

# The *Lophuromys flavopunctatus* THOMAS 1888 s.l. species complex : a craniometric study, with the description and genetic characterization of two new species (Rodentia - Muridae - Africa)

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## Abstract

We revised the taxonomy of the East African *Lophuromys flavopunctatus* species complex using craniometric data of nearly 3000 specimens grouped in 49 operational taxonomical units (OTU's) covering the whole of its geographical distribution.

Our study demonstrates that the differences in age and sex composition of OTU's are of no consequence for the branching of the obtained phenetic trees. This observation permitted us to screen the whole of the *L. flavopunctatus* s.l. species complex, to evaluate the validity of the already known taxa and to describe two species new to science.

Our study complements this traditional morphological approach with mitochondrial nucleotide sequences to characterize the two new species and several OTU's.

**Keywords:** Rodentia, East Africa, *Lophuromys*, taxonomy, craniometry, cytochrome b, genetics.

## Résumé

La taxinomie du 'complexe d'espèces' *Lophuromys flavopunctatus* a été réévalué en nous basant sur les données craniométriques d'environ 3000 crânes groupés en 49 unités taxinomiques opérationnelles (UTO's).

Notre étude a démontré que des différences de composition des UTO's, (âge et sexe) n'influencent pas la structure des arbres phénétiques (UPGMA) obtenus. Cette observation nous a permis d'évaluer la validité systématique des différents taxa et de décrire deux nouvelles espèces.

Nous avons employé des séquences mitochondriales afin de mieux caractériser nos deux nouvelles espèces et plusieurs UTO's.

**Mots-clés:** Rodentia, Afrique de l'Est, *Lophuromys*, taxinomie, craniométrie, cytochrome b, génétique.

## INTRODUCTION

The "speckled brush furred" African rats have been grouped in the *Lophuromys flavopunctatus* THOMAS 1888 s.l. species complex by VERHEYEN *et al.* (1996). Representatives of this complex are widely distributed from North-Eastern Angola through Southern Congo, Northern Zambia, Malawi, Northern Mozambique, Tanzania, Burundi, Ruanda, Eastern

Congo, Northern Congo, Uganda, Southern Kenya and Ethiopia. The distributional range of the Ethiopian populations is separated from that of the rest of the species complex by dry lowlands.

*L. flavopunctatus* s.l. prefers moist, marshy and grassy biotopes. Vegetation composition, structure and density seem not to be too important. In these optimal biotopes the "speckled brush furred" rats are generally by far the most dominant rodent. The actual geographical distribution of *Lophuromys flavopunctatus* s.l. seems to be solely determined by rainfall (density and pattern) and not by altitude, temperature or biotope structure (DIETERLEN, 1976).

Over the whole distributional range of this species group, fifteen taxa have been described based on the considerable variation in pelage colouration and external measurements. For a full listing of these taxa, their type-localities, geographical co-ordinates we refer to Appendix 1.1 and fig. 1. We do not include *Neanthomys giaquinto* TOSCHI 1946 from Addis Ababa, which description was solely based upon an artifact: the absence of a tail in the type specimen (TOSCHI, 1963). The skull measurements of the type-specimens, as measured by us, are listed in Appendix 1.2.

In their general taxonomic review of the Murids of the world, MUSSER & CARLETON (1993) consider that most of these taxa fall into synonymy with *flavopunctatus* THOMAS 1888 adding however that "... the appreciable character variation among samples probably reflects more than one species" (ib., p.605).

A recent study on the Ethiopian *Lophuromys flavopunctatus* species complex (LAVRENCHENKO *et al.*, 1998) demonstrated that *Lophuromys chrysopus* OSGOOD 1936 and *Lophuromys brevicaudus* OSGOOD 1936 are clearly distinct Ethiopian endemic species. *Lophuromys melanonyx* PETER 1972, a morphometrically well defined endemic species, was at that time intentionally not included in that analysis. For Southern Ethiopia, we mentioned the presence of what we provisionally considered to be representatives of *Lophuromys flavopunctatus brunneus* and even a fourth taxon classified tentatively as *Lophuromys* species D but possibly identical to typical *Lophuromys flavopunctatus* s.s.

The present study intends to complete the taxonomical revision of the *Lophuromys flavopunctatus* species group over its entire geographical range except for the "speckled brush

furred" rats from Mt Ruwenzori (our OTU 14) to be described elsewhere.

Our study illustrates the practical problems that stand between the many biological species concepts and the practical considerations of taxonomists that are faced with the task to describe taxa based on specimen collections. As in this study, the most often practiced approach is the description of rodent species based on morphometrical data, ideally taken from a sufficient large number of specimens. This approach enables us to deal with the disparities and inadequacies that characterize some of the early taxonomical descriptions.

The poor quality of many of the type specimens led us to implement multivariate cranio-metrical analyses for this revision. Because the cranium is often the only more or less usable part of a type specimen, we selected a number of reliable measurements which will allow us to compare between even severely damaged skulls. In view of the well-documented skull variability (growth and sexual dimorphism), we had to give a statistical dimension to our approach by including sufficiently large samples (OTU's = Operational Taxonomical Unit's) of measurable skulls, that cover the whole geographical range of the species group (in total 49 OTU's were used). An essential consequence of our approach is that we will try, through a number of specific canonical analyses and by subsequent plotting of the type-skulls, to discuss the status of the described taxa and to identify, for some of those taxa, OTU's which can be considered to represent these taxa.

We complement this traditional approach by the genetic characterization of a species new to science with partial mitochondrial cyt b sequences. These molecular data cannot substantiate the claim that the morphologically described species are biologically valid. However, whenever the studied OTU's possess fixed genetic differences, these nucleotide sequences can be used as an additional diagnostic feature to characterize newly described taxa. To test the hypothesis that observed differences between the studied taxa are meaningful, we first analyzed the nucleotide variation among specimens of some conspecific populations for which sufficient samples were available.

## MATERIAL AND METHODS

### The specimens

As the results of many fieldtrips in central Africa, realized between 1965 and 1995 by the Research group on African Rodents (RUCA, Department of Biology, University of Antwerp, Belgium), we established an extensive specimen collection. All specimens were prepared for study at the University of Antwerp before they were deposited at the Royal Africa Museum (Tervuren, Belgium). This study is largely based on these collections, but when necessary, our study material was completed with skulls from other collections. Our results are based on information from about 3150 skulls, of which 2.700 were suited for our analyses

In Appendix 2 we have grouped the specimens examined and measured per OTU. For each OTU the number of specimens, classified by sex and age, is provided. For the description of

the acronyms, that identify the musea and institutions where these specimens are curated, we refer to VERHEYEN *et al.* (1996). Appendix 3 gives an alphabetical list of the collecting localities, followed by their geographical co-ordinates; between brackets is the OTU number into which the locality is included. Fig.2 describes the geographical distribution of the OTU's studied.

### Craniometry

All skulls are grouped into age-classes using tooth eruption and tooth wear patterns as described in VERHEYEN *et al.* (1996). Also in the present study, the observed cusp structure of the upper cheekteeth and more especially in M<sup>1</sup> is very variable, which implies that the age-classifying method, with its well established theoretical and practical limitations, can at best be used to give a general impression.

The present study uses the same cranial and external measurements and the same acronyms as described in VERHEYEN *et al.* (1996). We draw special attention to p.246 where we discuss how we selected the used cranial measurements. The measurements were taken with callipers with digital reading graduated to hundreds of millimetres, but were recorded with a precision of 0,05 mm.

To facilitate the interpretation of our results, we supplied a full description of our measurements with drawings of a *Lophuromys flavopunctatus* skull (see appendices 4.1. and 4.2. in VERHEYEN *et al.* 1996). Table 1 (App. 4) briefly recapitulates the cranial measurements used here. Basic statistics, Student-t tests, One-way Analysis of Variance, Student-Newsman-Keuls a posteriori test (SOKAL & ROHLF, 1969), Multiple Discriminant or Canonical Analysis were performed on a PC with the statistical package STATISTICA 5.5 from 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. The metrical data-sets of the operational units used in this study (see Appendix 2) are not fully published but can be obtained through e-mail (hulsel@ruca.ua.ac.be).

In order to clarify the multi-group graphs, we do not show the individual scores, but draw the 95% equiprobable ellipses. In certain cases we prefer to construct a tree diagram, based on the Mahalanobis squared distances between the centroids, using the Unweighted Pair Group Arithmetic Average method (SNEATH & SOKAL, 1973). This accounts for all the relevant axes in the canonical hyperspace. Sometimes missing data are replaced by group means.

### DNA methods

The twenty four specimens that were used for this part of our study were collected during various expeditions in East Africa in 1984 (Ruanda), 1985 (D. R. Congo), 1989 (Tanzania), 1991 (Kenya), 1994 (Tanzania) (see listing of specimens in table 5). Tissues were stored at -80°C (or in 80% ethanol at 4°C). Samples from specimens from Ethiopia were supplied by Corti and Bekele.

DNA was isolated from ethanol-preserved muscle or liver tissues by standard proteinase K digestion, followed by phenol-chloroform extraction and ethanol precipitation (SAMBROOK *et al.*, 1989) or by the Chelex method (WALSH *et al.*, 1991). We amplified and sequenced a 402 bp long segment of the cyt b gene (from position 14139 to 14540 on the mitochondrial DNA sequence of *Mus musculus* (BIBB *et al.*, 1981). The cyt b primers are L13724 [5'-cgaagcttgatgaaaaaccatcgttg-3'] and H14139 [5'-aaactgcagccctcagaatgatattgtcctca-3'] (KOCHER *et al.*, 1989) and the PCR reaction was done using the protocols given in KOCHER *et al.* (1989). The samples were sequenced with the H14139-primer using a standard CycleSequencing protocol (Amersham Pharmacia Biotech), following the manufacturer's protocol, 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. Sexual dimorphism and growth in the skull of *Lophuromys flavopunctatus*

Because previous studies considered that sexual dimorphism in *Lophuromys flavopunctatus* and *Lophuromys sikapusi* skulls is insignificant, it has become customary to lump sexes in the OTU's that were used in our previous studies (VERHEYEN *et al.*, 1996, 1997, 2000, LAVRENCHENKO, *et al.*, 1998). Since the present data set is the first to contain certain OTU's with a sufficiently large number of skulls, we will be able to test statistically whether or not lumping data from both sexes affects the outcome of our canonical analyses.

The biggest OTU available for this purpose comprises 377 complete skulls (209M-168F) and was collected in and around Tshibati (see App. 2) mostly by our colleagues U. RAHM and F. DIETERLEN. We split the data of this OTU by sex and age classes and calculated the basic statistics of the skull measurements and of the in the field collected external measurements (Appendix 4 and Table 2).

Sexual differences seem to be nearly absent not only for the skull measurements but also for the external measurements. The only exceptions are in age class 3, where sexual dimorphism is highly significant for "choanae breadth" (M18) and "distance between coronoid and angular process in the mandibula" (M24). Consequently both measures were excluded in our further canonical analyses. We also note that in age-class 3 male animals are about 10% heavier than females.

Our data also suggest that the growth of the skull of a specimen, once it has fully erupted teeth, will remain rather limited. In both sexes, most measures show a small but steady growth from class 1 up to class 3. As expected, the molars and bullae do not increase in size whereas the upper incisor caliber (M21) shows a small size increase.

To evaluate if and how strong the sex and age of specimens

influence the outcome of canonical analyses (graph. 1.1) we first compare the six subgroups distinguished in table 2. It is reassuring to observe that there is a huge overlap between sexes and also between age-groups; only root 1 is influenced by growth but in a very moderate way.

To investigate how results of multivariate analyses are influenced by OTU's with different age-sex composition, and whether the results can be used for taxonomical purposes we made a canonical analysis between three geographical clearly different OTU's (Uluguru, Mutura, Tshibati) in which we could also distinguish between age-sex subgroups. The resulting phenetic tree (graph. 1.2) shows clearly that differences in sex- and (or) age-composition of the compared OTU's have no influence on the outcome of our analysis and demonstrates that subtle shape differences in skull configuration, independent from sex and age, are effectively reflected by canonical graphs and phenetic trees.

Graph.1.3 goes a step further and adds the species dimension into the analysis by including OTU 4 (Kisangani RB) and OTU 37 (*L. brevicaudus*). Again we observe that the resulting phenetic tree is not influenced by sex or age composition. It is therefore safe to conclude that we can compare OTU's of different age and sex composition and still obtain results that we can use in a taxonomical context.

### 2. The taxonomical status of the type specimens of the *L. flavopunctatus* species-complex

Since the previous study on the Ethiopian representatives of the *Lophuromys flavopunctatus* species complex (LAVRENCHENKO *et al.* 1998) we have completed our craniometrical data-base to address some unresolved problems. One of our primary concerns is the allocation of the Ethiopian *Lophuromys* type-specimens to one of our OTU's, in order to allow a clear-cut taxonomical revision of the whole *flavopunctatus*-group.

However, first we have to establish that none of our Ethiopian OTU's belong to the *Lophuromys sikapusi*-species group represented in Eastern Africa by *Lophuromys ansorgei*. Graph. 2.1 depicts the results of a canonical analysis that involves an OTU representing *L. ansorgei* with the different OTU's we were able to compile of Ethiopian *Lophuromys*. The graph convincingly shows that the two species groups are clearly separated from each other and that the skull of the controversial type specimen of *L. major* (see App.1.1 and fig.1) pertains certainly to the *sikapusi* species group and is not related to any of the Ethiopian *Lophuromys* we studied.

Graph. 2.2 shows that OTU 37, OTU 38+39, and OTU 35 are directly identified by the type skulls as belonging to respectively the species *L. brevicaudus*, *L. chrysopus* and *L. melanonyx*. The type skulls of *L. brunneus* and *L. simensis* plot well within OTU 36, suggesting that *simensis* is possibly a synonym of *brunneus*. The type skulls of *L. flavopunctatus* and *L. zaphiri* fit within OTU 34, implying that the latter is synonymous with the former. Additional analyses (forward and backward) with other OTU's as outgroups confirm these conclusions.

In graph. 3.1 we introduced some non-Ethiopian OTU's

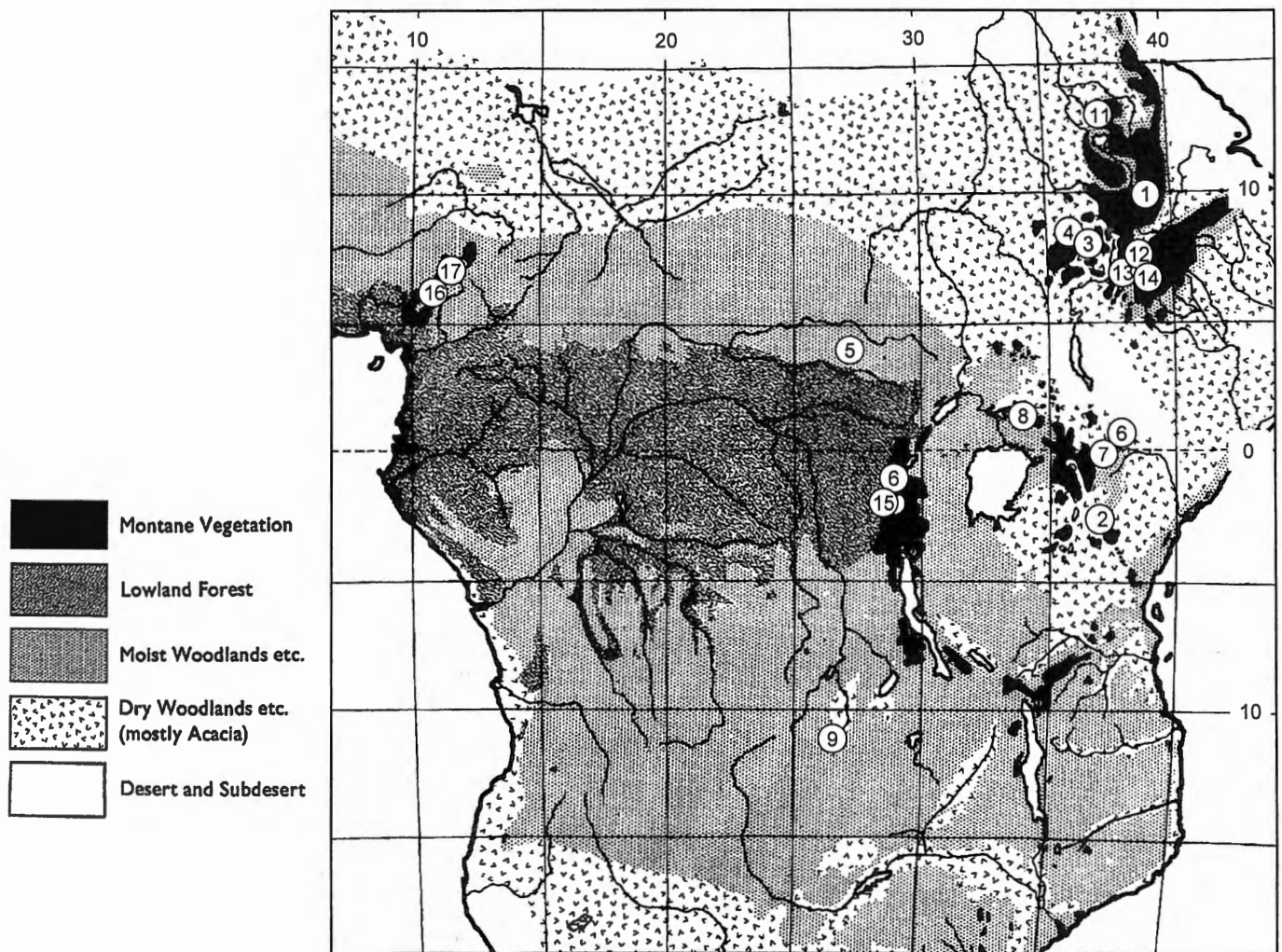


Fig. 1. Map showing the geographical situation of the type localities of the different taxa of the *Lophuromys flavopunctatus* species complex. For the co-ordinates and approximate altitudes we refer to Appendix 1.1. Based on Map B (p. XIII) of HALL & MOREAU (1970).

1. *flavopunctatus* THOMAS 1888
2. *aquilus* TRUE 1892
3. *zaphiri* THOMAS 1906
4. *brunneus* THOMAS 1906
5. *major* THOMAS *et al.* 1907
6. *laticeps* THOMAS *et al.* 1907

7. *zena* DOLLMAN 1909
8. *rubecula* DOLLMAN 1909
9. *rita* DOLLMAN 1910
10. *margarettae* HELLER 1912
11. *simensis* OSGOOD 1936
12. *brevicaudus* OSGOOD 1936

13. *chrysopus* OSGOOD 1936
14. *melanonyx* PETTER 1972
15. *cinereus* DIETERLEN *et al.* 1974
16. *eisentrauti* DIETERLEN 1978
17. *dieterleni* VERHEYEN *et al.* 1997

(OTU 6: Tshibati; OTU 20: Solai; OTU 26: Usambara E.) covering as much as possible the geographical variation of the taxonomically recognized non-Ethiopian taxa next to some relevant Ethiopian taxa such as *L. brevipaudus* (OTU 37) and *L. chrysopus* (OTU 38+39). We decided not to include the OTU's 34, 35 and 36 (respectively typical for *flavopunctatus*, *melanonyx* and *brunneus*) because we found that they tend to lump the non-Ethiopian OTU's, reducing seriously the usefulness of the graphs for the intended plotting of the non-Ethiopian type-specimens.

The critical type-specimen of *L. aquilus* TRUE 1892 (type locality: Mt Kilimanjaro) situates itself right in the centre of graph.3.1 but clearly outside OTU 37 (*brevicaudus*). On the other hand it might be concordant with OTU's 38 and 39

(*chrysopus*) as well as with the other OTU's. However, when we consider also the Kilimanjaro (Mweka) specimens, which are possibly topo-typical for *aquilus*, we have to conclude that *aquilus* identifies with one of the east African OTU's and not with OTU 38+39 (*chrysopus*). We will go further into this matter in the conclusions of this paper.

Most of the other east African type-specimens (*laticeps*, *zena*, *rita*, *margarettae*) fall within the east African OTU's (6, 20, 26) and are probably to be considered synonymous with *aquilus*. The only exception is *rubecula*, described in 1909 by DOLLMAN from Mt Elgon, which plots within *chrysopus* (OTU 38+39).

As to the two type-specimens from northern Cameroon (*eisentrauti*, *dieterleni*) they plot outside the east African and

Ethiopian OTU's and should probably be considered belonging to a different species group. Unfortunately, we do not possess the necessary skull series to investigate this issue further.

In graph. 3.2 we try to go into more detail by making a canonical analysis between Kenyan populations (OTU 19: Cherangani Hills; OTU 20: Solai; OTU 21: Aberdare Range; OTU 22: Mt Kenya) and the Ethiopian *chrysopus* (OTU 38: Harena; OTU 39: Beletta). In this graph it becomes clear that the Aberdare Range and Mt Kenya series are characteristic for *zena* DOLLMAN 1909, whereas the Cherangani Hills population and Solai are concordant with *margarettae* HELLER 1912. It becomes also apparent that *rubecula* DOLLMAN 1909 (Mt Elgon) has to be allocated to the *chrysopus* species group and the same applies probably to *eisentrauti* DIETERLEN 1979 and to *dieterleni* VERHEYEN *et al.* 1997.

In graphs 4.1 and 4.2 we have tried to allocate the more or less damaged skulls of certain type specimens to some geographically selected OTU's by making specific canonical analyses. Graph.4.1 allows us not only to show that the type-specimen of *rita* DOLLMAN 1910 fits well, as expected, within OTU 11 (Congo S.) and *laticeps* THOMAS *et al.* 1907 within OTU 8 (Mutura). More importantly the crucial type skull of *aquilus* TRUE 1892 fits nicely within the Usambara E population (OTU 26), which is geographically the closest to the Mount Kilimanjaro from which we have unfortunately no adequate topo-typical series. Finally, we show in graph.4.2 that very probably *cinereus* is to be considered a synonym of *L. laticeps* confirming what was already suspected by DIETERLEN (1987).

Summarized, we can safely conclude that the five Ethiopian OTU's, identified on craniological and other morphological characters, represent respectively the following taxa: OTU 34: *L. flavopunctatus*, OTU 35: *L. melanonyx*, OTU 36: *L. brunneus*, OTU 37: *L. brevicaudus*, OTU 38+39: *L. chrysopus*. We have not found any specimens related to the *L. sikapusi* species group in the Ethiopian *Lophuromys* collection we were able to study. Moreover *L. zaphiri* is in our opinion synonymous with *L. flavopunctatus* and *L. simensis* is possibly also a synonym of *L. brunneus*. We did not attempt to determine the geographical distribution of each of the recognized taxa since we do not possess enough reliable data for the whole of Ethiopia.

Concerning the non-Ethiopian taxa of the studied species group we have demonstrated that the studied populations can be identified with the following taxa: OTU 26: *aquilus*, OTU 8: *laticeps*, OTU 11: *rita*, OTU 21-22: *zena*, OTU 19-20: *margarettae*. We also have shown that the severely damaged *cinereus* type skull falls clearly within OTU 8 and is thus to be considered synonymous with *laticeps*. The *rubecula* type skull from Elgonyi (Mt Elgon) is however situated consistently within the OTU's (38+39) typical for Ethiopian *chrysopus*; however, the other Mt Elgon specimens (OTU 18) that we could measure seem to be referable to *margarettae* (see following chapter).

Finally, we mention that both type skulls of *dieterleni* and *eisentrauti* appear to be near *chrysopus* (OTU 38+39). We are convinced that both belong to a clearly differentiated strain of *chrysopus* but for the moment we are not able to go

deeper into this for lack of adequate series from N. Cameroon.

### 3. Craniometrical variation within the *L. flavopunctatus* s.l. species complex

We choose to tackle this problem by making canonical analyses including as many OTU's as possible distributed over the entire geographical range of the species complex and then visualizing the results by tree diagrams based upon the Mahalanobis squared distances between the obtained centroids (UPGA). The usefulness of this approach is limited by the size of the OTU's (numbers of adult and complete skulls) versus the number of cranial variables (measurements) taken per skull. Indeed, the number of observations per OTU has to be preferably greater than the number of variables (i.e. measurements) per skull, otherwise the matrix of within variation of this OTU tends to be singular.

Keeping in mind our results concerning the importance of sexual dimorphism and skull-growth we eliminated from the start the measurements M18 (CHOB) and M24 (PCPA).

Each OTU used in our analyses comprises only fully adult and complete skulls and contains a sufficient number of specimens to make statistically valid analyses. When necessary we maximalised OTU's either by eliminating some measures responsible for excluding some otherwise complete skulls or by replacing missing data by the mean of the group.

Fig. 2 shows schematically the geographic distribution of the OTU's over the Eastern and Central African region. By far most of these OTU's are homogenous as to the geographical origin of the included specimens. Only for Congo S (OTU 11) we had to group specimens from rather wide-spread or varied geographical origin to obtain statistically valid series. In total we compiled for this study 46 OTU's out of which 33 group twenty or more complete adult skulls and another 5 with at least 16 usable adult skulls; the 8 remaining OTU's are composed of about 10 skulls. All our OTU's were screened for measuring errors and recording oddities.

In a first approach (graph.5.1) we include only the 33 "major" OTU's which contain a minimum of 20 skulls each. In a second step we add another 5 OTU's grouping a minimum of 16 skulls each (graph.5.2). Finally, the 8 "minor" OTU's with about 10 skulls each (graph.5.3) are included in the analysis. Graph.5.1 is based upon the morphometrical comparison of 33 OTU's, using 20 skull measurements (see table 1). We also identified, hoping to facilitate the interpretation of the resulting phenetic tree, the OTU's that we found to be representative for the 5 major east African type-populations (see 2). Our first observation is the clear morphometrical separation between the Ethiopian species *melanonyx*, *brevicaudus*, *flavopunctatus* from all the other OTU's. This also applies to *chrysopus*; however, *chrysopus* W. and E. form a well defined clade not only with the Ethiopian species *brunneus*, but also with the "zena" populations of Mt Kenya and the Aberdare Range. The sister clade of the *chrysopus-zena-brunneus* group is formed by the totality of all the other non-Ethiopian OTU's that we examined. We note that both clades are linked at a rather high linkage distance of 100.

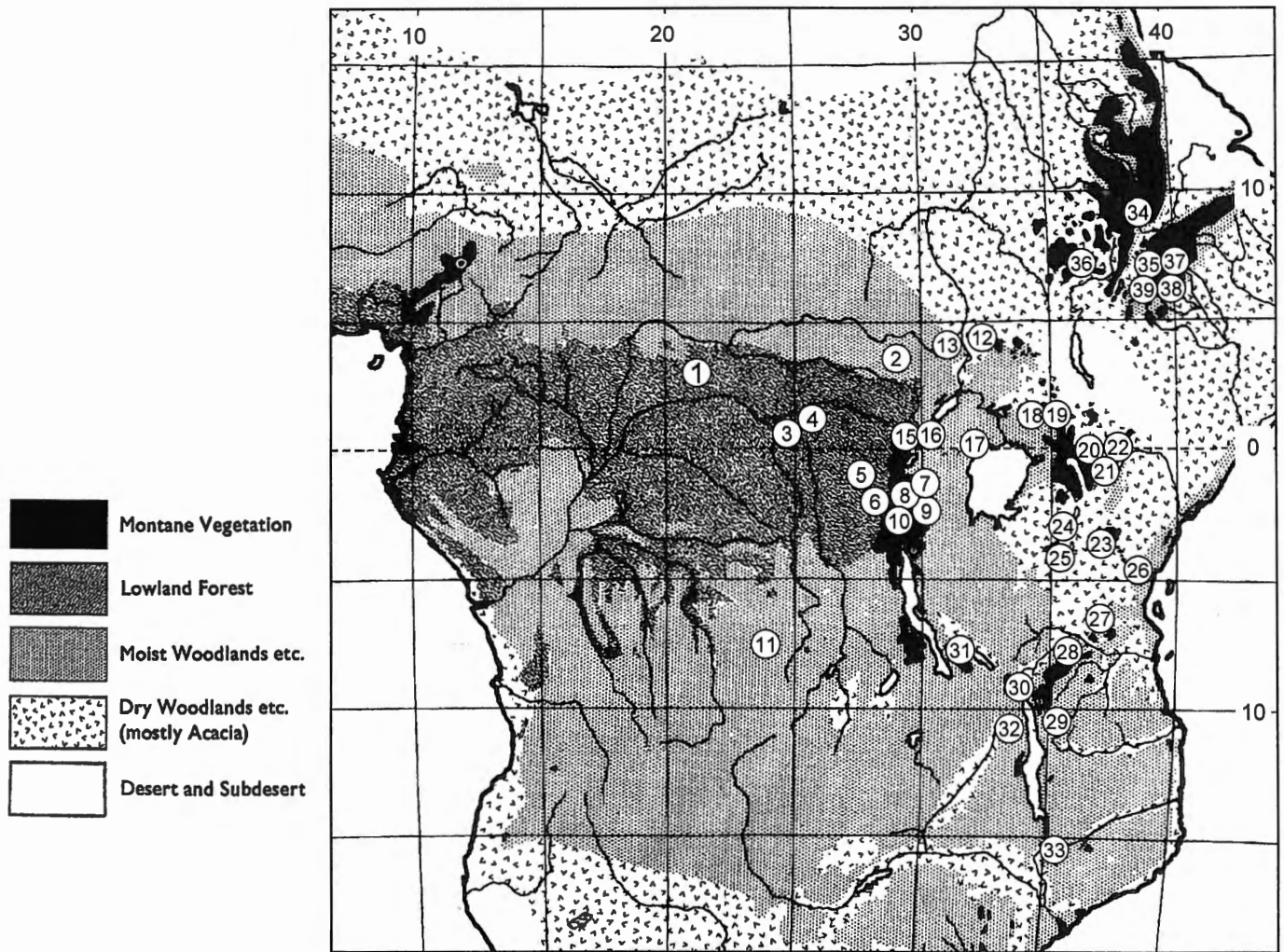


Fig. 2. The geographical distribution of the OTU's of the *L. flavopunctatus* species complex as used in this study. For the exact composition of the individual OTU's, we refer to Appendix 2 and for the co-ordinates of the collecting localities, see Appendix 3. Based on Map B (p. XIII) of HALL & MOREAU (1970).

1	Congo NW.	10	Uwinka (Nyungwe Forest)	20	Solai	30	Rungwe Mt
2	Congo NE.	11	Congo S.	21	Aberdare Range	31	Ufipa Plateau
3	Kisangani LB	12	Gilo (Imatong Mts)	21.1	Gatamaiyu	32	Nyika Plateau
4	Kisangani RB	13	Iwatoka	21.2	Aberdare Range (BMNH)	33	Zomba
5	Irangi	14	Ruwenzori Mt (p.m.)	22	Kenya Mt	34	<i>L. flavopunctatus</i> s.s.
6	Tshibati	15	Rutshuru	22.1	Kenya Mt (BMNH)	35	<i>L. melanonyx</i>
6.1	Kahuzi Mt	16	Kigesi	23	Meru Mt	36	<i>L. brunneus</i>
7	Virunga Volcanoes	17	Uganda	23.1	Kilimanjaro Mt (Mweka)	37	<i>L. brevicaudus</i>
8	Mutura	17.1	Bugala Isl.	24	Ngorongoro Rim	38	<i>L. chrysopus</i> E.
8.1	Kinigi	18	Elgon Mt	25	Hanang Mt	39	<i>L. chrysopus</i> W.
8.2	Kidaho	19	Cherangani Hills	26	Usambara E. Range		
9	Butare	19.1	Kaptagat	27	Uluguru Range		
9.1	Ruanda E.			28	Mufindi		
				29	Peramiho		

Within the non-Ethiopian clade of graph. 5.1, two branches are quite distinct from all the others: first OTU 4 (Kisangani RB) and OTU 5 (Irangi), secondly OTU 23 (Mt Meru). The other non-Ethiopian OTU's group into geographically related clades such as (Mutura - Uwinka - Kinigi - Butare - Kidaho - Ruanda E), (Tshibati - Rutshuru - Virunga Volc. -

Kigesi), (Congo S - Rungwe Mt - Nyika Plat.), (Cherangani Hills - Solai - Kenya Mt), (Ngorongoro Rim - Gilo) and (Usambara E. - Uluguru). However, in some cases OTU's, such as Kisangani LB and Ufipa Plateau, cluster in a rather unexpected way. We also found that the introduction or exclusion of one or more critical non-Ethiopian OTU's into the

analysis often resulted in a reshuffling of low-level branching between the observed geographical clades, but it never affected the clear branching and identity of OTU 23 (Meru Mt.) or OTU 4 (Kisangani RB) and OTU 5 (Irangi).

In graph.5.2 we introduced 38 OTU's, containing each at least 16 adult complete skulls and using 16 cranial measurements. The results of graph.5.1 and 5.2 are identical: the 5 newly introduced populations Entebbe (OTU 17), Hanang Mt (OTU 25), Peramiho (OTU 29), Congo NW (OTU 1), Aberdare Range (OTU 21.2) do not differ significantly from the other non-Ethiopian OTU's while some OTU's, e.g. Hanang (OTU 25) and Aberdare Range (OTU 21.2) fit geographically rather well with the already existing groups. In general however, we see a rather important exchange of OTU's between the geographical clades we could discern in graph.5.1 and thus a breaking down of their geographical identity.

Graph. 5.3 represents a tree-diagram for 46 OTU's based on a backward canonical analysis of 11 cranial measurements and on 8 new OTU's with each a minimum of 10 adult skulls. This analysis not only confirms the results of graphs 5.1 and 5.2, but also suggests that not one of the 8 newly introduced OTU's is clearly differentiated from the other non-Ethiopian populations. We note however, that the geographic clades in the non-Ethiopian OTU's that we clearly could discern in graph. 5.1, tend to dissolve in graph. 5.2 to disappear almost completely in graph. 5.3. This progressive loss of information can be explained by dwindling numbers of specimens per OTU, which entails a restriction of the number of used measures.

Summarized, we conclude that we can identify craniometrically from the examined non-Ethiopian populations at least 3 samples, viz. OTU 4 (Kisangani RB), OTU 5 (Irangi) and OTU 23 (Meru Mt), which can be considered for formal taxonomic recognition.

#### 4. Genetic results

The observed intraspecific genetic variation in the studied cyt b fragment is significantly lower than the differentiation observed at the interspecific level (appendix 4, tables 5 and 6). Among eight specimens from three populations of *zema* we detect only 10 variable sites, 7 of which are substitutions at the third codon position, 3 are substitutions at the first codon position (data not shown). The number of parsimony informative sites in the context of the seven other studied OTU's is reduced to 6 sites. Both measures of variability are low in comparison with the differentiation observed among the other OTU's, including representatives of the taxa *flavopunctatus*, *laticeps*, *aquilus*, *rita*, *margarettae* and the OTU's 4 and 24 that are discussed further.

Among the 402 bp long cyt b sequences from *flavopunctatus*, *laticeps*, OTU 4 (Kisangani Right Bank), *aquilus*, *zema*, *margarettae*, *aquilus*, OTU 23 (Meru Mt), *rita*, *margarettae* and *zema* we observe 54 parsimony informative sites, 14 at the first codon position, one at the second codon position and 39 at the third codon position (appendix 4, table 5).

The observed nucleotide changes result in 12 amino acid substitutions, all of which (except one leucine-isoleucine

change in OTU 4 – Kisangani RB) are differences between taxa or OTU's (data not shown). The amount of nucleotide substitutions observed ranges between 2.3 and 8.1 %. In all cases, the sequences of (putative) conspecifics are considerably more similar than sequences of different OTU's (appendix 4, tables 5 and 6).

The OTU's and taxa represented by more than one partial cyt b sequence share a typical set of informative sites. The fact that little variation is observed among the eight *zema* specimens indicates that the observed differences, even when based upon a single specimen, are likely to be significant, and diagnostically reliable differences.

#### 5. Description of *Lophuromys dudui* n.sp.

##### Holotype

RUCA D1739; adult female; alc. specimen; skull complete; collected by DUDU AKAIBE (26 March 1986) in Masako (00.36 N - 25.13 E; alt. 440 m) in the rainforest of the Tshoporiver; collecting number D1739.

##### Paratypes

10 specimens from the same locality as the type-specimen and collected by DUDU Akaibe between 12 December 1985 and 23 August 1986.

RUCA D1170 (ad.male; skull + alc.spec.; coll.nr D1170)  
 RUCA D1290 (ad.male; skull + alc.spec.; coll.nr D1290)  
 RUCA D1315 (ad.male; skull + alc.spec.; coll.nr D1315)  
 RUCA D1332 (ad.male; skull + alc.spec.; coll.nr D1332)  
 RUCA D1649 (ad.male; skull + alc.spec.; coll.nr D1649)  
 RUCA D1734 (ad.female; skull + alc.spec.; coll.nr D1734)  
 RUCA D1771 (ad.female; skull + alc.spec.; coll.nr D1771)  
 RUCA D1902 (ad.female; skull + alc.spec.; coll.nr D1902)  
 RUCA D2322 (ad.female; skull + alc.spec.; coll.nr D2322)  
 RUCA D2974 (ad.female; skull + alc.spec.; coll.nr D2974)

For the craniometrical data of the type and paratypes we refer to App.1.3.

##### Type locality

The holotype and the paratypes were collected in the Masako forest (in primary as well as old secondary forest).

##### Etymology

We dedicate this new species to our colleague and friend Prof. Dr. DUDU AKAIBE in appreciation of his continuous efforts to promote scientific research on small mammals in extremely difficult circumstances.

##### Diagnosis

*L. dudui* is a new species of "speckled and short-tailed brush-furred rat" that belongs to the so called *Lophuromys flavopunctatus* species complex. Consequently it is clearly differentiated cranially and dentally from 1° the *Lophuromys nudicaudus-huttereri* species complex 2° the small *L. rahmi* endemic to the mountainous region of Kivu (Congo) 3° the *sikapusi-ansorgei-angolensis-roseveari* species complex. Within the *flavopunctatus* species complex, it can easily be characterized a.o., by its (1) smallish skull, (2) short maxillary and mandibular tooththrow, (3) short ears and (4) short hind-

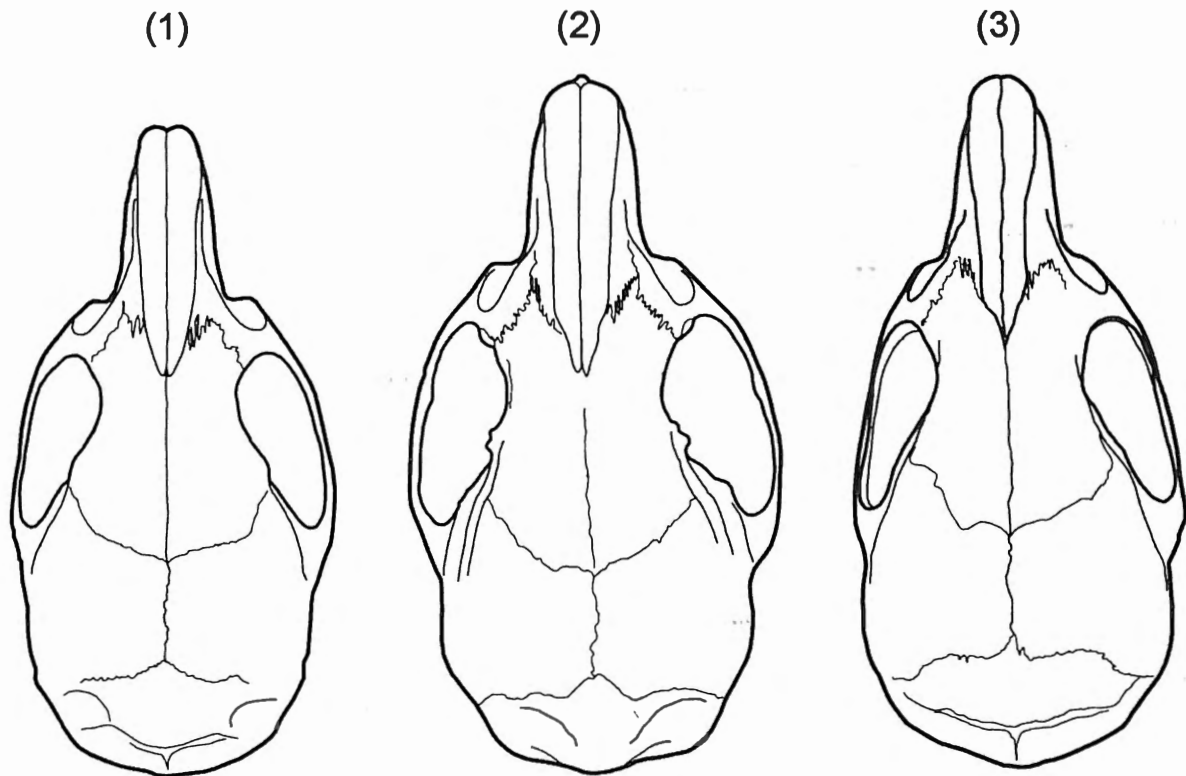


Fig. 3. Schematic representation of the dorsal views of representative skulls for (1) *Lophuromys dudui* (type: D1739), (2) *laticeps* (KMMA30366) and (3) *L. verhageni* (RUCA14327).

foot. For full details : see table 3 in App.4, graphs 6 and 8. For the genetic characterization see table 5 and 6 in App. 4

#### Discussion of the morphological characters (table 3, fig. 3)

It is impossible to include in this chapter a description of the external characters such as the colouration of the pelage, the feet, ears etc... Indeed, the type-specimens, fixed in formalin and then stored and transported for a long period in inadequate containers, have taken a more or less rusty tinge.

In table 3 we have included statistics of the external measurements of our new taxon, but we stress that these data have to be used with caution. Indeed, these field measurements were taken by different research groups using slightly different measuring techniques. Nevertheless we can conclude that *L. dudui* is on the overall clearly smaller when compared with *laticeps* (Mutura: OTU 8): from 5% (HB) to 7,5% (TL) to 10% (HF) to 20% (EL) smaller.

The morphology of the skull (fig.4) situates this new taxon within the *L. flavopunctatus* species complex, but when compared with representative skulls of a topo-typical population of *laticeps* (OTU 8) we can characterize our new taxon in the following way:

- (1) smaller, more slender skull with a more delicate rostrum;
- (2) less pronounced supraorbital ridges and less prominent notches;
- (3) smaller upper molars and relatively wider palate.

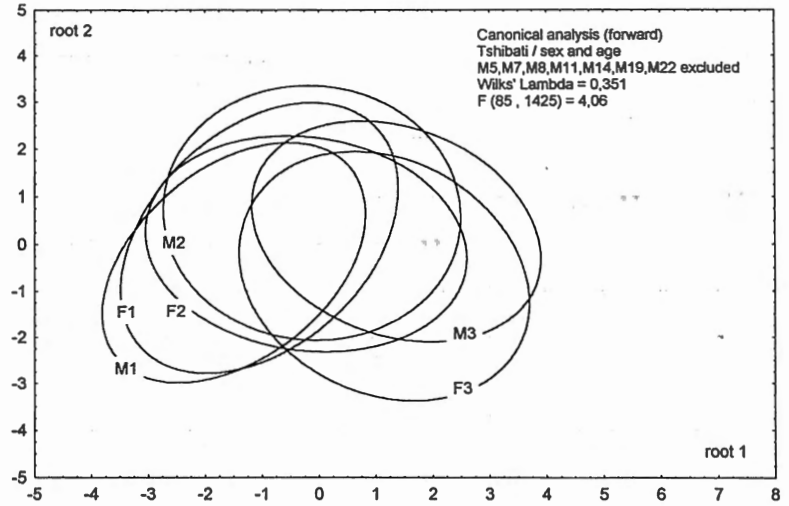
#### Univariate analysis (table 3)

The basic statistics show the variation coefficients to be far below 10% except for the "choanae breadth" (nr 18) which is a rather unreliable measure. When comparing the basic data of the skull-measurements of *dudui* to our standard population of *laticeps* (OTU 8: Mutura) we notice that the skull of *dudui* is about 5 to 10% smaller for length as well as breadth and height measures (with a maximum of 20% for DINC: depth of the upper incisor = M21). Only for measures of the skull basis, represented here by M10 (PALA), M18 (CHOB) and in a lesser degree by M12 (UPDA), we find that both taxa have about the same size.

The comparison between *dudui* and OTU 5 (Irangi) reveals that, although both are rather close in our multivariable analyses (graphs 5.1-5.2-5.3), they differ rather importantly in the univariate approach (table 3). Indeed, we see that in 9 out of the 24 cranial measures (M3, M4, M5, M6, M7, M10, M13, M14, M24) there is statistically no significant difference between both OTU's but that 9 out of the remaining 15 measurements are statistically highly different (M1, M8, M9, M11, M15, M16, M20, M21, M23). Summarizing, we can describe the skull of OTU 5 (Irangi) to be on the overall metrically closer to *dudui* than to our standard population of *laticeps* (OTU 8: Mutura) meaning that its skull is clearly smaller than the latter. However, for certain measures it is markedly less different (M1, M8, M9, M11, M16, M17, M19, M20, M21) from OTU 8 (Mutura). Finally, we see that Irangi (OTU 5) is well differentiated from *dudui* by two

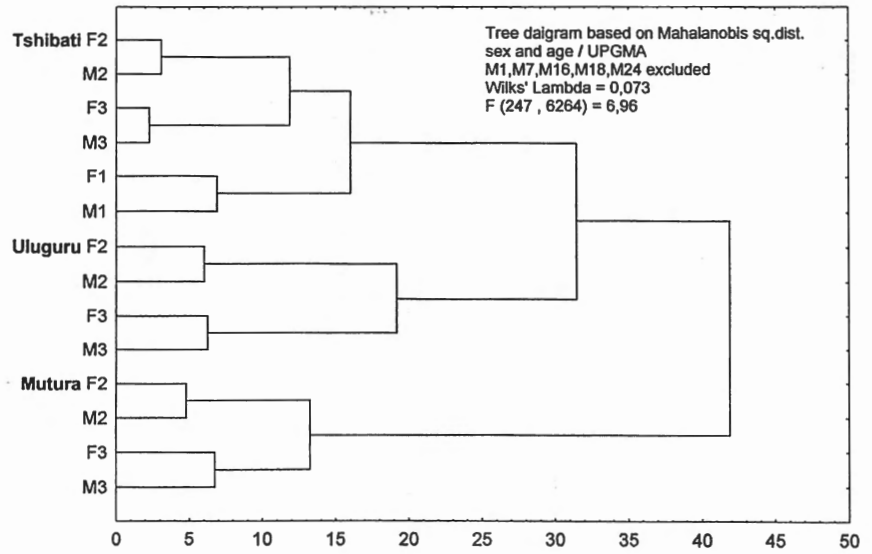


Graph. 1.1.  
Graphical representation of a canonical analysis of the six subgroups of OTU 6 (Tshibati) as we recognized in table 2.



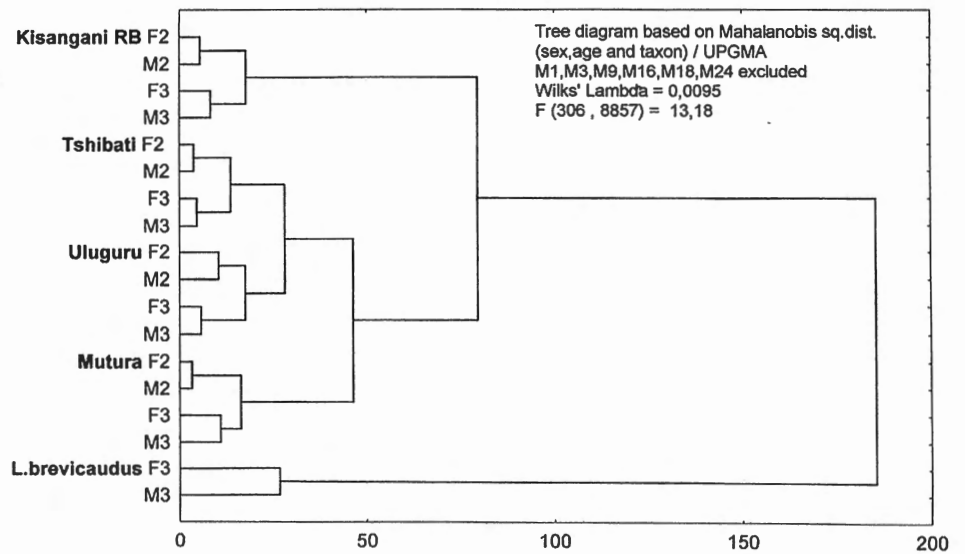
Graph.1.1

Graph. 1.2.  
Phenetic tree based on Mahalanobis squared distances between the age-sex subgroups of three geographically different OTU's of taxonomically not different populations of "speckled" *Lophuromys*.



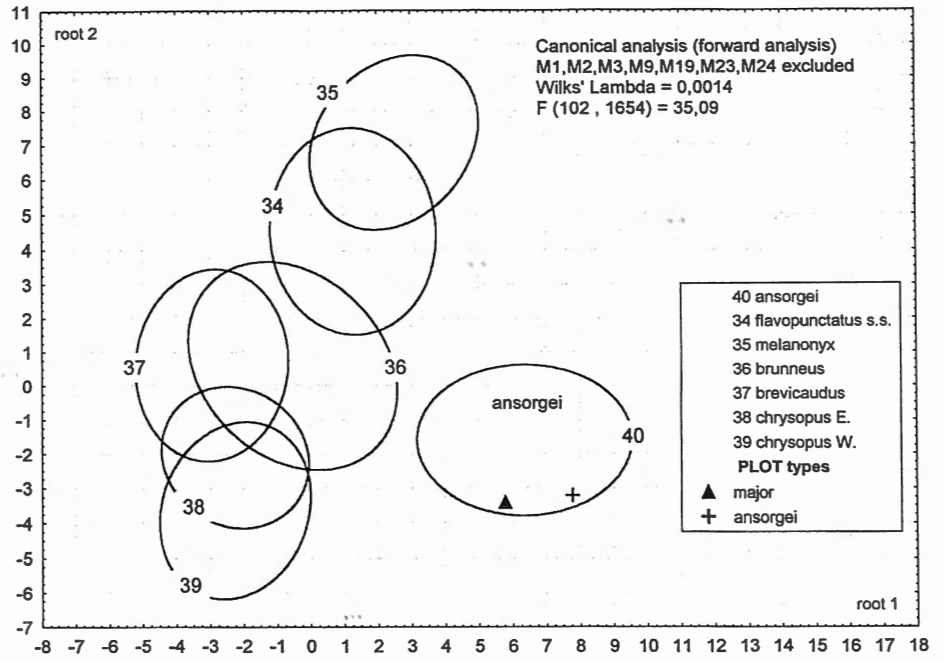
Graph.1.2

Graph. 1.3.  
Phenetic tree based on Mahalanobis squared distances between age-sex subgroups of three geographically distant OTU's of the same taxon and two taxonomically different populations of "speckled" *Lophuromys*.



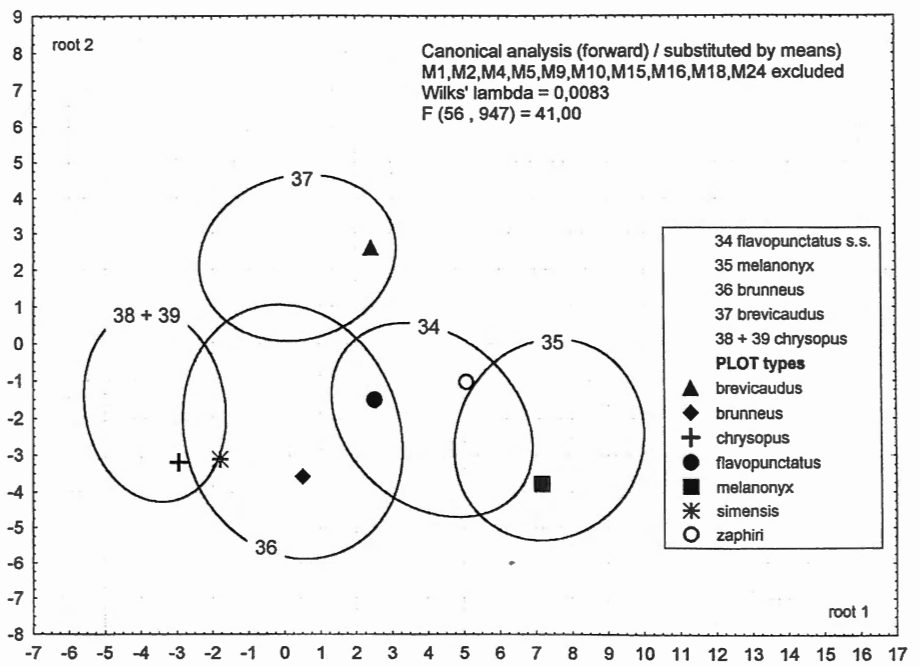
Graph.1.3

Graph. 2.1.  
Graphic representation of a forward canonical analysis performed on the "speckled" Ethiopian *Lophuromys* OTU's (34, 35, 36, 37, 38, 39) compared with a representative of the *L. sikapusi* species - complex (OTU 40).

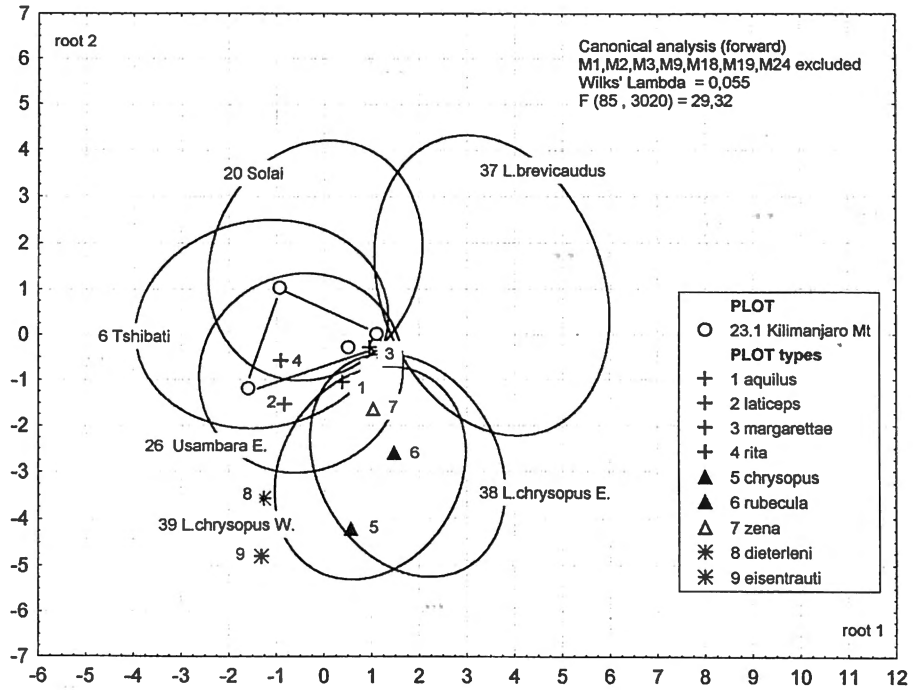


Graph.2.1

Graph. 2.2.  
Graphic representation of a forward canonical analysis of five Ethiopian "speckled" *Lophuromys* OTU's (34, 35, 36, 37, 38, 39) providing the background to allocate by plotting the Ethiopian types of the species-group.

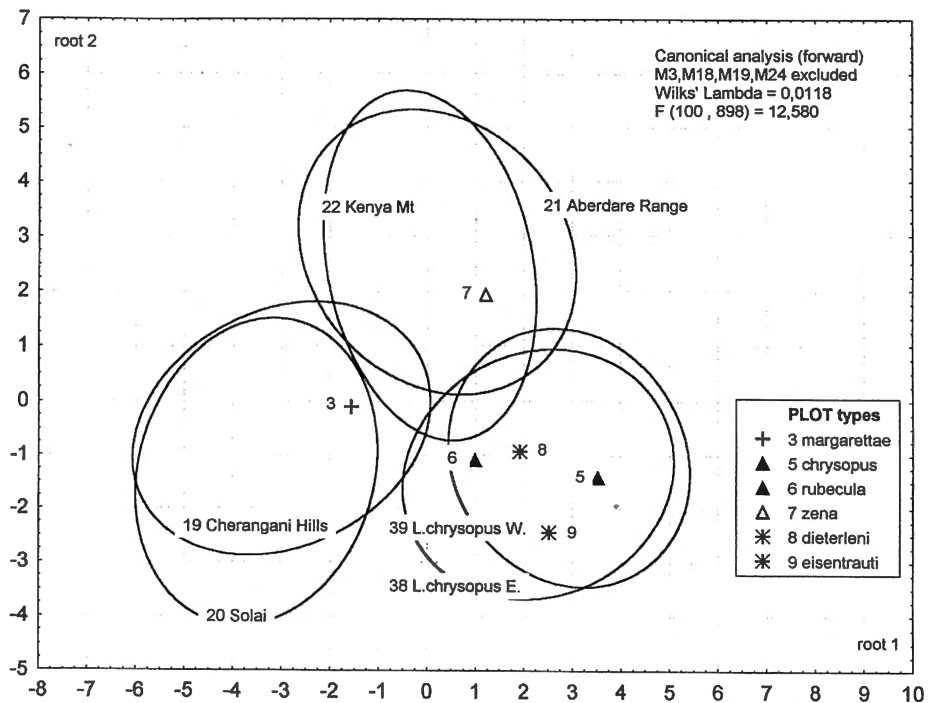


Graph.2.2

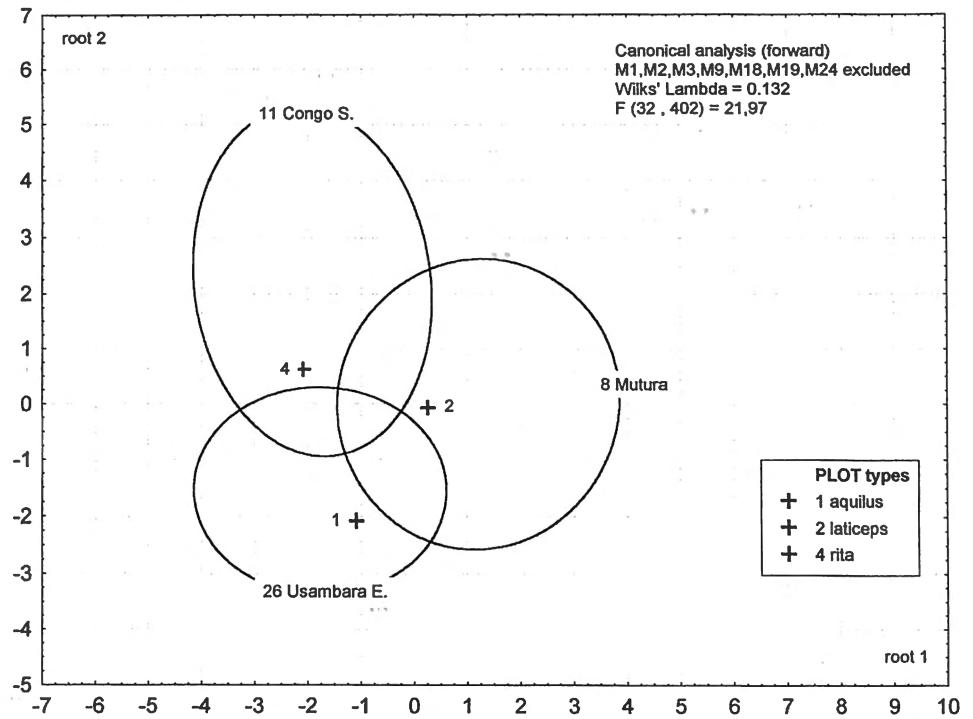


Graph. 3.1 and 3.2. Canonical analyses providing the necessary background to situate by plotting most of the non-Ethiopian type-specimens of the *L. flavopunctatus* species group (see text for discussion).

Graph.3.1

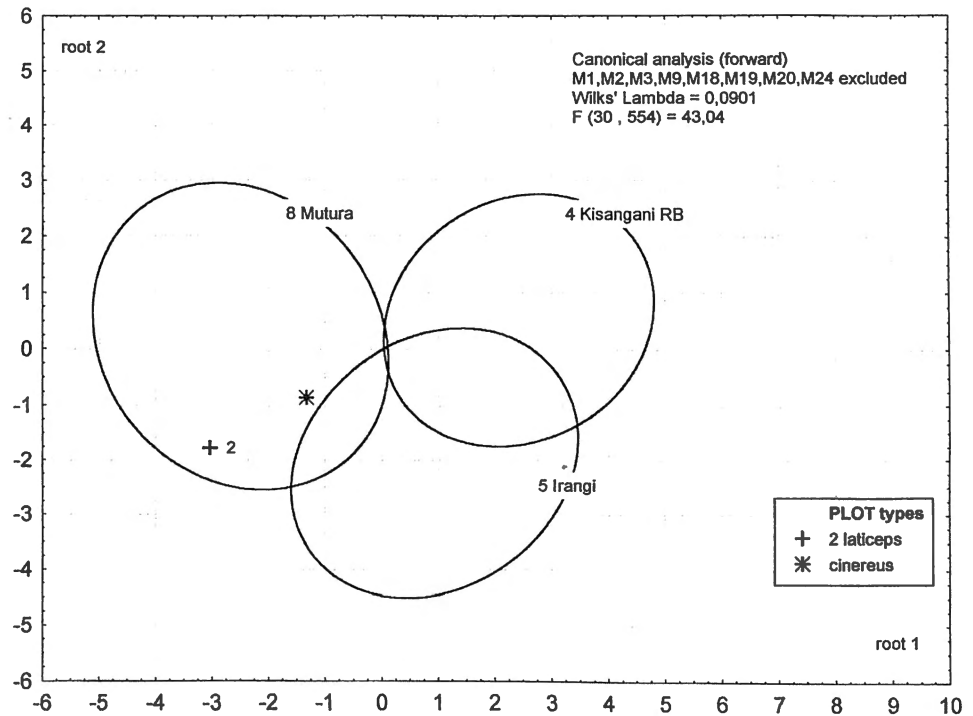


Graph.3.2



Graph.4.1

Graph. 4.1 and 4.2.  
 Canonical analyses attempting to link by plotting some of the non-Ethiopian types to some of our OTU's (see text).



Graph.4.2

measures (M15 and M23) representing the rostral width indicating that the average skull of OTU 5 (Irangi) is rather close to *dudui* but with a significantly more slender rostrum.

#### Discriminant analysis (graphs 6 and 7)

For diagnostic reasons we performed through forward analysis a discriminant function between our new taxon *dudui* (OTU 4: Kisangani RB) and the population of Mutura (OTU 8) representing the taxon *laticeps*. The results represented in graph 6 indicate that 100% of the individual skulls can be correctly classified by the obtained discriminant function using 15 out of the 24 available measurements. We note also that the most important discriminating measures are: M12 (UPDA), M7 (DIA2), M21 (DINC), M11 (UPTE).

In graph 7 we demonstrate further that *dudui* is also easily differentiated craniometrically from OTU 5 (Irangi) and that both populations can be identified 100% correctly through a discriminant function using 14 out of the 24 available measurements, the most important discriminating measures being M21 (DINC), M12 (UPDA), M13 (M1BR), M15 (BNAS).

#### Multiple discriminant analysis (graph 8)

We performed a canonical analysis by comparing the population of *dudui* (OTU 4: Kisangani RB) with 1° the Mutura (OTU 8) series which is probably topotypical for *laticeps* and which represents the east African taxa 2° the Irangi-population (OTU 5) and 3° the Mt Meru population (OTU 23) representing the new east African taxon that we will describe next.

We see that in this graph *dudui* is not only clearly differentiated from topotypical *laticeps* (OTU 8) but also from the Mt Meru-population (OTU 23). As to OTU 5 (Irangi) it coincides with *dudui* slightly overlapping with OTU 8 and OTU 23. However, the results of the same analysis, but comparing roots 2 versus 3 show that Irangi identifies closely with *dudui*. Finally, plotting of the specimens of OTU 2 (Congo NE) demonstrates that *dudui* is probably present in the whole of the forested areas north-east of Kisangani.

#### Genetic characterization (appendix 4, tables 5, 6)

All OTU's and taxa represented by more than one partial cyt b sequence share a typical set of informative sites. Therefore, it is not surprising that the comparison of the partial cyt b sequences of the two specimens representing *dudui* with sequences of relevant described taxa and OTU's from the same region show the utility of molecular markers to identify this new taxon.

The observation that only little variation exists among the eight *zena* specimens indicates that the differences for *dudui*, even when based upon only two specimens, are likely to be significant, and diagnostically reliable differences

Interestingly, these molecular data suggest that *dudui* is clearly distinct (average p distance = 0.054) from *flavopunctatus*, but also differs significantly from *aquilus* and *laticeps* (average p-distances are respectively 0.063 and 0.032). The implications of these data for the phylogenetic relationships between *dudui* and other *Lophuromys* taxa will

be the subject of a separate study using more and other nucleotide sequences.

#### Additional information

Through some additional canonical comparisons including surrounding OTU's (o.a. 1, 3, 7, 11, 15) we acquired the certainty that the populations living in the mountainous rift region and on the left bank of the Congo river are distinctly different from *dudui*. By plotting we found also evidence that our new taxon is present in the northeastern region of Congo (OTU 2) as far as the Garamba-Blukwa-Djugu-region.

Furthermore, plotting of individual skulls (KMMA 38.734, 738, 739, 770) allowed us to allocate a small series of Visiki (00.23 N - 29.12 E. 1100 m alt) to *dudui* whereas all the measured skulls originating from localities on the western flank of the rift mountains seem to belong to *laticeps*, from which *dudui* is significantly genetically differentiated (7.8% uncorrected sequence divergence). On the other hand the series of Irangi (OTU 5) (alt 850 m) which can be considered to be more or less representative for the population of the southeastern lowland rainforest of Congo separates itself as a rather well defined population (graph 8).

For the moment we consider *dudui* to be sufficiently craniometrically and genetically different from other OTU's and described taxa to be allocated the status of species whereas the Irangi population is probably a local form (subspecies) of *dudui*. However, it remains always possible that new data (e.g. caryology or additional genetic analyses) might change the taxonomic status of our new form.

#### 6. Description of *Lophuromys verhageni* n.sp.

##### Holotype

KMMA 96-037-M-3848; adult female; alc.specimen; skull complete; collected by Ron VERHAGEN (9 March 1996) on Mount Meru (03.13'47" S - 36.41'34" E - alt.2600 m), collecting number RUCA 14.329.

##### Paratypes

22 specimens collected by Ronald VERHAGEN.

KMMA 96-037-M3832 (ad.male; alc. + cr.; col.nr.14.295)  
 96-037-M3833 (ad.fem.; alc. + cr.; col.nr. 14.307)  
 96-037-M3834 (ad.fem.; alc. + cr.; col.nr. 14.308)  
 96-037-M3835 (ad.male; alc. + cr.; col.nr. 14.309)  
 96-037-M3836 (ad.fem.; alc. + cr.; col.nr. 14.312)  
 96-037-M3837 (ad.fem.; alc. + cr.; col.nr. 14.313)  
 96-037-M3838 (ad.? ; alc. + cr.; col.nr. 14.319)  
 96-037-M3839 (ad.male; alc. + cr.; col.nr. 14.320)  
 96-037-M3840 (ad.male; alc. + cr.; col.nr. 14.321)  
 96-037-M3841 (ad.male; alc. + cr.; col.nr. 14.322)  
 96-037-M3842 (ad.fem.; alc. + cr.; col.nr. 14.323)  
 96-037-M3843 (ad.male; alc. + cr.; col.nr. 14.324)  
 96-037-M3844 (ad.male; alc. + cr.; col.nr. 14.325)  
 96-037-M3845 (ad.male; alc. + cr.; col.nr. 14.326)  
 96-037-M3846 (ad.fem.; alc. + cr.; col.nr. 14.327)  
 96-037-M3847 (ad.fem.; alc. + cr.; col.nr. 14.328)  
 96-037-M3849 (ad.male; alc. + cr.; col.nr. 14.347)  
 96-037-M3850 (ad.male; alc. + cr.; col.nr. 14.348)  
 96-037-M3851 (ad.male; alc. + cr.; col.nr. 14.352)

96-037-M3852 (ad.male; alc. + cr.; col.nr. 14.353)  
 96-037-M3853 (ad.male; alc. + cr.; col.nr. 14.354)  
 96-037-M3856 (ad.male; alc. + cr.; col.nr. 14.368)

For the craniometrical data of the type and paratypes: see App. 1.4.

### Type locality

All specimens were collected on the 8 and 9 March 1996 on Mt Meru (03°13'47"S-36°41'34"E at the altitude of 2.600 m (grid 8) except for col.nrs 14.347 and 14.348; these were collected on 10 March 1996 in grid 10 (03°13'54"S-36°42'39"E at the altitude of 3.050 m).

The collector describes grid 8 as situated in a grassy glade of about 2.500 m<sup>2</sup>, dotted here and there with low bushes and several small pools heavily surrounded by papyrus, the whole surrounded by moist mountain forest with little undergrowth and here and there small patches of open grassy spaces.

### Etymology

We have the pleasure to dedicate this new species to our colleague and friend Ronald VERHAGEN, who has contributed greatly to our ecological knowledge on African small mammals in Tanzania.

### Diagnosis

*Lophuromys verhageni* is a new species of "speckled and short-tailed brush-furred rat" of the *L. flavopunctatus* species complex and as such can be easily differentiated cranially and dentally from all the other species complexes of the genus *Lophuromys*.

Within the east African representative OTU's we can characterize our new species easily as a somewhat bigger animal with a slightly bigger but more slender skull with weak supraorbital ridges. (See also table 4, fig. 3, graph.8 and 9)

### Discussion of morphological characters

(Appendix 4, table 4; fig. 3)

We have not found reliable colour or pattern differences in the pelage that would allow us to characterize this population. Indeed, our specimens have been fixed in formalin and conserved in alcohol so that comparisons with dry type skins become rather difficult and unreliable.

In table 4 we compare the basic statistics of the external measurements of the Mt Meru sample with similar data obtained by our research teams for the Mutura (OTU 8) population. We find that *verhageni* is about 10% bigger than what we found for our topo-typical *laticeps* population; only for the tail length (TL) there seems not to be a significant difference. We note however that the CV% are high for HB, TL and EL and that only the hindfoot length (HF) gives results which are reliable.

The morphology of the skull and teeth situates *verhageni* within the *L. flavopunctatus* complex. A morphological comparison with typical *laticeps* skulls (OTU 8) shows that the skull of *verhageni* is slightly bigger but with a more slender

aspect and with less pronounced supraorbital ridges (fig. 3).

### Univariate analysis (Appendix 4, table 4)

A comparison with the toptotypical population of *laticeps* (Mutura: OTU 8) shows that *verhageni* is for most breadth measures significantly smaller than the latter (M8, M9, M15, M18, M20, M23) but bigger for most length-measures (M1, M2, M3, M4, M6, M7). The most significant measures characterizing *verhageni* are however M5 (PAFL), M14 (ZYPL), M21 (DINC) and M22 (ROHE).

We note that for some teeth measures (M11, M13) *verhageni* is not significantly different as well as for bullae length (M9: BULL) and nasal length (M16: LNAS). Finally, it is remarkable that for M21 (DINC) *verhageni* is significantly smaller and for M17 (LOTE) significantly bigger.

Summarizing we can characterize *verhageni* as having a somewhat larger but more slender skull with a finer rostrum, a weaker zygomatic plate and a rather heavier set of lower molars than *L. laticeps*.

### Discriminant analysis (graph. 9)

In this graph we attempt to characterize *verhageni* by comparing it to our toptotypical population of *laticeps* (Mutura: OTU 8). The results show that close to 100% of the individual skulls can be correctly identified by the discriminant function (forward analysis) by using 13 out of the 24 available measurements. We note also that the most important discriminating measures are: M14 (ZYPL), M13 (M<sub>1</sub>BR), M23 (ROBR), M12 (UPDA) and M17 (LOTE).

### Multiple discriminant analysis (graph. 8)

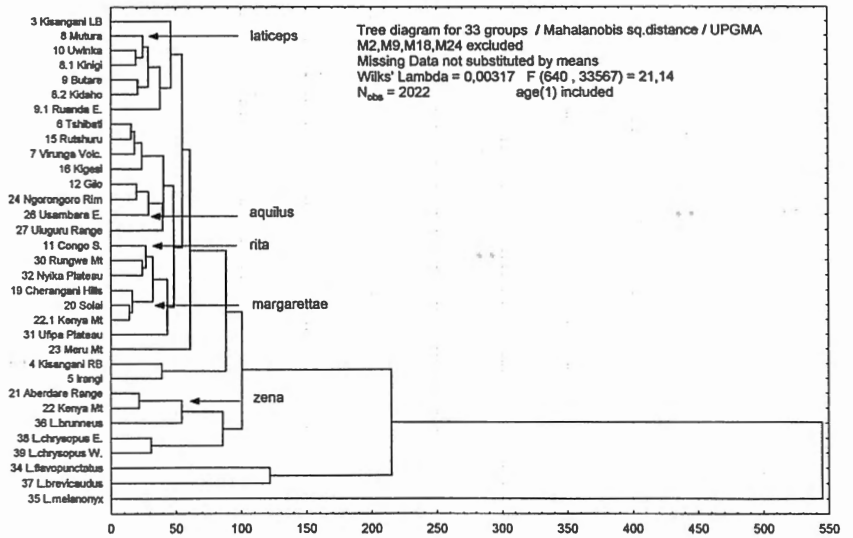
We refer to graph.8 where we show that *verhageni* (OTU 23) is not only well differentiated from a population toptotypical for *laticeps* (Mutura: OTU 8) but also from *L. dudu* (Kisangani RB: OTU 4).

### Genetic characterization (Appendix 4, tables 5 and 6)

As observed above, all OTU's and taxa represented by more than one partial cyt b sequence share a typical set of informative sites. The comparison of the partial cyt b sequences of the two specimens representing *verhageni* with sequences of relevant described taxa and OTU's from the same region (i.e. *laticeps*, *aquilus* and *dudu*) show the utility of molecular markers to identify this new taxon.

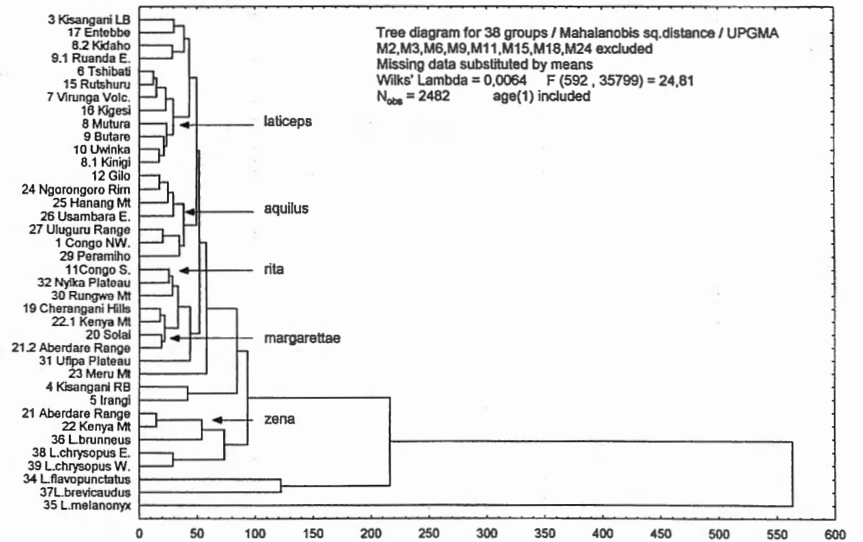
Since only little variation exists among the conspecifics tested here (tables 5 and 6), we suggest that the differences observed between *verhageni* and related taxa, such as the geographically closely situated *aquilus* (separated by approximately 60 km) are meaningful (p distance = 0.045). It is important to note that the genetic distance observed between *verhageni* and *aquilus* is considerably higher than p distances between the assayed *zenu* populations (average p distance = 0.001) that are separated by approximately the same geographic distance [approximately 50-60 km separate Aberdares from Mount Kenya]. Also the genetical differences between *verhageni* with *laticeps* and *dudu* (p-dis-

Graph. 5.1.  
UPGMA dendrogram based upon the craniometric comparison of 33 OTU's, using a minimum of 20 skull measures.



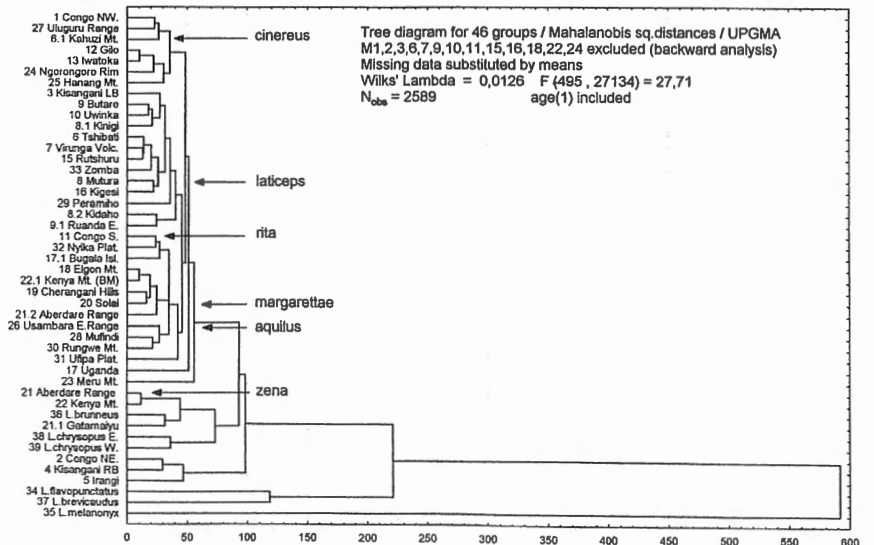
Graph.5.1

Graph. 5.2.  
UPGMA dendrogram based upon the craniometric comparison of 38 OTU's, using a minimum of 16 skull measures.

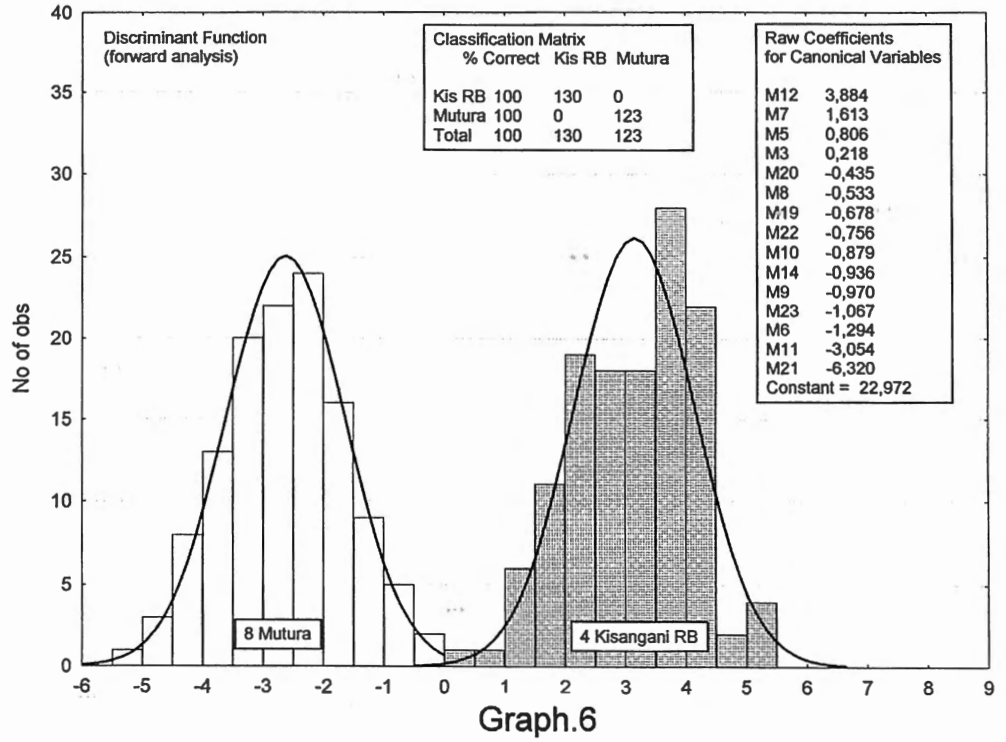


Graph.5.2

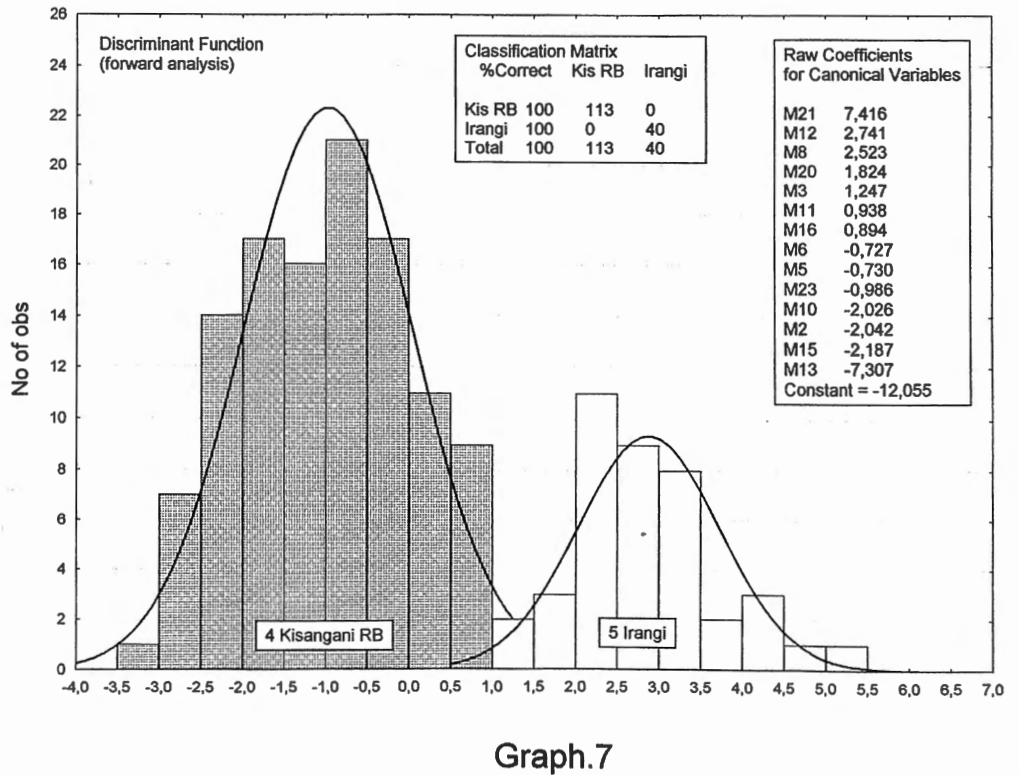
Graph. 5.3.  
UPGMA dendrogram based upon the craniometric comparison of 46 OTU's, using a minimum of 10 skull measures.



Graph.5.3

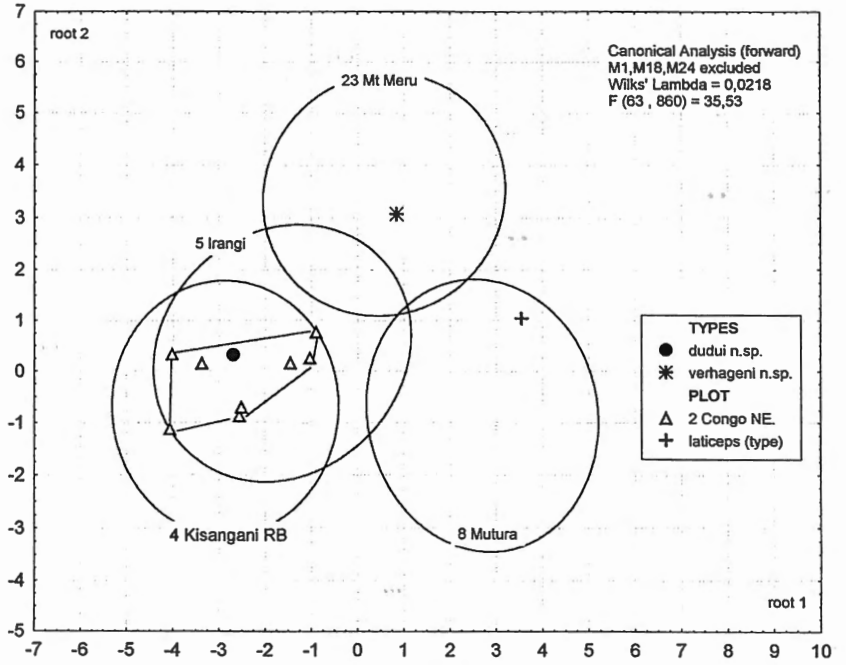


Graph. 6. Graphic representation of the discriminant function allowing the characterization of *L. dudui* n.sp. versus a topo-typical sample of *laticeps* (OTU 8), together with the canonical coefficients.



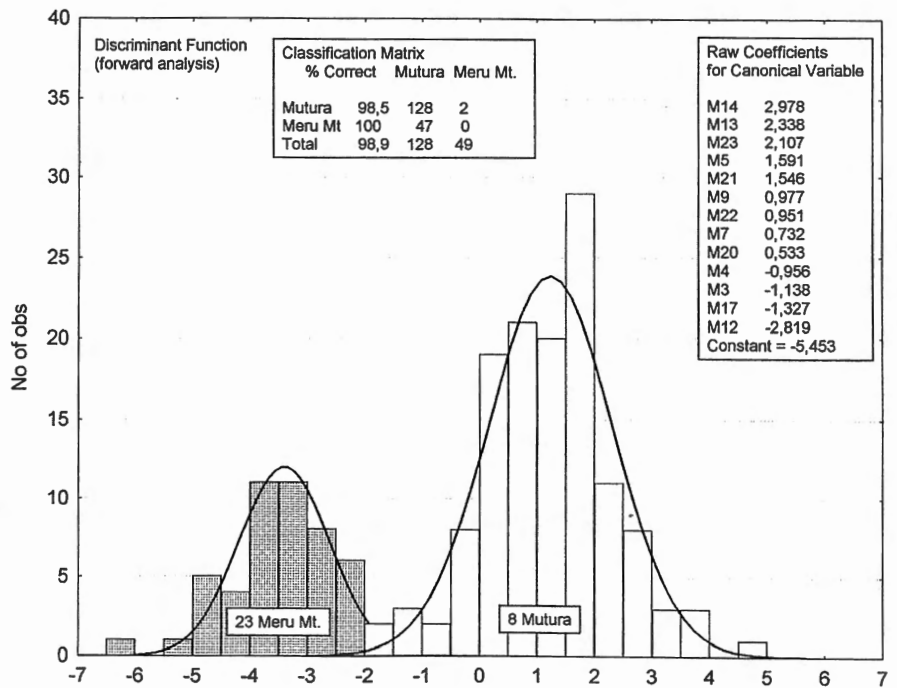
Graph. 7. Graphic representation of the discriminant function characterizing between *L. dudui* n.sp. versus the population of "Irangi" (OTU 5).





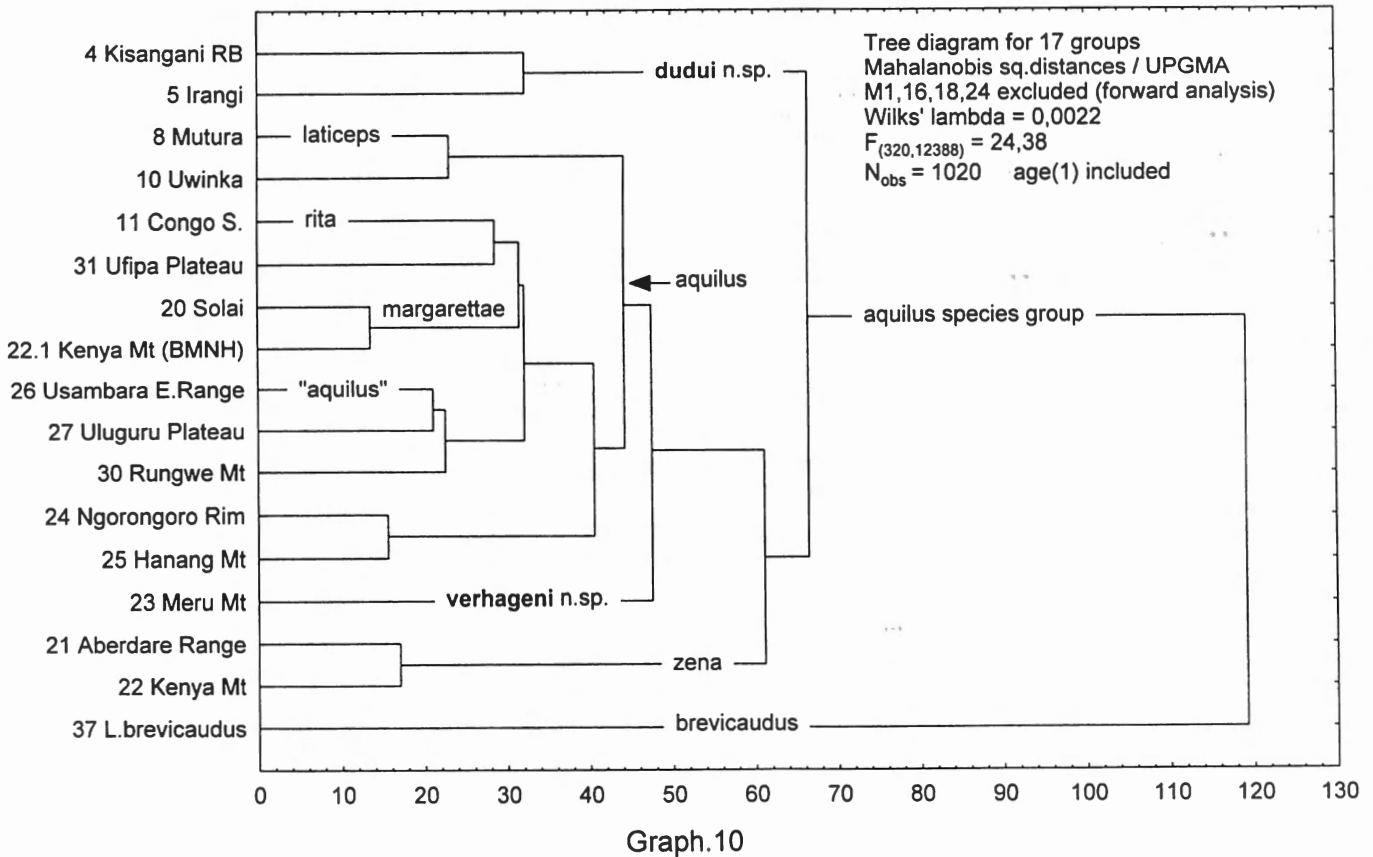
Graph. 8.  
Graphical representation of a canonical analysis on our new species *verhageni* (OTU 23 : Mt Meru) and *dudui* (OTU 4 : Kisangani RB) and a population of the taxon *laticeps* (OTU 8 : Mutura).

Graph.8



Graph. 9.  
Graphical representation of the discriminant function (forward analysis) between the Mutura population (OTU 8), representing the taxon *laticeps* and the new taxon *verhageni* of Mt Meru (OTU 23). Are also represented the coefficients for the canonical transformation, necessary for the diagnosis of the new taxon.

Graph.9



Graph. 10. UPGMA dendrogram based upon OTU's representing the known and our newly described east African taxa and using *brevicaudus* (OTU 37) as an outgroup.

tances are respectively = 0.078 and 0.059), even when based upon a single specimen, are likely to be reliable diagnostic differences.

Finally, the significance of the amount of genetical differentiation between *verhageni* and the nearby *aquilus* population (Mweka) is illustrated by the fact that the nucleotide substitutions observed between these two taxa result in not less than 4 inferred amino acid substitutions (p-distance = 0.031).

#### DISCUSSION AND CONCLUSIONS

The combination of craniometric and quantitative methods with genetical data, has proven to be a valuable approach to evaluate the current taxonomy of the *L. flavopunctatus* s.l. species complex.

One of the most important results of this study is that it illustrates the power and limitations of our methodology and approach. Indeed, concerning the use of craniometrical data in taxonomical work on rodents, our study demonstrates – at least for the studied taxa – that the differences in age and sex composition of OTU's (as long as these are sufficiently large; i.e. Nobs >20) are of no consequence for the branching of the phenetic trees based on the Mahalanobis squared distances between the centroids. This observation permitted us to screen the whole of the *L. flavopunctatus* s.l. species com-

plex and to evaluate the validity of the already known taxa, to detect new taxa and to describe two *Lophuromys* species new to science.

Although it was not our main objective to go into the taxonomy of the Ethiopian representatives of the species complex, we had to consider a possible overlap with other east African taxa. *L. flavopunctatus* THOMAS 1888 turned out to be typical for Ethiopia and *L. zaphiri* THOMAS 1906 appears to be synonymous with it. The taxa *brunneus* THOMAS 1906, *brevicaudus* OSGOOD 1936, *chrysopus* OSGOOD 1936 and *melanonyx* PETER 1972 are craniometrically well differentiated from *flavopunctatus*. However, there is a closer craniometrical similarity between the latter and *brevicaudus*. All these Ethiopian taxa are considered to be differentiated at the species level, but the taxon *simensis* OSGOOD 1936 is possibly synonymous with *brunneus*. None of these taxa proved to belong to the *L. sikapusi* species complex; *L. major* THOMAS & WROUGHTON 1907 is not represented in the Ethiopian *Lophuromys* populations we analysed.

The craniometrical study of the type skulls from non - Ethiopian origin shows that *laticeps* THOMAS & WROUGHTON 1907, *rita* DOLLMAN 1910, *margarettae* HELLER 1912 and *cinereus* DIETERLEN *et al.* 1974 are probably synonyms with *aquilus* TRUE 1892. However, the fact that each of the type specimens of *zena* DOLLMAN 1909, *rubecula* DOLLMAN 1909, *eisentrauti* DIETERLEN 1978 and *dieterleni* VERHEYEN *et al.*

1997 plots within the OTU 's 38+39 representing Ethiopian *chrysopus* suggests that this caryotypically well defined species has a much wider distribution than believed so far.

Graph.10 represents a phenetic tree incorporating the OTU's of the known and our newly described east African taxa and comparing these with a well-defined outgroup from Ethiopia (OTU 37: *brevicaudus*). This graph is an example of a multitude of different phenetic trees that can be obtained through changing or adding to the selection of east African OTU's; however, all the resulting trees are always fundamentally similar.

In the first place we note that the Ethiopian *L. brevicaudus* (OTU 37) is, as expected, different and clearly separated from all the east African taxa. Next, it is apparent that the east African populations of the "speckled" *Lophuromys* regroup in four taxonomical and geographical entities:

- 1° *dudui*: represents a taxon that inhabits the region of the rain-forest situated between the right bank of the Congo river and the western foothills of the rift mountains (OTU's 4 and 5);
- 2° *zena*: groups the mountain populations of the Aberdare Range and Mt Kenya (OTU's 21 and 22);
- 3° *verhageni*: represents the population that lives on Mount Meru
- 4° *aquilus*: contains the rest of the OTU's, and covers the remainder of the known geographical range of the "speckled" *Lophuromys*.

We especially draw attention to the fact that in Kenya the "speckled" *Lophuromys* from the lower regions around Aberdare Range and Mt Kenya (OTU's 20 and 22.1) are allocated to "*aquilus*" whereas the specimens, caught higher up the flanks of both mountains (OTU's 21 and 22), are identified as belonging to *zena*. From graph 5.1 we know that *zena* is morphometrically most similar to Ethiopian *brunneus* (OTU 36) and forms, be it on a higher level of differentiation, a clade with Ethiopian *chrysopus* (OTU's 38+39).

It is obvious that we need more information, preferably chromosomal and genetical, before we can settle whether *brunneus* THOMAS 1906 has taxonomical priority over *zena* DOLLMAN 1909 and what the taxonomic position of the east African *rubecula* DOLLMAN 1909 is in connection with Ethiopian *chrysopus* OSGOOD 1936.

As to our newly described taxon, *dudui* is morphometrically and genetically sufficiently separated from the other non - Ethiopian OTU's, that it should be differentiated at the species level. This conclusion is supported by its rather important geographical range covering the rainforest from the right bank of the Congo river to the western foothills of the rift mountains and reaching to the north as far as Garamba and to the south as far as the Maniema region.

Also *L. verhageni* (OTU 23: Mt Meru) is craniometrically well defined, but is manifestly closer to *aquilus* than to *zena* and *dudui*. Moreover, it appears to have reached a genetical level of differentiation similar to levels observed among other rodent species (SMITH & PATTON, 1991). All the other formerly recognized east African taxa such as *laticeps*, *rita*, *margarettae*, *cinereus* are to be considered conspecific with *aquilus*. Consequently, we have refrained to describe and name the branch grouping the populations of Mt Hanang (OTU 25) and Ngorongoro Rim (OTU 24), because these

OTU's never form a well defined higher level grouping such as we found for *dudui* and *verhageni*.

Finally, graph.5.1 shows clearly that all the east African "speckled" *Lophuromys* form together with the Ethiopian *brunneus* and *chrysopus* what we call the "*aquilus*" species group, contrasting with the rest of the Ethiopian species *melanonyx*, *brevicaudus* and *flavopunctatus*. We will develop this further into a forthcoming publication concerning the speckled *Lophuromys* of the Mount Ruwenzori.

Our study complements the traditional morphological approach with a genetic tool to characterize two new species and several OTU's. The partial mitochondrial cyt b sequences used here do not provide direct evidence to support our view that the described species are biologically valid. However, the fact that the mitochondrial cyt b fragment of our new species is significantly different when compared to sequences of related taxa, is suggestive to this effect.

It is documented that mitochondrial cyt b evolves at a similar rate in a wide array of vertebrates (JOHNS & AVISE, 1998). The observed amount of sequence divergence among the *Lophuromys* species and populations studied here is well within the range observed for other mammal species, including some rodents (SMITH & PATTON, 1991). Indeed, it has been reported that the cyt b sequence divergence between mammal species ranges between 0-0.32 (p distances), and for sister taxa, these values range between 0-0.2 with a mode at about 0.035 for mammals (JOHNS & AVISE, 1998). Interestingly our results appear to agree with findings suggesting that cyt b sequence divergences among South American Akodontine rodent species are in the same range or higher (0.03 > p > 0.21, SMITH & PATTON, 1991). However, as correctly pointed out (FERGUSON, 2002) genetic distances as such do not allow us to distinguish between species-level and population-level differences. An important problem is that it is easy to imagine how populations may have been geographically isolated for long periods of time, while they presumably constitute a single species (AVISE *et al.*, 1998). Although the evidence provided by our cyt b sequences supports that the investigated taxa and OTU's have experienced a long-term genetic isolation, the inclusion of genetic distances to the presented craniometrical evidence does not allow us to make absolute statements whether or not a population has attained the species status (FERGUSON, 2002).

Nevertheless, our observation that the investigated OTU's and taxa differ in fixed genetic characters that can be detected by their nucleotide sequences and morphological differences does provide some support about the taxonomic status of the investigated taxa. All taxa for which more than a single specimen was assayed share character states (synapomorphies), a situation that appears to be compatible with the phylogenetic species concept (CRACRAFT, 1983). The presence, and relative stability of the synapomorphies not only implies genetic differentiation, but suggests a lack of gene flow between these taxa.

#### ACKNOWLEDGEMENTS

We express our gratitude to the curators of the mammal collections of the museums who gave us the opportunity to

study the type-specimens and collections in their care. Many colleagues have been very helpful, understanding and very patient with us. We particularly wish to thank M. CARLETON (Smithsonian Institution, National Museum of Natural History, Washington DC, USA), C. DENYS and M. TRANIER (Muséum d'Histoire naturelle, Paris, France), F. DIETERLEN (Staatliches Museum für Naturkunde, Stuttgart, Germany), P. JENKINS (British Museum of Natural History, London, U.K.), S. McLAREN (Carnegie Museum of Natural History, Pittsburgh, USA), G. MUSSER (American Museum of Natural History, New York, USA), B. PATTERSON and J. KERBIS (Field Museum of Natural History, Chicago, USA), W. VAN NEER (Koninklijk Museum voor Midden Afrika, Tervuren, Belgium). We also acknowledge the work of T. DILLEN in the molecular laboratory of the Royal Belgian Institute of Natural Sciences. Finally our gratitude also goes to our colleagues Prof.dr. H. LEIRS and Prof.dr. R. VERHAGEN for their technical and administrative assistance and support to finalize this work. This study was funded by FWO-V project 2.0004.91 and by a DWTC project entitled "Evaluating the effect of Pleistocene climate changes on speciation patterns in selected African vertebrates".

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## APPENDIX 1

Types	Mus.	reg.nr	Country	Locality	Co-ordinates	Alt.±	S	A	Cr	P
<b>flavopunctatus</b>	BMNH	60.5.4.101	Ethiopia	Shoa, prob. Ankober ± 100 mi NE of Addis Ababa	10.05N-39.45E	3000	-	2	x	x
<b>zaphiri</b>	BMNH	6.11.1.41	Ethiopia	Bodeli-Walamo, E. of upper Omo river	07.30N-38.00E	2500	M	2	x	x
<b>brunneus</b>	BMNH	6.11.1.42	Ethiopia	Manno-Jimma	07.39N-36.47E	2000	M	3	x	x
<b>simensis</b>	FMNH	28.550	Ethiopia	Mt Geech-Ras Dachan Mt- Simien Mts	13.14N-38.40E	3000	M	2	x	x
<b>brevicaudus</b>	FMNH	28.573	Ethiopia	Mt Albasso-Chilalo Mts	07.55N-39.27E	3300	F	2	x	x
<b>chrysopus</b>	FMNH	28.592	Ethiopia	Allata-Sidamo	06.40N-38.35E	2500	-	1	x	x
<b>melanonyx</b>	MHNP	1972.250	Ethiopia	Dinshu-Bale Mt	07.07N-39.45E	3200	M	2	x	x
<b>zena</b>	BMNH	6.7.8.27	Kenya	Aberdare Range (East side of - near Nyeri)	00.26S-36.56E	2500	M	3	x	x
<b>rubecula</b>	BMNH	10.4.1.165	Kenya	Elgonyi (Mt Elgon)	00.58N-34.40E	2300	M	2	x	x
<b>margarettae</b>	USNM	181.793	Kenya	Mt Gargues	00.58N-37.20E	2000	M	3	x	x
<b>aquilus</b>	USNM	34.723	Tanzania	Mt Kilimanjaro	03.02S-37.20E	2650	M	2	x	x
<b>major</b>	BMNH	7.7.8.177	Congo	Bwanda – Ubangi river (?=Bwendi)	04.01N-06.43E	750?	-	3	x	x
<b>laticeps</b>	BMNH	7.6.14.35	Congo	Lake Kivu	01.35S-28.30E	1450	F	3	x	x
<b>rita</b>	BMNH	9.1.3.36	Congo	Lufupa river – Katanga	11.12S-25.17E	1350	M	3	x	x
<b>cinereus</b>	SMNS	18.046	Congo	Mukaba marsh – P.N.Kahuzi-Biega	02.15S-28.41E	2200	F	1	x	x
<b>eisentrauti</b>	MAKB	74.436	Cameroun	Mt Lefo near Bamenda	05.55N-10.09E	2550	M	2	x	x
<b>dieterleni</b>	ZFMK	69.289	Cameroun	Mt Oku	06.12N-10.32E	2050	M	2	x	x

Types	Mus.	reg.nr	Country	Description
<b>flavopunctatus</b>	BMNH	60.5.4.101	Ethiopia	<i>Lophuromys flavopunctatus</i> THOMAS 1888 and THOMAS 1902 (p.314)
<b>zaphiri</b>	BMNH	6.11.1.41	Ethiopia	<i>Lophuromys zaphiri</i> THOMAS 1906 (p.304)
<b>brunneus</b>	BMNH	6.11.1.42	Ethiopia	<i>L. flavopunctatus brunneus</i> THOMAS 1906 (p.306)
<b>simensis</b>	FMNH	28.550	Ethiopia	<i>L. flavopunctatus simensis</i> OSGOOD 1936 (p.238)
<b>brevicaudus</b>	FMNH	28.573	Ethiopia	<i>L. brevicaudus</i> OSGOOD 1936 (p.241)
<b>chrysopus</b>	FMNH	28.592	Ethiopia	<i>L. aquilus chrysopus</i> OSGOOD 1936 (p.242)
<b>melanonyx</b>	MHNP	1972.250	Ethiopia	<i>L. melanonyx</i> PETTER 1972
<b>zena</b>	BMNH	6.7.8.27	Kenya	<i>L. aquilus zena</i> DOLLMAN 1909 (p.550)
<b>rubecula</b>	BMNH	10.4.1.165	Kenya	<i>L. rubecula</i> DOLLMAN 1909 (p.551)
<b>margarettae</b>	USNM	181.793	Kenya	<i>L. aquilus margarettae</i> HELLER 1912
<b>aquilus</b>	USNM	34.723	Tanzania	<i>L. aquilus</i> TRUE 1892
<b>major</b>	BMNH	7.7.8.177	Congo	<i>L. major</i> THOMAS & WROUGHTON 1907 (p.382)
<b>laticeps</b>	BMNH	7.6.14.35	Congo	<i>L. aquilus laticeps</i> THOMAS & WROUGHTON 1907 (p.383)
<b>rita</b>	BMNH	9.1.3.36	Congo	<i>L. rita</i> DOLLMAN 1910
<b>cinereus</b>	SMNS	18.046	Congo	<i>L. cinereus</i> DIETERLEN et al. 1974
<b>eisentrauti</b>	MAKB	74.436	Cameroun	<i>L. sikapusi eisentrauti</i> DIETERLEN 1978
<b>dieterleni</b>	ZFMK	69.289	Cameroun	<i>L. dieterleni</i> VERHEYEN et al. 1997

Appendix 1.1. : Listing of data concerning the description of the types of the *Lophuromys flavopunctatus* – species group included in this study. For the definition of the acronyms of the institutions and museums and the age classes we refer to VERHEYEN et al. 1996.

( S = sex; A = age; Cr = cranium; P = skin; F = female; M = male).

Types	Mus.	reg.nr	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12
<i>flavopunctatus</i>	BMNH	60.5.4.101				12,25	6,75	8,00	9,65	5,50	15,15	3,25	5,25	7,15
<i>zaphiri</i>	BMNH	6.11.1.41	30,15	28,65	24,45	13,45	6,45	7,55	9,20	5,65		3,05	5,75	7,05
<i>brunneus</i>	BMNH	6.11.1.42				13,05	6,70	8,10	9,75	6,35			5,65	
<i>simensis</i>	FMNH	28.550	29,40	28,10	24,00	12,45	6,70	7,95	9,30	5,95	14,95	2,90	5,15	6,65
<i>brevicaudus</i>	FMNH	28.573	29,70	28,35	24,20	12,75	6,10	7,55	9,65	5,35	13,75	2,80	5,35	6,20
<i>chrysopus</i>	FMNH	28.592	29,60	27,45	23,80	11,95	6,50	7,55	8,45	6,10	14,40	3,20	4,80	6,60
<i>melanonyx</i>	MHNP	1972.250		32,15	28,15	14,55	7,15	8,85	10,60	5,65	16,40	3,15	6,30	7,40
<i>zena</i>	BMNH	6.7.8.27	29,80	28,55	24,35	12,35	6,40	7,45	8,95	6,00	15,10	3,05	5,35	6,75
<i>rubecula</i>	BMNH	10.4.1.165	28,25	27,15	22,95	11,45	5,65	7,25	8,45	5,65	13,35	3,15	4,85	6,45
<i>margarettae</i>	USNH	181.793	29,70	28,40	24,35	12,75	6,75	8,05	9,30	5,70	14,25	2,85	5,15	6,80
<i>aquilus</i>	USNH	34.723				12,30	6,40	7,85	9,10	5,90	14,10	3,15	4,70	6,50
<i>major</i>	BMNH	7.7.8.177				14,30	7,65	8,95	10,60	7,05		3,70	5,60	7,85
<i>laticeps</i>	BMNH	7.6.14.35	29,05	27,30	23,30	11,85	5,80	7,10	8,60	6,20	15,10	3,15	5,15	6,85
<i>rita</i>	BMNH	9.1.3.36	29,45	28,40	24,05	12,35	6,15	7,70	9,15	6,15		3,25	5,35	7,00
<i>cinereus</i>	SMNS	18.046				11,75	6,30	7,15	8,40	5,80		3,05	4,85	6,45
<i>eisentrauti</i>	MAKB	74.436	26,80	24,25	20,65	10,90	5,45	6,40	7,60	6,30	13,30	3,15	4,60	6,35
<i>dieterleni</i>	ZFMK	69.289	30,90	29,40	24,80	12,60	6,40	7,85	9,30	6,85	16,00	3,20	4,70	6,85

Types	Mus.	reg.nr	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22	M23	M24
<i>flavopunctatus</i>	BMNH	60.5.4.101	1,90	2,95	2,90	13,15	4,85	1,65		12,45	1,30	6,55	4,85	
<i>zaphiri</i>	BMNH	6.11.1.41	1,95	3,45	3,15	12,05	5,10	1,55	6,55	12,65	1,20	6,45	5,20	
<i>brunneus</i>	BMNH	6.11.1.42	2,00	3,35	2,95	11,95	4,95				1,15	6,45	4,50	9,65
<i>simensis</i>	FMNH	28.550	1,75	3,25	2,85	11,95	4,70		5,30	12,35	1,30	6,35	4,50	8,60
<i>brevicaudus</i>	FMNH	28.573	1,80	3,15	2,55	11,95	4,50		5,90	12,15	1,25	6,00	4,10	8,75
<i>chrysopus</i>	FMNH	28.592	1,70	3,05	2,65	11,35	4,60		5,55	12,70	1,25	6,25	4,20	8,50
<i>melanonyx</i>	MHNP	1972.250	2,10	3,50	2,90		5,65	1,60	5,90	13,00	1,25	6,70	5,35	9,80
<i>zena</i>	BMNH	6.7.8.27	1,70	2,70	2,65	12,25	4,70	1,55	6,95	12,80	1,55	6,10	5,00	8,15
<i>rubecula</i>	BMNH	10.4.1.165	1,65	2,95	2,60	11,15	4,20	1,45	7,15	12,25	1,25	5,60	4,55	
<i>margarettae</i>	USNH	181.793	1,75	2,85	2,80	12,15	4,90		5,15	12,15	1,20	6,05	4,90	8,90
<i>aquilus</i>	USNH	34.723	1,65	2,75	2,80	12,30	4,35		5,45	12,85	1,35	6,15	4,95	
<i>major</i>	BMNH	7.7.8.177	2,00	3,05	3,45	14,65	5,10	1,90		12,85	1,45	7,25		
<i>laticeps</i>	BMNH	7.6.14.35	1,70	2,90	2,95	11,15	4,55	1,50	6,45	13,30	1,35	6,25	5,05	8,75
<i>rita</i>	BMNH	9.1.3.36	1,80	2,85	2,60	11,80	4,65	1,95	7,00	13,05	1,20	6,15	5,05	
<i>cinereus</i>	SMNS	18.046	1,70	2,50	2,70	10,65	4,30	1,15			1,35	6,20	4,65	7,75
<i>eisentrauti</i>	MAKB	74.436	1,60	2,45	2,65	10,40	4,20	1,55	4,95	12,15	1,30	5,90	4,70	7,45
<i>dieterleni</i>	ZFMK	69.289	1,75	3,45	2,85	12,75	4,45	1,05	5,00	13,25	1,45	6,70	5,35	8,95

**Appendix 1.2.** : Listing of the craniometrical data of the type specimens of the *Lophuromys flavopunctatus* species group, as measured by us.

MUS	NUMB	LOCAL	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
RUCA	D1739	MASAKO	29.20	27.80	23.85	12.30	6.25	8.00	9.45	5.70	14.90	3.50
RUCA	D1170	MASAKO	28.75	27.35	23.70	11.80	5.90	7.70	9.05	5.55		3.20
RUCA	D1290	MASAKO	27.60	25.85	21.70	11.00	5.75	6.80	8.25	5.65	13.10	2.80
RUCA	D1315	MASAKO	28.70	27.85	23.40	11.90	6.30	7.80	9.25	6.00	14.75	3.30
RUCA	D1332	MASAKO	27.55	25.85	21.55	11.25	6.15	7.05	8.30	5.55	13.30	3.00
RUCA	D1649	MASAKO	28.10	26.90	22.90	11.80	5.65	7.40	8.75	5.20	14.00	3.05
RUCA	D1734	MASAKO	28.00	26.40	22.25	11.00	5.85	7.20	8.40	5.65	13.80	3.10
RUCA	D1771	MASAKO	27.05	25.85	21.80	10.85	5.55	7.05	8.35	5.75	13.55	3.00
RUCA	D1902	MASAKO	28.80	27.20	23.00	11.45	6.20	7.40	8.80	5.45	14.25	3.05
RUCA	D2322	MASAKO	28.25	27.40	23.15	11.40	5.80	7.45	9.10	5.85	13.95	3.30
RUCA	D2974	MASAKO	29.80	28.40	23.90	12.25	6.60	8.00	9.60	5.60	14.15	3.20

NUMB	M11	M12	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22	M23	M24
D1739	4.35	6.90	1.60	2.70	2.70	11.70	4.20	1.50	4.80	12.80	1.10	6.00	4.80	7.85
D1170	4.50	6.50	1.60	2.20	2.65	11.40	4.05	1.50		12.00	0.90	6.15	4.65	
D1290	4.70	6.45	1.70	2.60	2.60	10.55	4.45	1.25		12.15	0.90	5.70	4.60	
D1315	4.45	6.60	1.60	2.40	2.90	11.45	4.05	1.50	4.95	12.85	1.20	6.15	4.85	7.70
D1332	4.50	6.50	1.70	2.25	2.40	10.90	4.25	1.50	4.70	12.25	1.00	5.65	4.45	
D1649	4.30	6.40	1.60	2.25	2.50	11.00	4.15	1.20	4.90	12.55	1.10	5.50	4.70	7.85
D1734	4.55	6.55	1.60	2.40	2.70	11.10	4.05	1.40	4.50	12.40	1.05	5.80	4.70	7.50
D1771	4.35	6.35	1.65	2.65	2.50	9.95	4.00	1.50	4.65	12.25	0.95	5.50	4.45	7.25
D1902	4.75	6.45	1.60	2.50	2.65	11.60	4.30	1.35	4.50	12.70	0.95	5.70	4.55	7.95
D2322	4.50	6.85	1.65	2.65	2.50	11.20	4.15	1.25	4.80	12.25	1.10	6.00	4.75	7.90
D2974	4.65	6.60	1.65	2.60	2.55	12.50		1.50	4.65	12.40	1.15	6.00	4.70	

**Appendix 1.3.** : Listing of the craniometrical data of the type and paratypes of *Lophuromys dudui* n.sp.



MUS	NUMB	LOCAL	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
KMMA	96-037-M-3848	Mt.MERU	29.65	28.40	23.90	12.40	5.60	7.65	9.10	5.90	14.35	3.10
KMMA	96-037-M-3832	Mt.MERU	30.45	29.25	24.95	12.80	6.00	8.25	9.35	6.20	14.50	3.00
KMMA	96-037-M-3833	Mt.MERU	30.55	29.65	25.05	13.00	5.85	8.05	9.50	6.15	15.35	3.35
KMMA	96-037-M-3834	Mt.MERU	28.75	27.50	23.20	12.00	5.60	7.50	8.85	5.75	13.70	2.60
KMMA	96-037-M-3835	Mt.MERU	30.80	29.50	25.30	13.00	5.45	7.80	9.35	6.10	15.00	3.05
KMMA	96-037-M-3836	Mt.MERU	29.70	28.20	24.00	12.60	5.50	7.50	8.90	6.15	14.00	2.75
KMMA	96-037-M-3837	Mt.MERU	27.95	26.15	22.05	11.30	5.25	6.75	8.00	5.70	13.50	2.60
KMMA	96-037-M-3838	Mt.MERU	28.55	26.65	22.50	11.60	5.35	7.10	8.45	5.75	13.55	3.00
KMMA	96-037-M-3839	Mt.MERU	29.75	28.00	23.90	12.15	5.45	7.15	8.55	6.00	14.25	2.85
KMMA	96-037-M-3840	Mt.MERU	29.40	28.00	23.90	12.30	5.45	7.40	8.85	6.20	13.95	2.70
KMMA	96-037-M-3841	Mt.MERU	29.75	28.35	24.10	12.45	5.70	7.50	8.85	5.95	14.35	2.75
KMMA	96-037-M-3842	Mt.MERU	30.50	29.45	25.05	13.00	6.25	7.85	9.30	5.95	15.00	3.20
KMMA	96-037-M-3843	Mt.MERU	30.15	29.35	25.20	12.85	5.65	7.95	9.70	6.40	15.05	3.25
KMMA	96-037-M-3844	Mt.MERU	31.10	29.85	25.40	12.90	6.00	8.05	9.45	5.90	14.50	2.95
KMMA	96-037-M-3845	Mt.MERU	29.65	28.80	24.30	12.50	5.30	7.60	9.15	6.15	14.85	3.05
KMMA	96-037-M-3846	Mt.MERU	28.95	27.55	23.55	11.85	5.65	7.15	8.40	6.00	14.00	2.85
KMMA	96-037-M-3847	Mt.MERU	29.50	27.70	23.60	12.05	5.75	7.25	8.45	5.80	13.80	2.85
KMMA	96-037-M-3849	Mt.MERU	30.15	28.75	24.50	12.50	5.80	7.75	8.75	5.80		2.95
KMMA	96-037-M-3850	Mt.MERU		30.10	25.90	12.90	6.25	8.10	9.90	5.90	15.00	3.00
KMMA	96-037-M-3851	Mt.MERU	28.95	26.90	22.90	12.00	5.25	6.90	8.25	6.00	14.00	2.65
KMMA	96-037-M-3852	Mt.MERU	29.50	28.20	24.05	12.25	5.50	7.70	8.90	5.80	14.75	2.80
KMMA	96-037-M-3853	Mt.MERU	31.30	30.10	25.70	12.70	5.90	8.40	9.75	5.75	15.00	3.05
KMMA	96-037-M-3856	Mt.MERU	31.10	29.75	25.75	13.20	6.15	8.20	9.45	5.75	14.85	3.15

NUMB	M11	M12	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22	M23	M24
96-037-M-3848	5.35	6.95	1.80	2.85	2.90	11.85	4.60	1.20	5.30	12.55	1.20	6.20	5.00	8.85
96-037-M-3832	4.95	7.00	1.85	2.80	2.80	12.40	4.55	1.35	5.20	12.80	1.20	6.65	5.00	8.95
96-037-M-3833	5.40	7.00	1.70	2.90	2.90	12.50	4.50	1.20	5.65	13.00	1.40	6.50	5.15	8.75
96-037-M-3834	4.85	6.40	1.65	2.40	2.50	11.25	4.40	1.20	5.25	12.40	1.15	5.90	4.85	8.15
96-037-M-3835	5.10	7.15	1.85	2.70	3.05	12.20	4.75	1.30	5.90	12.85	1.30	6.60	5.05	8.85
96-037-M-3836	5.10	6.60	1.70	2.75	2.90	12.05	4.70	1.30	5.25	12.55	1.25	6.20	4.70	
96-037-M-3837	5.30	6.60	1.80	2.40	2.50	10.65	4.55	1.60	5.15	12.70	1.10	5.50	4.65	7.85
96-037-M-3838	5.00	6.50	1.70	2.50	2.50	11.10	4.55	1.35	5.10	12.50	1.15	5.80	4.60	7.95
96-037-M-3839	5.35	6.75	1.80	2.70	2.95	12.00	4.70	1.35	5.30	12.80	1.30	6.00	4.85	8.65
96-037-M-3840	5.00	6.60	1.75	2.55	2.90	11.65	4.50	1.25	5.40	12.75	1.20	6.15	4.85	
96-037-M-3841	5.15	6.85	1.95	2.60	2.90	11.50	4.70	1.40	5.40	12.60	1.20	6.20	5.00	9.00
96-037-M-3842	5.20	7.10	1.75	2.90	2.80	11.95	4.35	1.20	5.10	12.70	1.35	6.20	4.85	9.15
96-037-M-3843	5.25	7.20	1.90	2.80	2.85	11.70	4.75	1.40	5.40	12.70	1.40	6.35	5.20	9.05
96-037-M-3844	5.00	6.80	1.75	2.90	2.80	12.40	4.25	1.40	5.45	12.60	1.30	6.25	4.95	8.75
96-037-M-3845	5.55	7.20	1.85	2.65	2.60	11.50	4.60	1.40	5.10	12.60	1.25	6.10	4.90	9.05
96-037-M-3846	5.50	6.70	1.75	2.60	2.70	11.30	4.70	1.30	5.25	12.80	1.20	6.20	5.00	8.20
96-037-M-3847	4.95	6.60	1.70	2.70	2.50	11.70	4.40	1.55	5.30	12.50	1.20	6.00	5.00	8.40
96-037-M-3849	5.15	6.50	1.65	2.60	2.50	12.50	4.35	1.30	5.20	12.65	1.35	6.30	4.55	9.00
96-037-M-3850	5.10	7.00	1.85	2.85	2.75		4.65	1.35	5.75	12.90	1.30	6.45	5.15	9.25
96-037-M-3851	5.20	6.55	1.80	2.50	2.65	11.10	4.65	1.20	5.20	13.05	1.25	5.85	4.85	
96-037-M-3852	4.90	6.70	1.70	2.65	2.65	11.70	4.50	1.30	5.45	12.85	1.20	6.25	5.05	8.20
96-037-M-3853	5.05	6.95	1.80	2.85	2.70	12.85	4.50	1.25	5.70	12.60	1.30	6.75	5.30	9.35
96-037-M-3856	5.35	7.05	1.75	2.75	2.80	12.50	4.65	1.40	5.10	12.50	1.40	6.45	4.85	8.85

**Appendix 1.4.** : Listing of the craniometrical data of the type and paratypes of *Lophuromys verhageni* n.sp.

## APPENDIX 2 : LISTING OF THE SPECIMENS, GROUPED PER OPERATIONAL TAXONOMICAL UNIT (OTU)

## OTU 1 "Congo NW."

M(9), F(9); cl1(3), cl2(10), cl3(4), cl4(1)

TANDALA,	USNM,	463590, 463603, 537879,
YALOSEMBA,	CNHM,	86734, 86735,
	USNM,	463591-599, 537874-877,

## OTU 2 "Congo NE."

M(3), F(8), sex?(6); cl1(3), cl2(12), cl3(2)

BAFWASENDE,	FMNH	E129
BLUKWA,	KMMA	9611, 9612, 12833, 12834
BUTA,	KMMA,	8923,
DJUGU,	KMMA,	10719,
GARAMBA,	KMMA,	78.39.M.395,
KIFUKU,	KMMA,	9099, 9100, 9183,
KOTELI,	KMMA,	8878, 8881, 8885, 8916,
MEDJE,	KMMA,	4519,
PANGA,	KMMA,	9107, 9144, 9145,

## OTU 3 "Kisangani Left Bank"

M(18), F(17), sex?(1); cl1(6), cl2(18), cl3(12)

KISANGANI 5A,	RUCA,	Z0585, Z0586
KISANGANI 5B,	RUCA,	Z0696, Z0697, Z0699, Z0808, Z0809, Z0811, Z2573, Z2575, Z2677, Z2680, Z2681, Z2683, Z2687-92, Z2694, Z2746-50, Z6617-18, Z6768, Z8756, Z8759, Z9262, Z9263, Z9268, Z9271, Z9274

## OTU 4 "Kisangani Right Bank"

M(72), F(66), sex?(6); cl1(24), cl2(67), cl3(42), cl4(11)

KISANGANI 1A,	RUCA,	Z0208, Z8990, Z8992, Z9534, Z9535, Z9537,
KISANGANI 2A,	RUCA,	Z1004-05, Z2079, Z2085, Z2087-88, Z2092-93, Z2095, Z2097-98, Z2101, Z2104, Z2108, Z2110-11, Z2605, Z2607, Z2651, Z2726-28, Z2893, Z3309, Z3463, Z3581, Z3585, Z3892, Z3894, Z4112, Z8552, Z8611-12, Z9725-28, Z9731-33, Z9735-38,
KISANGANI 2B,	RUCA,	Z10160, Z10162, Z2239, Z2240-42, Z5879, Z5882, Z7486, Z7980, Z7984-85
KISANGANI 3A,	RUCA,	Z0375, Z0377-79, Z0382, Z0384-86, Z0391, Z2546, Z2556, Z2558, Z2563-64, Z2634, Z2711, Z2761, Z5377, Z5384, Z5386, Z5389, Z5650, Z5656, Z5660, Z8446-47, Z8454,
KISANGANI 3B,	RUCA,	Z1839, Z1840, Z7212-13, Z7803, Z9945-47, Z9950, Z9952-54, Z9956, Z9960,
KISANGANI 3C,	RUCA,	Z0969, Z0971, Z0973, Z0974,
KISANGANI 4A,	RUCA,	Z10729, Z10733, Z10737, Z10746, Z1318-20, Z1548, Z3146, Z6162-65, Z6243, Z6246-47, Z7012, Z7016, Z7642, Z7644, Z7649, Z7654, Z9394, Z9400,
MASAKO,	RUCA,	D1170, D1290, D1315, D1332, D1649, D1734, D1739, D1771, D1902, D2322, D2974, 6669,
YANGAMBI,	KBIN,	7014, 7015,

## OTU 5 "Irangi"

M(20), F(26), sex?(1); cl1(5), cl2(22), cl3(15), cl4(5)

IRANGI,	SMNS,	12980-83, 12985-86, 12991-92, 12999, 13002-04, 13008, 13011, 13016, 13019-20, 13023, 13028-30, 13033, 13035, 13037-39, 13041, 13043, 13045-46, 13048, 13493, 18157, 18159-60, 18163, 18167, 18171, 18183
	KMMA,	28385, 30384-85, 30387, 31811, 31814, 31817, 31821, 1823

## OTU 6 "Tshibati"

M(210), F(173), sex?(18); cl1(106), cl2(152), cl3(131), cl4(12)

BUKARABWA,	KMMA,	30405, 31770, 31772-73, 31775-76, 31778-84, 31787-93
BUSHUSHU,	KMMA,	28981
CHIRERA,	KMMA,	31732-33, 31735, 31742-59
FOMULAC,	KMMA,	30295, 30305-08, 30310-11
IDJWI Island,	KMMA,	17890-92
LEMERA,	KMMA,	28016, 30260-61, 30265, 30267-69, 30271-75, 30278-79, 30282, 30285, 30287-89
LUSHALA,	USNM,	535876

LUSHEBERE, LWIRO,	KMMA, 28980 KMMA, 31952-53, 31959, 31961-63, 31965-70, 31974, 31981, 31985-86, 31993-94, 31996, 31999, 32002-03, 32006-07, 32010, 32013, 32015, 32017, 32020, 32022, 32024, 32026, 32028, 32030, 32037, 32064, 32070, 32072-73, 32076-82, 32089, 32092, 32095-99, 32100-101, 32103-104, 32106-108, 32110-111, 32114-116, 32119, 32123, 32125
MUGABA, MUGANZA, NYAMBASHA,	USNM, 535878-79 USNM, 498735 USNM, 375485, 535894-96 KMMA, 30224, 30226-36, 30238, 30242, 30244-46, 30248-53, 30256, 30258, 30500, 30518
TSHIBATI,	KMMA, M15, M32, M38, M51, M55, M60, M64, M71, M80, M81, M94, M99, M130, M138, M164, M166, M180, M191, M201, M205, M218, M221, M223, M225, M226, M227, M229, M233, M241, M334, M340, M366, M370, M407, M415, M419, M448, M451, M452, M454, M487, M489, M509, M510, M514, M532, M536, M537, M540, M556, M567, M622, M628, M647, M650, M660, M665, M669, M670, M699, M700, M740, M743, M745, M757, M795, M828, M837, M838, M843, M860, M875, M896, M909, M1011, M1029, M1064, M1077, M1106, M1142, M1144, M1153, M1207, M1214, M1252, M1263, M1267, M1269, M1278, M1300, M1301, M1305, M1313, M1318, M1320, M1326, M1338, M1348, M1370, M1372, M1379, M1400, M1409, M1423, M1460, M1464, M1470, M1474, M1597, M1601, M1637, M1657, M1675, M1695, M1753, M1765, M1769, M1771, M1773, M1782, M1795, M1809, M1814, M1869, M1876, M1890, M1923, M1943, M1952, M1968, M1980, M1985, M1993, M2004, M2008, M2025, M2031, M2035, M2044, M2078, M2085, M2086, M2087, M2089, M2100, M2102, M2131, M2145, M2147, M2152, M2182, M2183, M2192, M2193, M2202, M2204, M2209, M2217, M2222, M2225, M2232, M2233, M2236, M2243, M2250, M2255, M2278, M2292, M2294, M2789, 32139, 32144, 32153, 32155, 32159, 32162-63, 32165-67, 32172, 32175, 32184, 32188, 32191, 32195-96, 32199, 32201, 32204-05, 32207, 32209, 32211-12, 32214, 32218-20, 32222-24, 32226, 32229, 32231-33, 32236-38, 32241-43, 32245, 32250, 32257-61, 32263, 32265-66, 32268, 32276-77, 32285, 32289, 32290, 32295-96, 32300, 32302, 32306-08

**OTU 6.1 "Kahuzi Mt"**

M(4), F(6), sex?(1); cl1(3), cl2(1), cl3(6), cl4(1)

KAHUZI,	SMNS, 18623-25, 18629, 22313 KMMA, 28970, 28971, 28974, 28978, 28979, 28988
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**OTU 7 "Virunga Volcanoes"**

M(84), F(69), sex?(44); cl1(27), cl2(93), cl3(61), cl4(14)

GAHINGA,	KMMA, 1737 RUCA, 4861, 4862, 4863, 4864, 4869, 4870-71, 4872-75, 4917-18, 4950, 4954-55, 5027-30, 5032, 5041, 5094-95, 5098-100, 5104, 5131
GASIZA,	RUCA, 4901, 4902-08, 4938-41, 4947, 4970, 4972-73, 5013, 5015, 5058, 5087, 5152-54, 5163, 5172-73, 5221, 5225, 5245
KARISIMBI,	BMNH, 65.929 KMMA, 8036 AMNH, 82745, 82746
KARISOKE,	RUCA, 3640, 3642, 3648, 3654, 3658, 3660, 3663, 3666, 3668-70, 3672-75, 3680, 3691-92, 3695-96, 3698, 3700, 3702, 3707-08, 3710, 3713-14, 3717, 3721, 3921, 3923
MIKENO,	BMNH, 11.12.3.339, 11.12.3.398, 11.12.3.403, 11.12.3.405, 11.12.3.406, 11.12.3.408, 11.12.3.409, 11.12.3.412, 11.12.3.415, 65.911, 65.913, 65.915, 65.917, 82749, 82750
MUHABURA,	KMMA, A1742, B1742 RUCA, 4676-77, 4679-81, 4683, 4685-86, 4748, 4750, 4798, 4811, 4844-45, 4847
MUSHUMANGA, NYAMLGIRA,	KMMA, 820.11.M.805, A176C, A179C, B176C, B179C KMMA, 75.2, 820.11.M.425, 820.11.M.427-429, 820.11.M.433, 820.11.M.436-438
RUKUMI,	KMMA, 272-273, 274A, 274B, 284A, 284B, 284C, 289-90, 292.1, 294B, 302, 303B, 306, 309, 310C, 310D, 312B

VISOKE, RUCA, 2842-43, 2859-63, 2889-91, 2893, 2895-96, 2898-99, 2902-03, 2907, 2937-42, 2973, 2976, 2998-99, 3000, 3002, 3046, 3635-36, 3739-40, 3898, 3901, 3914

### OTU 8 "Mutura"

M(67), F(62), sex?(2); cl1(15), cl2(67), cl3(36), cl4(13)

MUTURA, KMMA, 74.020.M.693, 74.020.M.697, 74.020.M.699, 74.020.M.700, 74.020.M.701-703, 74.020.M.707  
 RUCA, R352-354, R356-358, R360, R365-366, R368, R371-372, R382, R417-422, R426, R429-432, R434-438, R453-454, R461, R465-466, R468, R472-476, R479, R481-484, R488, R505-507, R509, R511-515, R517, R519-520, R523, R527-530, R532-533, R536, R550, R602, R612, R615-616, R620, R624, R644-646, R648-650, R653-654, R656-660, R663, R666, R671, R682, R684-685, R692-693, R695, R703, R714-715, R717-718, R720-729, R738-739, R742-743, R745, R749-751, R753, R755-756, R758, R768, R823, R832, R837,

### OTU 8.1 "Kinigi"

M(59), F(49), sex?(2); cl1(41), cl2(48), cl3(15), cl4(6)

KINIGI, RUCA, 2336-40, 2342, 2344-45, 2348-51, 2355-56, 2358-59, 2361, 2415, 2420, 2422-24, 2435-37, 2443, 2446, 2478, 2489, 2601, 2608-09, 2611-14, 2681-83, 2688-89, 2691, 2695-99, 2701-05, 2707-08, 2719-25, 2734-37, 2742-49, 2774-75, 2780-82, 2784, 2786, 2795, 2832-35, 2854, 2875-76, 2878-79, 2881, 2935, 3058, 3072, 3815, 3826-27, 3829-31, 3838, 3849, 3861, 3864-65, 3869-70, 3874, 3876, 3885

### OTU 8.2 "Kidaho"

M(20), F(17); cl1(1), cl2(17), cl3(15), cl4(4)

KIDAHO, RUCA, 3096, 3177-78, 3180-81, 3247-48, 3250, 3377, 3382, 3384, 3393, 3478, 3552, 4545, 4547, 4550-52, 4579, 4587-90, 4592, 4616, 4633, 4667-70, 4792-93, 4796, 4799, 4800, 4825-27

### OTU 9 "Butare"

M(24), F(33), sex?(1); cl1(6), cl2(36), cl3(22), cl4(9)

BUTARE, KMMA, M 262, M 267, M 283, M 302, M1017, 1036-37, 1046, 1048, 1055-56, 21204, 23197, 23198, 38778  
 GAKURAZO, KMMA, 74.020.M98, 74.020.M101, 74.020.M106  
 GASARENDA, KMMA, 74.020.M1020, 74.020.M1023, 74.020.M310,  
 GITESI, KMMA, 74.020.M163, 74.020.M164  
 GITOVU, KMMA, 74.020.M96, 74.020.M97  
 KAYOVE, RUCA, 4120, 5276, 5283-86  
 KIBUYE, KMMA, 80.55.M.221  
 KIGOMBE, KMMA, 74.020.M.120, 74.020.M.130, 74.020.M.140, 74.020.M.148, 74.020.M.151, 74.020.M.153, 74.020.M.155, 74.020.M.156  
 KIKONGO, KMMA, 820.11.M.412  
 KITABI, RUCA, 1012-13, 1018-19, 1022, R867, R890, R891, R912, R914, R921, R928, R955, R966, R972, R973, R975, R992, R993, R995, R996, R997,  
 MAMBA, KMMA, 74.020.M.298, 74.020.M.299  
 NYANGE, RUCA, 1955, 1996, 2013, 2014, 2036  
 RUKANDE, KMMA, 74.020.M.294  
 RWASAVE, KMMA, 74.020.M.300  
 TARE, KMMA, 74.020.M.307

### OTU 9.1 "Rwanda E."

M(16), F(9), sex?(2); cl1(3), cl2(14), cl3(10)

KABUGA, KBIN, 16162  
 KABUYE, RUCA, 5375, 5379  
 MASAKA, BMNH, 11.12.3.224  
 MUHAZI, KMMA, 38873  
 KMMA, 74.020.M.108

RUKIRA,	RUCA,	1571, 1604, 1695, 1697, 1770, 1791, 3940, 3965, 3984, 3985, 4016, 4040
RULIBA,	RUCA,	5331, 5336-37, 5350, 5362-63, 5369, 5384

**OTU 10 "Uwinka" (Nyungwe Forest)**

M(37), F(17), sex?(6); cl1(4), cl2(28), cl3(24), cl4(4)

GATAKA,	KMMA,	74.020.M.232, 74.020.M.234, 74.020.M.235, 74.020.M.247
KAGANO,	KMMA,	74.020.M.219
KIGAMBA,	KBIN,	19887
LUNGWE,	KMMA,	20684
NTANGO,	RUCA,	2502, 2504-05, 2507-08, 2510, 2551-53, 2559, 2562, 2564
ROUTABANSOUGERA,	RUCA,	4195, 4214, 4216, 4232-33, 4235-36, 4245-46, 4248-49, 4251, 4278, 4286, 4288-90, 4293, 4315-16, 4321, 4349- 50, 4360, 4363
UWINKA,	KMMA,	74.020.M.209, 74.020.M.1003
	RUCA,	R148, R149, R152, R154, R169, R170, R174, R188, R208, 2066, 2146, 2148, 2153, 2241, 2251, 2288

**OTU 11 "Congo S."**

M(18), F(12), sex?(5); cl1(10), cl2(21), cl3(6), cl4(1)

CHISHIMBI,	AMNH,	161457, 161458
DILOLO,	KMMA,	11639, 28939
DUNDO,	BMNH,	63.1110
KAFUBU,	KBIN,	18745
KAZIBA,	KBIN,	11176
KIFUMRUANSI (riv.),	KMMA,	23583
KISWISHI,	KMMA,	23763
KOMI,	KMMA,	9946
KONGOLO,	KMMA,	19392
LUBUMBASHI,	KMMA,	23118
LUKOLELA,	AMNH,	86888
LULUABOURG,	BMNH,	2676
	KMMA,	7157, 7159, 7162
	AMNH,	86186
LUWOHOSHI,	KMMA,	23759
MUBALE,	KBIN,	11174
MUKANA,	KBIN,	11175
MUKULI,	AMNH,	55736, 55737
MUNAMA,	KBIN,	14876
MWINILUNGA,	BMNH,	39.507-511, 46.560-562
NGOME,	RUCA,	1549
SOLWESI,	BMNH,	50.929, 50.930, 59.103, 59.104
TSHUAPA,	KMMA,	9208

**OTU 12 "Gilo" (Imatong Mts)**

M(55), F(55); cl1(23), cl2(54), cl3(27), cl4(6)

GILO,	SMNS,	27084-88, 27091-99, 27100-102, 27104-109, 27115-116, 27990, 27992, 27994, 27996, 28001, 28004-05, 28007-08, 28010-11, 28014, 28028-29, 28035-36, 28041, 28044, 28054, 28056, 30065, 30539, 30540-42
KATIRE,	SMNS,	28016, 28018-19, 28021, 28023-24, 28026, 28061-62, 28066
KINYETI,	SMNS,	30009-14, 30528, 30531-33, 30535-37
NAGISHOT,	SMNS,	27074-78, 27080-81, 30017-22, 30025-31, 30544-51, 30554-55, 30557-59, 30561
TALANGA,	SMNS,	27110, 28059, 28064

**OTU 13 "Iwatoka"**

M(7), F(6), sex?(4); cl1(3), cl2(4), cl3(7), cl4(2), cl7(1)

IWATOKA,	SMNS,	30562-67
KAJIKO,	SMNS,	27113, 27114, 28093, 28095,
WATOKA,	SMNS,	28080-82, 28087-89, 28092,

**OTU 15 "Rutshuru"**

M(25), F(16), sex?(5); cl1(5), cl2(19), cl3(20), cl4(2)

RUTSHURU,	AMNH, 82722,
	BMNH, 11.12.3.418, 11.12.3.420-421, 11.12.3.426, 11.12.3.430,
	11.12.3.432, 11.12.3.435-437
	KBIN, 4489, 4490, 4495, 4498,
	KMMA, 820.11.M.373-376, 820.11.M.378-381, 820.11.M.383,
	820.11.M.444-446, 820.11.M.450-455, 820.11.M.457-462,
	11853, 13818, 13862, 13968, 13972, 16995, 17003, 17004,
	17016,

**OTU 16 "Kigesi"**

M(21), F(24), sex?(1); cl1(7), cl2(18), cl3(19), cl4(2)

ECHUYA,	BMNH, 63.842-43, 63.845, 63.847, 63.849-51
KAMIKONI,	KMMA, 820.11.M408,
KIDUKA,	BMNH, 11.12.3.460-461
KIGESI,	BMNH, 11.12.3.225, 11.12.3.236-37, 11.12.3.529-30,
	11.12.3.533, 11.12.3.535-36, 63.852-53, 63.855, 63.857-
	60, 63.862-65,
	FMNH, 157756,
KIRWA,	AMNH, 89857-60,
KUMBA,	BMNH, 11.12.3.450
MPALO,	AMNH, 89863,
MUTANDA,	BMNH, 11.12.3.445-449, 11.12.3.452-455
MUVO,	KMMA, 820.11.M.424

**OTU 17 "Uganda"**

M(9), F(6); cl1(1), cl2(6), cl3(6), cl4(2)

ENTEbbe,	BMNH, 11.12.3.462, 64.563-564, 64.566-568,
KAMPALA,	BMNH, 66.1277, 66.1279, 66.1283-1284, 66.1286-1288,
	66.1295-1296,
MABIRA,	MCZC, 40799,
ZIKA,	BMNH, 64.556-560, 64.562,

**OTU 17.1 "Bugala Isl."**

M(5), F(8); cl1(2), cl2(6), cl3(4), cl4(1)

BUGALA,	BMNH, 67.1384, 67.1385, 67.1389, 67.1390, 67.1391, 67.1393,
	67.1395, 67.1399, 67.1401, 71.1066, 71.1070, 71.1071,
	71.1072

**OTU 18 "Elgon Mt"**

M(9), F(4), sex?(1); cl1(1), cl2(9), cl3(4)

BENET,	BMNH, 6331, 6332
ELGON Mt.,	BMNH, 10.4.1.1.149, 36.3.16.27A
	KMMA, 5152-54
ELGONYI,	BMNH, 10.4.1.161-164, 10.4.1.169-171
KOITOGOSH,	BMNH, 66.3727
NALASANYI,	BMNH, 11.12.3.226, 11.12.3.465

**OTU 19 "Cherangani Hills"**

M(18), F(13); cl1(6), cl2(15), cl3(7), cl4(3)

AROR VALLEY,	BMNH, 71.2014,
KAIBIBICH,	BMNH, 69.455-459, 71.1983, 71.1986-87, 71.1990, 71.1992-93,
	71.1996-98, 71.2000-01,
KAIBOS,	BMNH, 71.2016-2020,
KAMELIGON,	BMNH, 71.2003-2010, 71.2012

**OTU 19.1 "Kaptagat"**

M(3), F(1), sex?(2); cl1(2), cl2(1), cl3(3)

KAPTAGAT,	RUCA, K2, K3, K10-K14,
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**OTU 20 "Solai"**

M(21), F(25), sex?(1); cl1(1), cl2(18), cl3(26), cl4(2)

SOLAI,	BMNH,	11.12.8.58-67, 11.12.8.70-71, 11.12.8.73, 11.12.8.75, 11.12.8.77-80, 11.4.7.95, 11.4.7.97-98, 11.4.7.100-106, 11.4.7.108-109, 65.933-935, 65.938-941, 65.943-949, 65.951, 65.953, 65.955,
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**OTU 21 "Aberdare Range"**

M(14), F(13), sex?(4); cl1(11), cl2(8), cl3(10), cl4(2)

ABERDARE, MOORLAND, RUHURUINI,	RUCA RUCA RUCA,	R28146, R28148-150, R28206-211, R28214-215, R28219, R28221, R28157-158, R28165-169, R28173, R28175, R28179-180, R28182, R28185, R28186, R28190, R28200, R28202,
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**OTU 21.1 "Gatamaiyu"**

M(8), F(3); cl1(2), cl2(5), cl3(4)

GATAMAIYU,	RUCA,	R28439, R28441, R28444, R28453, R28456-57, R28462, R28471, R28489, R28497, R28500,
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**OTU 21.2 "Aberdare Range" (BMNH)**

M(10), F(10); cl2(7), cl3(12), cl4(1)

ABERDARE,	BMNH,	10.5.3.131-132, 10.5.3.134A-B, 10.5.3.135, 10.5.3.138, 10.5.3.140-146, 10.5.3.148, 10.5.3.150, 10.5.3.207-210, 65.963,
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**OTU 22 "Kenya Mt"**

M(21), F(12), sex?(3); cl1(5), cl2(13), cl3(18)

CHOGORI	RUCA	R28509-10, R28512-15, R28517, R28521-22, R28525, R28528, R28535-38, R28542-43, R28592, R28596-97, R28601,
KENYA Mt, METEOR. STATION	RUCA RUCA,	R28137, R28140, R28142, R28368, R28370-71, R28373, R28375, R28379, R28382, R28386,
NM GATE	RUCA	R28401-02, R28407, R28418,

**OTU 22.1 "Kenya Mt" (BMNH)**

M(22), F(11); cl1(2), cl2(18), cl3(13)

FIRMIN HUT, KENYA Mt,	KBIN, BMNH,	18676, 0.2.1.28, 0.2.1.30-31, 11.4.7.107, 73.1155, 73.1160-61, 73.1163-64, 73.1167, 73.1169, 73.1171-74, 73.1183, 73.1185, 78.3205-06, 78.3208-12,
NAROMORU TRACK, SIRIMON TRACK,	HZMB, KBIN, BMNH, BMNH, KBIN,	A21212, 15597, 74.697-98, 62.104, 62.106-107, 18675,

**OTU 23 "Meru Mt"**

M(35), F(15), sex?(1); cl1(8), cl2(18), cl3(19), cl4(6)

MERU Mt,	ZFMK,	60.45-51, 60.54-55, 60.57-61, 60.63-70, 60.72-73, 63.179-180, 63.182-184,
	RUCA,	14295, 14307-09, 14312-13, 14319-29, 14347-48, 14352- 54, 14368,

**OTU 23.1 "Kilimanjaro Mt"**

M(2), F(2), sex?(1); cl2(3), cl3(2)

MWEKA,	RUCA,	14355, 14364, 14378, 14398, 14399,
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**OTU 24 "Ngorongoro Rim"**

M(17), F(12); cl1(4), cl2(22), cl3(3)

NGORONGORO,	AMNH,	55719,
	BMNH,	63.3255, 63.3262, 65.3252, 65.3256-58, 65.3261,
		65.3263, 65.3265, 65.3268-71, 65.3275, 75.1030-37,
		75.1039-43,
	KBIN,	15596,

**OTU 25 "Hanang Mt"**

M(9), F(8), sex?(3); cl2(11), cl3(8), cl4(1)

GERODOM,	RUCA,	7281, 7362, 7366, 7369, 7371, 7388,
HANANG,	RUCA,	7287, 7289, 7293, 7297, 7303, 7313, 7314, 7316, 7318,
		7327, 7328, 7395, 7400, 7404,

**OTU 26 "Usambara E."**

M(33), F(28); cl1(5), cl2(30), cl3(25), cl4(1)

EMAU,	RUCA,	6054, 8110, 8170, 8624,
GOLOGOLO,	RUCA,	7901, 7958, 7963, 8138, 8139, 8552,
MAGAMBA,	RUCA,	7504, 7511, 7516, 7520-21, 7526, 7601, 7611-12, 7619-
		20, 7685-86, 7693, 7699, 7716-19, 7760, 7769, 7826,
		7828, 7927,
MANOLO,	RUCA,	6104, 6143, 7802, 7805, 7809, 7815-16, 7819, 7878,
		7886, 7948, 8040-42, 8117, 8182, 8564, 8567, 8574,
		8597,
VITI,	RUCA,	7555, 7568, 7666-67, 7670, 8523, 8528, 8547,

**OTU 27 "Uluguru Range"**

M(71), F(94); cl1(13), cl2(59), cl3(77), cl4(15), cl?(1)

BONDWA,	RUCA,	T914, T919, T1402, T1427, T1438, T1440, T2390, T4279,
		T4288, T4289, T4290, T4296, 13929, 14454, 14463,
		14464, 14468, 14472, 14487, 14555, 14556, 14557,
		14569, 14570,
KIDEGE,	RUCA,	3283, 3405, 3429,
KIRUGUVUMI,	RUCA,	3328, 3331, 3378, 14392,
MBETE,	RUCA,	922-23, 928, 929, 963, 975-78, 1029-30, 2302, 2308,
		2318, 2321, 2324, 2341, 2343-48, 2356, 2359, 2362,
		2724-27, 2734-36, 2747-49, 2751-55, 2762, 2765-67,
		2770, 3632-33, 3648, 3659, 3661, 3695, 3697, 3704,
		3716, 3730, 4031, 5745-47, 6543, 6599, 6607-08, 6612,
		6621, 6667, 6713, 6722,
MORNINGSIDE,	RUCA,	T898, T899, T900, T904, T936, T1443-45, T4795-98,
		T4803, T4807-08, T4811, 960, 979-987, 999, 1032-33,
		2314, 2316, 2331-33, 2335, 2352-54, 2366, 2368-70,
		3758-61, 3768, 3776, 3781-82, 3784, 12260-63, 12278,
		14444-46, 14566, 14576, 14579,
NYAMBALA,	RUCA,	3416, 3420,

**OTU 28 "Mufindi"**

M(8), F(7); cl1(2), cl2(7), cl3(6)

MUFINDI,	RUCA,	10873, 10876-77, 10882, 10907, 10909, 10914, 10945,
		10972, 10980, 10983, 11000, 11006, 11014, 11030,

**OTU 29 "Peramiho"**

M(9), F(8); cl1(3), cl2(9), cl3(3), cl4(2)

NAKAHUGA,	RUCA,	5861, 5896, 5897,
PERAMIHO,	RUCA,	5793-94, 5802, 5828, 5868, 5870, 5872, 5874, 5892,
		5918, 5933, 5961, 5967, 5968,

**OTU 30 "Rungwe Mt"**

M(34), F(37); cl1(4), cl2(40), cl3(23), cl4(4)

IBUMBA,	RUCA,	6281, 6283, 6288-89, 6293, 6296-97, 6447, 6457, 6470-
		71, 6475, 6477, 6483, 6498, 6505-07, 6510, 6512-13,
		6554, 6558-59, 6561,
RUNGWE,	RUCA,	5943, 6167, 6169-71, 6205, 6220, 6253-54, 6257-58,



SUMA, MCZC, 6260, 6262, 6270-71, 6298, 6301, 6305, 6356-58, 6369,  
 RUCA, 6371-73, 6377, 6387, 6389, 6428-30, 6434-35,  
 26378,  
 6172, 6177-78, 6181, 6185, 6199, 6237, 6316, 6328,  
 6331, 6336, 6439,

**OTU 31 "Ufipa Plateau"**

M(24), F(15), sex?(2); cl1(8), cl2(25), cl3(5), cl4(3)

CHINGOMBE, RUCA, 13201, 13203, 13205, 13239, 13240-43, 13264, 13288-  
 90,  
 MBIZI, BMNH, 58.368, 58.371,  
 RUCA, 13001-03, 13010, 13018, 13021, 13028-29, 13033-34,  
 13037-38, 13043-45, 13086, 13088-90, 13129-30, 13133,  
 13165, 13170, 13188-89, 13218, 13254,

**OTU 32 "Nyika Plateau"**

M(15), F(14), sex?(1); cl1(1), cl2(22), cl3(4), cl4(3)

CHELINDA, TMUS, TM41751, TM41755,  
 CHITIPA, TMUS, TM41741,  
 NYIKA, BMNH, 66.1021-1025, 66.1027-1029, 66.1031-1038, 66.1040-  
 1048, 66.1050-1051,

**OTU 33 "Zomba"**

M(7), F(4), sex?(1); cl1(4), cl2(5), cl3(2), cl4(1)

MBANGE, KBIN, 3177,  
 ZOMBA, AMNH, 162329, 162331, 162333-38, 162340-42,

**OTU 34 *L. flavopunctatus* s.s.**

M(8), F(8); cl1(1), cl2(7), cl3(8)

ADDIS ABEBA, BMNH, 2.9.9.31, 2.9.9.32, 2.9.9.34, 37.2.24.76, 37.2.24.77, 50.57  
 ANKOBER, SMNS, 23892  
 DEBRA MARKOS, BMNH, 28.1.11.118-120  
 MENAGESHA, ZMUM, S165871, S165968-70,  
 SABATA, BMNH, 70.753  
 YAH YAH, BMNH, 2.9.9.35

**OTU 35 *L. melanonyx***

M(9), F(12); cl1(3), cl2(8), cl3(9), cl4(1)

BALE, ZMUM, S162508-513, S162515-520, S162522-526  
 DINSHU, BMNH, 72.1265, 72.1265, 78.947,  
 MHNP, 1972.262,  
 HARENNA, ZMUM, S162507,  
 SHIYA valley, BMNH, 72.1267,

**OTU 36 *L. brunneus***

M(13), F(16); cl1(5), cl2(8), cl3(14), cl4(2)

BELETTA, ZMUM, S164928, S164930-933, S164936-938, S164941-943,  
 S164945, S165961-967, S165975-977  
 BONGA, ZMUM, S165972-974  
 JIMMA, SMNS, 23384, 23385, 23400, 23402,

**OTU 37 *L. brevicaudus***

M(50), F(59), sex?(11); cl1(23), cl2(37), cl3(52), cl4(7), cl?(1)

BALE, ZMUM, S162435, S162437, S162442, S162444, S162448,  
 S162451-452, S162455, S162458, S162462-464,  
 S162466-472, S162474-75, S162477, S162479, S162481,  
 S162484-85, S162488, S162490, S162492-93, S162495-  
 99, S162501, S162503-04, S162530-546, S162593,  
 S162719, S162720, S164482, S164812-820, S164823-82-  
 6, S164848-852, S164920-925,  
 BALE GOBA, SMNS, 23359, 23361-366, 23369-371, 23373-377, 23379, 23899,  
 23900,,

CHILALO, SMNS, 35946-950, 35952-954, 35960, 35964-969  
 GOBA, BMNH, 64.872, 64.873, 76.42, 76.51  
 URGANA, BMNH, 72.1245, 72.1247,

OTU 38 *L.chrysopus* E.

M(25), F(23), sex?(1); cl1(2), cl2(28), cl3(16), cl4(3)

HARENNA, ROMA, ET23, ET31  
 ZMUM, S162410, S162411, S162414-424, S162426-434,  
 S164827-847, S164918, S164919, S164926, S164927,

OTU 39 *L.chrysopus* W.

M(13), F(13), sex?(2); cl1(2), cl2(9), cl3(14), cl4(3)

BELETTA, ZMUM, S164946, S164948, S164950-957  
 SHEKO, ZMUM, S167314-330,

OTU 40 *L.ansorgei*

M(37), F(46), sex?(1); cl1(34), cl2(33), cl3(13), cl4(4)

CRATER TRACK BMNH 65.1373-74, 65.1377-78, 65.1380-81, 65.1385, 65.1386-  
 89, 77.1812-14, 77.1816-17, 77.1819-33, 77.1835-37,  
 77.1839, 77.1842-44, 77.1847, 77.1849-50, 77.1852,  
 77.1856-57, 77.1861-63, 77.1865, 77.1868, 77.1871,  
 77.1873, 77.1876-78, 77.1880, 77.1882, 77.1884,  
 77.1888-89, 77.1892-93, 77.1897-98, 77.1900-01,  
 77.1903-04, 77.1906, 77.1908-12, 77.1914, 77.1916,  
 77.1918-19, 77.1923-24, 77.1926-28, 77.1932, 77.1934,

## APPENDIX 3 : LISTING OF THE COLLECTING LOCALITIES

LOCALITY + (OTU)	CO-ORDINATES	LOCALITY +(OTU)	CO-ORDINATES
ABERDARE Range (21, 21.2)	00.19S-36.42E	KAIBOS (19)	01.12N-35.08E
ADDIS ABEBA (34)	09.02N-38.43E	KAJIKO (13)	03.51N-30.36E
ANKOBER (34)	09.34N-39.43E	KAMELIGON (19)	01.11N-35.07E
AROR Valley (19)	00.57N-35.38E	KAMIKONI (16)	01.16S-29.19E
BAFWASENDE (2)	01.09N-27.12E	KAMPALA (17)	00.19N-32.34E
BALE (35, 37)	07.01N-39.59E	KAPTAGAT (19.1)	00.24N-35.27E
BELETTA (36, 39)	07.32N-36.33E	KARISIMBI (7)	01.31S-29.25E
BENET (18)	01.20N-34.33E	KARISOKE (7)	01.28S-29.29E
BLUKWA (2)	01.44N-30.40E	KATIRE (12)	04.02N-32.47E
BONDWA (27)	07.06S-37.42E	KAYOVE (9)	01.48S-29.21E
BONGA (36)	07.15N-36.14E	KENYA Mt. (22, 22.1)	00.10S-37.19E
BUGALA (17.1)	00.40S-32.20E	KIBUYE (9)	02.03S-29.21E
BUKARABWA (6)	02.20S-28.50E	KIDAHU (8.2)	01.23S-29.47E
BUSHUSHU (6)	02.02S-28.52E	KIDEGE (27)	07.10S-37.30E
BUTA (2)	02.47N-24.50E	KIDUKA (16)	01.15S-29.42E
BUTARE (9)	02.34S-29.43E	KIFUKU (2)	01.26N-29.40E
CHELINDA (32)	10.19S-33.48E	KIFUMRUANSHI river (11)	11.27S-27.51E
CHILALO (37)	07.50N-39.20E	KIGAMBA (10)	03.08S-30.34E
CHINGOMBE (31)	07.45S-31.34E	KIGESI (16)	01.16S-29.45E
CHIRERA (6)	02.14S-28.48E	KIGOMBE (9)	02.30S-29.31E
CHISHIMBA (11)	10.08S-30.55E	KIKONGO (9)	02.30S-29.31E
CHITIPA (32)	04.35S-33.16E	KINIGI (8.1)	01.26S-29.36E
CHOGORI (22)	00.09S-37.24E	KINYETI (12)	03.56N-32.52E
DEBRA MARKOS (34)	10.20N-37.42E	KIRUGUVUMI (27)	07.10S-37.30E
DILOLO (11)	10.42S-22.20E	KIRWA (16)	01.15S-29.38E
DINSHU (35)	07.07N-39.45E	KISANGANI 1A (4)	00.45N-24.40E
DJUGU (2)	01.55N-30.30E	KISANGANI 2A (4)	00.50N-25.15E
DUNDO (11)	07.24S-20.47E	KISANGANI 2B (4)	00.45N-26.20E
ECHUYA (16)	01.15S-29.45E	KISANGANI 3A (4)	00.30N-25.30E
ELGON Mt. (18)	01.20N-34.39E	KISANGANI 3B (4)	00.15N-25.40E
EMAU (26)	04.38S-38.16E	KISANGANI 3C (4)	00.40N-26.00E
ENTEbbe (17)	00.05N-32.29E	KISANGANI 4A (4)	00.15N-25.45E
FIRMIN Hut (22.1)	00.10S-37.19E	KISANGANI 5A (3)	00.15S-24.30E
FOMULAC (6)	02.12S-28.53E	KISANGANI 5B (3)	00.15N-24.50E
GAHINGA (7)	01.24S-29.40E	KISWISHI (11)	11.29S-27.27E
GAKURAZO (9)	02.10S-29.45E	KITABI (9)	02.34S-29.26E
GARAMBA (2)	04.11N-30.00E	KOITOGOSH (18)	01.20N-34.39E
GASARENDA (9)	02.29S-29.34E	KOMI (11)	03.20S-23.48E
GASIZA (7)	01.25S-29.40E	KONGOLO (11)	05.20S-27.00E
GATAKA (10)	02.20S-29.05E	KOTELI (2)	02.51N-24.34E
GATAMAIYU (21.1)	00.59S-36.42E	KUMBA (16)	01.08S-29.54E
GERODOM (25)	04.30S-35.23E	LAIKIPIA (20.1)	00.30N-36.30E
GILO (12)	04.02N-32.51E	LEMERA (6)	02.28S-28.49E
GITESI (9)	02.05S-29.20E	LUBUMBASHI (11)	11.40S-27.28E
GITOVU (9)	02.15S-29.55E	LUKOLELA (11)	00.01S-17.15E
GOBA (37)	06.58N-39.59E	LULUABOURG (11)	05.53S-22.26E
GOLOGOLO (26)	04.48S-38.16E	LUNGWE (10)	03.03S-29.48E
HANANG Mt. (25)	04.28S-35.20E	LUSHALA (6)	02.13S-28.49E
HARENNA (35, 38)	06.42N-39.44E	LUSHEBERE (6)	01.58S-28.54E
IBUMBA (30)	09.09S-33.41E	LUWOHOSHI (11)	11.40S-27.44E
IDJWI Island(6)	02.09S-29.04E	LWIRO (6)	02.17S-28.48E
IMATONGO Mts (12)	04.06N-32.51E	MABIRA (17)	00.28N-32.57E
IRANGI (5)	01.54S-28.28E	MAGAMBA (26)	04.45S-38.17E
IWATOKA (13)	03.45N-30.38E	MAMBA (9)	02.29S-29.56E
JIMMA (36)	07.39N-36.47E	MANOLO (26)	04.36S-38.14E
KABUGA (9.1)	01.56S-30.42E	MASAKA (9.1)	01.59S-30.11E
KABUYE (9.1)	02.00S-30.24E	MASAKO (4)	00.36N-25.13E
KAFUBU (11)	11.45S-27.34E	MBANGE (33)	16.56S-35.14E
KAGANO (10)	02.24S-29.08E	MBETE (27)	06.52S-37.41E
KAHUZI Mt.(6.1)	02.15S-28.41E		
KAIBIBICH (19)	01.11N-35.07E		

LOCALITY + (OTU)	CO-ORDINATES	LOCALITY +(OTU)	CO-ORDINATES
MBIZI (31)	07.52S-31.41E	NYIKA Plateau (32)	10.34S-33.44E
MEDJE (2)	02.25N-27.18E	GA (2)	01.52N-26.23E
MENAGESHA (34)	08.57N-38.33E	PERAMIHO (29)	10.38S-35.28E
METEOR. STATION (22)	00.10S-37.13E	ROUTABANSOUGERA (10)	02.26S-29.11E
MERU Mt. (23)	03.15S-36.45E	RUHURUINI (21)	00.23S-36.49E
MIKENO (7)	01.29S-29.23E	RUKANDE (9)	02.34S-29.43E
MOORLAND (21)	00.28S-36.44E	RUKIRA (9.1)	02.13S-30.35E
MORNINGSIDE (27)	06.53S-37.40E	RUKUMI (7)	01.29S-29.27E
MPALO (16)	01.08S-30.03E	RULIBA (9.1)	01.57S-30.00E
MUBALE (11)	08.44S-26.56E	RUNGWE (30)	09.10S-33.37E
MUFINDI (28)	08.35S-35.20E	RUTSHURU (15)	01.11S-29.27E
MUGANZA (6)	02.22S-28.53E	RWASAVE (9)	02.34S-29.43E
MUGUBA (6)	02.18S-28.36E	SABATA (34)	08.55N-38.40E
MUHABURA (7)	01.22S-29.41E	SHEKO (39)	07.04N-35.30E
MUHAZI (9.1)	01.51S-30.20E	SHIYA Valley (35)	06.57N-39.45E
MUKANA (11)	09.13S-27.07E	SIRIMON Track (22.1)	00.03S-37.17E
MUKULI (11)	07.30S-29.40E	SOLAI (20)	00.06S-37.14E
MUNAMA (11)	11.47S-27.59E	SOLWESI (11)	12.10S-26.24E
MUSHUMANGA (7)	01.23S-29.12E	SUMA (30)	09.10S-33.40E
MUTANDA (16)	01.13S-29.40E	TALANGA (12)	04.01N-32.43E
MUTURA (8)	01.26S-30.28E	TANDALA (1)	03.02N-19.21E
MUVO (16)	01.14S-29.14E	TARE (9)	02.34S-29.41E
MWEKA (23.1)	03.02S-37.20E	TSHIBATI (6)	02.14S-28.48E
MWINILUNGA (11)	11.44S-24.26E	TSHUAPA (11)	03.25S-24.30E
NAGISHOT (12)	04.20N-33.32E	URGANA (37)	06.57N-39.45E
NAKAHUGA (29)	10.39S-35.27E	UWINKA (10)	02.29S-29.12E
NALASANYI (18)	00.51N-33.33E	VISOKE (7)	01.27S-29.30E
NAROMORU Track (22.1)	00.09S-37.12E	VITI (26)	04.44S-38.16E
NGOME (11)	05.03S-18.51E	WATOKA (13)	04.09N-30.40E
NGORONGORO Rim (24)	03.13S-35.31E	YAH YAH (34)	09.55N-38.15E
NM GATE (22)	00.10S-37.09E	YALOSEMBA (1)	02.35N-21.51E
NTANGO (10)	02.36S-29.13E	YANGAMBI (4)	00.47N-24.24E
NYAMBALA (27)	07.10S-37.30E	ZIKA (17)	00.07N-32.32E
NYAMBASHA (6)	02.07S-28.54E	ZOMBA (33)	15.22S-35.22E
NYAMLGIRA (7)	01.25S-29.12E		
NYANGE (9)	02.03S-29.33E		

## APPENDIX 4

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 <sup>1</sup> and cutting edge of upper incisor
M 8 *	INTE	smallest interorbital breadth
M 9 *	ZYGO	zygomatic breadth
M10 *	PALA	smallest palatal breadth
M11 *	UPTÉ	length of upper cheekteeth
M12 *	UPDA	breadth of upper dental arch
M13 *	M <sup>1</sup> BR	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 height
M23 *	ROBR	greatest rostrum breadth
M24	PCPA	distance between coronoid and angular processes

Table 1. A summary of the measurements used in this study. For a full description we refer to VERHEYEN *et al.* (1996). The measurements marked with \* were primarily retained for the multivariate analyses.

## OTU 6 Tshibati

AGE = 1	MALES					sign.	FEMALES					AGE = 1
	N	Mean	Min	Max	SD		N	Mean	Min	Max	SD	
M1	54	29.06	25.90	31.35	0.957	--	34	29.14	26.85	30.35	0.814	M1
M2	60	27.56	24.60	30.05	1.005	--	39	27.49	25.20	29.95	1.062	M2
M3	59	23.17	20.45	25.60	0.957	--	39	23.15	20.90	25.30	0.971	M3
M4	60	11.70	10.20	13.50	0.527	--	39	11.70	10.95	13.35	0.495	M4
M5	60	6.18	5.05	6.95	0.323	--	39	6.12	5.35	6.85	0.361	M5
M6	60	7.43	6.45	8.35	0.386	--	39	7.38	6.55	8.25	0.391	M6
M7	60	8.75	7.75	10.30	0.474	--	39	8.70	7.55	9.80	0.446	M7
M8	60	5.93	5.35	6.40	0.223	--	39	5.95	5.55	6.40	0.208	M8
M9	59	14.11	12.85	15.10	0.536	--	37	14.11	13.00	15.75	0.612	M9
M10	60	2.89	2.50	3.30	0.197	--	39	2.92	2.50	3.45	0.188	M10
M11	60	4.87	4.20	5.25	0.198	--	39	4.85	4.25	5.30	0.208	M11
M12	60	6.51	6.10	7.00	0.203	--	39	6.55	6.05	7.20	0.201	M12
M13	60	1.68	1.50	1.90	0.074	--	39	1.69	1.50	1.90	0.083	M13
M14	60	2.60	2.10	3.00	0.191	--	39	2.62	2.10	3.30	0.224	M14
M15	60	2.67	2.45	3.10	0.142	--	39	2.72	2.40	3.10	0.131	M15
M16	54	11.53	10.00	12.85	0.564	--	35	11.65	10.00	13.20	0.602	M16
M17	60	4.37	4.05	4.75	0.170	--	39	4.36	3.95	4.80	0.197	M17
M18	60	1.35	1.00	1.80	0.174	--	39	1.35	1.05	1.65	0.148	M18
M19	60	5.06	4.70	5.70	0.187	--	39	5.00	4.60	5.40	0.197	M19
M20	60	12.90	12.30	13.60	0.316	--	39	12.92	12.05	13.60	0.334	M20
M21	60	1.16	1.00	1.30	0.069	--	39	1.15	1.00	1.40	0.090	M21
M22	60	6.06	5.40	6.85	0.308	--	39	6.09	5.25	6.75	0.343	M22
M23	60	4.98	4.30	5.55	0.268	--	39	4.97	4.45	5.60	0.259	M23
M24	60	8.33	7.20	9.45	0.500	--	38	8.36	7.20	9.10	0.468	M24
W	26	51.9	30	75	8.8	--	15	50.5	36	61	6.6	W
HB	26	114.3	94	129	8.9	--	15	112.5	90	137	12.0	HB
TL	27	67.0	55	79	6.0	--	13	67.2	59	75	5.0	TL
HF(+n)	27	22.6	20	24	1.01	--	15	22.4	21	24	1.06	HF(+n)
EL	26	16.5	15	18	0.86	--	15	16.4	15	18	0.91	EL

AGE = 2	MALES					sign.	FEMALES					AGE = 2
	N	Mean	Min	Max	SD		N	Mean	Min	Max	SD	
M1	78	29.61	27.95	31.55	0.808	--	60	29.61	27.65	31.40	0.826	M1
M2	83	28.27	26.65	30.10	0.844	--	62	28.15	25.20	30.10	0.912	M2
M3	83	23.90	22.40	25.70	0.740	--	62	23.75	21.20	25.60	0.873	M3
M4	83	11.99	10.50	12.85	0.413	--	62	11.94	11.10	13.00	0.401	M4
M5	83	6.34	5.75	7.25	0.315	--	62	6.27	5.35	6.85	0.298	M5
M6	83	7.62	6.80	8.60	0.354	--	62	7.63	6.80	8.30	0.349	M6
M7	83	9.06	8.15	10.10	0.412	--	62	8.99	8.10	9.75	0.382	M7
M8	83	6.06	5.55	6.60	0.232	--	62	6.02	5.45	6.50	0.224	M8
M9	77	14.67	13.50	15.75	0.519	--	61	14.53	13.65	15.60	0.463	M9
M10	83	3.06	2.65	3.45	0.182	--	62	3.02	2.70	3.45	0.181	M10
M11	83	4.90	4.50	5.20	0.168	--	62	4.91	4.45	5.45	0.197	M11
M12	83	6.72	6.05	7.25	0.212	--	60	6.75	6.30	7.20	0.209	M12
M13	83	1.70	1.55	1.90	0.072	--	62	1.72	1.60	1.90	0.072	M13
M14	83	2.74	2.20	3.20	0.200	--	62	2.73	2.30	3.15	0.218	M14
M15	83	2.75	2.40	3.10	0.146	--	62	2.72	2.45	3.05	0.138	M15
M16	79	11.91	10.95	13.15	0.525	--	60	11.95	10.90	13.35	0.534	M16
M17	83	4.34	4.00	4.75	0.144	--	62	4.37	4.05	4.75	0.144	M17
M18	83	1.33	0.90	1.75	0.190	--	62	1.39	0.75	1.80	0.188	M18
M19	83	5.09	4.65	5.50	0.184	--	62	5.12	4.50	5.75	0.212	M19
M20	83	12.94	12.35	14.10	0.317	--	62	12.99	12.30	13.65	0.324	M20
M21	83	1.22	1.05	1.45	0.089	--	62	1.21	1.10	1.35	0.071	M21
M22	83	6.31	5.65	6.85	0.260	--	62	6.27	5.60	7.20	0.277	M22
M23	83	5.09	4.35	5.60	0.231	--	62	5.05	4.50	5.55	0.220	M23
M24	80	8.70	7.60	9.60	0.419	--	59	8.66	7.20	9.65	0.422	M24
W	35	61.3	46	74	6.9	--	30	57.4	41	76	8.3	W
HB	34	119.9	103	134	8.6	--	29	118.0	102	132	8.7	HB
TL	31	66.5	40	78	9.1	--	24	72.2	34	141	22.8	TL
HF(+n)	35	22.5	21	24	0.89	--	31	22.7	20	25	1.01	HF(+n)
EL	33	16.7	15	19	1.08	--	31	16.9	15	19	1.06	EL

AGE = 3	MALES					sign.	FEMALES					AGE = 3
	N	Mean	Min	Max	SD		N	Mean	Min	Max	SD	
M1	57	30.35	28.30	32.00	0.757	--	60	30.23	27.70	31.85	0.807	M1
M2	62	29.02	26.75	30.30	0.736	--	65	28.87	26.70	30.45	0.810	M2
M3	62	24.66	22.70	26.00	0.700	--	65	24.48	22.15	26.05	0.727	M3
M4	62	12.28	11.00	13.25	0.430	--	65	12.32	11.10	13.25	0.464	M4
M5	62	6.47	5.90	7.00	0.267	--	64	6.49	5.70	7.40	0.338	M5
M6	62	7.92	7.15	8.60	0.297	--	65	7.95	7.15	8.75	0.373	M6
M7	62	9.38	8.60	10.10	0.346	--	65	9.38	8.60	10.60	0.422	M7
M8	62	6.15	5.65	6.60	0.201	--	65	6.13	5.55	6.95	0.265	M8
M9	60	15.06	13.80	16.20	0.522	--	62	15.00	13.10	16.30	0.560	M9
M10	62	3.13	2.75	3.50	0.178	--	65	3.15	2.65	3.60	0.215	M10
M11	62	4.95	4.55	5.35	0.156	--	65	4.93	4.50	5.35	0.192	M11
M12	62	6.93	6.45	7.65	0.211	--	63	6.94	6.50	7.35	0.218	M12
M13	62	1.72	1.60	1.90	0.069	--	65	1.71	1.50	1.85	0.070	M13
M14	62	2.83	2.30	3.40	0.221	--	65	2.82	2.30	3.30	0.218	M14
M15	62	2.84	2.50	3.10	0.148	--	65	2.82	2.45	3.25	0.156	M15
M16	58	12.37	11.10	13.65	0.463	--	60	12.33	10.75	13.60	0.585	M16
M17	62	4.38	4.00	4.80	0.159	--	65	4.37	4.00	4.90	0.179	M17
M18	62	1.37	0.90	1.75	0.166	**	65	1.48	0.80	2.05	0.224	M18
M19	62	5.17	4.65	5.55	0.186	--	65	5.20	4.75	5.65	0.170	M19
M20	62	13.03	12.40	13.65	0.316	--	65	13.08	12.25	13.90	0.332	M20
M21	62	1.25	1.00	1.45	0.087	--	65	1.24	1.10	1.50	0.082	M21
M22	62	6.56	6.00	7.15	0.264	--	65	6.51	5.80	7.15	0.271	M22
M23	62	5.15	4.60	5.55	0.187	--	65	5.19	4.70	5.65	0.224	M23
M24	59	8.98	8.00	9.85	0.356	*	63	8.82	7.85	9.55	0.352	M24
W	27	67.1	54	77	6.7	*	23	62.5	47	78	7.4	W
HB	27	124.2	110	137	7.6	--	23	123.0	105	136	8.9	HB
TL	26	76.3	42	280	42.5	--	19	66.1	47	82	8.5	TL
HF(+n)	28	22.5	15	24	1.77	--	23	22.3	19	24	1.15	HF(+n)
EL	25	17.0	15	19	1.02	--	22	16.9	13	19	1.32	EL

Table 2. Basic statistics of craniometrical and external metrical data of a "speckled" *Lophuromys* population of the Tshibati region (OTU 6) (see App.2). This large population has been split up by sex and age-class so that the influence of sexual dimorphism can be evaluated.

OTU 8 Mutura							OTU 4 Kisangani RB								
age 2+3	N	Mean	Min	Max	SD	CV%	N	Mean	Min	Max	SD	CV%	sign.	%diff means	
M1	103	30.07	27.70	31.75	0.800	2.7	87	27.95	26.25	29.80	0.764	2.7	***	-7.04	
M2	103	28.61	26.35	30.30	0.808	2.8	108	26.67	24.80	28.40	0.766	2.9	***	-6.80	
M3	103	24.19	21.55	25.80	0.777	3.2	104	22.64	20.55	24.00	0.724	3.2	***	-6.41	
M4	103	12.06	11.00	13.00	0.421	3.5	109	11.38	10.25	12.30	0.412	3.6	***	-5.68	
M5	103	6.26	5.55	6.80	0.274	4.4	109	5.91	5.30	6.75	0.320	5.4	***	-5.61	
M6	103	7.80	6.85	8.50	0.313	4.0	109	7.40	6.70	8.15	0.302	4.1	***	-5.06	
M7	103	9.20	8.00	10.10	0.371	4.0	109	8.79	7.80	9.65	0.363	4.1	***	-4.49	
M8	103	6.05	5.55	6.55	0.215	3.6	109	5.55	5.10	6.00	0.203	3.7	***	-8.33	
M9	103	15.11	13.85	16.05	0.469	3.1	106	13.68	12.45	14.90	0.495	3.6	***	-9.46	
M10	103	3.14	2.65	3.60	0.187	5.9	109	3.12	2.65	3.55	0.174	5.6	ns	-	
M11	103	5.07	4.50	5.65	0.208	4.1	109	4.47	4.05	5.00	0.210	4.7	***	-11.71	
M12	103	6.76	6.30	7.30	0.201	3.0	109	6.59	6.05	7.05	0.215	3.3	***	-2.56	
M13	103	1.75	1.45	2.00	0.090	5.1	109	1.65	1.45	1.80	0.071	4.3	***	-5.61	
M14	103	2.87	2.40	3.40	0.191	6.7	109	2.53	2.15	3.00	0.186	7.4	***	-11.92	
M15	103	2.90	2.60	3.25	0.144	5.0	109	2.68	2.40	3.00	0.122	4.5	***	-7.75	
M16	103	12.18	11.00	13.40	0.513	4.2	89	11.05	9.60	12.60	0.500	4.5	***	-9.28	
M17	103	4.47	3.90	4.90	0.185	4.1	108	4.09	3.75	4.55	0.174	4.3	***	-8.62	
M18	102	1.40	0.90	1.85	0.189	13.5	109	1.40	0.90	1.80	0.159	11.4	ns	-	
M19	97	5.20	4.75	5.85	0.198	3.8	108	4.82	4.35	5.30	0.183	3.8	***	-7.30	
M20	103	13.03	12.40	13.80	0.287	2.2	108	12.26	11.65	12.90	0.286	2.3	***	-5.91	
M21	103	1.28	1.10	1.50	0.090	7.0	109	1.02	0.85	1.20	0.079	7.8	***	-20.15	
M22	103	6.61	5.65	7.25	0.325	4.9	109	5.89	5.15	6.35	0.239	4.1	***	-10.95	
M23	103	5.47	4.80	6.20	0.312	5.7	109	4.96	4.25	5.50	0.259	5.2	***	-9.32	
M24	102	8.69	7.85	9.50	0.335	3.9	103	7.72	6.95	8.60	0.327	4.2	***	-11.15	
HB	96	115.0	99	136	6.23	5.4	92	108.9	89	124	6.68	6.1	***	-5.28	
TL	73	65.9	54	76	4.70	7.1	52	61.0	51	72	4.37	7.2	***	-7.43	
HF	95	21.1	19.1	23.3	0.69	3.3	85	18.9	17.2	20.9	0.67	3.5	***	-10.19	
EL	93	17.0	15.1	18.6	0.75	4.4	61	13.5	11.0	16.2	1.27	9.4	***	-20.66	

OTU 4 Kisangani RB							OTU 5 Irangi								
age 2+3	N	Mean	Min	Max	SD	CV%	N	Mean	Min	Max	SD	CV%	sign.	%diff means	
M1	87	27.95	26.25	29.80	0.764	2.7	34	28.64	26.80	30.45	0.843	2.9	***	2.5	
M2	108	26.67	24.80	28.40	0.766	2.9	37	26.97	24.85	28.95	0.904	3.4	*	1.1	
M3	104	22.64	20.55	24.00	0.724	3.2	36	22.92	20.95	24.10	0.841	3.7	ns	-	
M4	109	11.38	10.25	12.30	0.412	3.6	37	11.53	10.75	12.30	0.435	3.8	ns	-	
M5	109	5.91	5.30	6.75	0.320	5.4	37	5.88	5.35	6.50	0.280	4.8	ns	-	
M6	109	7.40	6.70	8.15	0.302	4.1	37	7.32	6.50	8.15	0.371	5.1	ns	-	
M7	109	8.79	7.80	9.65	0.363	4.1	37	8.77	7.80	9.65	0.411	4.7	ns	-	
M8	109	5.55	5.10	6.00	0.203	3.7	37	5.89	5.30	6.35	0.248	4.2	***	6.2	
M9	106	13.68	12.45	14.90	0.495	3.6	37	14.22	13.15	15.45	0.549	3.9	***	3.9	
M10	109	3.12	2.65	3.55	0.174	5.6	37	3.08	2.65	3.50	0.183	5.9	ns	-	
M11	109	4.47	4.05	5.00	0.210	4.7	37	4.63	4.35	5.15	0.223	4.8	***	3.4	
M12	109	6.59	6.05	7.05	0.215	3.3	34	6.68	6.25	7.35	0.218	3.3	*	1.4	
M13	109	1.65	1.45	1.80	0.071	4.3	37	1.66	1.50	1.90	0.084	5.1	ns	-	
M14	109	2.53	2.15	3.00	0.186	7.4	37	2.52	2.20	2.90	0.177	7.0	ns	-	
M15	109	2.68	2.40	3.00	0.122	4.5	37	2.57	2.30	3.00	0.129	5.0	***	-3.8	
M16	89	11.05	9.60	12.60	0.500	4.5	34	11.62	10.40	13.05	0.583	5.0	***	5.2	
M17	108	4.09	3.75	4.55	0.174	4.3	37	4.20	3.80	4.70	0.211	5.0	**	2.6	
M18	109	1.40	0.90	1.80	0.159	11.4	37	1.31	1.00	1.65	0.183	14.0	**	-6.0	
M19	108	4.82	4.35	5.30	0.183	3.8	37	4.91	4.45	5.30	0.186	3.8	**	1.9	
M20	108	12.26	11.65	12.90	0.286	2.3	37	12.77	12.10	13.55	0.350	2.7	***	4.2	
M21	109	1.02	0.85	1.20	0.079	7.8	37	1.13	1.00	1.30	0.072	6.4	***	10.4	
M22	109	5.89	5.15	6.35	0.239	4.1	37	6.03	5.50	6.40	0.234	3.9	**	2.4	
M23	109	4.96	4.25	5.50	0.259	5.2	37	4.78	4.40	5.15	0.195	4.1	***	-3.7	
M24	103	7.72	6.95	8.60	0.327	4.2	36	7.75	7.10	8.40	0.353	4.6	ns	-	

Table 3. Basic statistics of cranial and external metrical data of a typical “speckled” *Lophuromys* population (OTU 8: Mutura; age classes 2+3), compared to our new species *L. dudu* (OTU 4: Kisangani RB; age classes 2+3) and a further comparison between craniometrical data of the latter and our population of Irangi (OTU 5: Irangi; age classes 2+3).

OTU 8 Mutura							OTU 23 Mt Meru							sign.	%diff means
age 2+3	N	Mean	Min	Max	SD	CV%	N	Mean	Min	Max	SD	CV%			
M1	103	30.07	27.70	31.75	0.800	2.7	35	30.45	28.95	31.60	0.648	2.1	***	1.25	
M2	103	28.61	26.35	30.30	0.808	2.8	35	29.26	27.55	30.60	0.692	2.4	***	2.25	
M3	103	24.19	21.55	25.80	0.777	3.2	35	24.91	23.55	26.25	0.649	2.6	***	2.98	
M4	103	12.06	11.00	13.00	0.421	3.5	37	12.58	11.85	13.20	0.312	2.5	***	4.28	
M5	103	6.26	5.55	6.80	0.274	4.4	37	5.94	5.30	6.45	0.278	4.7	***	-5.03	
M6	103	7.80	6.85	8.50	0.313	4.0	37	7.92	7.15	8.45	0.295	3.7	***	1.58	
M7	103	9.20	8.00	10.10	0.371	4.0	37	9.35	8.40	9.90	0.330	3.5	***	1.63	
M8	103	6.05	5.55	6.55	0.215	3.6	37	5.91	5.60	6.40	0.193	3.3	***	-2.32	
M9	103	15.11	13.85	16.05	0.469	3.1	36	14.65	13.95	15.35	0.354	2.4	***	-3.03	
M10	103	3.14	2.65	3.60	0.187	5.9	37	3.12	2.70	3.50	0.183	5.9	ns	-	
M11	103	5.07	4.50	5.65	0.208	4.1	37	5.05	4.65	5.55	0.211	4.2	ns	-	
M12	103	6.76	6.30	7.30	0.201	3.0	37	6.90	6.60	7.20	0.151	2.2	***	2.10	
M13	103	1.75	1.45	2.00	0.090	5.1	37	1.76	1.65	1.95	0.071	4.0	ns	-	
M14	103	2.87	2.40	3.40	0.191	6.7	37	2.69	2.40	2.90	0.124	4.6	***	-6.44	
M15	103	2.90	2.60	3.25	0.144	5.0	37	2.82	2.60	3.05	0.110	3.9	***	-2.66	
M16	103	12.18	11.00	13.40	0.513	4.2	36	12.12	11.30	13.10	0.440	3.6	ns	-	
M17	103	4.47	3.90	4.90	0.185	4.1	37	4.58	4.25	4.85	0.139	3.0	***	2.42	
M18	102	1.40	0.90	1.85	0.189	13.5	37	1.26	0.90	1.45	0.134	10.7	***	-10.61	
M19	97	5.20	4.75	5.85	0.198	3.8	37	5.24	4.90	5.90	0.226	4.3	ns	-	
M20	103	13.03	12.40	13.80	0.287	2.2	37	12.79	12.45	13.15	0.203	1.6	***	-1.84	
M21	103	1.28	1.10	1.50	0.090	7.0	37	1.24	1.15	1.40	0.072	5.8	***	-3.05	
M22	103	6.61	5.65	7.25	0.325	4.9	37	6.30	5.90	6.75	0.186	3.0	***	-4.70	
M23	103	5.47	4.80	6.20	0.312	5.7	37	4.98	4.55	5.30	0.168	3.4	***	-8.99	
M24	102	8.69	7.85	9.50	0.335	3.9	29	8.85	8.20	9.35	0.249	2.8	***	1.79	
HB	96	115.0	99	136	6.23	5.4	37	126.2	112	140	6.58	5.2	***	9.82	
TL	73	65.9	54	76	4.70	7.1	33	70.1	43	81	6.21	8.9	ns	-	
HF	95	21.1	19.1	23.3	0.69	3.3	36	22.5	21.0	24.7	0.74	3.3	***	7.00	
EL	93	17.0	15.1	18.6	0.75	4.4	36	18.7	14.3	22.0	1.77	9.4	***	10.29	

Table 4. Basic statistics of cranial and extern metrical data of a typical "speckled" *Lophuromys* population (OTU 8: Mutura; age classes 2+3) compared to our new species *verhageni* (OTU 23 : Mt Meru; age class 1 excluded).

OTU	TAXON	11	1111111111	1111222222	2233333333	3333333333	3333
OTU 34	<i>flavopunctatus</i> MENAGHESHA ET1	TCCCTTGTCT	TACCCCGTAT	CCCTCACCTT	TAATTACTAT	GGTACTATAT	CCCC
OTU 9	<i>laticeps</i> KIBUYE RW5379	AT.TC..C..	CG...T...	T..A...TCC	.G....A..	.AACACG.GC	ATTT
OTU 4	<i>dudui</i> KISANGANI/RB Z2556	AT.TC..C..	CG...T...	..C...TC.	.G....CC.	.A..AC....	AT.T
OTU 23.1	<i>aquilus</i> MWEKA 14364	ATT..CACT.	...T.TAC.C	T..C...TCC	C..A...CG.	AA..TC....	G..T
OTU 23	<i>verhageni</i> MERU 14313	ATT..C.CT.	C..A.T.C.C	..C...T.C	C..A...C..	.A....G...G..T	
OTU 3	<i>rita</i> KISANGANI/LB Z2575	AT.TC..A..	AG...T.CG.	.T.C...TC.	.G..ATTC	.A..AC.G..	AT.T
OTU 11	<i>rita</i> NGOME KIK1549	AT.TC..C..	AG...T.CG.	.T.C...TCC	..A..TC.C	.A..AC....	AT.T
OTU 19.1	<i>margarettae</i> KAPTAGAT K10	A..TC..C.C	CG.A.T...C	T..CTGT.CC	.....A..	.A..AC....	AT.T
OTU 21	<i>zena</i> ABERDARES R28182	A..TC..C.C	CGTATT...C	..ACT...CC	..A...C..	.A..AC....	AT.T
OTU 21.1	<i>zena</i> ABERDARES R28185	A..TCC..C.C	CGTATTA..C	..ACTG..CC	..A...C..	.A..AC....	AT.T
OTU 22	<i>zena</i> MOUNT KENYA R28382	A..TC..C.C	CGTATT...C	..CTG..CC	..A...C..	.A..AC....	AT.T
	<i>zena</i> MOUNT KENYA R28426	A..TC..C.C	CGTATT...C	..CTG..CC	..A...C..	.A..AC....	AT.T
	<i>zena</i> MOUNT KENYA R28377	A..TC..C.C	CGTATT...C	..ACTG..CC	..A...C..	.A..AC....	AT.T

Table 5. List of the parsimony informative sites of the studied mitochondrial cytochrome *b* DNA fragment for the species *L.dudui* and *L.verhageni* compared against representatives of relevant species (listed are OTU-number, species name, locality and specimen number) in the region. The lower half of the table illustrates the low observed variability within and among populations of *L.zena*, illustrating the likelihood that within species variation can be expected to be low enough to allow species diagnosis using mtDNA sequences, even when based on only one or two specimens. DNA sequences can be obtained from the authors (erik.verheyen@naturalsciences.be)



OTU	TAXON	LOCALITY	NUMBER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
OTU 34	<i>flavopunctatus</i>	MENAGHESHA	ET1		.006	.013	.013	.012	.012	.014	.013	.014	.013	.013	.013	.013	.013	.013	.014	.013	.013	.013	.013	.013	.013
	<i>flavopunctatus</i>	MENAGHESHA	ET6	.015		.012	.012	.011	.011	.012	.012	.013	.013	.011	.013	.012	.012	.012	.013	.012	.012	.012	.012	.012	.012
OTU 9	<i>laticeps</i>	KIBUYE	RW5379	.073	.063		.000	.009	.009	.013	.013	.011	.011	.010	.011	.011	.011	.011	.012	.012	.012	.012	.011	.011	
	<i>laticeps</i>	KIBUYE	RW5377	.073	.063	.000		.009	.009	.013	.013	.011	.011	.010	.011	.011	.011	.011	.012	.012	.012	.012	.011	.011	
OTU 4	<i>dudui</i>	KISANGANI/3A	Z2556	.061	.051	.033	.033		.004	.012	.012	.009	.010	.008	.010	.009	.009	.009	.010	.010	.010	.010	.009	.010	
	<i>dudui</i>	KISANGANI/3A	Z2558	.058	.048	.030	.030	.008		.012	.012	.010	.009	.007	.010	.009	.009	.009	.010	.009	.009	.009	.009	.009	
OTU 23.1	<i>aquilus</i>	MWEKA	14364	.081	.066	.078	.078	.063	.063		.010	.014	.014	.012	.013	.013	.013	.013	.013	.013	.013	.012	.013	.013	
OTU 23	<i>verhageni</i>	MERU	14313	.068	.058	.078	.078	.061	.058	.045		.014	.013	.012	.013	.013	.012	.012	.013	.013	.013	.013	.012	.013	
OTU 3	<i>rita</i>	KISANGANI/5B	Z2575	.081	.071	.053	.053	.035	.038	.081	.081		.004	.007	.012	.012	.012	.012	.013	.012	.012	.012	.012	.012	
	<i>rita</i>	KISANGANI/5B	Z2674	.078	.068	.051	.051	.038	.035	.081	.078	.008		.007	.012	.012	.012	.012	.013	.012	.012	.012	.012	.012	
OTU 11	<i>rita</i>	NGOME	KIK1549	.068	.053	.043	.043	.025	.023	.063	.061	.020	.018		.011	.010	.010	.010	.011	.010	.010	.010	.010	.010	
OTU 19.1	<i>margarettae</i>	KAPTAGAT	K10	.073	.068	.048	.048	.040	.038	.078	.076	.066	.063	.051		.007	.008	.008	.009	.008	.008	.008	.008	.008	
	<i>margarettae</i>	KAPTAGAT	K2	.071	.066	.048	.048	.035	.033	.071	.073	.061	.058	.045	.018		.007	.007	.008	.007	.007	.007	.007	.007	
OTU 21	<i>zena</i>	ABERDARES	R28182	.068	.058	.051	.051	.033	.030	.071	.063	.058	.056	.038	.028	.020		.000	.006	.004	.004	.005	.004	.004	
	<i>zena</i>	ABERDARES	R28169	.068	.058	.051	.051	.033	.030	.071	.063	.058	.056	.038	.028	.020	.000		.006	.004	.004	.005	.004	.004	
	<i>zena</i>	ABERDARES	R28185	.081	.071	.061	.061	.045	.043	.073	.071	.071	.068	.051	.035	.028	.013	.013		.006	.006	.007	.006	.004	
OTU 21.1	<i>zena</i>	GATAMAIYU	R28456	.073	.063	.056	.056	.038	.035	.076	.068	.063	.061	.043	.028	.020	.005	.005	.013		.004	.005	.004	.004	
	<i>zena</i>	GATAMAIYU	R28489	.073	.063	.056	.056	.038	.035	.071	.068	.063	.061	.043	.028	.020	.005	.005	.013	.005		.004	.004	.004	
OTU 22	<i>zena</i>	MOUNT KENYA	R28382	.073	.063	.056	.056	.038	.035	.066	.068	.063	.061	.043	.028	.020	.010	.010	.018	.010	.005		.004	.005	
	<i>zena</i>	MOUNT KENYA	R28426	.071	.061	.053	.053	.035	.033	.073	.066	.061	.058	.040	.025	.018	.008	.008	.015	.008	.008	.008		.004	
	<i>zena</i>	MOUNT KENYA	R28377	.073	.063	.053	.053	.038	.035	.076	.068	.063	.061	.043	.028	.020	.005	.005	.008	.005	.005	.010	.008		

Table 6. Genetic distances for all pairwise comparisons given as uncorrected p-distances (lower triangle) and standard errors (upper triangle).