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Systematics and distribution of *Mastomys* (Muridae, Rodentia) from Ethiopia, with the description of a new species

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Abstract

Studied was morphological, allozymic, and chromosomal variation of Ethiopian *Mastomys natalensis* sensu lato to clarify the systematics of this species complex. Three different species of *Mastomys* occur in Ethiopia. A new species, *Mastomys awashensis* n. sp., is described and compared with the other two, *M. erythroleucus* and *M. natalensis* which are widely distributed throughout most of Western, Central, and Eastern Africa. *Mastomys awashensis* n. sp. is endemic to the Ethiopian Rift Valley and is known only from two localities in the Upper Awash Valley. This newly described species differs from the other two Ethiopian *Mastomys* species by fixed alleles at Ldh-B and Got-1 loci and also by Hbb patterns and by relatively shorter tail bearing smaller scales. Besides that, the three species co-existing in the middle part of the Ethiopian Rift Valley can be distinguished biometrically with the use of multivariate analysis. The karyotype of *M. awashensis* (2 n = 32, NFa = 54) which is similar to that of *M. natalensis*, demonstrates, nevertheless, a number of unique characteristics differing it from any known representative of the *M. natalensis* species complex. The presented results from different disciplines support a previous supposition of a "mosaic" evolution under divergence in this species group.

Key word: *Mastomys*, Ethiopia, craniometry, allozymes, chromosomes

Introduction

The multimammate rat, genus *Mastomys* Thomas, 1915, is widely distributed throughout sub-Saharan Africa. It includes up to eight species (for review, see Musser and Carleton 1993). They are distinguished mainly by chromosomal and biochemical traits, so the data on their relations and peripheral distribution remain largely uncertain. Of these, four most closely related and weakly separable species *M. coucha* (Smith, 1836), *M. erythroleucus* (Temminck, 1853), *M. hildebrandtii* (Peters, 1878), and *M. natalensis* (Smith, 1834) constitute a presumably monophyletic group called the *M. natalensis* species complex that occupies most of the genus distribution region.

The situation with *Mastomys* taxonomy in Ethiopia is a matter of controversy, as well. All Ethiopian *Mastomys* were lumped under *M. natalensis* (Yalden et al. 1976). At present, two species are commonly acknowledged in Eastern and Central Africa, *M. erythroleucus* (2 n = 38) and *Mastomys* with 2 n = 32, NFa = 54 (Hubert et al. 1983). It has been supposed once that multimammate rats with latter karyotype belong to two separate species, *M. huberti* (Wroughton, 1908) and *M. natalensis* sensu stricto, inhabiting Western to Eastern and Southern Africa, respectively (Robbins and van der Straeten 1989; Leirs et al. 1991). Recently, the conspecificity of these two taxa was shown by cytogenetic, biometric, and hybridological analyses (Britton-Davidian et al. 1995; Granjon et al. 1996).

The present study provides allozymic, cytogenetic, and morphological information on the Ethiopian *Mastomys* sibling-species. *Mastomys* specimens collected in Ethiopia during 1987–1993 appeared to belong to three different species. Two of them corresponded to widespread species: *M. natalensis* (2 n = 32, NFa = 54) and *M. erythroleucus* (2 n = 38, NFa = 50). The other one (2 n = 32, NFa = 54, specific Hbb pattern) was shown to represent a separate species which is described here.

Material and methods

Field work in Ethiopia was carried out in the framework of the Joint Ethio-Russian Biological Expedition (JERBE). Specimens were captured at the following localities: 1. Awash National Park: 09°00′ N 40°10′ E; 2. Koka Lake area: 08°23′ N 39°09′ E; 3. Ambo area: 08°56′ N 37°58′ E; 4. Gambela area: 07°53′ N 34°22′E; 5. Lower Omo Valley: 05°00′ N 36°07′ E; 6. Nechisar National Park: 05°53′ N 37°38′ E. All specimens referred to in the present publication are stored at the Zoological Museum of Moscow University (ZMMU) and the Natural History Museum, Addis Ababa (NHMAA).

Allozymic study: According to allozyme characters the whole sample of Ethiopian *Mastomys* was divided into three groups corresponding presumably to three species: *M. erythroleucus* (locality 2: N = 27); *M. natalensis* (2: N = 6, 3: N = 79); *Mastomys* n. sp. (1: N = 4, 2: N = 7). Standard vertical polyacrylamide and horizontal starch gel electrophoresis and standard protein staining techniques (DAVIS 1964; PEACOCK et al. 1965; SELANDER et al. 1971; HARRIS and HOPKINSON 1978) were used to assay 20 enzymatic and non-enzymatic proteins from blood and kidney tissues. The enzymatic proteins (their respective abbreviations and tissue used are given in parentheses) were adenylate kinase (Ak, kidney); creatine kinase (Ck, kidney); glucosephosphate isomerase (Gpi, kidney); glycerol-3-phosphate dehydrogenase (Gpd, kidney); glutamate-oxaloacetate transaminase (Got-1, Got-2, kidney); isocitrate dehydrogenase (Idh-1, Idh-2, kidney); lactate dehydrogenase (Ldh-A, Ldh-B, kidney); malate dehydrogenase (Mdh-1, Mdh-2, kidney); malic enzyme (Me-1, blood); phosphoglucomutase (Pgm, kidney); purine nucleoside phosphorylase (Np, blood); phosphogluconate dehydrogenase (Pgd, blood); sorbitol dehydrogenase (Sdh, kidney); superoxide dismutase (Sod-1, Sod-2, kidney). The non-enzymatic protein was haemoglobin (Hbb). The specimens from localities 4 (*M. erythroleucus*: N = 48, *M. natalensis*: N = 15) and 6 (*M. erythroleucus*: N = 12) were analyzed only as to their haemoglobin patterns. Genetic relationships between *Mastomys* species were investigated using *Praomys albipes* (Ruppell, 1842) (localities 7 [Addis Ababa]: N = 26, 3: N = 26) and *Praomys fumatus* (Peters, 1878) (locality 2: N = 2) as the representatives of the closest related genus for comparison.

Cytogenetic study: The chromosomal analysis was performed on *M. erythroleucus* from localities 2 (10 males, 5 females), 5 (1 male), 6 (5 males, 3 females); *M. natalensis* from 2 (1 male, 3 females), 3 (3 males, 1 female), and *Mastomys* n. sp. from 1 (3 males, 1 female), 2 (5 males, 4 females). Somatic metaphases were prepared from bone marrow by the usual air-drying technique according to FORD and HAMERTON (1956) or through short-termed tissue culture from dead animals (KOZLOVSKY 1974). Slides were stained with 4% Giemsa in phosphate buffer with pH = 7.0. C-banding was obtained according to SUMNER (1972).

Morphological study: Four standard external measurements were obtained from freshly killed rats: head-body length (L), tail length (C), hind foot length without claws (Pl), ear length (Au). The following standard skull characters were measured: condylobasal length (Cb), length of nasals (LoNos), length of frontals (LoFr), length of parietals (LoPar), length of anterior palatal foramen (LoFIn), length of diastema (LoDia), length of maxillary toothrow (LoM^{1-3}), greatest breadth of nasals (LaNos), zygomatic breadth (LaZig), width of ramus superior of processus zygomaticus ossis maxillaris (Lars), width of the zygomatic arch (Laaz), interorbital breadth (LaIor), length of mandibula (LoMd), length of mandibular toothrow (LoM_{1-3}), length of the third lower molar (LoM_3). All external and three cranial measurements (Cb, LaZig, LoMd) were recorded using a digimatic calliper, the other were taken by micrometer in binocular microscope MBS-9 (Russia). Based upon the degree of tooth wear, the specimens were grouped into three age classes: sub-adults, adults, and seniles. Only adult individuals were used for subsequent analyses.

Numerical analyses: Genetic distances among populations and species were calculated using BIOSYS programme (SWOFFORD and SELANDER 1981). Statistic significance of differences among sexes and species by morphometric traits was evaluated by Student's t-test. Principal component analyses

were performed on external and cranial measurements of adult *Mastomys* specimens from the Ethiopian Rift Valley (localities 1, 2, and 6) using the subprogramme FACTOR of SPSS programme package (Nie et al. 1975) to evaluate unevenness of distribution of the specimens in the phenetic hyperspace of morphometric characters.

Results

Allozymic data

Only three of the 20 loci analyzed (Got-2, Mdh-2, and Sod-2) were found to be monomorphic for the same allele in *Praomys* and *Mastomys* species. The allele frequencies of both polymorphic and discriminant loci in the populations analyzed are given in table 1. Eight loci (Ak, Ck, Gpi, Idh-2, Ldh-A, Mdh-1, Pgd, and Hbb) discriminate the genera *Mastomys* and *Praomys*, five loci (Got-1, Ldh-B, Np, Pgd, and Hbb) discriminated at least two of the three *Mastomys* species. *Mastomys* n. sp. and *M. natalensis* from the middle part of the Ethiopian Rift Valley differ mutually by alternative alleles flxed for all these loci. The lack of heterozygous individuals at five diagnostic loci suggests the species rank of these sympatric taxa with similar karyotypes (2 n = 32). One locus (Hbb) appeared to be diagnostic for each of the three Ethiopian *Mastomys* species.

Table 1. Allele frequencies at 16 loci and frequencies of electrophoretically detectable phenotypes at Hbb licus in 8 populations belonging to 5 species of *Mastomys* and *Praomys* genera

	Species / Locality							
	Mastomys natalensis		*M. awashensis*		*M. erythroleucus*	*Praomys albipes*		*P. fumatus*
Locus, allele	3	2	2	1	2	3	7	2
Ak								
N	6	2	7	4	25	10	10	2
100	1.000	1.000	1.000	1.000	1.000	–	–	–
80	–	–	–	–	–	1.000	1.000	1.000
Ck								
N	79	5	7	4	27	26	29	2
156	–	–	–	–	–	1.000	1.000	1.000
100	1.000	–	1.000	1.000	1.000	–	–	–
56	–	1.000	–	–	–	–	–	–
Got-1								
N	79	6	7	4	27	26	29	2
138	–	–	–	–	0.019	–	–	–
100	0.987	1.000	–	–	0.981	–	–	–
87	–	–	1.000	1.000	–	0.962	1.000	1.000
67	0.013	–	–	–	–	0.038	–	–
Gpd								
N	79	5	7	4	26	26	29	2
145	–	–	–	–	–	0.077	–	–
135	–	–	–	–	–	0.058	–	–
113	–	–	–	–	0.962	–	–	–
100	1.000	0.900	–	–	0.038	0.846	1.000	1.000
67	–	0.100	1.000	1.000	–	–	–	–
44	–	–	–	–	–	0.019	–	–

Table 1. (continued)

	Species / Locality							
	Mastomys natalensis		*M. awashensis*		*M. erythroleucus*	*Praomys albipes*		*P. fumatus*
Locus, allele	3	2	2	1	2	3	7	2
Gpi								
N	79	5	7	4	27	26	29	2
112	–	–	–	–	–	–	0.190	–
58	–	–	–	–	–	1.000	0.810	1.000
–23	1.000	1.000	1.000	1.000	1.000	–	–	–
Idh-1								
N	79	6	7	4	26	26	29	2
100	–	–	–	–	–	0.077	0.224	–
78	0.814	1.000	0.714	1.000	0.923	0.712	0.466	1.000
64	0.186	–	0.286	–	0.077	0.212	0.310	–
Idh-2								
N	79	4	6	4	23	26	29	2
–50	1.000	1.000	1.000	1.000	1.000	–	–	–
–100	–	–	–	–	–	1.000	1.000	1.000
Ldh-A								
N	79	6	7	4	27	26	29	2
100	–	–	–	–	–	1.000	1.000	–
70	1.000	1.000	1.000	1.000	1.000	–	–	–
40	–	–	–	–	–	–	–	1.000
Ldh-B								
N	79	6	7	4	27	26	29	2
108	–	–	1.000	1.000	–	0.038	0.070	–
100	0.987	1.000	–	–	1.000	0.962	0.830	1.000
86	0.013	–	–	–	–	–	0.100	–
Me-1								
N	79	6	7	4	27	26	29	2
89	–	–	–	–	–	1.000	1.000	–
81	0.057	–	–	–	–	–	–	–
62	0.943	1.000	1.000	1.000	1.000	–	–	1.000
Mdh-1								
N	79	5	7	4	27	26	29	2
95	–	–	–	–	–	1.000	1.000	1.000
88	1.000	1.000	1.000	1.000	1.000	–	–	–
Np								
N	3	6	7	3	26	2	21	2
113	1.000	1.000	–	–	–	1.000	0.900	–
105	–	–	–	–	–	–	–	0.250
100	–	–	1.000	1.000	1.000	–	0.100	–
94	–	–	–	–	–	–	–	0.750
Pgd								
N	79	6	7	4	27	26	29	2
120	–	–	–	–	–	–	–	1.000
100	–	–	1.000	1.000	1.000	–	–	–
95	1.000	1.000	–	–	–	–	–	–
90	–	–	–	–	–	1.000	1.000	–

Table 1. (continued)

	Species / Locality							
	Mastomys natalensis		*M. awashensis*		*M. erythroleucus*	*Praomys albipes*		*P. fumatus*
Locus, allele	3	2	2	1	2	3	7	2
Pgm								
N	79	6	7	4	26	26	29	2
110	0.006	0.333	–	–	–	–	–	–
100	0.981	0.667	1.000	1.000	1.000	1.000	1.000	1.000
87	0.013	–	–	–	–	–	–	–
Sdh								
N	79	5	7	4	25	26	29	2
100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	–
80	–	–	–	–	–	–	–	1.000
Sod-1								
N	79	6	7	4	27	26	29	2
100	1.000	1.000	1.000	1.000	1.000	–	–	1.000
72	–	–	–	–	–	0.308	–	–
56	–	–	–	–	–	0.692	1.000	–
Hbb								
N	79	6	7	2	22	26	29	2
100/60 (1)	1.000	1.000	–	–	–	–	–	–
70/85	–	–	–	–	–	1.000	1.000	–
80/100 (4)	–	–	1.000	1.000	–	–	–	–
70/80	–	–	–	–	–	–	–	1.000
80/115 (2)	–	–	–	–	1.000	–	–	–

N – number of specimens examined. See text numbers of sampling localities. In parenthesis Hbb phenotypes are given according to Lavrenchenko et al. (1992).

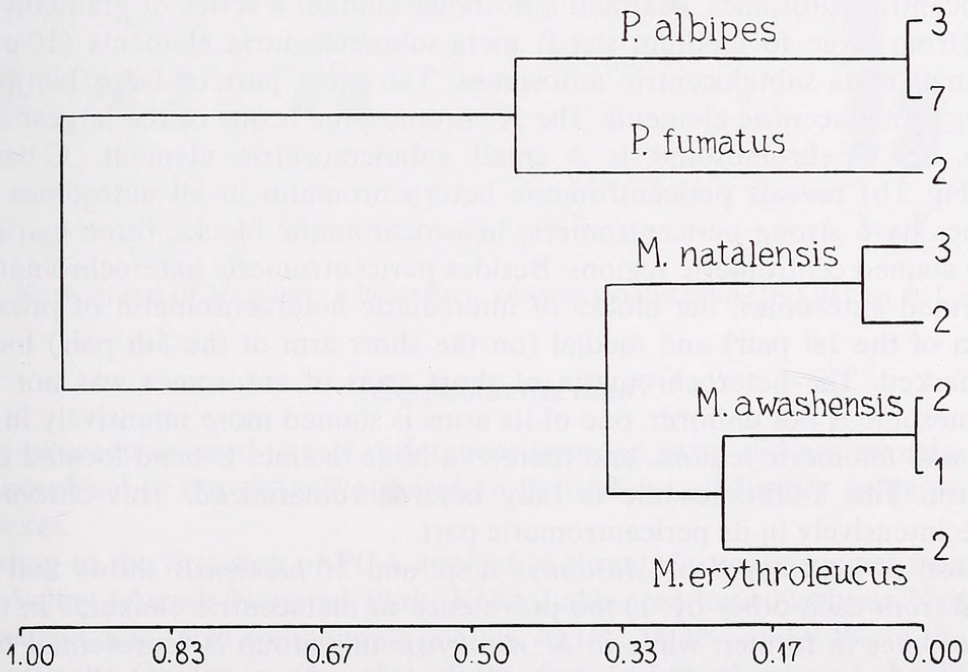

Fig. 1. UPGMA phenogram based on Nei's genetic distances between Ethiopian populations of *Mastomys* and *Praomys* species. The scale to be values of genetic distances (Nei 1972). See text for numbers of localities.

UPGMA dendrogram (Fig. 1) generated on the Nei's genetic distances matrix (NEI 1972) clearly shows that all *Mastomys* species are more closely related to each other than to Praomys. These results confirm the validity of the genus *Mastomys* as a monophyletic group.

The value of Nei's genetic distance between *M. erythroleucus* and *M. natalensis* is 0.258. *Mastomys* n. sp. genetically is more similar to *M. erythroleucus* (Dnei = 0.225) and is more distant from *M. natalensis* (Dnei = 0.402).

The scale of genetic distances between the three Ethiopian *Mastomys* is equal to that found between *Mastomys* species from Senegal (DUPLANTIER et al. 1990 b). Ethiopian *Mastomys* n. sp. shares common fixed haemoglobin electromorph (Hbb 4) with *M. coucha* from South Africa (GORDON 1978; GREEN et al. 1978, 1980; GORDON and WATSON 1986) and differs from the Ethiopian populations of *M. erythroleucus* (Hbb 2, 3) and *M. natalensis* (Hbb 1) (LAVRENCHENKO et al. 1992).

Chromosomal data

Ethiopian *M. erythroleucus* is characterized by 2 n = 38 which generally corresponds to results from previous studies of this species from other regions (MATTHEY 1965, 1966; KRAL 1971; TRANIER 1974; HUBERT et al. 1983; DUPLANTIER et al. 1990 a; BRITTON-DAVIDIAN et al. 1995). Therefore, we consider here the data on the two *Mastomys* species with a karyotype of 2 n = 32 only.

In *M. natalensis* (Fig. 2 a), the karyotype comprises 7 pairs of large submetacentric, 5 pairs of medium sized meta-submetacentric, and 3 small acrocentric pairs of autosomes. The smallest pair of autosomes has very short arms and sometimes it can be described as a subtelocentric. The sex chromosomes are both large, X being metacentric and Y being acrocentric. C-banding (Fig. 2 b) reveals all chromosome pairs carrying pericentromeric heterochromatin, and the short arms of chromosomes Nos. 1, 3, 4, 6 and 7 are extremely heterochromatic. The intercalaric heterochromatin of autosomes is indistinguishable. The X-chromosome is weakly stained, intensity of its staining is increased in centromeric and telomeric regions. The Y-chromosome appears fully heterochromatic.

In *Mastomys* n. sp., the chromosomal set (Fig. 3 a) includes 12 pairs of biarmed and 3 pairs of acrocentric autosomes. Biarmed autosomes contain a series of gradually decreasing in size (from large to medium sized) meta-submetacentric elements (10 pairs) and 2 pairs of small meta-subtelocentric autosomes. The most part of large biarmed autosomes belong to metacentric elements. The X-chromosome is one of the largest meta-submetacentrics, the Y-chromosome is a small submetacentric element. C-banding of karyotype (Fig. 3 b) reveals pericentromeric heterochromatin in all autosomes. Most of the autosomes have strong pericentromeric heterochromatic blocks, three biarmed pairs have weakly stained centromeric regions. Besides pericentromeric heterochromatin in two pairs of biarmed autosomes, the blocks of intercalaric heterochromatin of proximal (on the long arm of the 1st pair) and medial (on the short arm of the 5th pair) localization were also marked. The heterochromatin of short arms of autosomes was not revealed. The X-chromosome is not uniform: one of its arms is stained more intensively in the pericentromeric and telomeric regions, and there is a large distinct C-band located distally in the other arm. The Y-chromosome is fully heterochromatinized. This chromosome is stained more intensively in its pericentromeric part.

Comparison of karyotypes of *Mastomys* n. sp. and *M. natalensis* shows that they are distinguished from each other by: 1) the prevalence of metacentric elements in the group of large autosomes in former, while in *M. natalensis* this group is represented by mainly submetacentric elements; 2) the form of the Y-chromosome which is small submetacentric in *Mastomys* n. sp. and large acrocentric in *M. natalensis*; 3) the C-banding pattern which shows absence of heterochromatin of additional short arms in *Mastomys* n. sp.

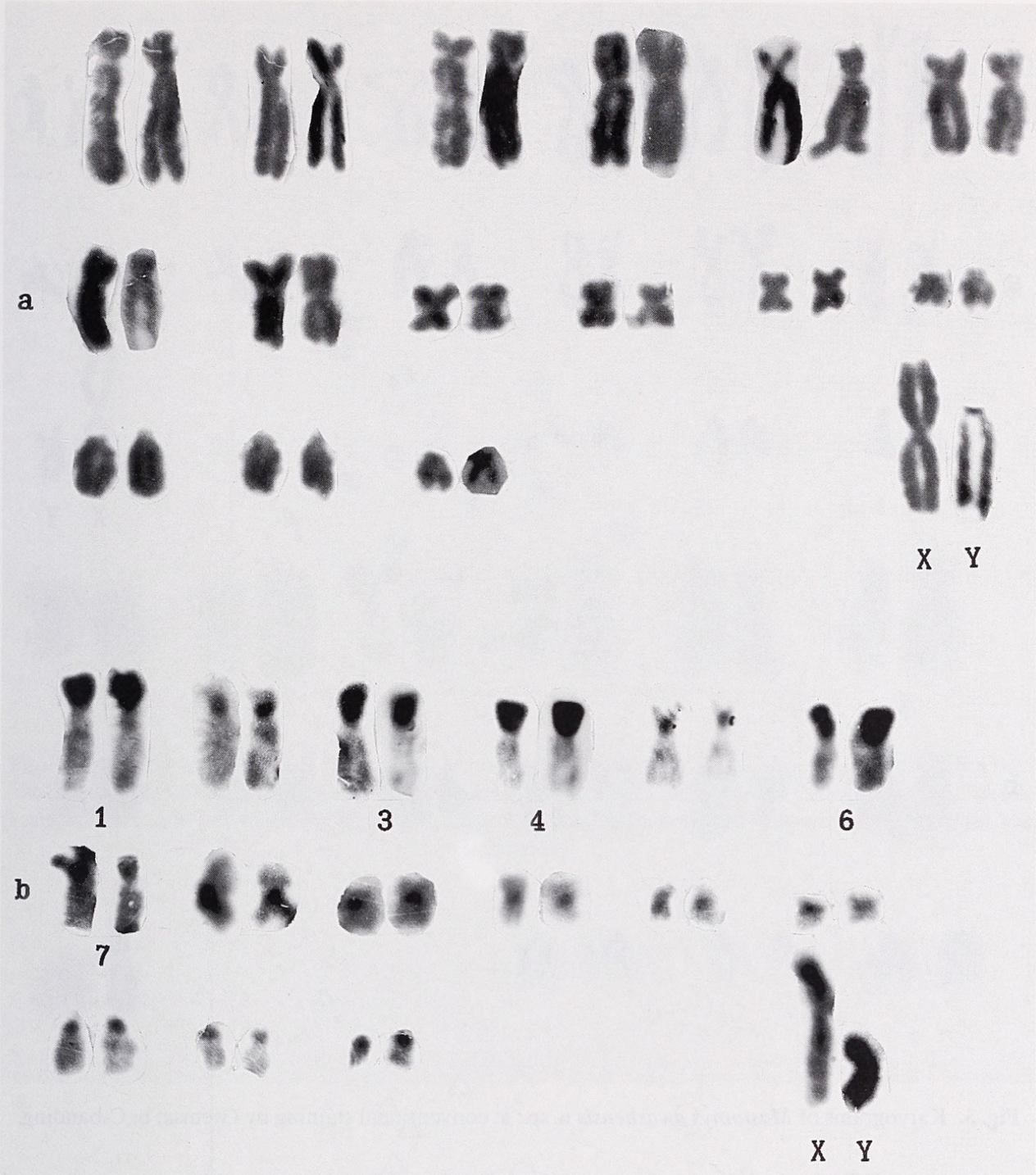

Fig. 2. Karyograms of *Mastomys natalensis*: a: conventional staining by Giemsa; b: C-banding.

Morphometric data

Univariate procedures used to test differences between sexes did not reveal any effect of sexual dimorphism in our data. We therefore carried out all further analyses by combining both sexes.

According to the first step of PCA applied to three *Mastomys* species from the Ethiopian Rift Valley (Awash National Park, Koka Lake area, and Nechisar National Park), the first, second, and third components contain 43.1%, 11.3%, and 9.4% of the total variation, respectively. On the scatter plot of the first and third axes of the PCA (Fig. 4), *M. natalensis* is clearly separated from the remaining taxa. As to the latter, the specimens identified as *Mastomys* n. sp. and *M. erythroleucus* form one solid group.

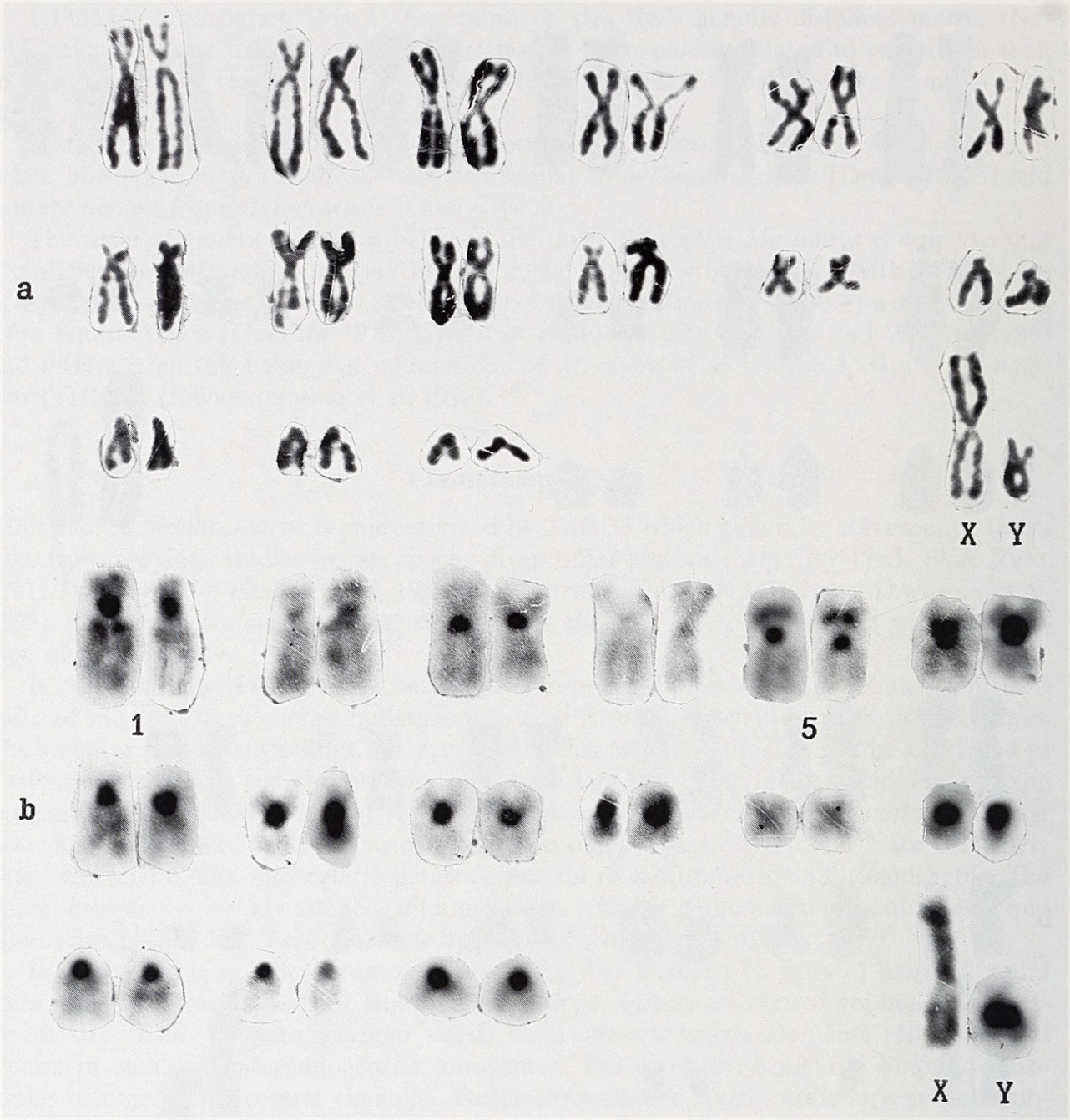

Fig. 3. Karyograms of *Mastomys awashensis* n. sp.: a: conventional staining by Giemsa; b: C-banding.

A second PCA was elaborated to examine discrimination between *Mastomys* n. sp. and *M. erythroleucus*. For this, we used only specimens from the Upper Awash Valley (Koka Lake area and Awash National Park). The first component accounts for 39.9% of the total variation, the second one accounts for more 13.1%. The scatter plot of the first two principal components (Fig. 5) shows *Mastomys* n. sp. and *M. erythroleucus* are clearly separated.

So, these analyses indicate unambiguously three *Mastomys* species to occur together in the Upper Awash Valley that are distinguished biometrically.

Description of the new species

Mastomys awashensis Lavrenchenko, Likhnova, and Baskevich, n. sp.

Mastomys sp. 2, Lavrenchenko et al. 1992: 90; Lavrenchenko and Baskevich 1996: 278.

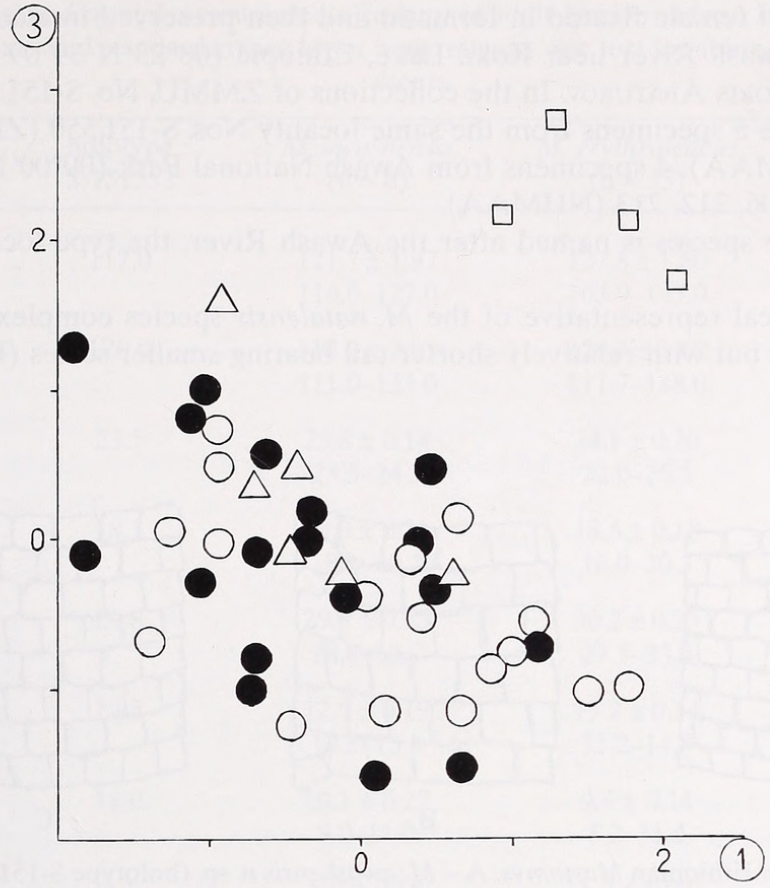

Fig. 4. Bivariate scatter plot of relative positions of specimens of the three *Mastomys* species from the Ethiopian Rift Valley in the projection of principal components I and III. *M. erythroleucus*: localities 2 (empty circles) and 6 (black circles); *M. natalensis*: locality 2 (squares); and *M. awashensis*: localities 1, 2 (triangles).

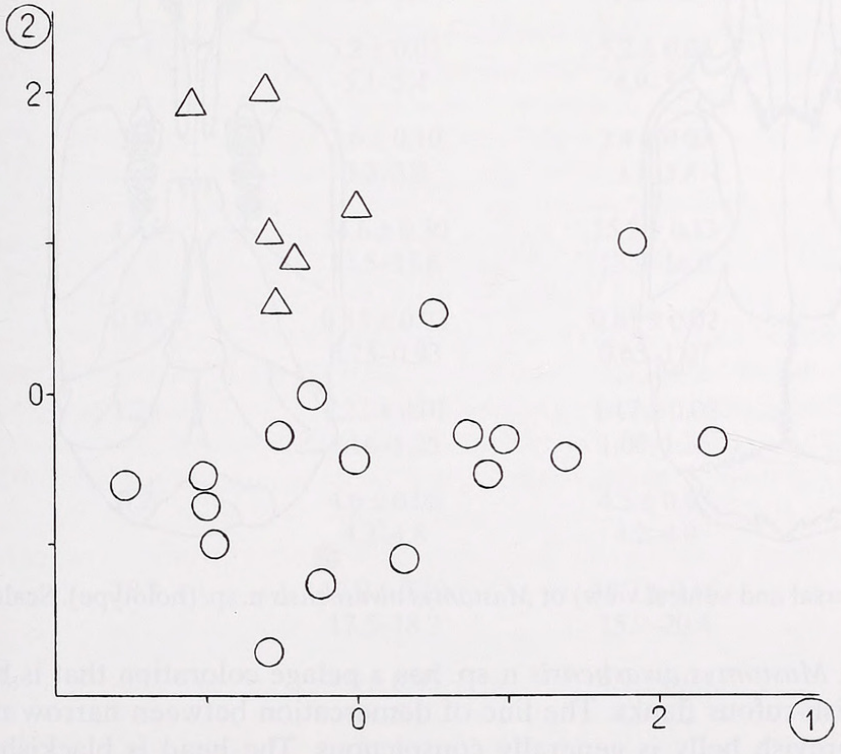

Fig. 5. Bivariate scatter plot of relative positions of specimens of two *Mastomys* species from the Upper Awash Valley in the projection of the first two principal components. See Fig. 4 for symbols.

Holotype: Adult female fixated in formalin and then preserved in alcohol collected at the bank of the Awash River near Koka Lake, Ethiopia (08°23′ N 39°09′ E) on the 15th May 1990 by Dr. Boris Abaturov. In the collections of ZMMU, No. S-151 552.

Paratypes: More 5 specimens from the same locality Nos. S-151 550 (ZMMU) and 480, 481, 482, 503 (NHMAA); 4 specimens from Awash National Park (09°00′ N 40°10′ E), collector's Nos. 205, 206, 212, 213 (NHMAA).

Etymology: The species is named after the Awash River, the type locality of the new taxon.

Diagnosis: Typical representative of the *M. natalensis* species complex, similar in size to *M. erythroleucus* but with relatively shorter tail bearing smaller scales (Fig. 6).

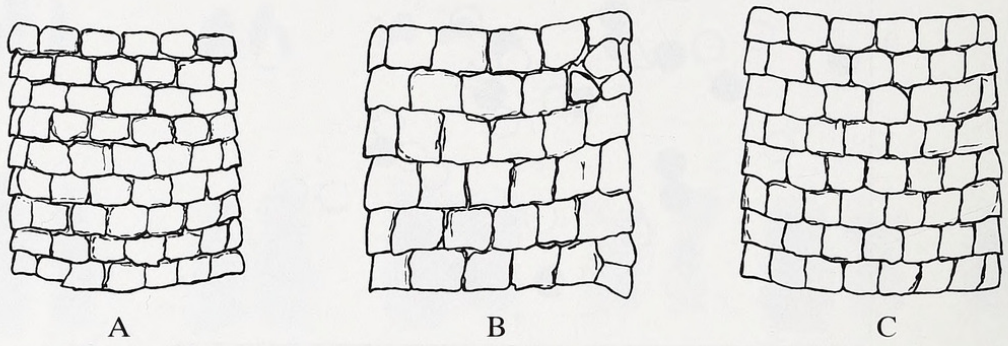

Fig. 6. Tail scales of Ethiopian *Mastomys*. A – *M. awashensis* n. sp. (holotype S-151 552, ZMMU); B – *M. erythroleucus* (S-151 555, ZMMU); C – *M. natalensis* (235, laboratory of mammal microevolution, Institute of Ecology and Evolution RAS). Scale bar = 1 mm.

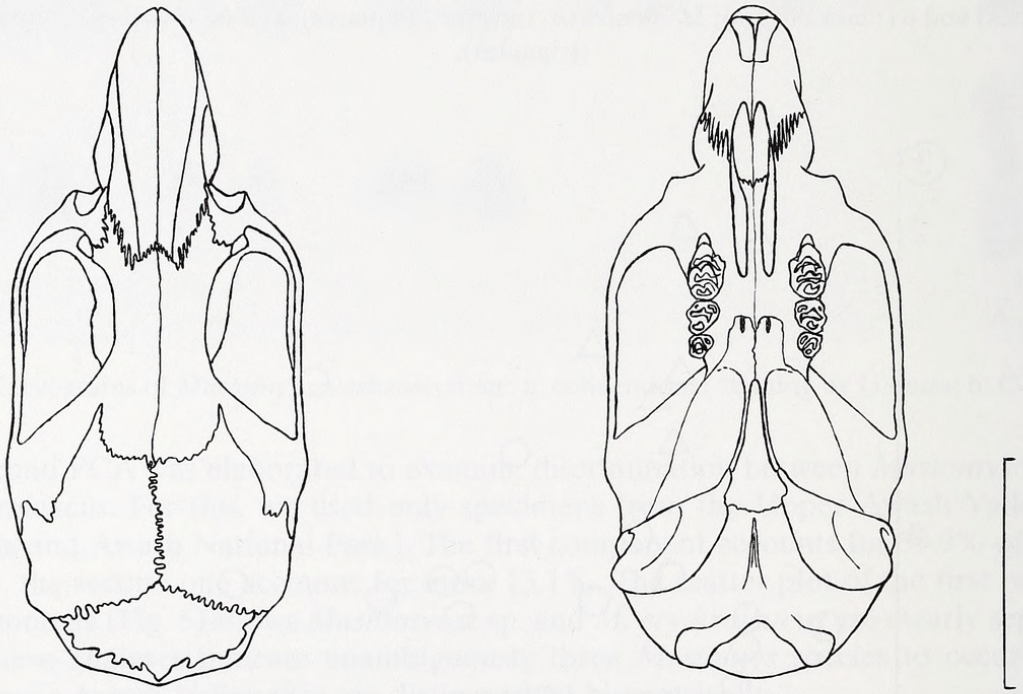

Fig. 7. Skull (dorsal and ventral view) of *Mastomys awashensis* n. sp. (holotype). Scale bar = 10 mm.

Description: *Mastomys awashensis* n. sp. has a pelage coloration that is blackish on the back, with greyish-rufous flanks. The line of demarcation between narrow rufous band on the flank and greyish belly is generally conspicuous. The head is blackish dorsally, with yellowish-rufous cheek: Dorsal side of the hands and feet is white, the claws are light. The skull (Fig. 7) with straight and strongly rounded dorsal edge of anterior margin of zygo-

Table 2. External and cranial measurements (in mm) of adult *Mastomys* from Ethiopian Rift Valley (upper lines:means and standard errors; lower lines: ranges). See text for abbreviations of measurements

Symbole	holotype S-151552	*M. awashensis* (n = 6)	*M. erythroleucus* (n = 35)	*M. natalensis* (n = 4)
L	117.0	121.7 ± 1.97 116.0–127.0	127.8 ± 1.80 103.9–145.0	132.3 ± 4.11 123.0–143.0
C	120.0	118.2 ± 2.01 111.0–123.0	129.3 ± 1.62 111.7–148.0	121.0 ± 4.51 114.0–134.0
Pl	23.5	23.8 ± 0.14 23.5–24.3	24.1 ± 0.20 22.0–26.5	23.9 ± 0.31 23.1–24.5
Au	18.1	19.0 ± 0.31 18.1–20.2	18.5 ± 0.18 16.0–20.3	19.1 ± 0.97 17.0–21.3
Cb	29.8	29.8 ± 0.25 28.8–30.7	30.2 ± 0.25 27.7–33.4	31.9 ± 0.39 30.8–32.7
LoNos	13.5	12.9 ± 0.19 12.2–13.5	13.2 ± 0.14 11.2–14.8	14.1 ± 0.19 13.7–14.4
LoFr	11.0	10.1 ± 0.27 9.0–11.0	9.8 ± 0.14 8.2–11.4	11.1 ± 0.10 10.8–11.3
LoPar	5.2	5.9 ± 0.18 5.2–6.3	5.7 ± 0.08 4.6–6.3	5.9 ± 0.20 5.3–6.2
LoFIn	8.3	7.9 ± 0.09 7.7–8.3	7.6 ± 0.12 6.0–8.7	7.3 ± 0.03 7.3–7.4
LoDia	8.8	8.8 ± 0.13 8.5–9.4	8.6 ± 0.09 7.6–9.8	9.7 ± 0.10 9.4–9.9
LoM^{1-3}	5.4	5.2 ± 0.05 5.1–5.4	5.2 ± 0.02 4.9–5.5	5.6 ± 0.04 5.5–5.7
LaNos	3.4	3.6 ± 0.10 3.2–3.9	3.4 ± 0.03 3.1–3.8	3.6 ± 0.04 3.4–3.6
LaZig	13.5	14.6 ± 0.30 13.5–15.6	15.2 ± 0.13 13.9–16.6	16.4 ± 0.10 16.2–16.6
Lars	0.90	0.85 ± 0.03 0.75–0.93	0.81 ± 0.02 0.65–1.07	1.00 ± 0.04 0.91–1.09
Laaz	1.25	1.22 ± 0.01 1.16–1.25	1.17 ± 0.02 1.00–1.35	1.50 ± 0.04 1.42–1.58
LaIor	4.2	4.6 ± 0.08 4.2–4.8	4.5 ± 0.03 4.2–4.8	4.6 ± 0.03 4.5–4.6
LoMd	18.2	17.9 ± 0.10 17.5–18.2	18.2 ± 0.16 15.9–20.4	20.2 ± 0.12 19.9–20.3
LoM_{1-3}	5.1	4.9 ± 0.05 4.8–5.1	4.9 ± 0.03 4.6–5.2	5.0 ± 0.07 4.9–5.2
LoM_3	1.30	1.22 + 0.03 1.08–1.30	1.19 + 0.01 1.05–1.34	1.40 + 0.05 1.33–1.55

matic plate, narrow mesopterygoid fossa, anterior palatine foramina extending to middle of M^1, palatine bone reaching no further forward than the middle of M^2. Tubercles t 1 and t 4 of the upper first molars are clearly compressed. Cusp t 4 of M^2 is large and lies more or less in line with the second lamina, t 3 of M^2 is reduced and lies in line with t 1 and t 5.

On average, the new species is smaller than *M. natalensis* from the Upper Awash Valley (Tab. 2). The differences are statistically significant for all skull measurements with the exception of LoPar, LaNos, LaIor and LoM_{1-3}. On the contrary, tail length is the only measurement discriminating *M. awashensis* from *M. erythroleucus* from the same area ($t = 2.77$, $P = 0.009$).

The new species differs from *M. erythroleucus* and *M. natalensis* both in its genital morphology and spermatozoal structure (Lavrenchenko and Baskevich 1996) and by fixed alleles at Ldh-B and Got-1 loci and also by Hbb pattern. The karyotype of *M. awashensis* (2 n = 32, NFa = 54) which is similar to that of *M. natalensis* demonstrates, nevertheless, a number of unique characteristics differing it from any known representative of the *M. natalensis* species complex.

Distribution: At present, according to available data, the new *Mastomys* species is confined to a small part of the Upper Awash Valley. All known specimens were captured at two sites: eastern bank of Koka Lake and Awash National Park. We failed to trap any *Mastomys* in the area along the Awash River northward from Awash National Park to Gewane area (10°05′ N 40°33′ E) during 1988–1995 field seasons. Most probably, this area is too arid for any representatives of the *M. natalensis* species complex. On the other hand, Dorst (1972) believes that three sympatric *Mastomys* species occur at the northern bank of Lake Abaya (Merab Abaya: 06°27′ N 37°48′ E). These species might be *M. erythroleucus*, *M. natalensis*, and *M. awashensis*, although we found only *M. erythroleucus* in the neighbouring area (Nechisar National Park: 05°53′ N 37°38′ E) in 1993.

Habitat: The new species inhabits Awash riverbank covered by natural vegetation (Acacia-Commiphora thornbush with high grass) and adjacent agricultural lands. Six other rodent species *Tatera robusta* (Cretzschmar, 1830), *Acomys* sp., *Arvicanthis dembeensis* (Ruppell, 1842), *Praomys fumatus*, *Mastomys erythroleucus*, and *M. natalensis* were captured at the same localities. *M. awashensis* appeared to be outdoor occupant only, whereas the two other Ethiopian *Mastomys* species were found both in natural habitats, agricultural lands, and in the buildings of human settlements.

Discussion

All three Ethiopian multimammate rats considered above belong to the *M. natalensis* species complex, a recently evolved lineage of *Mastomys* which is characterized by larger size of molars and labio-lingual compression of dental tubercles (Denys and Jaeger 1986). Peculiar characteristics of these species exhibit apparent lack of congruence between morphological, allozymic, and chromosomal data. Thus, *M. erythroleucus* and *M. natalensis* share a common genital morphology, differing from that of *M. awashensis* (Lavrenchenko and Baskevich 1996). On the other hand, *M. awashensis* is most closely related to *M. erythroleucus* according to allozymic and morphometric data. Conversely, *M. awashensis* is more similar to *M. natalensis* with respect to chromosomal characteristics (2 n, NFa) and the size of tail scales. This disparity supports our previous supposition about a "mosaic" pattern of evolution under diversification in the *M. natalensis* species complex (Lavrenchenko and Baskevich 1996).

Of three *Mastomys* species occurring in Ethiopia, two (*M. natalensis* and *M. erythroleucus*) are widely distributed throughout the most part of Western, Central, and Eastern Africa. The third one, *M. awashensis*, was found in a restricted area of the Upper Awash Valley. This distribution closely matches the distribution pattern of another

species, 68-chromosomal *Acomys* sp. (Sokolov et al. 1993). Yalden and Largen (1992), in their review of endemic mammals of Ethiopia, claimed that all indubious endemics of this country are rather strictly associated with open habitats at high altitude (19 species) or with remnant forests (9 species). It has been considered that Awash Valley and other Ethiopian dry lowlands are not the most likely habitats for the occurrence of endemic mammals (Yalden and Largen 1992). Our findings of *Mastomys awashensis* and *Acomys* sp. (2 n = 68) show that the Upper Awash Valley with its unique rodent fauna is an integral part of the Ethiopian region with high faunistic diversity and endemism.

The newly described *M. awashensis* must be classified as Vulnerable (VU), criterion D-2 (IUCN Red List Category) because of the small area of its occurrence, the agricultural development of this area, and the non-commensal life style. However, it is difficult to assess what conservation measures might be necessary for this new Ethiopian endemic species without gathering further information on its population levels and habitat requirements.

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Zusammenfassung

Systematik und Verbreitung von Mastomys (Muridae, Rodentia) in Äthiopien mit Beschreibung einer neuen Art

Es wurde die morphologische, allozymische und chromosomale Variation von drei äthiopischen *Mastomys*-Arten aus dem *M. natalensis*-Komplex untersucht. Eine neue Art *Mastomys awashensis* n. sp. wird beschrieben und verglichen mit den anderen beiden *M. erythroleucus* und *M. natalensis*. Diese sind auch in großen Teilen des westlichen, zentralen und östlichen Afrika weit verbreitet. *Mastomys awashensis* n. sp. ist hingegen endemisch im äthiopischen Rift-Tal und wurde dort nur von zwei Örtlichkeiten des oberen Awash-Tales bekannt. Diese neu beschriebene Art unterscheidet sich von den anderen beiden äthiopischen *Mastomys*-Arten durch fixierte Allele an den Loci Ldh-B und Got-1 sowie durch Hbb-Muster und einen relativ kürzeren Schwanz mit kleineren Schuppen. Weiterhin können die drei Arten mit gemeinsamem Vorkommen im mittleren Rift-Tal biometrisch nach multivariater Analyse von Körper- und Schädelmaßen unterschieden werden. Der Karyotyp von *M. awashensis* (2 n = 32, NFa = 54), der dem von *M. natalensis* ähnelt, zeigt dennoch eine Anzahl von eigenen Charakteristika, die ihn von allen anderen bekannten Repräsentanten des *M. natalensis*-Komplexes unterscheidet. Die mit verschiedenen Methoden erhobenen Befunde lassen eine „mosaikartige" Evolution mit divergenter Radiation in dieser Artengruppe vermuten.

References

Britton-Davidian, J.; Catalan, J; Granjon, L.; Duplantier, J.-M. (1995): Chromosomal phylogeny and evolution in the genus *Mastomys* (Mammalia, Rodentia). J. Mammalogy **76**, 248–262.

Davis, B. J. (1964): Disc-electrophoresis. II. Method and application to human serum proteins. Ann. N. Y. Acad. Sci. **121**, 404–408.

Denys, G.; Jaeger, J. J. (1986): A biostratigraphic problem: the case of the East African Plio-Pleistocene rodent faunas. Modern Geology **10**, 215–233.

Dorst, J. (1972): Notes sur quelques rongeurs observes en Ethiopie. Mammalia **36**, 182–192.

Duplantier, J. M.; Britton-Davidian, J.; Granjon, L. (1990 a): Chromosomal characterization of three species of the genus *Mastomys* in Senegal. Z. zool. Syst. Evolut.-forsch. **28**, 289–298.

Duplantier, J. M.; Granjon, L.; Mathieu, E.; Bonhomme, F. (1990 b): Structures genetiques comparees de trois especes de rongeurs africains du genre *Mastomys* au Senegal. Genetica **81**, 179–192.

Ford, C. E.; Hamerton, J. L. (1956): A colchicine hypotonic citrate, squash sequence for mammalian chromosomes. Stain Technology **31**, 247–251.

Gordon, D. H. (1978): Distribution of sibling species of the *Praomys* (*Mastomys*) *natalensis* group in Rhodesia (Mammalia: Rodentia). J. Zool. (London) **186**, 397–401.

Gordon, D. H.; Watson, C. B. R. (1986): Identification of cryptic species of rodents (*Mastomys*, *Aethomys*, *Saccostomys*) in the Kruger National Park. S. Afr. J. Zool. **21**, 95–99.

Granjon, L; Duplantier, J. M.; Catalan, J.; Britton-Davidian, J.; Bronner, G. N. (1996): Conspecificity of *Mastomys natalensis* (Rodentia: Muridae) from Senegal and South Africa: Evidence from experimental crosses, karyology and biometry. Mammalia **60**, 697–706.

Green, C. A.; Gordon, D. H.; Lions, N. F. (1978): Biological species in *Praomys* (*Mastomys*) *natalensis* (Smith), a rodent carrier of Lassa virus and bubonic plague in Africa. Amer. J. Trop. Med, Hyg. **27**, 627–629.

Green, C. A.; Keogh, H.; Gordon, D. H.; Pinto, M.; Hartwig, E. K. (1980): The distribution, identification and naming of the *Mastomys natalensis* species complex in southern Africa (Rodentia: Muridae). J. Zool. (London) **192**, 17–23.

Harris, H.; Hopkinson, D. A. (1978): Handbook of enzyme electrophoresis in human genetics. Amsterdam: North-Holland Publ. Comp.: N. Y., Amer. Elsevier Publ. Comp., Inc.

Hubert, B.; Meylan, A.; Petter, F.; Poulet, A.; Tranier, M. (1983): Different species in genus *Mastomys* from Western, Central and Southern Africa (Rodentia, Muridae). Ann. Mus. Roy. Afr. Centr. **237**, 143–148.

Kozlovsky, A. I. (1974): The possibility of determination of karyotypes of small mammals after death. Zool. Zh. **53**, 1871–1872 (in Russ.).

Kral, B. (1971): Non-Robertsonian variability of karyotype in rats of the subgenus *Mastomys*. Zool. Listy **20**, 39–49.

Lavrenchenko, L. A.; Baskevich, M. I. (1996): Variation of generative system structure in some species of the genus *Mastomys* Thomas, 1915 (Rodentia, Muridae). Mammalia **60**, 277–288.

Lavrenchenko, L. A.; Likhnova, O. P.; Orlov, V. N. (1992): Hemoglobin patterns: a possible implication in systematics of multimammate rats *Mastomys* (Muridae, Rodentia). Zool. Zh. **71**, 85–93. (in Russ.).

Leirs, H.; Heyrman, C.; Verhagen, R.; Verheyen, W. (1991): Lack of geographic variation in Tanzanian *Mastomys*: zoogeographic consequences. Belgian J. Zoology **122** (suppl. 1), 27.

Matthey, R. (1965): Etudes de cytogenetique sur des Muridae africains appartenant aux genres *Arvicanthis*, *Praomys*, *Acomys* et *Mastomys* (Rodentia). Mammalia **29**, 228–249.

Matthey, R. (1966): Gytogenetique et taxonomie des rats appartenant au sous-genre *Mastomys* Thomas (Rodentia – Muridae). Mammalia **30**, 105–119.

Musser, G. G.; Carleton, M. D. (1993): Subfamily Murinae. In: Mammal species of the World. A taxonomic and geographic reference. 2 nd ed. Ed. by D. E. Wilson and D. M. Reeder. Washington, London: Smithsonian Inst. Press. Pp. 564–675.

Nei, M. (1972): Genetic distance between populations. Amer. Nat. **106**, 283–292.

Nie, H. N.; Hull, C. H.; Jenkins, J. G.; Steinbrenner, K.; Bent, D. H. (1975): SPSS. Statistical Package for the Social Sciences. 2 nd ed. New York: McGraw-Hill.

Peacock, A. C.; Bunfing, S. L.; Queen, K. G. (1965): Serum protein electrophoresis in acrilamide gel: patterns from normal human subject. Science **147**, 1451–1453.

Robbins, C. B.; van der Straeten, E. (1989): Comments on the systematics of *Mastomys* Thomas 1915 with the description of a new African species. Senckenbergiana biol. **69**, 1–14.

Selander, R. K.; Smith, M. H.; Yang, S. Y.; Johnson, W. E.; Gentry, J. B. (1971): Biochemical polymorphism and systematics in the genus *Peromyscus*. 1. Variation in the old-feld mouse (*Peromyscus polinotus*). Stud. Genet. 6. Univ. Texas Publ. **7103**, 49–90.

Sokolov, V. E.; Orlov, V. N.; Baskevich, M. I.; Afework Bekele; Assefa Mebrate (1993): A karyological study of the spiny mouse *Acomys* Geoffroy 1838 (Rodentia Muridae) along the Ethiopian Rift Valley. Tropical Zoology **6**, 227–235.

Sumner, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Exp. Cell. Res. **75**, 304–306.

Swofford, D. L.; Selander, R. K. (1981): BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. **72**, 281–283.

Tranier, M. (1974): Parente des *Mastomys* du Maroc et du Senegal (Rongeurs, Murides). Mammalia **38**, 558–560.

Yalden, D. W.; Largen, M. J. (1992): The endemic mammals of Ethiopia. Mammal. Rev. **22**, 115–150.

Yalden, D. W.; Largen, M. J.; Kock, D. (1976): Catalogue of the mammals of Ethiopia. 2. Insectivora and Rodentia. Monitore Zoologico Italiano (nuova serie) Suppl. **8**, 1–118.

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