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Systematic and distributional notes on the *Lophuromys flavopunctatus* Thomas, 1888 species-complex in Ethiopia (Muridae - Rodentia)

by L.A. LAVRENCHENKO, W.N.VERHEYEN & J. HULSELMANS

Abstract

The morphological variation of some Ethiopian populations of *Lophuromys flavopunctatus* sensu lato was studied to clarify certain aspects of the systematics of this species-complex. Multivariate analyses of the craniometrical data of our specimens and comparisons with the type specimens, demonstrate that *Lophuromys brevicaudus* and *L. chrysopus* are to be considered valid species both endemic to Ethiopia; moreover these two species can be distinguished on pelage colour and external characters. The former is a specialized heathland form confined to Chilalo, Gedeb and Bale Mountains (eastern plateau) covering a range of altitudes (2,400 m to 3,750 m ASL), the latter is widespread in lower tropical forests (1,680 to 2,760 m ASL) on both sides of the Rift Valley. There are indications that *L. chrysopus* has differentiated into two distinct subspecies on either side of the Rift. The question on *L. flavopunctatus* sensu stricto is raised; the 68-chromosomal form from the Beletta Forest (western plateau) is conditionally assigned to be *L. flavopunctatus brunneus*. The occurrence in the same area of a fourth species, *Lophuromys* sp. D is a possibility. It is obvious that the Ethiopian plateau represents a centre of diversification and endemism and an area of high diversity of the genus *Lophuromys*.
Key words: Rodentia, Muridae, *Lophuromys*, systematics, morphometrics, biodiversity, endemics, Ethiopia.

Résumé

Notes concernant la systématique et la distribution du groupe d'espèces *Lophuromys flavopunctatus Thomas,* 1888 (Muridae, Rodentia) en Ethiopie.
La variation morphologique de quelques populations éthiopiennes de *Lophuromys flavopunctatus* sensu lato a été étudiée, afin d'élucider certains aspects de la systématique de ce groupe d'espèces. Des analyses multivariées des données craniométriques de nos spécimens, ainsi que la comparaison avec les spécimens types, montrent que *Lophuromys brevicaudus* et *L. chrysopus* sont à considérer comme des espèces valides, toutes deux endémiques en Ethiopie; en outre, l'on peut distinguer ces deux espèces par la couleur de leur pelage et leurs caractéristiques externes. La première espèce est une forme spécialisée des bryères, limitée à Chilalo, Gedeb et les Montagnes Bale (plateau oriental), rencontrée à diverses altitudes (2.400 à 3.750 m d'altitude), la seconde est une espèce répandue dans les forêts tropicales inférieures (1.680 m à 2.760 m d'altitude) de part et d'autre de la Vallée du Rift. Il existe des indications selon lesquelles *L. chrysopus* s'est différencié en deux sous-espèces distinctes, de chaque côté du Rift. La question concernant *L. flavopunctatus* sensu stricto est soulevée; la forme aux 68 chromosomes de la Forêt Beletta (plateau occidental) est considérée provisoirement comme étant *L. flavopunctatus brunneus*. La présence, dans la même région, d'une quatrième espèce, *Lophuromys* sp. D, est possible. Il est évident que le plateau éthiopien constitue un centre de diversification et d'endémisme que c'est une région où le genre *Lophuromys* est particulièrement varié.
Mots clés: Rodentia, Muridae, *Lophuromys*, systématique, morphométrie, biodiversité, espèces endémiques, Ethiopie.

Introduction

The subgenus *Lophuromys* PETERS, 1874 (sensu DIETERLEN 1987) groups three taxonomically complicated species-complexes, i. e. *L. sikapusi* (TEMMINCK, 1853) sensu lato (s. lat.), *L. nudicaudus* HELLER, 1911 s. lat. and *L. flavopunctatus* THOMAS, 1888 s. lat. (VERHEYEN et al. 1996). Representatives of the last 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 and CARLETON 1993).
The Ethiopian populations of *Lophuromys flavopunctatus* s. lat. are separated from the rest of the range of the species-complex by dry lowlands (KINGDON 1974) and demonstrate considerable variation in pelage colour and external measurements. Eight taxa have been described from Ethiopia, based on these characters: *L. flavopunctatus* THOMAS, 1888 from Shoa (probable type locality Ankober); *L. zaphiri* THOMAS, 1906 from Bodeli (Wallamo), *L. aquilus brunneus* THOMAS, 1906 from Manno (Western Ethiopia); *L. flavopunctatus simensis* OSGOOD, 1936 from Ras Dashan (Simien); *L. brevicaudus* OSGOOD, 1936 from Mt Albasso (Badda); *L. aquilus chrysopus* OSGOOD, 1936 from Allata (Southern Ethiopia); *Neanthomys giaquintoi* TOSCHI, 1946 from Addis Ababa and *Lophuromys melanonyx* PETTER,1972 from Bale Mt.. However, the description of *Neanthomys giaquintoi* was solely based upon an artefact: the absence of a tail in the type specimen (TOSCHI 1963).

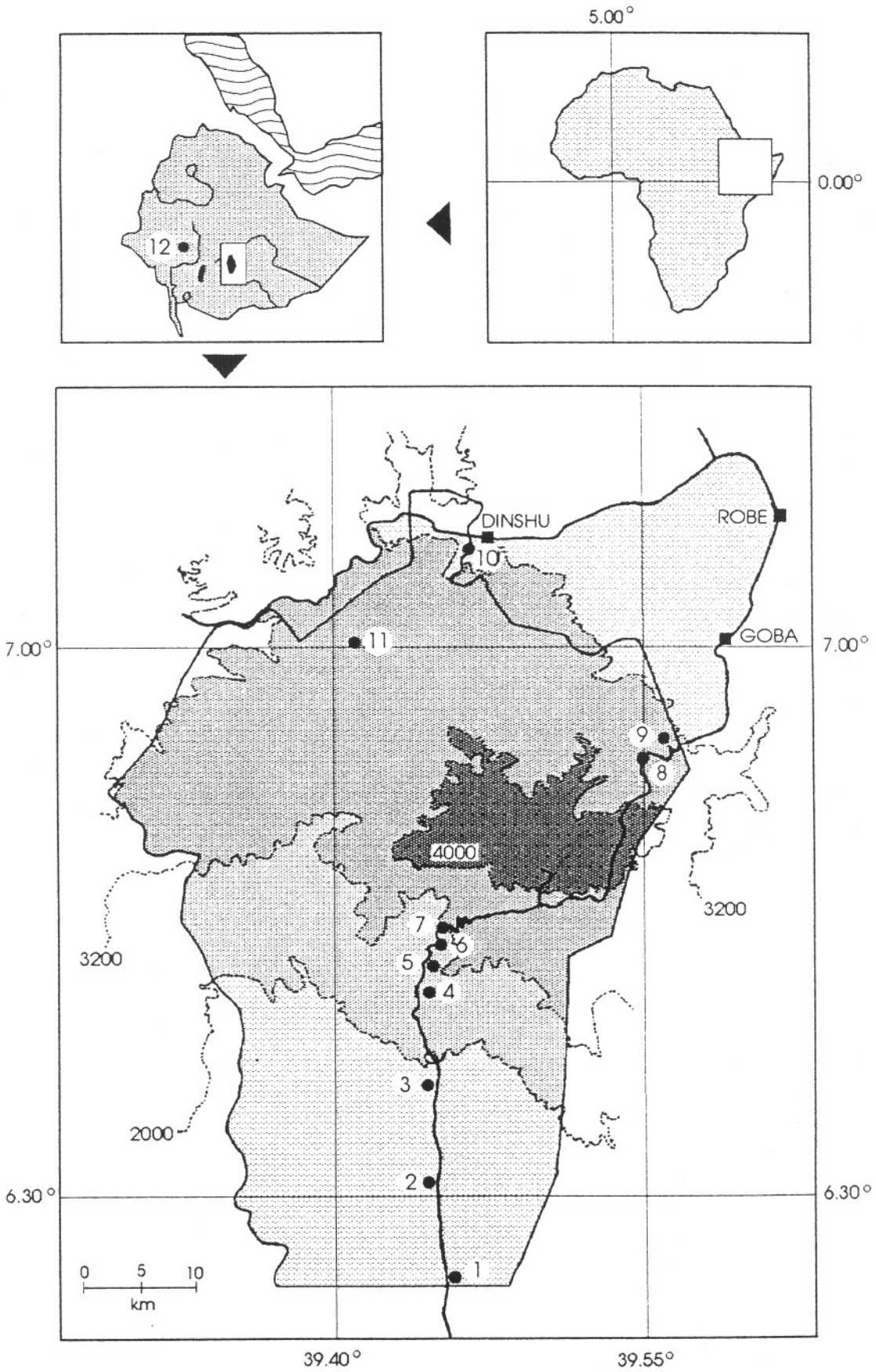

Fig. 1. A map of Ethiopia, showing the collecting localities. The numbers refer to the co-ordinates and altitudes of the localities as described in the text.

YALDEN et al. (1976) stated "Despite the proliferation of names, it seems clear that all refer to one very variable species. Specimens from a single locality vary considerably in colour and ventral fur, which is typically reddish-orange, maybe pale lemon-yellow in some individuals". Recently, in the final part of the Catalogue of Ethiopian Mammals (YALDEN et al. 1996), all these taxa were lumped under *L. flavopunctatus*. However, recent multivariate morphometrics show extensive morphological differentiation of the Ethiopian populations of *L. flavopunctatus* s. lat. with the Bale population being the most distinct (AFEWORK BEKELE and CORTI 1994). Nevertheless, these authors continue to assign all these populations to the single species *L. flavopunctatus*.

During extensive trapping sessions of small mammals in Southern and Western Ethiopia, between 1995 and 1997, the senior author collected sizable series of *Lophuromys*. On most of this material cytogenetic and allozymic analyses were performed (LAVRENCHENKO et al. 1997; ANISKIN et al. 1997). The results show extensive genetic differentiation between two populations of the *L. flavopunctatus* species-complex confirming their full species rank. Careful analyses of OSGOOD's (1936) original descriptions show that *L. brevicaudus* and *L. chrysopus* are the appropriate names for these forms. Furthermore, the collected samples include also material on two other putative taxa of the *L. flavopunctatus* species-complex.

The present study provides morphological and morphometric information on these four Ethiopian *Lophuromys* taxa and their distributional patterns. *L. melanonyx* PETTER, 1972, which is morphologically well differentiated from the above mentioned species, will not be discussed in this publication although it also makes part of the *L. flavopunctatus* species-complex. Data on morphology, ecology and phylogenetic relationships of this large specialized species, known only from a restricted range in the Bale Mountains, will be published elsewhere.

Material and methods

Field work in Ethiopia was carried out in the framework of the Joint Ethio-Russian Biological Expedition (JERBE) during 1995-1997. A total of 198 *L. flavopunctatus* s. lat. was captured in the following localities (see fig. 1).

BALE MOUNTAINS

1. The Harenna Forest near Shisha River (1,680 m ASL, 6°27'N 39°44'E). The lower belt of the mixed montane evergreen tropical rain forest with *Podocarpus gracilior, Croton macrostachys, Okotea keniensis, Zanthoxylum leprieuri, Filicia decipiens, Allophilus rubifolius, Rhus ruspolii, Toddalia asiatica.*
2. The Harenna Forest between Shisha and Shawe Rivers (1,780 m ASL, 6°31'N 39°44'E). The upper part of the lower belt of the mixed montane evergreen tropical rain forest with *Podocarpus falcatus, Aningeria adolfi-friederici, Okotea keniensis, Olea welwitschii, Syzygium guineense, Croton macrostachys, Coffea arabica.*
3. The Harenna Forest near Shawe River (1,935 m ASL, 6°38'N 39°44'E). The lower part of the middle belt of the mixed montane evergreen tropical rain forest with *Aningeria adolfi-friederici, Podocarpus falcatus, Prunus africanus, Schefflera miryantha, Polyscias fulva, Allophilus abyssinicus, Ficus* sp., *Dracaena afromontana, D. steudneri, Vepris dainellii, Solanecio mannii.*
4. *Schefflera - Hagenia* belt of the Harenna Forest near Katcha clearing (2,400 m ASL, 6°42'N 39°44'E) with *Milletia ferruginea, Hagenia abyssinica, Schefflera abyssinica, Aningeria adolfi-friederici, Bersama abyssinica, Erythrina brucei, Polyscias fulva, Ficus thonningi, Allophilus abyssinicus, Brucea antidysenterica, Galiniera saxifraga, Acanthus emineus.*
5. The middle belt of the Harenna Forest (2,620 m ASL, 6°44'N 39°44'E) with *Hagenia abyssinica, Schefflera volkensii, S. abyssinica, Bersama abyssinica, Rapanea melanophloeas, Brucea antidysenterica, Maytenus capillipes* and bamboo *Arundinaria alpina.*
6. The upper part of *Schefflera - Hagenia* belt of the the Harenna Forest (2,760 m ASL, 6°45'N 39°44'E) with *Hagenia abyssinica, Schefflera volkensii, Rapanea melanophloeas, Discopodium penninerve, Hypericum revolutum, Pentas schimperiana, Maytenus arbutifolia, Pittosporum viridiflorum, Erica trimera, Rubus steudneri.*
7. Ericaceous belt of the Harenna Forest (3,250 m ASL, 6°46'N 39°45'E). *Erica* bush with *Erica arborea, Alchemilla haumannii, Helichrysum formosissimum, H. splendidum, Echinops longisetus.*
8. Ericaceous belt of northern slope of the Sanetti Plateau (3,750 m ASL, 6°54'N 39°55'E) with *Erica trimera, Alchemilla haumannii, Helichrysum citrispinum, H. gofense.*
9. *Erica* bush near Chorchora Mt. (3,500 m ASL, 6°56'N 39°56'E) with *Erica arborea, Alchemilla haumannii, Helichrysum citrispinum, H. splendidum, Kniphofia isoetifolia.*
10. Mosaic grassland / forest habitats around Dinsho (3,170 m ASL, 7°06'N 39°47'E). Typical undifferentiated afromontane forest with *Juniperus procera, Hypericum revolutum, Maytenus arbutifolia, Rosa abyssinica* and open grassy patches with *Euphorbia dumalis, Festuca abyssinica, Koeleria capensis, Poa schimperana, Exotheca abyssinica.*
11. Upper Wabe Valley. Swamp shore areas in Kotera (3,500 m ASL, 7°00'N 39°41'E) with *Erica trimera, Helichrysum citrispinum, Artemisia schimperi , Alchemilla haumannii, Kniphofia foliosa.*

BELTE GERA FOREST BLOCK

12. The humid afromontane Beletta Forest (2,050 m ASL, 7°32'N 36°33'E). The mixed montane evergreen tropical rain forest with *Schefflera abyssinica, Syzygium guineense, Polyscias fulva, Allophylus abyssinicus, Aningeria adolfi-friederici, Brucea antidysenterica, Dracaena afromontana, Solaneceo gigas, Croton macrostachys, Ficus* sp., *Malacantha alnifolia, Vernonia amygdalina, Clausena anisata, Vepris dainelii, Coffea arabica.*

All our specimens are deposited in the collections of the Zoological Museum of Moscow University (ZMMU) and the Koninklijk Museum voor Midden-Afrika, Tervuren-Belgium (KMMA).

Taking into account the original descriptions (OSGOOD 1936) and the chromosome / allozyme characters (LAVRENCHENKO et al. 1997; ANISKIN et al. 1997) our sample of Ethiopian *L. flavopunctatus* s. lat. was

divided into three groups corresponding tentatively to three species: *L. chrysopus* (locality 1: n=1, loc2: n=6, loc3: n=17, loc4: n=8, loc5: n=7, loc6: n=11, loc12: n=12); *L. brevicaudus* (locality 4: n=2, loc6: n=1, loc7: n=8, loc8: n=10, loc9: n=24, loc10: n=49, loc11: n=24); *L. flavopunctatus brunneus* (locality 12: n=17). One specimen from locality 12 differs from these forms in its skull characteristics, cranial and external measurements but unfortunately the skin and karyotype are not available. In the present publication this sole specimen will be referred to as *Lophuromys* sp. D.

Six standard external measures were obtained from the freshly killed rats:

weight (W), head+body length (HB), tail length (Tl), hind-foot length without nail (HF(-n)), hind-foot lenght with nail (HF(+n)), ear length (EL). Statistical comparisons of these external measurements were made by means of the Student-t test.

On each skull twenty four craniometrical and dental dimensions were measured (table 1). Univariate procedures used to test sexual dimorphism did not reveal significant differences between sexes in our data; we therefore lumped sexes for further analyses. The description of the craniological measurements tooth-wear classes, as well as the statistical methods: follow VERHEYEN, COLYN and HULSELMANS (1996). Where needed, we provide more details in the legends of the figures and graphs.

Table 1. - Recapitulation and short description of the measurements as used in this study. For a full description we refer to VERHEYEN et al. (1996). Only measurements marked with * were retained for the multivariate analyses.

NUMBER		ACRONYMS	MORPHOMETRICAL CHARACTERS
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
M10		PALA	smallest palatal breadth
M11	*	UPTE	length of upper cheekteeth
M12		UPDA	breadth of upper dental arch
M13	*	M^1BR	greatest breadth of first upper molar
M14	*	ZYPL	smallest breadth of zygomatic plate
M15	*	BNAS	greatest breadth of nasals
M16	*	LNAS	greatest length of nasals
M17		LOTE	length of mandibular teeth
M18		CHOB	greatest breadth of choanae
M19		BULL	length of auditory bulla
M20		BRCA	greatest breadth of braincase
M21		DINC	depth of upper incisor
M22		ROHE	mediosagittal projection of rostrum heigth
M23		ROBR	greatest rostrum breadth
M24		PCPA	distance between coronoid and angular processes

EXTERNAL MORPHOMETRY

Comparing the external dimensions of the studied *Lophuromys* species reveal a rather marked interspecific variation; the results are summarized in table 2. *Lophuromys chrysopus* is of similar general size (W and HB measures) as *L. brevicaudus* but differs from it by its longer tail and ears (t=18.95 and 4.61, respectively; p=0.000), and its longer HF(-n) (t=3.17, p=0.002); its shorter HF(+n) (t=3.06, p=0.003) reflects the relatively shorter claws of *L. chrysopus*. The tail length is the best character discriminating *L. chrysopus* from *L. brevicaudus* (table 2). On the other hand, *Lophuromys flavopunctatus brunneus* is considerably larger than *L. brevicaudus* ($p<0.001$ for all external measurements) and *L. chrysopus* ($p<0.01$ for Tl and HF(-n), and $p<0.001$ for all other measurements).

Several authors discussed the possible relation between the relative tail length and the geographical distribution of Ethiopian populations of *Lophuromys flavopunctatus* s. lat. (RUPP 1980, YALDEN 1988a, AFEWORK BEKELE and CORTI 1994). The tail and head-body length ratios (Tl/HB) of our samples of *Lophuromys* are given in table 3. YALDEN (1988a) demonstrated the trend to shorter tails at higher altitudes within the Bale Mountain region. We suspect however that Yalden's samples from Shisha, Shawe and partly from Katcha must be assigned to *L. chrysopus*, whereas his specimens from Dinshu, Goba and Worgona - are most probably *L. brevicaudus* (table 2 from YALDEN 1988a). It is further our opinion that the "Bale population" in the morphometrical analysis performed by AFEWORK BEKELE and CORTI (1994) is probably a mixed sample and encompasses specimens of *L. chrysopus* and of *L. brevicaudus* (fig. 4 from AFEWORK BEKELE & CORTI 1994).

VARIATION IN SKULL AND TOOTH-MORPHOLOGY

When comparing representative series of skulls of comparable age-classes *of L. flavopunctatus*, *L. chrysopus* and *L. brevicaudus*, we could only notice small differences in dimensions and proportions; important morphological differences however were not encountered. The only diagnostical characters that we could identify are the proportionally larger bullae in *L. brevicaudus* when compared to the other ethiopian *Lophuromys*-species.

Also our efforts to identify morphological characters with diagnostical value in the dentition were not successful. In fig.2 we compare a number of maxillary toothrows of the three studied Ethiopian species of *Lophuromys* to some

Table 2. External measurements of different taxa of the Ethiopian *Lophuromys flavopunctatus* species complex. W: weight; HB: head + body length; Tl: tail length; HF(-n): hind-foot length (- nail); HF(+n): hind-foot length (+ nail); EL: ear length).

Age-classes							
L. CHRYSOPUS							
(M+F)		W	HB	Tl	HF(-n)	HF((n)	EL
	mean±SE	35.54±0.94	108.25±1.36	77.00±1.98	21.17±0.22	23.09±0.28	17.11±0.16
s/ad	min-max	30.0 - 42.0	99.5 - 116.0	70.0 - 82.0	20.0 - 22.3	21.5 - 24.5	16.0 - 18.0
	n	12	12	6	12	11	12
	mean(SE	43.24±1.12	114.10±0.92	79.03±1.02	21.14±0.10	23.08±0.12	17.70±0.12
ad	min-max	34.0 - 65.0	100.0 - 128.0	71.7 - 86.5	19.0 - 23.0	21.0 - 25.2	16.5 - 20.0
	n	45	46	20	46	37	46
	mean±SE	43.33±2.73	117.50±2.50	-	21.47±0.29	23.10±0.67	17.67±0.88
sen	min-max	38.0 - 47.0	112.5 - 120.0	-	21.0 - 22.0	22.0 - 24.3	16.0 - 19.0
	n	3	3	-	3	3	3
L. BREVICAUDUS							
	mean±SE	36.14±1.07	107.17±1.35	56.90±1.16	20.47±0.12	23.16±0.14	16.56±0.12
s/ad	min-max	26.0 - 52.0	96.0 - 126.0	44.0 - 68.0	18.8 - 22.0	21.5 - 24.5	15.0 - 17.5
	n	25	26	21	26	26	26
	mean±SE	43.22±0.65	114.24±0.68	59.33±0.50	20.75±0.07	23.54±0.08	17.05±0.08
ad	min-max	29.0 - 60.0	96.0 - 134.0	50.0 - 66.0	19.0 - 22.0	21.3 - 25.0	15.0 - 19.0
	n	86	87	60	87	87	87
	mean±SE	45.00±5.49	116.40±4.61	60.00±2.12	21.20±0.25	23.86±0.35	17.70±0.58
sen	min-max	28.0 - 57.0	105.0 - 130.0	56.0 - 65.0	20.5 - 22.0	23.0 - 25.0	16.0 - 19.0
	n	5	5	4	5	5	5
L. FLAVOPUNCTATUS BRUNNEUS							
	mean±SE	47.0	105.0	-	21.8	24.0	17.0
s/ad	min-max	-	-	-	-	-	-
	n	1	1	-	1	1	1
	mean±SE	62.69±1.70	125.42±1.43	72.30±1.46	21.75±0.20	24.37±0.26	18.55±0.14
ad	min-max	47.0 - 69.0	117.0 - 131.0	69.0 - 76.0	21.0 - 23.0	22.8 - 26.0	18.0 - 19.5
	n	13	13	5	13	13	13
	mean±SE	70.33±2.60	129.67±1.20	-	22.47±0.29	25.00±0.38	18.83±0.33
sen	min-max	66.0 - 75.0	128.0 - 132.0	-	22.0 - 23.0	24.5 - 25.8	18.5 - 19.5
	n	3	3	-	3	3	3
LOPHUROMYS SP. D							
	mean±SE	66.0	128.0	65.0	21.0	24.0	18.0
ad	min-max	-	-	-	-	-	-
	n	1	1	1	1	1	1

Table 3. Tail and head-body length ratio (Tl/HB) of certain taxa of the *Lophuromys flavopunctatus* species complex from Ethiopia

	Age-classes (M+F)			
Species	s/ad	ad	sen	
	mean ± SE	0.71±0.02	0.68±0.01	-
L. chrysopus	min - max	0.67 - 0.79	0.61 - 0.76	-
	n	6	20	-
	mean±SE	0.53±0.01	0.52±0.01	0.51±0.01
L. brevicaudus	min - max	0.41 - 0.65	0.43 - 0.62	0.50 - 0.54
	n	21	60	4
	mean±SE	-	0.59±0.02	-
L. flavopunctatus brunneus	min - max	-	0.53 - 0.64	-
	n	-	5	-
	mean±SE	-	0.51	-
Lophuromys sp. D	min - max	-	-	-
	n	-	1	-

toothrows of type-specimens of Ethiopian *Lophuromys*-species. The specimens were selected to illustrate the variation present in cusp and ridge patterns. Here also we were unable to identify characters with diagnostical value. We can only notice that both *L. brevicaudus* and *L. chrysopus* have somewhat smaller molars than representatives of typical *Lophuromys flavopunctatus* (*flavopunctatus*, *brunneus*, *laticeps*, *zaphiri*).

CRANIOMETRICAL ANALYSES

Univariate analyses (tables 4 and 5) reveal that *L. flavopunctatus brunneus*, when compared to our series of *L. chrysopus* and *L. brevicaudus*, has the biggest skull for nearly all the measurements except for M8 (INTE), M10 (PALA), M18 (CHOB) and M19 (BULL). Tested with Student's t-test the difference between *L. flavopunctatus*

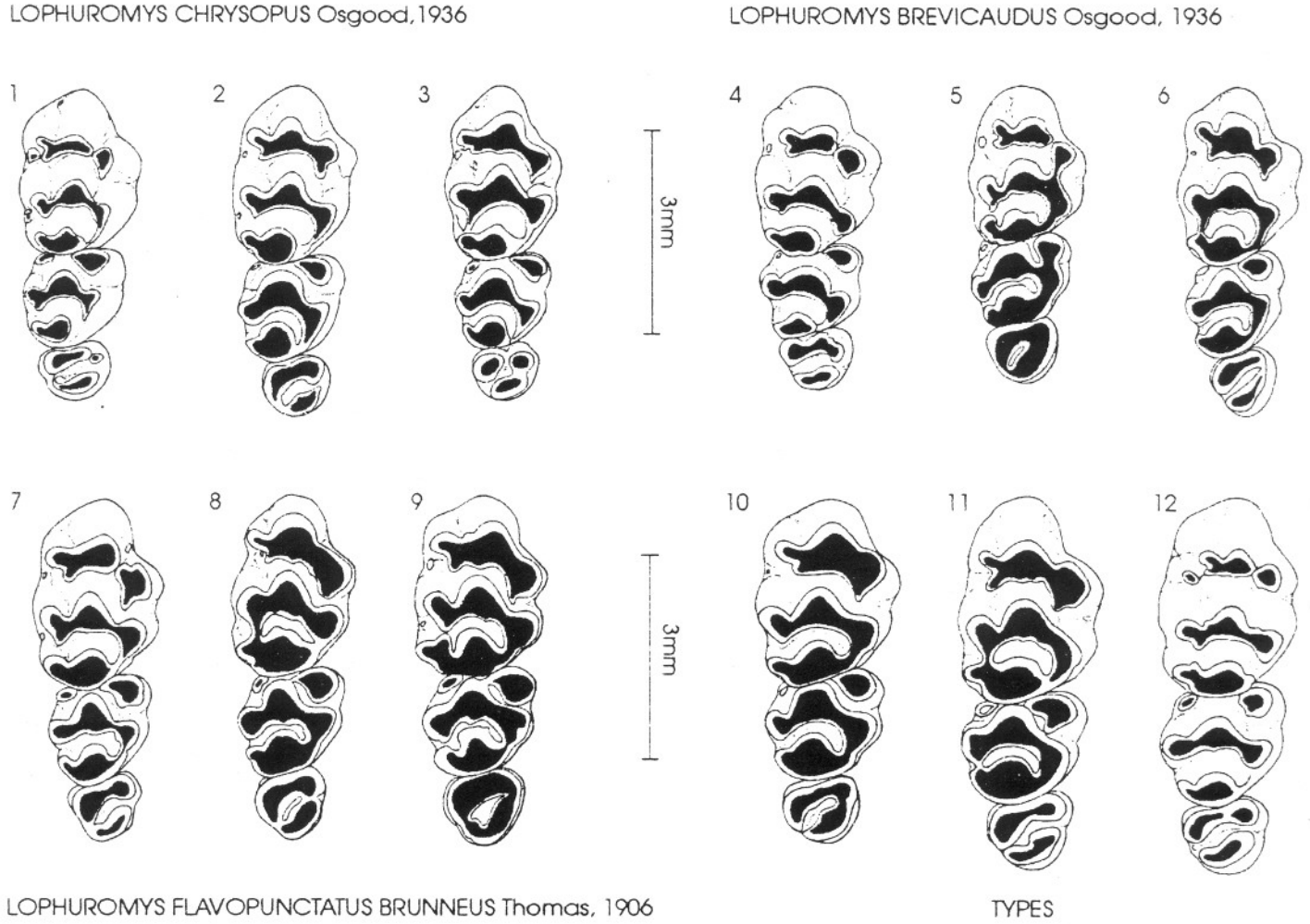

Fig. 2. – Comparative drawings of the right maxillary teeth of three representative specimens of *L. chrysopus* OSGOOD 1936; *L. brevicaudus* OSGOOD 1936; *L.flavopunctatus brunneus* THOMAS,1906 and the type-specimens of *L.flavopunctatus* THOMAS,1888; *L. aquilus brunneus* THOMAS,1906 and *L.flavopunctatus zaphiri* THOMAS,1906. The examples were choosen to cover as much as possible the observed variation in form and cusp-structure of the molars.

(1) L. *chrysopus*	KMMA M97087.0018	(Ethiopia - Beletta forest)
(2) L. *chrysopus*	KMMA M97087.0016	(Ethiopia - Harenna forest)
(3) *L. chrysopus*	KMMA M97087.0017	(Ethiopia - Harenna forest)
(4) *L. brevicaudus*	KMMA M97087.0007	(Ethiopia - Dinsho) female
(5) *L. brevicaudus*	KMMA M97087.0004	(Ethiopia - Dinsho) male
(6) *L. brevicaudus*	KMMA M97087.0003	(Ethiopia - Chorchora Mt.) female
(7) *L. flavopunctatus brunneus*	KMMA M97087.0012	(Ethiopia - Beletta forest) female
(8) *L. flavopunctatus brunneus*	KMMA M97087.0010	(Ethiopia - Beletta forest) male
(9) *L. flavopunctatus brunneus*	KMMA M97087.0011	(Ethiopia - Beletta forest) male
(10) *L. flavopunctatus* (type)	BMNH 60.5.4.101	(Ethiopia - Ankober ?)
(11) *L. aquilus brunneus* (type)	BMNH 6.11.1.42.	(Ethiopia - Manno)
(12) *L. flavopunctatus zaphiri* (type)	BMNH 6.11.1.41.	(Ethiopia - Bodeli)

Table 4. – Basic statistics of craniometrical data of *Lophuromys chrysopus* (Harenna and Beletta populations), *Lophuromys brevicaudus* (Bale population) and *Lophuromys flavopunctatus brunneus* (Beletta population). Only skulls of dental wear classes 2-3-4 were retained.

L.chrysopus (Harenna)							**L. chrysopus (Beletta)**					
	N	MEAN	MIN	MAX	STD	CV%	N	MEAN	MIN	MAX	STD	CV%
M1	43	29,38	28,15	30,50	0,6051	2,06	10	30,39	29,40	31,30	0,5701	1,88
M2	43	27,72	25,95	29,15	0,6839	2,47	10	28,52	27,60	29,50	0,6426	2,25
M3	43	23,63	22,25	25,35	0,7028	2,97	9	24,21	23,40	24,90	0,5849	2,42
M4	43	12,06	11,15	13,25	0,4455	3,69	10	12,26	11,60	12,80	0,4402	3,59
M5	43	6,06	5,60	6,70	0,2605	4,30	10	6,30	5,80	6,75	0,2929	4,65
M6	43	7,63	6,95	8,35	0,2795	3,67	10	7,82	7,15	8,15	0,3690	4,72
M7	43	8,72	7,90	9,55	0,3402	3,90	10	8,98	8,00	9,40	0,4934	5,50
M8	43	5,87	5,55	6,25	0,1516	2,58	10	6,14	6,00	6,30	0,1101	1,79
M9	43	14,07	12,50	14,80	0,4014	2,85	10	14,70	14,35	15,65	0,3797	2,58
M10	43	2,92	2,65	3,30	0,1526	5,23	10	2,96	2,75	3,25	0,1560	5,27
M11	43	4,89	4,55	5,35	0,1544	3,16	10	4,78	4,40	5,10	0,2150	4,50
M12	42	6,44	6,20	6,75	0,1511	2,35	10	6,48	6,25	6,95	0,2098	3,24
M13	43	1,63	1,45	1,70	0,0589	3,61	10	1,62	1,50	1,70	0,0632	3,90
M14	43	3,02	2,65	3,50	0,2159	7,14	10	3,02	2,80	3,30	0,1415	4,69
M15	43	2,64	2,25	3,00	0,1563	5,93	10	2,70	2,40	2,90	0,1509	5,59
M16	43	11,62	10,75	12,20	0,3197	2,75	10	12,40	11,95	12,95	0,3201	2,58
M17	43	4,32	4,10	4,75	0,1382	3,20	10	4,33	4,00	4,55	0,1751	4,04
M18	39	1,59	1,25	2,00	0,1878	11,84	10	1,50	1,10	1,80	0,2121	14,14
M19	43	5,19	4,80	5,65	0,1784	3,44	10	5,40	5,20	5,55	0,1012	1,88
M20	43	12,39	11,85	13,20	0,3231	2,61	10	12,75	12,30	13,10	0,2967	2,33
M21	43	1,31	1,10	1,50	0,0894	6,85	10	1,33	1,25	1,40	0,0587	4,41
M22	43	6,04	5,60	6,75	0,2099	3,48	10	6,09	5,75	6,45	0,2196	3,61
M23	43	4,69	4,25	5,20	0,2199	4,69	10	4,71	4,25	5,10	0,2650	5,63
M24	43	8,18	7,15	8,70	0,2991	3,66	9	8,56	8,10	9,50	0,4076	4,76

L.brevicaudus (Bale)							**L.flav.brunneus (Beletta)**					
	N	MEAN	MIN	MAX	STD	CV%	N	MEAN	MIN	MAX	STD	CV%
M1	33	29,37	27,95	30,95	0,7362	2,51	14	31,10	28,75	32,75	1,0862	3,49
M2	33	28,09	26,75	29,60	0,7878	2,80	16	30,00	27,05	31,65	1,1639	3,88
M3	33	24,09	22,95	25,25	0,6551	2,72	15	25,66	23,00	27,50	1,0479	4,08
M4	33	12,50	11,85	13,30	0,3520	2,82	16	13,04	11,60	13,80	0,5063	3,88
M5	33	6,24	5,50	6,85	0,3343	5,36	16	6,87	6,35	7,45	0,2976	4,33
M6	33	7,57	7,05	8,00	0,2966	3,92	16	8,23	7,25	8,70	0,3958	4,81
M7	33	8,83	8,10	9,60	0,3796	4,30	16	9,71	8,65	10,30	0,4651	4,79
M8	33	5,36	5,05	5,70	0,1556	2,90	16	6,04	5,70	6,35	0,2115	3,50
M9	33	14,19	13,60	15,15	0,3360	2,37	16	15,16	14,05	15,95	0,4024	2,66
M10	33	2,67	2,30	3,10	0,2469	9,23	16	2,71	2,40	3,05	0,1658	6,11
M11	33	4,98	4,65	5,45	0,2069	4,15	16	5,38	5,00	5,85	0,2295	4,27
M12	33	6,24	5,85	6,70	0,1992	3,19	16	6,73	6,20	7,10	0,2173	3,23
M13	33	1,69	1,55	1,85	0,0676	4,01	16	1,82	1,65	2,00	0,0790	4,35
M14	33	2,89	2,40	3,35	0,1851	6,41	16	3,18	2,75	3,70	0,2502	7,87
M15	33	2,60	2,35	3,00	0,1408	5,41	16	2,77	2,50	3,00	0,1354	4,88
M16	33	12,10	10,95	13,05	0,4645	3,84	14	12,59	11,05	13,65	0,7098	5,64
M17	33	4,29	4,05	4,55	0,1231	2,87	16	4,77	4,50	5,30	0,2128	4,46
M18	29	1,25	0,95	1,65	0,1966	15,71	16	1,42	1,15	1,70	0,1653	11,63
M19	33	5,84	5,15	6,35	0,2479	4,24	16	5,68	5,10	6,00	0,2632	4,63
M20	33	12,29	11,70	12,80	0,3049	2,48	16	12,83	12,20	13,40	0,3076	2,40
M21	33	1,22	1,15	1,40	0,0649	5,32	16	1,37	1,20	1,55	0,1044	7,65
M22	33	6,05	5,45	6,70	0,2733	4,52	16	6,35	5,55	7,00	0,3631	5,72
M23	33	4,54	4,30	4,85	0,1327	2,92	16	4,89	4,50	5,30	0,1908	3,90
M24	31	8,49	7,70	9,00	0,3450	4,07	16	9,06	7,70	9,65	0,4506	4,97

Table 5.–t-Student comparisons between the craniometrical data of *L. chrysopus* (Harenna versus Beletta), *L. chrysopus* versus *L. brevicaudus*, *L. chrysopus* (Harenna) versus *L. flavopunctatus brunneus* and *L. brevicaudus* versus *L. flavopunctatus brunneus*.

	chrysopus(Harenna)< >chrysopus(Beletta)							
var.	chryso(H)	chryso(B)	t-Stud	dF	P	n1	n2	
M1	29,38	30,39	-4,778	51	0,000	43	10	
M2	27,72	28,52	-3,358	51	0,001	43	10	
M3	23,63	24,21	-2,309	50	0,025	43	9	
M4	12,06	12,26	-1,250	51	0,217	43	10	n.s.
M5	6,06	6,30	-2,495	51	0,016	43	10	
M6	7,63	7,82	-1,815	51	0,075	43	10	n.s.
M7	8,72	8,98	-1,919	51	0,061	43	10	n.s.
M8	5,87	6,14	-5,327	51	0,000	43	10	
M9	14,07	14,70	-4,479	51	0,000	43	10	
M10	2,92	2,96	-0,813	51	0,420	43	10	n.s.
M11	4,89	4,78	1,812	51	0,076	43	10	n.s.
M12	6,44	6,48	-0,601	50	0,551	42	10	n.s.
M13	1,63	1,62	0,488	51	0,627	43	10	n.s.
M14	3,02	3,02	0,131	51	0,896	43	10	n.s.
M15	2,64	2,70	-1,172	51	0,247	43	10	n.s.
M16	11,62	12,40	-6,885	51	0,000	43	10	
M17	4,32	4,33	-0,132	51	0,895	43	10	n.s.
M18	1,59	1,50	1,258	47	0,215	39	10	n.s.
M19	5,19	5,40	-3,477	51	0,001	43	10	
M20	12,39	12,75	-3,157	51	0,003	43	10	
M21	1,31	1,33	-0,812	51	0,421	43	10	n.s.
M22	6,04	6,09	-0,710	51	0,481	43	10	n.s.
M23	4,69	4,71	-0,236	51	0,814	43	10	n.s.
M24	8,18	8,56	-3,298	50	0,002	43	9	

	chrysopus(Harenna)< >brevicaudus							
var.	chryso (H)	brevi	t-Stud	dF	P	n1	n2	
M1	29,38	29,37	0,088	74	0,930	43	33	n.s.
M2	27,72	28,09	-2,181	74	0,032	43	33	
M3	23,63	24,09	-2,917	74	0,005	43	33	
M4	12,06	12,50	-4,580	74	0,000	43	33	
M5	6,06	6,24	-2,585	74	0,012	43	33	
M6	7,63	7,57	0,818	74	0,416	43	33	n.s.
M7	8,72	8,83	-1,261	74	0,211	43	33	n.s.
M8	5,87	5,36	14,271	74	0,000	43	33	
M9	14,07	14,19	-1,398	74	0,166	43	33	n.s.
M10	2,92	2,67	5,257	74	0,000	43	33	
M11	4,89	4,98	-2,275	74	0,026	43	33	
M12	6,44	6,24	5,010	73	0,000	42	33	
M13	1,63	1,69	-3,861	74	0,000	43	33	
M14	3,02	2,89	2,937	74	0,004	43	33	
M15	2,64	2,60	0,952	74	0,344	43	33	n.s.
M16	11,62	12,10	-5,309	74	0,000	43	33	
M17	4,32	4,29	1,159	74	0,250	43	33	n.s.
M18	1,59	1,25	7,114	66	0,000	39	29	
M19	5,19	5,84	-13.297	74	0,000	43	33	
M20	12,39	12,29	1,425	74	0,158	43	33	n.s.
M21	1,31	1,22	4,665	74	0,000	43	33	
M22	6,04	6,05	-0,231	74	0,818	43	33	n.s.
M23	4,69	4,54	3,279	74	0,002	43	33	
M24	8,18	8,49	-4,123	72	0,000	43	31	

	chrysopus(Harenna)< >brunneus							
var.	chryso(H)	brun.	t-Stud	dF	P	n1	n2	
M1	29,38	31,10	-7,495	55	0,000	43	14	
M2	27,72	30,00	-9,290	57	0,000	43	16	
M3	23,63	25,66	-8,433	56	0,000	43	15	
M4	12,06	13,04	-7,232	57	0,000	43	16	
M5	6,06	6,87	-10,141	57	0,000	43	16	
M6	7,63	8,23	-6,512	57	0,000	43	16	
M7	8,72	9,71	-8,891	57	0,000	43	16	
M8	5,87	6,04	-3,467	57	0,001	43	16	
M9	14,07	15,16	-9,237	57	0,000	43	16	
M10	2,92	2,71	4,454	57	0,000	43	16	
M11	4,89	5,38	-9,418	57	0,000	43	16	
M12	6,44	6,73	-5,837	56	0,000	42	16	
M13	1,63	1,82	-9,771	57	0,000	43	16	
M14	3,02	3,18	-2,376	57	0,021	43	16	
M15	2,64	2,77	-3,070	57	0,003	43	16	
M16	11,62	12,59	-7,106	55	0,000	43	14	
M17	4,32	4,77	-9,437	57	0,000	43	16	
M18	1,59	1,42	3,041	53	0,004	39	16	
M19	5,19	5,68	-8,205	57	0,000	43	16	
M20	12,39	12,83	-4,702	57	0,000	43	16	
M21	1,31	1,37	-2,182	57	0,033	43	16	
M22	6,04	6,35	-4,081	57	0,000	43	16	
M23	4,69	4,89	-3,285	57	0,002	43	16	
M24	8,18	9,06	-8,736	57	0,000	43	16	

	brevicaudus< >brunneus							
var.	brevi	brun.	t-Stud	dF	P	n1	n2	
M1	29,37	31,10	-6,390	45	0,000	33	14	
M2	28,09	30,00	-6,778	47	0,000	33	16	
M3	24,09	25,66	-6,340	46	0,000	33	15	
M4	12,50	13,04	-4,403	47	0,000	33	16	
M5	6,24	6,87	-6,380	47	0,000	33	16	
M6	7,57	8,23	-6,474	47	0,000	33	16	
M7	8,83	9,71	-7,046	47	0,000	33	16	
M8	5,36	6,04	-12,697	47	0,000	33	16	
M9	14,19	15,16	-8,838	47	0,000	33	16	
M10	2,67	2,71	-0,560	47	0,578	33	16	n.s.
M11	4,98	5,38	-6,044	47	0,000	33	16	
M12	6,24	6,73	-7,943	47	0,000	33	16	
M13	1,69	1,82	-5,938	47	0,000	33	16	
M14	2,89	3,18	-4,651	47	0,000	33	16	
M15	2,60	2,77	-3,984	47	0,000	33	16	
M16	12,10	12,59	-2,826	45	0,007	33	14	
M17	4,29	4,77	-10,028	47	0,000	33	16	
M18	1,25	1,42	-2,933	43	0,005	29	16	
M19	5,84	5,68	2,072	47	0,044	33	16	
M20	12,29	12,83	-5,833	47	0,000	33	16	
M21	1,22	1,37	-6,013	47	0,000	33	16	
M22	6,05	6,35	-3,197	47	0,002	33	16	
M23	4,54	4,89	-7,406	47	0,000	33	16	
M24	8,49	9,06	-4,862	45	0,000	31	16	

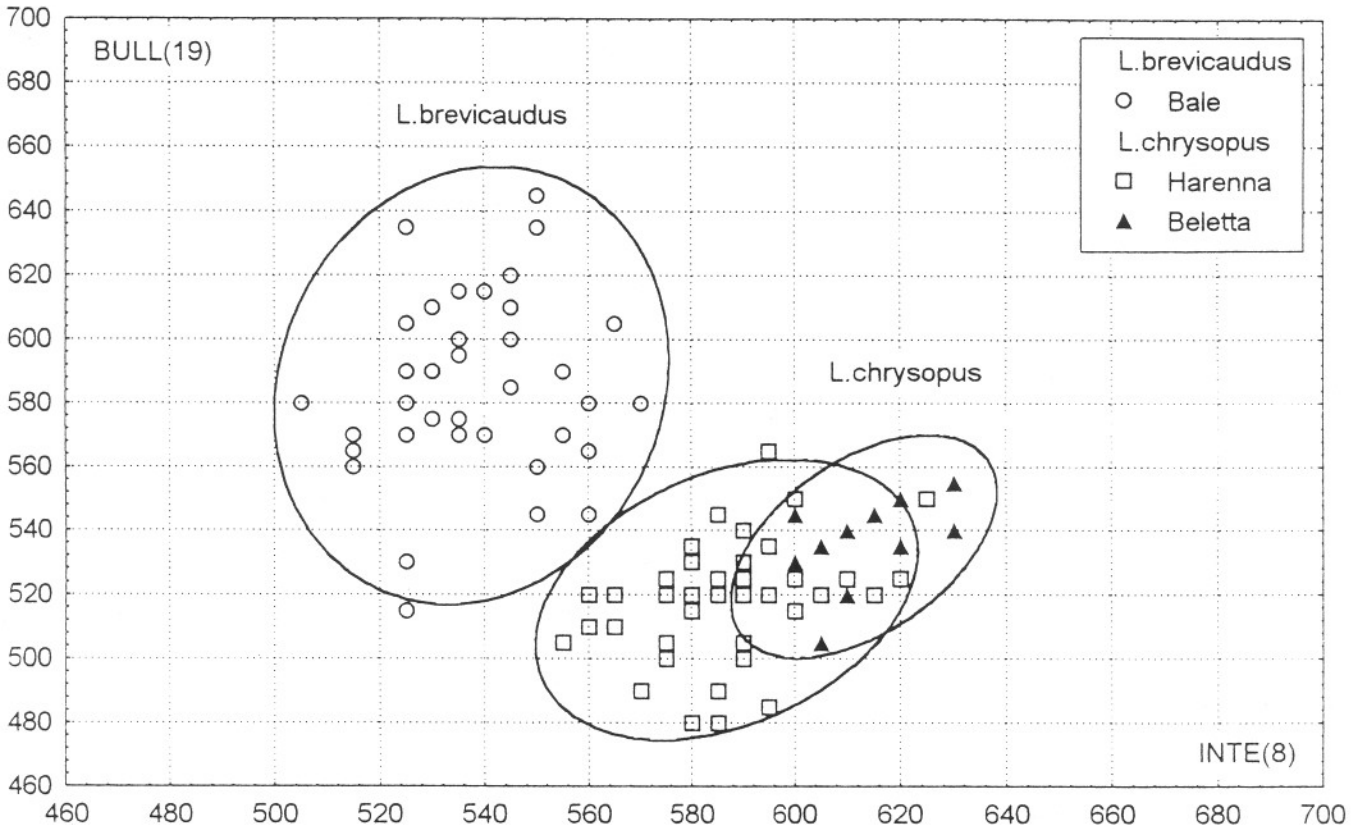

Fig. 3. – Scatter diagram visualizing the ratio-differences Bullae length (M19) and Interorbital breadth (M8) between *Lophuromys brevicaudus* (Bale) and *L. chrysopus* (Harenna and Beletta).

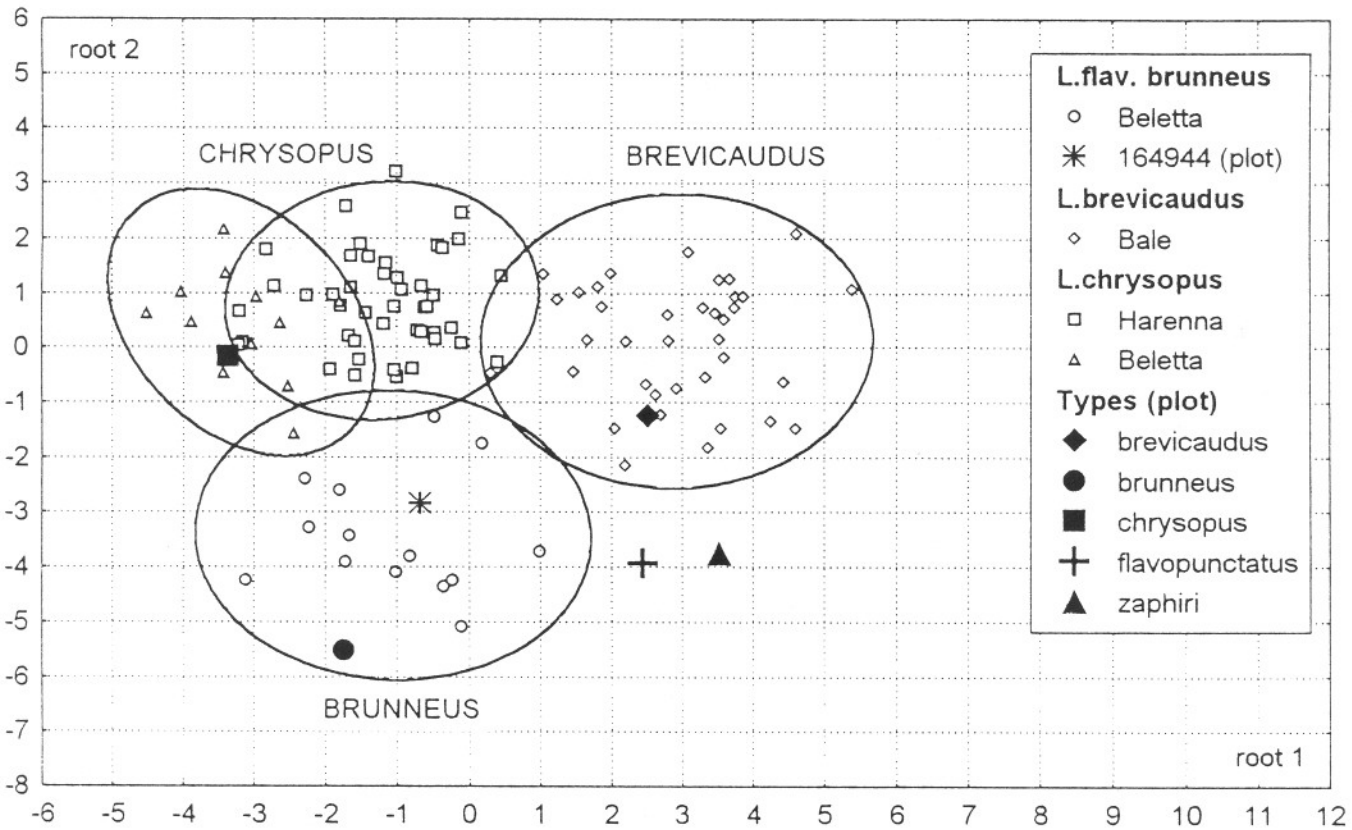

Fig. 4. Canonical analysis on a selected data set of *Lophuromys brevicaudus*, *Lophuromys chrysopus* (Harenna and Beletta) and *Lophuromys flavopunctatus brunneus* in order to situate by plotting the type-specimens of these species, possibly related subspecies and a critical specimen such as ZMMU 164944 (sp.D).

brunneus and *L. brevicaudus* is always highly significant, except for M10 (PALA).

L. brevicaudus and *L. chrysopus* have roughly the same skull-size. However *L. brevicaudus* differs significantly of *L. chrysopus* for the following measures:

- *L. brevicaudus* is significantly smaller than *L. chrysopus* for M8 (INTE), M10 (PALA), M12 (UPDA), M14 (ZYPL), M18 (CHOB), M21 (DiNC), M23 (ROBR).
- *L. brevicaudus* is significantly bigger than *L. chrysopus* for M2 (PRCO), M3 (HEBA),M4 (HEPA), M5 (PAFL), M11 (UPTE), M13 (M1BR), M16 (LNAS), M19 (BULL), M24 (PCPA).

For the other measurements *L. brevicaudus* and *L. chrysopus* do not differ.

When comparing the *L. chrysopus*-populations of Harenna and Beletta we find that the latter is significantly bigger for M1 (GRLS), M2 (PRCO), M3 (HEBA), M5 (PAFL), M8 (INTE), M9 (ZYGO), M16 (LNAS), M19 (BULL), M20 (BRCA), M24 (PCPA). However for 14 out of 24 measuremants there is no significant difference, be it that skulls of the Beletta-sample tend to be bigger.

Bivariate analyses show that an excellent separation between *L. brevicaudus* and *L. chrysopus* can be achieved by using the ratio between the variables Bullae-length (M19) and Interorbital breadth (M8). This is clearly visualized by the scatter diagram reproduced in fig. 3.

A forward canonical analysis (table 6 and fig. 4) was performed on the variance -covariance matrix of the raw

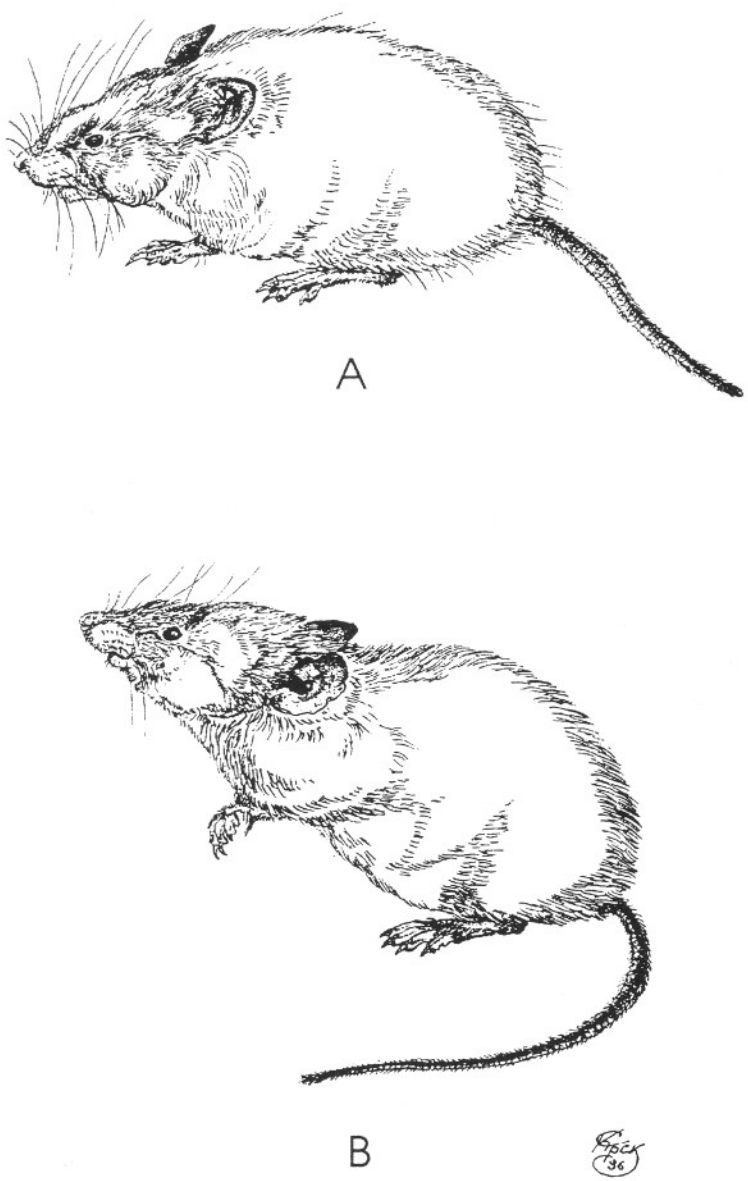

Fig. 5. – Drawings showing the habitus-differences between *Lophuromys brevicaudus* (A) *and Lophuromys chrysopus* (B).

Table 6.– Summary of the main results of the discriminant function analyses on a selected craniometrical data set between *L. chrysopus* (Harenna), *L. chrysopus* (Beletta), *L. brevicaudus* and *L. flavopunctatus brunneus*.

Wilks' Lambda: ,03432 approx. F (27,281) = 22,613 p<0,0000

Raw Coefficients for Canonical Variables

Variable	Root 1	Root 2	Root 3
M8 (INTE)	-0,0693	-0,0084	-0,0187
M13 (M1BR)	0,0310	-0,0891	-0,0060
M16 (LNAS)	-0,0020	-0,0011	-0,0279
M7 (DIA2)	0,0114	-0,0090	0,0024
M11 (UPTE)	0,0052	-0,0196	0,0347
M6 (DIA1)	-0,0088	0,0016	0,0390
M5 (PAFL)	-0,0086	-0,0132	-0,0081
M4 (HEPA)	0,0125	0,0021	-0,0074
M14 (ZYPL)	-0,0033	0,0127	0,0104
Constant	22,1248	39,3824	6,8266
Eigenval	4,9934	1,9238	0,6627
Cum.Prop	0,6588	0,9126	1,0000

Factor Structure Matrix : Correlations Variables - Canonical Roots (Pooled-within-groups correlations)

Variable	Root 1	Root 2	Root 3
M8 (INTE)	-0,8266	-0,3552	0,0243
M13 (M1BR)	0,1160	-0,6579	0,0438
M16 (LNAS)	0,0595	-0,4503	-0,5039
M7 (DIA2)	-0,0235	-0,5534	-0,0075
M11 (UPTE)	0,0593	-0,6210	0,2620
M6 (DIA1)	-0,1025	-0,4137	0,0507
M5 (PAFL)	-0,0103	-0,6198	-0,1082
M4 (HEPA)	0,1132	-0,4985	-0,0941
M14 (ZYPL)	-0,1347	-0,1906	0,2309

Squared Mahalanobis Distances (upper triangle)
F-values; df = 9,96 (lower triangle)

Group	chryso(H)	brevi	chryso(B)	brun
chryso(H)	----------	19,2825	11,1635	19,1856
brevi	39,1583	----------	41,5557	29,8653
chryso(B)	10,0757	35,9106	----------	25,4184
brun	19,7465	29,2558	15,5335	----------

data set of age classes 1-4. However in order to include certain damaged type specimens and because one of the samples was limited to 12 specimens the data set was reduced to 10 variables; of these the analysis discarded variable M15(BNAS).

The Wilks' Lambda criterion indicates a good discrimination between the groups. The coefficients for canonical transformation for root 1, which totals 66% of total variation and the correlations between the original variables and the canonical root 1 are negative and positive, which shows that root 1 not only expresses size but also shape variation between groups.

Projection of the individual data on the root 1 / root 2 scatterplot shows three clearly separated groups. The type specimens of *chrysopus*, *brevicaudus* and *brunneus*, plotted on this graph, fall within the scatters of these three groups : *brevicaudus* separates from *chrysopus* and *brunneus* along root 1, while root 2 discriminates the *chrysopus* populations from *brunneus*. The *chrysopus* populations of Beletta and Harenna are slightly separated.

CHARACTERIZATION OF *LOPHUROMYS BREVICAUDUS* OSGOOD, 1976

Lophuromys brevicaudus OSGOOD 1936: 241. Type locality: Mt Albasso.
Lophuromys flavopunctatus (nec THOMAS): partim YALDEN 1988a: 287; partim AFEWORK BEKELE & CORTI 1994: 677; LAVRENCHENKO et al. 1997: 220.
Lophuromys sp. B: ANISKIN et al. 1997: 819.

DESCRIPTION AND DIAGNOSIS

A medium-sized "speckled" *Lophuromys* with a relatively short tail (fig. 5A). The texture of the dorsal pelage is softer and shorter, the coloration being generally duller than in other Ethiopian representatives of the *Lophuromys flavopunctatus* species-complex. The underfur on the ventral and dorsal side is light grey. The coloration of the dorsal region is greyish-drab, abundantly "speckled" owing to the pale-coloured subterminal rings of the dorsal hairs which are unicolorous greyish below these rings (fig. 6B). The coloration of the ventral side of the body is in general greyish, but in some specimens the belly is cream coloured or yellowish; each ventral hair is white tipped and darkgrey at the base, like in *Lophuromys melanonyx*.

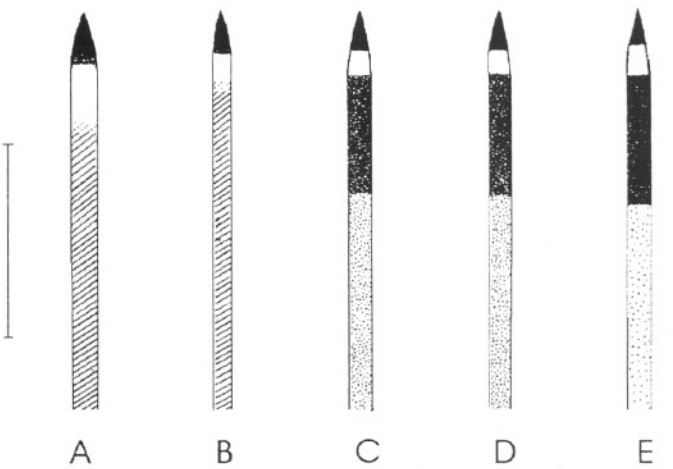

Fig. 6. – Schematic representation of the banding of the hairs of species *Lophuromys*. Colour bands were measured on a typical dorsal hair, halfway along the back. Hatch indicates grey pigmentation, stipple = red pigmentation in different intensities.
A - *L. melanonyx* (ZMMU 162510), B - *L. brevicaudus* (ZMMU 162502), C - *L. flavopunctatus brunneus* (KMMA 97087.0009) from the Beletta Forest, D - *L. chrysopus* (ZMMU 162413) from the Harenna Forest, E - *L. chrysopus* (KMMA 97087.0019) from the Beletta Forest.
Scale bar = 5 mm.

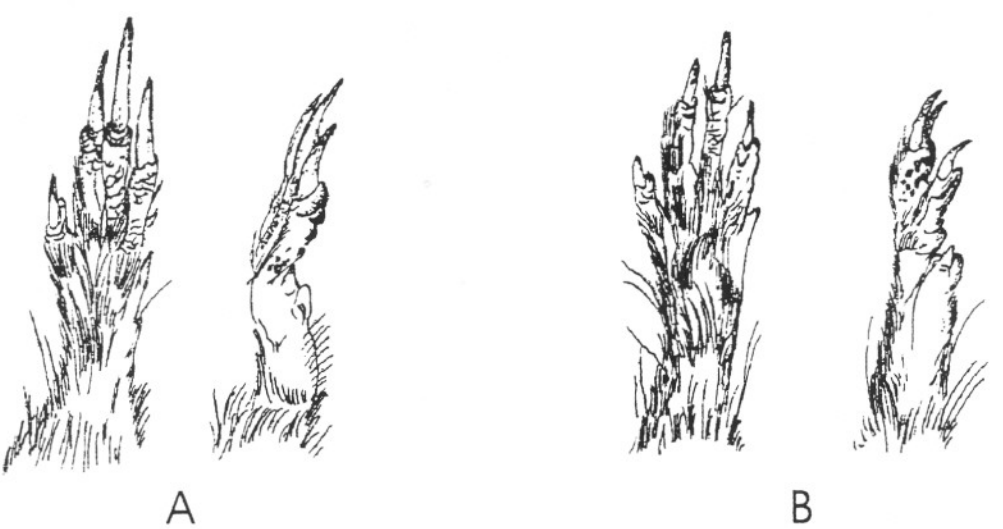

Fig. 7. – Schematic drawings of the fore-feet stressing the clearly longer claws of *Lophuromys brevicaudus* (A) when compared to *Lophuromys chrysopus* (B).

The dorsal part of the head has the same colour as the dorsal side. The chin and throat are more greyish than the belly owing to the reduction of the white tips of the hairs in this region; however, in some specimens there is a narrow reddish-orange collar which is contrasting with the basic colour of the belly and chin-region. The dorsal side of the forefeet is dark, whereas the dorsal side of the hindfeet is greyish with a central longitudinal darkish band. The light coloured claws are noticeably longer than in other taxa, especially on the forefeet (fig. 7A). The grey scales on the tail are darker above than below; the hairs on the dorsal side are black, on the ventral side nearly white.

Lophuromys brevicaudus differs from *L. flavopunctatus brunneus* in having a smaller and clearly narrower skull; the unusually large bullae are medially close to each other. *Lophuromys brevicaudus* has a skull of similar size as *L. chrysopus* but has a more slender rostrum and skull-basis, and somewhat heavier M^1 and bullae.

The karyotype of *L. brevicaudus* (2n=68, NFa=78; 8m, sm + 4st + 54a + Xst +Ya) is described by ANISKIN et al. (1997). Allozyme analysis has shown that G-6pd, Dia-2 and Alb loci and Hbb pattern are good genetic markers for the discrimination between *Lophuromys brevicaudus* and *L. chrysopus* from the Bale Mountains (LAVRENCHENKO et al. 1997).

DISTRIBUTION AND ECOLOGY

When describing this taxon OSGOOD (1936) mentioned two series, "one from the Chilalo Mountains and another from the Gedeb Mountains, the latter lying somewhat farther south and separated by the intervening valley of the Webbi Shebeli River". We found *L. brevicaudus* to be common in the Bale Mountains. It seems to have a rather restricted distribution, occurring only in a few neighbouring montane zones in south-central Ethiopia.

L. brevicaudus is a diurnal specialized rodent typical for the *Erica-Hypericum* zone (3,170 - 3,750 m ASL) of these mountain ranges where it is one of the most abundant small mammal species together with *Crocidura glassi* HEIM DE BALSAC, 1966 (YALDEN 1988a, LAVRENCHENKO et al. 1997). It occurs also, but in smaller numbers, in the lower *Schefflera-Hagenia* belt of the Harenna Forest (2,400 - 2,760 m ASL) where it coexists with its sibling-species *Lophuromys chrysopus* (table 7). There is further a restricted syntopy of *L. brevicaudus* with *L. melanonyx* on the swamp shore in the Upper Wabe Valley (locality 11) (LAVRENCHENKO et al. 1997).

MATERIAL EXAMINED

Locality 4: ZMMU 162444, KMMA 97087.0001; locality 6: ZMMU 164820; locality 7: ZMMU 164816, 164819, 164920-25; locality 8: ZMMU 162455-56, 162530-36, KMMA 97087.0008; locality 9: ZMMU 162462-68, 162470, 162472-73, 162480-84, 162537-39, 162593, 162605, 162720, KMMA 97087.0002, 97087.0003, 97087.0005; locality 10: ZMMU 162435-41, 162443, 162445-51, 162453-54, 162457-61, 162475-78, 162500-01, 162604, 162719, 164812-15, 164817-18, 164821-26, 164848-52, KMMA, 97087.0004, 97087.0007; locality 11: ZMMU 162485-99, 162502, 162540-46, KMMA 97087.0006.

CHARACTERIZATION OF *LOPHUROMYS CHRYSOPUS* OSGOOD, 1936

Lophuromys aquilus chrysopus OSGOOD 1936: 242. Type locality: Allata.

Lophuromys flavopunctatus (nec THOMAS): partium YALDEN 1988a: 287; partim AFEWORK BEKELE & CORTI 1994: 677.

Lophuromys sp. A: LAVRENCHENKO et al. 1997: 220; ANISKIN et al. 1997: 818.

DESCRIPTION AND DIAGNOSIS

A medium-sized "speckled" *Lophuromys* with a relatively long tail (fig. 5B). General colour of the back blackish-brownish, abundantly "speckled" owing to the light subterminal rings of the hairs. Below these rings the dorsal hairs are bright reddish basally and blackish in the terminal half in specimens from the Harenna Forest, and light reddish basally and black in the terminal half in those from the Beletta Forest (fig. 6D, E). The ventral colour is variable from yellow to light orange and from light pink to reddish in specimens from Harenna and Beletta, respectively. The underfur is light grey on the dorsum and light yellow on the ventral side. There is a marked contrast between the colour of the dorsal underfur and the reddish bases of the dorsal hairs. The dorsal part of

Table 7. –Relative abundance of *Lophuromys* spp. in the different altitudinal belts on the southern slope of the Bale Massif. See text and fig. 1 for numbers of localities.

Locality	1	2	3	4	5	6	7
Altitude (ASL)	1,680 m	1,780 m	1,935 m	2,400 m	2,620 m	2,760 m	3,250 m
L. chrysopus	1	6	17	8	7	11	0
L. brevicaudus	0	0	0	2	0	1	8

the head has the same colour as the dorsal side. The throat is more greyish than the belly owing to the grey basal parts of the hairs in this region. The dorsal side of the forefoot is dark, the dorsal side of the hindfoot is greyish-rufous, neatly contrasting with the blackish toes. The light claws are, especially on the forefeet (fig. 7B), noticeably shorter than in other Ethiopian representatives of the *Lophuromys flavopunctatus* species-complex. The grey scales on the tail are darker above than below; the hairs on the dorsal side are black, the top of each hair on the ventral side is white, but the basis has a dark grey or blackish colouration.

The skull of *Lophuromys chrysopus* is similar in size to *L. brevicaudus* but with a wider rostrum and skull base and more slender M^1 and somewhat more widely separated smaller bullae.

The karyotype of this species (2n=54, NFa=60; 8m, sm + 44a + Xa +Ya) from the Harenna Forest is described in ANISKIN et al. (1997). Our preliminary data indicate the presence of supernumerary B-chromosomes in the karyotypes of *L. chrysopus* from the Beletta Forest.

DISTRIBUTION AND ECOLOGY

This species is together with *Praomys albipes* (RUPPEL, 1842) one of the commonest rodents in the different altitudinal belts in the Harenna Forest from 1,680 m to 2,760 m ASL (table 7). According to the available data, *L. chrysopus* is known only from the Beletta Forest in the Belte Gera Region. Nevertheless, we expect that this species, widespread in the montane evergreen tropical rain forests on both the western and eastern plateaux in Ethiopia, will probably also occur in most of the south-western forests.

The unusual soft pelage of *L. chrysopus,* when compared to *L. brevicaudus*, confirms that it is a true tropical forest species. It is worth mentioning that the type locality of this taxon coincides with that of *Cercopithecus aethiops djamdjamensis* NEUMANN, 1902 an endemic of the Harenna Forest adapted to a closed-canopy montane forest (DANDELOT and PREVOST 1972, CARPANETO and GIPPOLITI 1994). In general, we can state that there is habitat segregation between *Lophuromys chrysopus* and *L.brevicaudus* in the Harenna Forest (table 7) but that *L. chrysopus* and *L. flavopunctatus brunneus* are syntopic in the Beletta Forest.

REMARKS

Multivariate morphometrics of the skull demonstrate that samples of *Lophuromys chrysopus* from Harenna and Beletta Forests are probably conspecific but also sufficiently different to eventually warrant subspecific characterization. Moreover, there are some external (peculiarities of colouration) and genetic (presence or absence of B-chromosome system) discrepancies between the populations from opposite sides of the Ethiopian Rift Valley which reinforce this hypothesis.

MATERIAL EXAMINED

Locality 1: KMMA 97087.0017; locality 2: ZMMU 162410-11, 162420-21, 162423; KMMA 97087.0016; locality 3: ZMMU 162412-13, 162415-19, 162426, 162434, 164839, 164842, 164845-46, 164926-27, KMMA 97087.0013, 97087.0014; locality 4: ZMMU 162422, 162424, 162427, 162429-32, KMMA 97087.0015; locality 5: ZMMU 164827-29, 164831, 164838, 164918-19; locality 6: ZMMU 164830, 164832-37, 164841, 164843-44, 164847; locality 12: ZMMU 164946, 164948, 164951-53, 164955-57, KMMA 97087.0018, 97087.0019, 97087.0020, 97087.0021.

CHARACTERIZATION OF *LOPHUROMYS FLAVOPUNCTATUS BRUNNEUS* THOMAS, 1906

Lophuromys flavopunctatus brunneus THOMAS 1906: 305. Type locality: Manno.

DESCRIPTION AND DIAGNOSIS

When we do not consider *L. melanonyx, Lophuromys flavopunctatus brunneus* is the largest known Ethiopian representative of this species-complex. The colour of the dorsal fur is blackish-brownish, abundantly "speckled" with the light subterminal rings of the hairs. Below these rings the dorsal hairs are bright reddish basally and blackish in the terminal half (fig. 6C). The hairs on the abdomen are uniformly rusty. The underfur is light grey above contrasting with the reddish basal portion of the dorsal bristles and the light yellow below. The dorsal part of the head has the same colour as the dorsal side. Chin and throat have the same colour as the ventral side. The dorsal side of the forefoot is dark, whereas the dorsal side of the hindfoot is greyish with a central longitudinal blackish band. The light claws are longer than normal, especially on the forefeet, very much like in *Lophuromys brevicaudus*. The grey scales on the tail are darker above than below; the hairs on the dorsal side are black, on the ventral side nearly white.

The large skull possesses wide and protruding rounded zygomatic arches.

A preliminary cytogenetic study has shown that the karyotype of *L. flavopunctatus brunneus* is composed of 68 chromosomes (same diploid number as *L. brevicaudus*): however more detailed analysis will be necessary to describe the possible differences between the karyotypes of *L. flavopunctatus brunneus* and *L. brevicaudus.*

The exact geographical co-ordinates of the type locality of *L. flavopunctatus* remain unknown. THOMAS (1903) indicated that "the type of this species . . . was probably from Ankober, about 100 miles N.E. of Addis Ababa." The type of this taxon has an incomplete skull without auditory bullae.

We use conditionally the name *L. flavopunctatus brunneus* for the 68-chromosomal form from the Beletta Forest

until the taxonomical position of *L. flavopunctatus* sensu stricto is clearly understood.
Finally we remark that one specimen from the same locality (ZMMU 164944) earmarked for the moment as *Lophuromys* sp. D differs from *L. flavopunctatus brunneus* in having a shorter tail (tables 2,3), a shorter and broader skull, a shorter and broader rostrum, and a strikingly rounded foramen magnum. We notice however that, when plotted on our canonical analysis (see fig.4) the specimen ZMMU 164944 falls well within the population of *L. flavopunctatus brunneus*. However we judge for the moment that the morphological differences may be important enough to suggest that three different *Lophuromys* species might be sympatric in the Beletta Forest.

MATERIAL EXAMINED

Locality 12: ZMMU 164928, 164930-31, 164933-36, 164938-39, 164941-43, 164945, KMMA 97087.0009, 97087.0010, 97087.0011, 97087.0012.

Discussion

The present study demonstrates that the *Lophuromys flavopunctatus* species-complex is represented in Ethiopia by at least three distinct species, *L. brevicaudus, L. chrysopus* and *L. flavopunctatus*. These species can be diagnosed by allozymic, cytogenetic, morphometric and morphological characters. It is probable that the number of taxa pertaining to the *L. flavopunctatus* species-complex will further increase after new field studies in the relic forests and isolated alpine plateaux of Ethiopia, combined with an adequate examination of all relevant museum material from this country. In this respect the sole specimen of *Lophuromys* sp. D (ZMMU 164944) may be a representative of an as yet undescribed species. Furthermore, DIETERLEN (1987) mentioned two specimens of *L. flavopunctatus* from Ankober showing "a phenotypical approach to *L. melanonyx*". Finally, the original description of *Lophuromys flavopunctatus simensis* Osgood, 1936 even suggests species rank for this population from the Simien Mountains (northern most distribution for the genus).
According to available distributional data, *Lophuromys brevicaudus* and *L. chrysopus* are endemic to Ethiopia. Of the 28 indubitable endemic mammals of Ethiopia, 19 are associated with open habitats at high altitude (above 2,000 m ASL), whereas only nine are associated with forests at lower altitudes (YALDEN and LARGEN 1992). YALDEN et al. (1996) concluded that Ethiopian forests have a rather impoverished mammal fauna. The high-altitude endemic of the eastern plateau *L. brevicaudus* is, like *Stenocephalemys griseicauda* PETTER, 1972, a typical member of the endemic rodent fauna of the heathlands. Of the nine endemic forest mammals, only two, *Praomys albipes* and *Desmomys harringtoni* (THOMAS, 1903), are widespread. The other forest endemics have a very restricted distribution or known only from their types [e.g. *Pelomys rex* (THOMAS, 1906) and *Crocidura macmillani* DOLLMAN, 1915] (YALDEN and LARGEN 1992). In particular, YALDEN (1988b) was amazed at the absence of specialist forest rodents in the relic Harenna Forest.
The recognition of *Lophuromys chrysopus* as a distinct endemic species demonstrates that the forest mammal fauna of Ethiopia is richer and more unique than has been assumed so far. The present current distribution of this forest species may be associated with some humid periods of the Pleistocene when forest covering extensive areas in Ethiopia would have allowed *Lophuromys chrysopus* to spread across the Rift Valley, which is presently a major zoogeographical barrier in Ethiopia. Discrepancies in coloration and chromosome characters between *L. chrysopus* populations from both sides of the Rift underline the importance of this zoogeographical barrier. We may add that several other endemic species of afro-alpine moorlands [e.g. *Canis simensis* Ruppell, 1838, *Tachyoryctes macrocephalus* (Ruppell, 1842) and *Muriculus imberbis* (Ruppell, 1842)] have distinct subspecies on either side of the Rift (YALDEN and LARGEN 1992). A similar divergence may have remained unnoticed in two widespread forest endemics, *Praomys albipes* and *Desmomys harringtoni*. The 68-chromosomal *Lophuromys* known only from the Beletta Forest is conditionally assigned to *L. flavopunctatus brunneus*. Future studies will be essential to determine the exact geographic range of this form and other putative taxa (such as *Lophuromys* sp. D); one or more of which may be endemic, while others may also exist also beyond the borders of Ethiopia.
It is obvious, that the relic forests and alpine plateaux of Ethiopia are real centres of diversification and endemism for the genus *Lophuromys*. In fact the number of sympatric species in Ethiopia is rather amazing for this genus. Three endemic species, *Lophuromys chrysopus, L. brevicaudus* and *L. melanonyx* occur in the Bale Mountains, replacing each other in the different altitudinal belts (tropical forest - heathland - afro-alpine zone) each time with a small overlap suggesting an adaptive pattern of speciation. On the other hand, two or three species, *L. chrysopus, L. flavopunctatus brunneus* (and possible *Lophuromys* sp. D) are syntopic in the Beletta Forest on the western and opposite side of the Rift Valley.
By now it has become clear that the final elaboration of the systematics of the *L. flavopunctatus* species-complex from Ethiopia will be a rather complex problem due to the proven sympatry between certain of its taxa. The erroneous conclusion about conspecificity of all Ethiopian *L. flavopunctatus* s. lat. in previous studies (RUPP 1980; AFEWORK BEKELE and CORTI 1994) resulted in our opinion from the use of mixed samples of specimens belonging to at least two species.
We can assume that the Ethiopian representatives of the genus *Lophuromys* present a complex of forms at different levels of taxonomical diversification (cytotypes with B-chromosome system, subspecies, species) resulting from various biogeographical interactions and making it a valuable model in evolutionary biology.

Conclusions

The presented data reveal a more complex taxonomical structure of Ethiopian *Lophuromys* than has been assumed so far. *L. brevicaudus* and *L.chrysopus* are considered to be distinct endemic species, which can be distinguished on allozymic and chromosome characters but also morphologically and biometrically. The former species is confined to a part of the eastern plateau, together with the endemic *L. melanonyx*, the latter is found in the tropical forests on both sides of the Rift Valley. Additionally, our data indicate that next to *L. flavopunctatus brunneus* possibly a fifth *Lophuromys* taxon (sp.D) occurs on the western plateau. All these "speckled" forms belong to the *L. flavopunctatus* species-complex.

This study on *Lophuromys* makes it perfectly clear that the fauna of Ethiopia is not that well known and that the biodiversity in this region of Africa could be far higher than suspected today.

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L.A. LAVRENCHENKO
Severtzov Institute of Ecology and Evolution
Russian Academy of Sciences
Leninsky Pr. 33, 117071 Moscow, Russia

W.N. VERHEYEN and J. HULSELMANS
RUCA - UA
Departement Biologie
Onderzoeksgroep Evolutiebiologie
Groenenborgerlaan 171, B-2020 Antwerpen, België
e-mail: hulsel@ruca.ua.ac.be