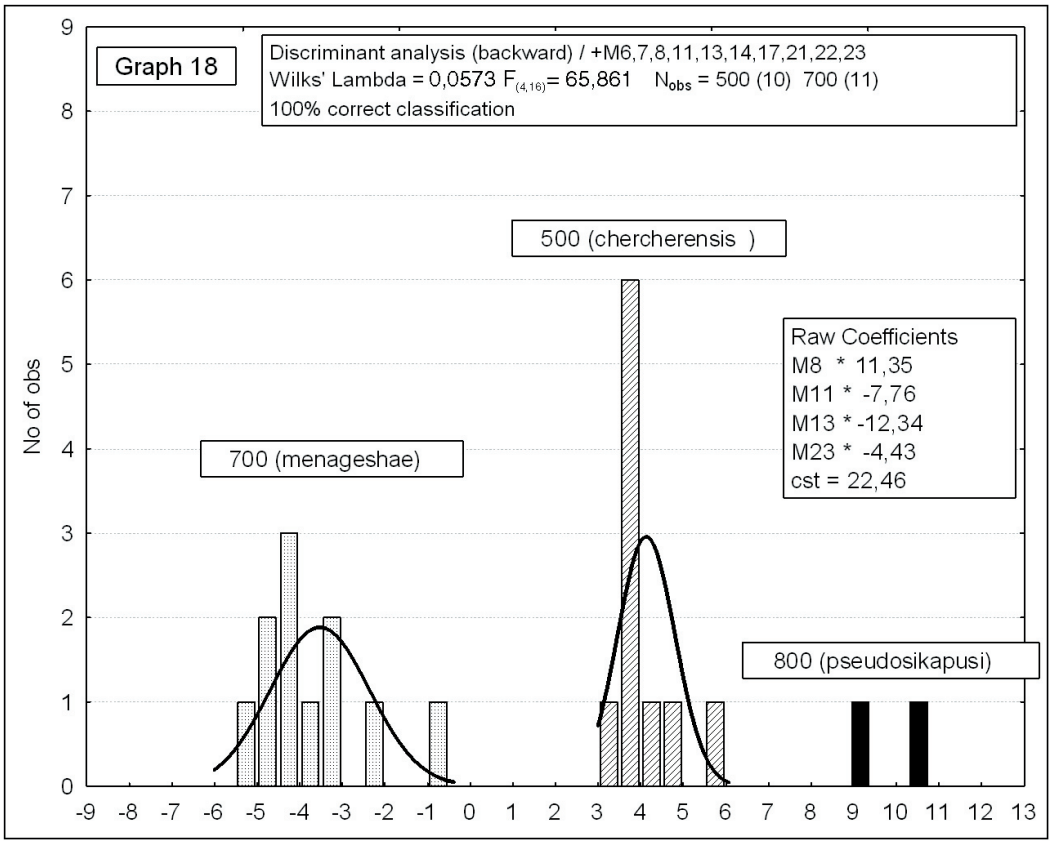
Also in the discriminant analyses (graphs 18 and 19) we see that *L. chercherensis* can easily be distinguished from *L. menageshae* and *L. simensis*. The backward discriminant analysis characterizing *L. chercherensis* versus *L. menageshae* needs only four measures (M8 (INTE), M11 (UPTE), M13 (M^1BR), M23 (ROBR)) to allow 100% correct classification (graph. 18). To differentiate between *L. chercherensis* and *L. simensis* (graph. 19) the forward analysis requires only 11 measures (M5, M6, M7, M10, M12, M13, M17, M19, M20, M22, M23) to realize 100% correct diagnosis.



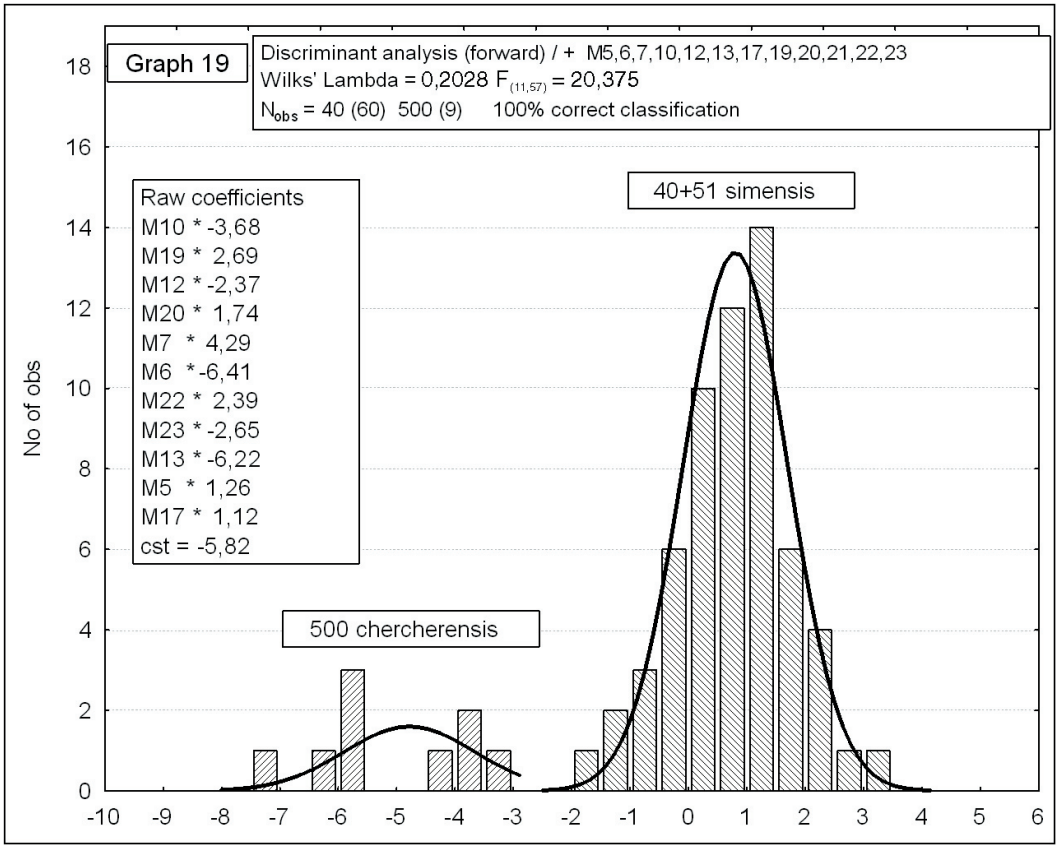
Graph 16.
Graphic representation of a principal component analysis (based on non-transformed data) of cranial measurements of *L. menageshae* n.sp. (OTU 700) and *L. chercherensis* n.sp. (OTU 500). Note that the *zaphiri*-type is found outside the ranges of these two new taxa.



Graph 17.
Graphic representation of a principal component analysis (based on log-transformed data) of cranial measurements of *L. menageshae* n.sp. (OTU 700) and *L. chercherensis* n.sp. (OTU 500).



Graph 18.
Graphic representation of the discriminant function (backward analysis) differentiating *L. menageshae* n.sp. (OTU 700) and *L. chercherensis* n.sp. (OTU 500). The four skull measurements needed for the 100 % correct diagnosis of these new taxa are also available. The two specimens of *L. pseudosikapusi* n.sp. (OTU 800) are plotted.



Graph 19.
Graphic representation of the discriminant function (forward analysis) differentiating *L. chercherensis* n.sp. (OTU 500) and *L. simensis* (OTU's 40+51). The raw canonical coefficients permitting 100 % correct diagnosis are also listed.

Genetic characterization

The obtained data on the partial cytochrome b sequences suggest that *L. chercherensis* is importantly differentiated from all known and newly recognized taxa of Ethiopian *L. flavopunctatus* s. lat. (average p-distances = 0.038-0.104). The genetic intraspecific variability within *L. chercherensis* is characterized by much lower p-distances (average p = 0.009). Therefore, it is not surprising that the studied cytochrome b fragment can be used as a set of markers to identify this new taxon (table 3). Our previous study revealed that the RAPD band pattern of *L. chercherensis* differs significantly from those of *L. chrysopus*, *L. flavopunctatus* s. str., *L. brunneus*, *L. simensis*, *L. menageshae* and *L.* cf. *sikapusi* (see figs 4, 5A, 6A, 7 in Lavrenchenko *et al.*, 2004).

Distribution and ecology

The new species has been found in two localities of the Chercher Mountains: 22 km northeast Hirna (09°19'43''N 41°15'53''E, 2700 m ASL) and the vicinities of Hirna (09°12'58''N 41°05'36''E, 2000 m ASL). Five specimens of *L. chercherensis* from the former locality were captured in highly disturbed *Podocarpus* forest. The only rodent species found together with *L. chercherensis* was *Praomys albipes* (Rüppell, 1842).

6.4. Description of *Lophuromys pseudosikapusi* n.sp.

Lophuromys cf. *sikapusi*: Lavrenchenko, 2003, Bonn. zool. Beitr. 50(4): 324.
Lophuromys cf. *sikapusi*: Lavrenchenko *et al.*, 2004, Biol. Journ. Linn. Soc. 83: 302.

Holotype

ZMMU S-179563; adult male; skull and dry skin; collected by L.A. Lavrenchenko (26 March 1999) in Sheko Forest (07°04'N 35°30'E, 1930 m ASL); collecting number 951.

Paratype

ZMMU S-179564; adult female; skull and dry skin; collected by L.A. Lavrenchenko (26 March 1999) in the same locality; collecting number 952.

Type locality

Sheko Forest, South-West Ethiopia (07°04'N 35°30'E, 1930 m ASL). The exact place of capture was in disturbed humid afromontane forest situated *ca.* 800 m northwards from the local agricultural office of the Sheko settlement.

Etymology

The specific epithet is derived from *L. sikapusi* and the Greek prefix *pseudo-*, meaning "false *L. sikapusi*".

Diagnosis

A large-sized representative of the *L. flavopunctatus* species complex with a relatively long tail, large ears and flattened skull. Differs from all other members of this species group by its "unspeckled" pelage.

Description

Externally *L. pseudosikapusi* n.sp. is an "unspeckled brush furred" rat. The dorsal pelage is blackish-reddish, the hairs are bright reddish at the base and blackish in the distal half without any light subterminal bands (fig. 2B). Ventral pelage is apricot, the hairs are yellowish basally and reddish in the terminal half. The chin and throat have the same colour as the ventral side. The blackish ears are relatively large (ca. 20 mm). The dorsal surface of the forefeet and hindfeet is light rufous. The claws are white and relatively short. The tail is relatively long (ca. 60% of HB). The hairs are blackish-brown on the upper tail surface and nearly white on the lower surface, however, since they are very short the tail appears almost "naked".

The large skull with broad orbital and palatal regions possesses a relatively narrow and flattened braincase and a narrow rostrum (Fig. 3.4). Measurements are given in table 7.4 and appendix 2.

The karyotype of *L. pseudosikapusi* n.sp. (2*n* = 70, NFa = 84; 10 m, sm + 6st + 52a + Xsm + Ya) is described by Lavrenchenko *et al.* (2004).

Univariate analysis

In table 6 and appendix 2 we see that the skull of *L. pseudosikapusi* has about the same general size as *L. menageshae*. Nevertheless, it is consistently bigger for the interorbital and palatal breadths M8 (INTE) and M10 (PALA), but smaller for all the cheekteeth measures (M11, M13, M17), braincase breadth M20

Table 8. Sympatry in Ethiopian *Lophuromys*. The table contains the numbers of sampling localities (see fig. 1 and table 1 for their abbreviations) where pairs of sympatric species were found to co-occur under syntopy; "(h)" indicates hypothesized contemporary hybridization.

Species	1	2	3	4	5	6	7	8	9
(1) *chrysopus* (2n=54)									
(2) *melanonyx* (2n=60)	-								
(3) *brevicaudus* (2n=68)	24,30	15,26							
(4) *flavopunctatus* s.str. 2n=68)	-	-	-						
(5) *brunneus* (2n=68)	5	-	-	5(h)					
(6) *simensis* (2n=70)	-	-	-	-	-				
(7) *menageshae* (2n=70)	-	-	-	1,28	-	-			
(8) *chercherensis* (2n=70)	-	-	-	-	-	-	-		
(9) *pseudosikapusi* (2n=70)	32	-	-	-	-	-	-	-	

(BRCA), rostrum breadth M23 (ROBR) and ramus-height of mandibula M24 (PCPA). The skull of *L. pseudosikapusi* is somewhat bigger than that of *L. simensis* and *L. chercherensis* (table 6), however, only the difference for M1 (GRLS), M8 (INTE), M10 (PALA), M12 (UPDA) and M16 (LNAS) is statistically significant under comparison with the former species. The absence of statistical significance for the difference in cranial characteristics between *L. pseudosikapusi* and *L. chercherensis* can be associated with a very small number (n=2 vs. n=10) of available specimens of these new taxa. Nevertheless, *L. pseudosikapusi* is considerably larger than *L. chercherensis* in some external characteristics (p=0.003 for ear length and p=0.01 for hind-foot length (without nail)) and has a significantly longer tail, both in overall length and relative to the head and body (p=0.004 and 0.001, respectively) (Tables 7.3 and 7.4).

Multivariate analysis

The result of the backward discriminant analysis characterizing *L. menageshae* versus *L. chercherensis* (graph 18) demonstrates that the two plotted specimens of *L. pseudosikapusi* are clearly separated from these two new species. Higher values of the canonical scores for *L. pseudosikapusi* are defined by its wider interorbital region (M8), weaker dentintion (M11, M13) and narrower rostrum (M23) comparatively to *L. menageshae* and *L. chercherensis*.

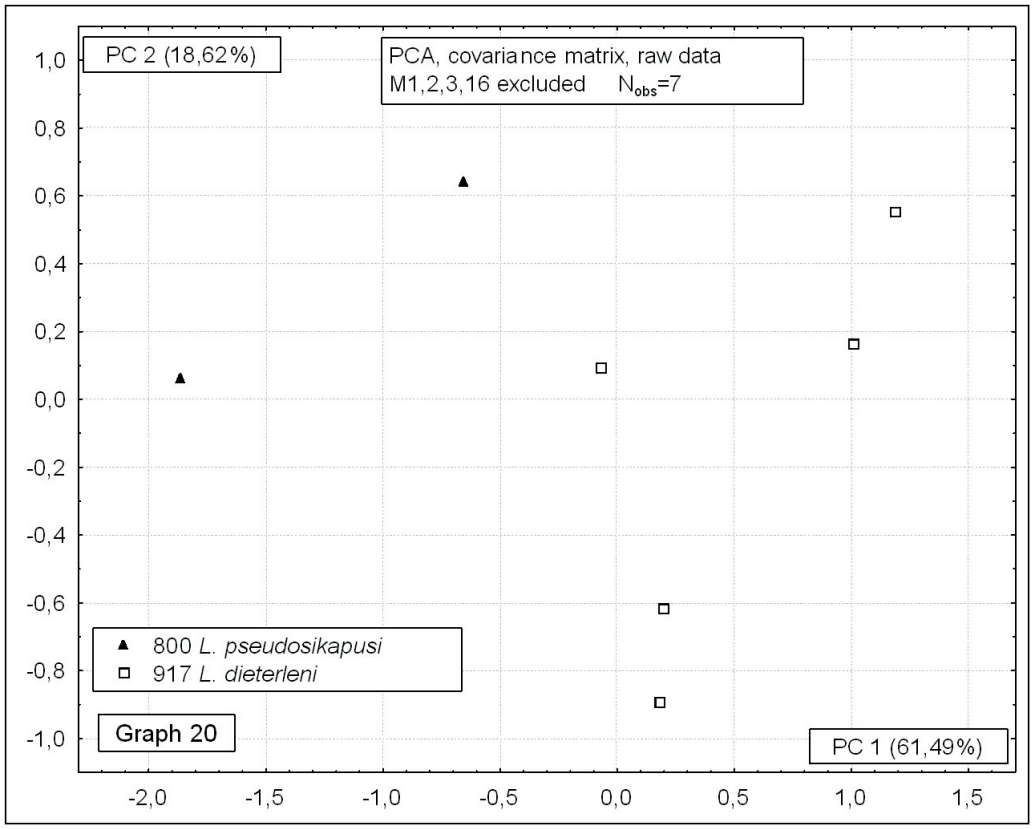
Finally, we compare *L. pseudosikapusi* n. sp. with another "unspeckled brush furred" rat, *L. dieterleni* from Mount Oku (West Cameroun), that shows cranial resemblance to the *L. flavopunctatus* species complex (Verheyen *et al.*, 1997). The results of the principal component analysis reveal that *L. pseudosikapusi* and *L. dieterleni* separate clearly along the PC 1 with no overlap between them (graph. 20). PC 1 can not be interpreted as a size factor, as it is characterized by positive correlation with M8 (INTE) and M23 (ROBR) (loading > 0.47) contrasted by negative correlation with M4 (HEPA), M5 (PAFL), M6 (DIA1), M7 (DIA2), M11 (UPTE), M12 (UPDA), M13 (M^1BR), M14 (ZYPL) and M17 (LOTE) (loadings < -0.60). Therefore, the difference between the two species along the first axis reflects the narrower but longer snout, the narrower orbital region, the larger zygomatic plate and the heavier cheekteeth rows in *L. pseudosikapusi* comparatively to *L. dieterleni* (see also table 6).

Genetic characterization

Two obtained partial cytochrome b sequences of *L. pseudosikapusi* are identical and differ importantly from those of other Ethiopian *Lophuromys* taxa (average p-distances = 0.036-0.102). Therefore, the gene fragment can be used as a set of markers to identify this new taxon (Table 3). Our previous study revealed significant differences in the RAPD profiles between *L. pseudosikapusi* and other studied Ethiopian species, *L. chrysopus*, *L. flavopunctatus* s. str., *L. brunneus*, *L. simensis*, *L. menageshae* and *L. chercherensis* (see Figs 4, 5A,B and 7 in Lavrenchenko *et al.*, 2004).

Distribution and ecology

Only known from the Sheko Forest. Despite intensive sampling efforts with the same methodology used in the Sheko Forest we failed to trap *L. pseudosikapusi* in forested site adjacent to the type locality - the Dishi area of the Godare Forest (07°21'N 35°13'E, 1200 m a.s.l.) which is, however, situated at a lower altitude. It remains possible that the currently known species range is incomplete. Nevertheless, we suppose, that it is extremely limited. Both known specimens of *L. pseudosikapusi* were captured in disturbed humid



Graph 20. Individual specimen scores projected onto the first and second principal components extracted from analysis of *L. pseudosikapusi* n.sp. (OTU 800) and *L. dieterleni*.

afromontane forest with notable abundance of parasitic *Ficus* and undergrowth dominated by *Coffea arabica*. In the Sheko Forest, the new species occurs together with at least seven other rodent species: *Dendromus melanotis* A. SMITH, 1834, *Lophuromys chrysopus* OSGOOD, 1936, *Praomys albipes* (RÜPPELL, 1842), *Mus mahomet* RHOADS, 1896, *Lemniscomys macculus* (THOMAS & WROUGHTON, 1910), *Desmomys yaldeni* LAVRENCHENKO, 2003, and *Otomys* sp.

DISCUSSION

1. Systematics and taxonomy

Our integrative approach (using craniometry and partial cytochrome b sequences combined with the results of previous chromosomal and RAPD-PCR analyses) reveals that morphological and genetic diversity among Ethiopian *L. flavopunctatus* s. lat. is far higher than suspected today. One of the most unexpected and interesting results of our study is evidence for extensive reticulate processes in this species group. Serious difficulties surround the making of taxonomic decisions on populations of hybrid origin (JONES *et al.*, 1995) and the determination of the species boundaries under such circumstances requires special consideration. At least three species, *L. simensis*, *L. menageshae* and *L. melanonyx*, were supposedly involved in ancient introgressive hybridization. Exposed differences in morphometric and RAPD patterns suggest the absence of contemporary gene flow between *L. simensis* and *L. menageshae*. The third species, *L. melanonyx*, is craniometrically and cytogenetically clearly differentiated from these two taxa. Besides that, specific appearance, ecology and behaviour of the specialized afroalpine form (PETTER, 1972; YALDEN & LARGEN, 1992; our unpublished data) make it somewhat aberrant among all other representatives of the *L. flavopunctatus* species complex. The karyotypic differences between *L. melanonyx* on one hand, and *L. simensis* and *L. menageshae* on the other (2n=60, NFa=90 versus 2n=70, NFa=84; see ANISKIN *et al.*, 1997; LAVRENCHENKO *et al.*, 2004), seem to be effective barriers to introgression. We hypothesize that some horizontal transfer of mtDNA between *L. melanonyx* and *L. menageshae* (or *L. simensis*) took place during a previous phase of their differentiation when the chromosomal differences were less pronounced. There is increasing evidence that mtDNA introgression

between "good" species of mammals may be more common that previously thought (e.g. TEGELSTROM, 1987; PATTON & SMITH, 1994; IWASA & SUZUKI, 2002; GOOD *et al.*, 2003; GAUBERT *et al.*, 2005; MELO-FERREIRA *et al.*, 2005). Therefore, we suppose that *L. melanonyx*, *L. menageshae* and *L. simensis* should be assigned full species rank.

The complex pattern of co-distribution of nuclear (RAPD) and mitochondrial markers assumes contemporary gene flow between 68-chromosomal *L. flavopunctatus* s. str. and *L. brunneus*. Moreover, the results of multivariate analysis of cranial morphology support the supposition (ch. 5). Exact distribution ranges of the two forms as well as precise location of contact zone between them remain unclear and require further investigation. Nevertheless, the evidence available at the time allows us to interpret relationships between *L. flavopunctatus* s. str. and *L. brunneus* as "parapatry with hybridization". It is noteworthy that the levels of morphological and genetic (average p-distance = 0.068) differentiation between these two forms are comparable with those between undoubted species of *Lophuromys*. Thus, the results of this study suggest that the taxa can be regarded as two semispecies belonging to superspecies *L. flavopunctatus* under diagnostic criteria outlined by HELBIG *et al.* (2002). In particular, the suggestion of the authors that "semispecies are terms that can be used to label qualitatively different categories of species whose evolutionary independence cannot be determined empirically" corresponds certainly to our case with *L. flavopunctatus* s. str. and *L. brunneus*.

There is no indication of previous or contemporary gene flow across species boundaries of the resting four taxa, *L. chrysopus*, *L. brevicaudus*, *L. chercherensis* and *L. pseudosikapusi*, which are represented by mutually monophyletic lineages in a tree of mitochondrial haplotypes (LAVRENCHENKO *et al.*, 2004). The genetic distances between them (average p-distances = 0.048-0.104) fall well within the range typical for allied species in muroids rodents (BRADLEY & BAKER, 2001). As they are also fully diagnosable using genetic (cytochrome b fragment), morphologic (craniometry, external morphology) and, partially, cytogenetic (C- and G-banding) character sets, the species rank for all these taxa cannot be questioned.

Thus, with inclusion of the new data and with an updated taxonomy we recognize the following nine *Lophuromys* species in Ethiopia, all of which are endemic to this country:

L. [f.] flavopunctatus THOMAS, 1888
L. [f.] brunneus THOMAS, 1906
L. simensis OSGOOD, 1936
L. brevicaudus OSGOOD, 1936
L. chrysopus OSGOOD, 1936
L. melanonyx PETTER, 1972
L. menageshae LAVRENCHENKO *et al.*, 2007
L. chercherensis LAVRENCHENKO *et al.*, 2007
L. pseudosikapusi LAVRENCHENKO *et al.*, 2007

2. Biogeography and possible evolutionary history

The number of species of *L. flavopunctatus* s. lat. inhabiting the area of the Ethiopian Plateau (n = 9) is comparable with that known for the rest of the much larger distribution range of this entire species complex (n = 12, see VERHEYEN *et al.*, 2007). Then, we can note the following differences between these two non-overlapping sets of species:

(1) The level of interspecific morphological diversity is significantly higher among Ethiopian taxa (ch. 3).
(2) Seven of the nine Ethiopian species are locally sympatric and syntopic with some other (table 8) whereas all non-Ethiopian species are strictly allopatric (VERHEYEN *et al.*, 2002, 2007).
(3) In contrast with the strong evidence for extensive reticulate processes within the Ethiopian Plateau (ch. 5), no indication to interspecies transfer of mtDNA was revealed among non-Ethiopian species.

The mentioned dissimilarities could be associated with both different evolutionary age of Ethiopian and non-Ethiopian *L. flavopunctatus* s. lat., and some intrinsic environmental properties of different areas within their distribution range. The results of our distribution-wide phylogeographic analysis (based on mtDNA data) of this species complex will be published elsewhere. We note here only that Ethiopian species, *L. chrysopus*, represents the most basal branch of the phylogenetic tree suggesting the Ethiopian Plateau to be the ancestral area for this species group. We can suppose that relatively long co-existence of distinct evolutionary lineages resulted in greater morphological diversity (as consequence of adaptive radiation), local sympatry and extensive reticulate processes within Ethiopian species. Contrariwise, the absence of reticulation among non-Ethiopian *L. flavopunctatus* s. lat. could be linked with their allopatric distribution as a result of the more recent evolutionary history of these species.

Whereas the distribution range of the species complex outside of Ethiopia includes isolated mountains and comparatively small plateaux (east of the Rift) or topographically relatively uniform lowlands (west of

the Rift), the Ethiopian Plateau represents vast montane massif with extremely diverse geomorphology that can potentially provide a larger numbers of ecological niches. Generally, one could expect that higher rates of *both* speciation and extinction will occur in the topographically more diverse area than in the one that is less so (VRBA, 1992). FJELDSÅ & LOVETT (1997) found that peak concentrations of recently evolved species of African forest birds and plants were often congruent with clusters of old relict species. They suggested that specific areas of topographical complexity, which may have localized environmental stability (caused mainly by a stable pattern of orographic rainfall or mist precipitation) over long-term climatic cycles, can simultaneously act as "species pumps" and refuges for ancient relict species. Therefore, the co-existence of a number of endemics (including neo-endemics and relics) in such areas may be associated with both high rates of speciation and low rates of extinction. We think that this scenario can also be applied to the Ethiopian *Lophuromys*. The occurrence of narrow-ranged phylogenetic relics with high habitat specialization among other groups of animals suggests that climate conditions are likely to have been stable over millions of years in some places in the southern part of the Ethiopian Plateau. A number of such examples are provided by endemic amphibian monotypic genera, brevicipitine *Balebreviceps* and bufonids *Spinophrynoides* and *Altiphrynoides* (LARGEN, 1998). As the presumed evolutionary age of the amphibian relics is certainly greater than that of *L. flavopunctatus* species complex (0.7-0.9 Myr, see LAVRENCHENKO *et al.*, 2004) and these two groups of vertebrates with relatively low dispersal capacity share currently the same habitats (montane forests and moorlands), we may suppose that their representatives have survived unfavourable Pleistocene episodes in the same refugia within the Ethiopian Plateau. The altitudinal shifts of the habitats in the area of extremely topographic variety may not only allow persistence of old lineages but are also expected to promote their splitting and differentiation because of distributional dissection. The repeated periods of spatial fragmentation, rejoining of montane habitats during middle and late Pleistocene could facilitate both speciation in the Ethiopian *Lophuromys* and the interspecies transfer of mtDNA between currently allopatric *L. simensis*, *L. menageshae* and *L. melanonyx*. Thus we can suppose that the evolutionary history of *L. flavopunctatus* s. lat. of the Ethiopian Plateau was featured by both intensive local speciation in the restricted area and accumulation of survived evolutionary lineages combined with subsequent reticulation among some of them. Of course, this rather speculative scenario should be tested by detailed phylogenetic analysis using extended set of molecular data (the study is in progress).

3. Conservation implications

The case study of *L. flavopunctatus* s. lat. provides some support to the supposition of FJELDSÅ *et al.* (1999) about correlation between centres of endemism and of human cultures. Indeed, the Ethiopian Plateau, being cradle of one of the most ancient sub-Saharan African cultures, harbours almost half of the known species of the group. Agriculture has been the main human activity in the area 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 & CORTI, 1997). Although most species of *L. flavopunctatus* s. lat. do not represent specialized forest forms (with the possible exception of *L. chrysopus* and *L. pseudosikapusi* – see below), none of them is able to exist actually in true agricultural landscapes widespread presently within the Ethiopian Plateau. All Ethiopian collection localities of either species in such areas are from very small reserves containing relictual forest and bush patches within the agricultural matrix. Overall, the distribution of the species complex in Ethiopia has been dramatically reduced during historical time being restricted currently to areas of remaining natural or semi-natural vegetation. We may assume that some local species with restricted range size (e.g. similar in this respect to existing *L. chercherensis* and *L. pseudosikapusi*) became recently extinct and, therefore, initial diversity of Ethiopian *Lophuromys* was even higher than observed today.

As the conservation status of Ethiopian *Lophuromys* has been recently assessed at the GMA African Workshop in 2004 (IUCN 2006. 2006 IUCN Red List of Threatened Species. <www.iucnredlist.org>), we discuss here only the newly described species or taxa for which the species rank is proposed in the present study. It is difficult to assess the status of *L. flavopunctatus* s.str, *L. brunneus* and *L. menageshae* under IUCN Red List guidelines (IUCN, 2001) because of the absence of the detailed information on their exact distribution ranges, current condition of natural habitats in crucial

areas and population levels of the species. Therefore, we recommend that these species are given Data Deficient (DD) category. Nevertheless, it is noteworthy that all of them seem to be closely associated with montane forests which are the most endangered environment of the country because of their rapid and massive destruction (STUART & ADAMS, 1990).

Although the distribution range of *L. simensis* was apparently reduced because of particularly strong human population pressures in northern Ethiopia, it comprises protected area of the Simien Mountains National Park. However, a significant part of the Park has been heavily grazed by goats and cattle or converted to agriculture (our data, April – May 2005). Although the rather eurytopic species occurs in various environments (from dry woodlands to montane grasslands and moorlands) (ch. 6.1), it is never found in cultivated and degraded habitat, even at high altitude. Taking into account that *L. simensis* is still locally abundant in remaining relatively intact area of the Park (our unpublished data) we propose to classify it as Near Threatened (NT).

L. chercherensis is known from two adjacent localities of the Chercher Mountains: the vicinities of Hirna (09°13'N 41°06'E, 2000 m ASL) and 22 km northeast Hirna (09°20'N 41°16'E, 2700 m ASL). In spite of the fact that four specimens of the species were collected by Hans Rupp in the former locality in 1974, we did not find any suitable habitat there during our field work in 2000. According to reports of local people, complete deforestation of the area took place during the last quarter of last century as a result of the past activity of a timber company. At the same time, we trapped only five specimens of *L. chercherensis* in the latter locality in a small highly disturbed *Podocarpus* forest. It is obvious that the distribution range of the species that initially encompassed a significant part of the Chercher Mountains was conspicuously reduced. Even assumed that *L. chercherensis* inhabits yet some other very scarce and small forest remnants of the region (e.g. Kuni-Muktar Mountain Nyala Sanctuary), the maximum area of its occupancy can be estimated as ca. 300 km^2. The long-term survival of this species in such small, isolated forest patches is unlikely. Thus, *L. chercherensis* must be classified as Endangered B2ab(iii).

The only two known specimens of *L. pseudosikapusi* were collected in the heavily degraded Sheko Forest (07°04'N 35°30'E, 1930 m ASL) characterized by notable abundance of parasitic *Ficus* and undergrowth dominated by *Coffea arabica*. Although accurate habitat requirements of *L. pseudosikapusi* remain unclear, its evident absence in the adjacent forested area situated at a lower altitude (ch. 6.4) permits to suppose that the species is highly specialized to specific habitats of only one type of humid afromontane forest. Some parallels might be drawn with another apparently specialized forest dweller, *Desmomys yaldeni*, which was found besides the Sheko Forest at the similar altitude in the vicinities of Gore (08°08'N 35°30'E, 1800 m ASL) (Lavrenchenko *et al.*, 2003). Although *L. pseudosikapusi* also can potentially occur in a few other locations close to the type locality, its range size seems to be very restricted (< 5000 km^2) and the rapid destruction of the humid afromontane forests in south-western Ethiopia might threaten this presumably stenobiotic species in the nearest future. Therefore, we propose to classify *L. pseudosikapusi* as Endangered B1ab(iii) in categories of IUCN Red List. All efforts should be made to protect the Sheko Forest where two narrow endemic rodent species, *L. pseudosikapusi* and *Desmomys yaldeni*, occur yet.

CONCLUSIONS

In our integrated systematic evaluation of the Ethiopian *Lophuromys* we were faced with difficulties of two different kinds: (1) effects of recent and ancient interspecies hybridization and (2) restricted size of a few key samples resulted apparently from the recent rarity of some species. Nevertheless, the multidisciplinary approach (using multivariate craniometry, mitochondrial and nuclear molecular markers, and cytogenetic data) allowed us to characterize all recognized taxa as fully diagnosable in multiple independent characters and to describe three new species. Our study revealed that Ethiopian members of *L. flavopunctatus* s. lat. represent at least nine distinct species endemic to the country. The number of related rodent species is notable even for such centre of endemism and biodiversity as the Ethiopian Plateau. Moreover, this "species flock" constitutes a remarkable example of multiple reticulation among muroid species inhabiting fairly restricted area. The evidence suggests that the mammalian fauna of Ethiopia is unique not only because of high level of endemism but also as a basis for novel evolutionary models. This reinforces the need for effective protection of the remaining montane forests constituted key environment of the most Ethiopian *Lophuromys* as some of which can become extinct in a short time after their discovery.

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Appendix 1

Listing of the Ethiopian specimens, grouped per Operational Taxonomical Unit (OTU).

OTU 34 *L. flavopunctatus* s. str.
M(2), F(3)
Addis Ababa (locality 1): BMNH 37.2.24.77.
Ankober (locality 4): SMNS 23892.
Menagesha Forest (locality 28): BMNH 70.753; ZMMU S-165968, S-165970.

OTU 35 *L. melanonyx*
M(9), F(12)
Bale Mts (localities 15, 25, 26): BMNH 72.1265, 72.1267, 78.947; MHNP 1972.262; ZMMU S-162507-513, S-162515-518, S-162520, S-162522-526.

OTU 36 *L. brunneus*
M(13), F(17)
Beletta Forest (locality 5): ZMMU S-164928, S-164930-933, S-164935-938, S-164941-943, S-164945, S-165961-967, S-165975-977.
Bonga (locality 7): ZMMU S-165972-974.
Jimma (locality 23): SMNS 23384, 23385, 23400, 23402.

OTU 37 *L. brevicaudus*
M(50), F(60), sex?(11)
Bale Mts (localities 15, 24, 26, 30): BMNH 64.872, 64.873, 72.1245, 72.1247, 76.42, 76.51; SMNS 23359, 23361-366, 23369-371, 23373-377, 23379, 23899, 23900; ZMMU S-162435, S-162437, S-162442, S-162444, S-162448, S-162451-452, S-162455, S-162458, S-162462-464, S-162466-472, S-162474-475, S-162477, S-162479, S-162481, S-162484-485, S-162488, S-162490, S-162492-493, S-162495-499, S-162501, S-162503-504, S-162530-546, S-162593, S-162719, S-162720, S-164482, S-164812-820, S-164823-826, S-164848-852, S-164920-925.
Chilalo Mts (locality 11): SMNS 35946-950, 35952-954, 35960, 35964, 35966-969.

OTU 38 *L. chrysopus* East
M(25), F(23), sex?(1)
Harenna Forest (localities 24, 33): ROMA ET23, ET31; ZMMU S-162410, S-162411, S-162414-424, S-162426-434, S-164827-847, S-164918, S-164919, S-164926, S-164927.

OTU 39 *L. chrysopus* West
M(13), F(13), sex?(1)
Beletta Forest (locality 5): ZMMU S-164946, S-164948, S-164950-957.
Sheko Forest (locality 32): ZMMU S-167314-330.

OTU 503 *L. chrysopus* Godare
M(9), F(4), sex?(2)
Godare Forest (locality 19): BMNH 75.3119, 75.3121; ZMMU S-168907-919.

OTU 40 *L. simensis* Simien
M(22), F(14)
Simien Mts (localities 10, 31): ZMMU S-178473-508.

OTU 51 *L. simensis* Tana
M(14), F(10)
Debre Tabor (locality 14): ZMMU S-171638, S-171640, S-171641, S-175384-396.
Guna, Mt (locality 20): ZMMU S-171633-636.
Vanzaye (locality 34): ZMMU S-171637, S-171639, S-171642, S-171643.

OTU 500 *L. chercherensis*
M(4), F(5), sex?(1)
Chercher Mts (localities 21, 22): SMNS 23415, 23894-897; ZMMU S-168902-906.

OTU 700 *L. menageshae*
M(6), F(5)
Addis Ababa (locality 1): BMNH 2.9.9.31, 2.9.9.32, 2.9.9.34, 37.2.24.76, 50.57.
Debre Markos (locality 12): BMNH 28.1.11.118, 28.1.11.119, 28.1.11.120.
Menagesha Forest (locality 28): ZMMU S-165969, S-165971.
Yah Yah (locality 35): BMNH 2.9.9.35.

OTU 800 *L. pseudosikapusi*
M(1), F(1)
Sheko Forest (locality 32): ZMMU S-179563, S-179564.

APPENDIX 2.1

Cranial (M1 to M16) measurements (mm) of the three new taxa, *L. menageshae*, *L. chercherensis* and *L. pseudosikapusi*. For the description of the measurements see Table 2.

MUSEUM + REG	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15	M16
***L.menageshae* n.sp.**																
holotype																
ZMMU S-165969	31.55	30.50	25.80	13.95	6.90	8.20	10.10	5.95	16.75	2.80	5.80	7.00	1.95	3.70	3.10	12.85
paratype																
ZMMU S-165971	31.95	31.50	26.85	14.25	7.35	8.50	10.30	5.80	16.10	3.15	5.75	7.20	1.95	3.90	3.10	13.65
additional specimens																
BMNH 2.9.9.31	31.00	31.15	26.60	13.20	6.60	8.10	9.60	6.00	15.75	2.50	5.80	7.00	2.10	3.50	3.05	12.60
BMNH 2.9.9.32	31.60	30.80	26.30	13.45	6.85	8.55	10.10	5.65	15.35	2.80	5.55	6.95	2.05	3.45	3.00	13.15
BMNH 2.9.9.34	31.30	30.75	26.10	13.35	6.70	8.30	10.10	5.85	15.55	2.90	5.60	7.00	2.05	3.35	2.90	12.85
BMNH 2.9.9.35	31.80	31.70	26.10	13.35	6.60	8.10	9.75	5.70	14.80	2.75	5.65	6.90	2.05	3.55	2.95	12.90
BMNH 37.2.24.76	31.05	30.45	26.05	13.35	7.10	8.60	10.20	5.45	15.50	2.80	5.30	7.05	1.95	3.20	2.95	12.30
BMNH 50.57	31.55	30.80	26.00	13.50	6.95	8.45	10.15	6.05	15.70	3.05	5.85	7.10	2.00	3.35	2.95	13.50
BMNH 28.1.11.118	33.15	32.65	27.75	14.40	7.70	8.85	10.90	5.90	16.35	2.85	5.75	7.30	2.10	3.75	2.95	12.85
BMNH 28.1.11.119		31.00		14.00	7.55	8.65	10.50	5.85	15.45	2.80	5.75	7.00	2.05	3.45	2.80	12.20
BMNH 28.1.11.120	31.25	30.95	26.35	13.90	7.60	8.50	10.40	5.70	15.65	2.90	5.40	7.10	1.90	3.55	2.85	12.25
***L.chercherensis* n.sp.**																
holotype																
ZMMU S-168902	30.55	29.85	25.45	12.95	6.50	8.15	9.40	6.25	14.90	3.25	5.60	7.25	1.90	3.15	3.00	13.20
paratypes																
ZMMU S-168903	30.65	30.30	26.00	12.95	6.50	8.05	10.00	6.30	15.45	3.25	5.80	7.35	1.90	3.60	3.00	12.40
ZMMU S-168904	29.15	28.70	24.35	12.10	6.00	7.60	8.90	5.80	14.20	3.90	5.25	6.70	1.85	3.05	2.60	11.50
ZMMU S-168905	30.15	29.55	25.30	12.85	6.40	7.85	9.20	5.90	15.35	3.10	5.50	7.10	1.80	3.15	2.75	12.30
ZMMU S-168906	27.85	26.95	22.30	11.15	5.80	7.15	8.35	5.50	13.80	2.55	5.00	6.30	1.75	2.95	2.65	10.50
additional specimens																
SMNS 23415	30.10	29.10	24.65	12.20	5.95	7.80	9.25	5.75	14.75	3.15	5.15	6.90	1.80	3.10	2.90	12.45
SMNS 23894		30.40	25.75	13.10	6.85	8.20	9.70	6.05	16.25	3.10	5.15	7.20	1.90	3.20	2.80	
SMNS 23895	31.90	30.85	26.00	12.90	6.65	8.40	9.95	6.05	16.20	3.35	5.40	7.35	1.75	3.40	3.20	13.20
SMNS 23896	29.00	27.75	23.40	11.95	6.20	7.55	9.10	5.75		2.70	5.25	6.75	1.85	2.80	2.70	11.80
SMNS 23897	28.85	27.85	23.30	11.70	5.85	7.65	8.80	5.70	14.50	2.85	4.90	6.70	1.75	3.05	2.80	11.20
***L.pseudosikapusi* n.sp.**																
holotype																
ZMMU S-179563	31.75	30.55	26.10	13.50	6.85	8.55	10.40	6.40	15.80	3.55	5.25	7.50	1.85	3.60	3.00	13.50
paratype																
ZMMU S-179564	31.25	30.40	25.90	12.95	6.70	8.20	9.65	6.20	15.35	3.20	5.15	6.95	1.75	3.35	3.10	12.80

APPENDIX 2.2

Cranial (M17 to M24) and external measurements (mm), and weight (g) of the three new taxa, *L. menageshae*, *L. chercherensis* and *L. pseudosikapusi*. For the description of the measurements see Table 2.

MUSEUM + REG	M17	M18	M19	M20	M21	M22	M23	M24		W	HB	TL	HF-n	HF+n	EL
***L.menageshae* n.sp.**															
holotype ZMMU S-165969	5.20	1.20	6.00	14.00	1.50	6.55	5.20	9.55		72	129	67	20	22	16.5
paratype ZMMU S-165971	5.35	1.20	6.00	12.85	1.50	6.95	5.20	9.60		77	138	72	21	23	17
additional specimens															
BMNH 2.9.9.31	5.25	1.55	6.00	13.35	1.25	6.85	5.35	9.95		-	-	-	-	-	-
BMNH 2.9.9.32	5.15	1.40	6.15	13.75	1.25	6.85	5.05	10.10		-	-	-	-	23	18
BMNH 2.9.9.34	5.05	1.40	5.80	13.50	1.35	6.60	5.30	9.45		-	-	-	-	23	18
BMNH 2.9.9.35	4.85	1.15	5.95	13.35	1.25	6.75	5.10	9.90		-	-	-	-	-	18
BMNH 37.2.24.76	4.85	1.25	5.45	13.75	1.10	6.60	5.50	-		-	134	63	-	22	15
BMNH 50.57	5.05	1.65	6.00	14.15	1.20	6.65	5.75	-		-	143	70	-	22	20
BMNH 28.1.11.118	5.15	1.35	5.80	14.20	1.35	7.25	5.30	10.90		-	131	75	-	24	17
BMNH 28.1.11.119	5.10	1.70	5.85	13.40	1.30	7.00	5.15	-		-	-	-	-	-	-
BMNH 28.1.11.120	4.85	1.45	5.60	13.10	1.20	6.80	5.15	-		-	131	60	-	22	17
***L.chercherensis* n.sp.**															
holotype ZMMU S-168902	4.65	1.45	5.60	12.30	1.55	6.90	4.95	8.95		65	124	-	21	24	18
paratypes													-		
ZMMU S-168903	5.00	1.00	5.30	12.70	1.45	6.30	4.95	9.35		65	130	-	21	24	17
ZMMU S-168904	4.50	1.55	5.10	12.30	1.20	7.25	4.70	8.20		60	127	65	20	23	18
ZMMU S-168905	4.90	1.45	5.20	12.65	1.45	6.20	4.70	8.20		65	130	65	20	22	18
ZMMU S-168906	4.75	1.70	4.90	12.00	1.25	5.55	4.70	7.65		36	114	-	20	22	18
additional specimens															
SMNS 23415	4.60	1.30	4.95	12.70	1.30	6.00	4.90	8.45							
SMNS 23894	4.75	1.05	5.50	13.25	1.40	6.60	5.25	9.50		72	140	-	20	23	-
SMNS 23895	4.75	1.45	5.20	12.30	1.25	6.70	5.50	9.35		78	145	-	21	24	-
SMNS 23896	4.90	1.30	5.35	13.05	1.20	6.00	4.65	8.50		41	119	60	20	22	-
SMNS 23897	4.45	1.10	4.85	12.25	1.10	6.15	4.95	8.10		61	126	60	20	22	-
***L.pseudosikapusi* n.sp.**															
holotype ZMMU S-179563	4.85	1.45	5.65	13.00	1.40	6.85	4.75	8.90		67	138	86	23	25	19.5
paratype ZMMU S-179564	4.50	1.35	5.45	12.40	1.50	6.45	5.00	8.95		53	130	78	21	23.5	20