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Re-evaluation of the *Lophuromys nudicaudus* HELLER, 1911 species-complex with a description of a new species from Zaire (Muridae - Rodentia)

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Abstract

In order to define precisely a new murid species from the Zaire lowland rainforest, a revision of the systematics of the related *Lophuromys nudicaudus* was essential. Analysis of the morphological and metrical data of the types and other museum-specimens showed that *Lophuromys huttereri* sp.nov. is a well-defined species inhabiting probably the greater part of the lowland rainforest of the South-Central faunal region south of the Zaire River.

Lophuromys nudicaudus on the other hand has a zoogeographical distribution covering probably the whole of the West-Central lowland rainforest between the north bank of the Zaire River and the Cross River (Gabon/RioMuni/R.C.A./ Cameroon/ Congo). Since one *nudicaudus* specimen (KMMA 6251) was collected in Basoko, far to the east of this region, it is probable that further collecting will prove it to be also present in the lowland rainforest on the right bank of the Zaire between the Ubangui and the Aruwimi rivers. Finally, there are indications (1) that specimens from the region between the Cross and Sanaga rivers differ sufficiently from typical *nudicaudus* to warrant taxonomical recognition under the subspecific name *tullbergi* and (2) that the Bioko-population, described under the subspecific name *parvulus*, is very close to its mainland counterpart and should therefore be put into synonymy with *tullbergi*.
Keywords: Rodentia, Muridae, *Lophuromys*, systematics, morphology, morphometrics, biogeography, Central Africa.

Resumé

Afin de pouvoir définir avec précision une nouvelle espèce de Muridae de la forêt équatoriale du Zaïre, une révision de la systématique de l'espèce apparentée, *Lophuromys nudicaudus*, s'imposait. L'analyse des données morphologiques et métriques des types et d'autres spécimens muséologiques a montré que *Lophuromys huttereri* sp.nov. est une espèce bien distincte, habitant probablement la plus grande partie de la forêt équatoriale de la région "South-Central", au sud de la rivière Zaïre.

Par contre, l'aire zoogéographique de *Lophuromys nudicaudus* recouvre probablement la totalité de la forêt équatoriale de la région "West-Central" entre la rive droite (septentrionale) de la rivière Zaïre et la rivière Cross (Gabon/Rio Muni/R.C.A./ Cameroun/Congo). Etant donné qu'un spécimen de *nudicaudus* (KMMA 6251) a été récolté à Basoko, situé loin à l'est de cette région, il est probable que des récoltes ultérieures démontreront sa présence également dans la forêt équatoriale de la rive droite du Zaïre entre les rivières Ubangui et Aruwimi. Enfin, certains indices laissent supposer (1) que les spécimens provenant de la région entre les rivières Cross et Sanaga sont suffisamment différents du *nudicaudus* typique pour justifier leur reconnaissance taxinomique sous le nom subspécifique de *tullbergi*, et (2) que la population de Bioko, décrite sous le nom subspécifique de *parvulus*, est très proche de son équivalent continental et devrait, par conséquent, être considérée comme synonyme de *tullbergi*.
Mots-clefs: Rodentia, Muridae, *Lophuromys*, systématique, morphologie, morphométrie, biogéographie, Afrique Centrale.

Introduction

The genus *Lophuromys* PETERS 1874, which represents an aberrant, somewhat isolated taxon within the African murids (ELLERMAN 1941; DIETERLEN 1976; DENYS et al. 1992) encompasses species-complexes with wide-ranging distributions, as well as isolated mountain-dwelling species. *Lophuromys* could provide excellent "marker" taxa to investigate speciation and biogeographical patterns, using molecular techniques such as DNA-sequencing, on condition however that its systematics are well understood and documented. Unfortunately, much confusion continues to persist in murid taxonomy (see MUSSER and CARLETON 1993) and the genus *Lophuromys* is no exception.

For this reason we undertook an exhaustive systematic study of the genus *Lophuromys* by examining all the type-specimens, the extensive reference-material available in scientific institutions and by making complementary collections during field trips to crucial regions of central and eastern Africa. We are confident that this approach will give precise biogeographical information as to possible contact and (or) hybrid zones between taxa, making future sampling more efficient and in the long run provide the framework for a systematic revision of the genus *Lophuromys* in which morphology and molecular data are integrated and balanced.

In 1984 Marc COLYN collected, in an attempt to evaluate the significance of the Zaire River as a zoogeographical barrier, an important series of murid specimens in the vicinity of Kisangani (Zaire). This collection included a

number of *Lophuromys* specimens from the left bank of the Zaire showing resemblances with *Lophuromys nudicaudus*, a species with a known distribution at that time restricted to the West-Central lowland rainforest. A preliminary comparison of these specimens with the type of *Lophuromys nudicaudus* HELLER, 1911 and a limited number of voucher-specimens of this species, revealed the existence of an important amount of odontological and craniological variation. A re-evaluation of the relevant type-specimens and the presently available voucher-specimens, as well as a review of the literature, were needed to come to a balanced opinion as to the systematic status of our Zaire specimens.

Taxonomic context

In 1911 three species of "unspeckled and short-tailed" *Lophuromys* were nearly simultaneously described but *Lophuromys nudicaudus* HELLER precedes by a few months *Lophuromys naso* THOMAS and *Lophuromys tullbergi* MATSCHIE.

HELLER (1911) stresses in his description of *L. nudicaudus* that it differs from the other known species by its smallness, its much harsher fur and the naked aspect of its tail. We have to assume that he was comparing his new species with the other "unspeckled" forms such as *L. sikapusi* (TEMMINCK, 1853), *L. afer* (PETERS, 1866), *L. ansorgei* DE WINTON, 1896 and obviously with *Lophuromys pyrrhus* HELLER, 1911 which he described simultaneously with *nudicaudus*.

THOMAS (1911) compared his new species *L. naso* directly with *L. nudicaudus*. He stated that in size and other characters it is similar but that its teeth are peculiarly cuspidate. As the most distinguishing tooth characters, he mentions that the incisors are a little more thrown forwards and more importantly that the M^1 has small outer accessory cusps very unusually developed. Regarding the skull, he stressed the peculiar slender low muzzle, its flattened upper profile, even concave at a point above the front end of the palatal foramina and anterior zygoma-root, as in *L. nudicaudus*.

MATSCHIE (1911), before describing *Lophuromys sikapusi manteufeli* as a new subspecies from the Muansa-region (Tanzania), had to decide whether *L. afer* (PETERS, 1866) should be considered a synonym of *L. sikapusi* (TEMMINCK, 1853). He compared the arguments of DE POUSARGUES (1896), who thought *afer* to be a synonym of *sikapusi*, a conclusion already formerly reached by JENTINK (1888), with those of TULLBERG (1893). The latter based his opinion solely on 6 *Lophuromys* specimens, collected by SJÖSTEDT in Kitta, Mbonge and Ndian of the Rio del Rey area of the northern coastal region of Cameroon. He concluded that these specimens fit closely the type description of *L. afer* and consequently TULLBERG classified these specimens under this name. However, MATSCHIE (1911), re-examining the same material, decided that the Rio del Rey specimens should be considered to belong to a new species that he described under the name of *Lophuromys tullbergi*. To prove his point, he emphasized that this new species is clearly smaller than *L. afer* and that its M^2 has only 2 external cusps instead of the 3 that can be observed in *afer* and *sikapusi*. Although mentioning *L. nudicaudus* and *L. naso* in his listing of "unspeckled" species, he did not attempt any further comparison with his newly described species. It is also noteworthy that, although having access to new information forwarded to him by his colleague STEHLIN identifying Akropong in Ghana as the type locality of *L. afer*, he continued to consider this species to be different from *L. sikapusi* described from Dabocrom, also situated in Ghana.

SCHWARZ (1920), CABRERA (1929), GOOD (1947) and MONARD (1951) refer only to the existence of *L. nudicaudus* in the Cameroon region but refrain from any taxonomic comment. HATT (1940) on the other hand retains *L. nudicaudus* and *L. naso* as full species and synonymizes *L. tullbergi* with *nudicaudus* although stressing that his opinion on *tullbergi* is "necessarily based on published information alone".

ELLERMAN (1941) in his taxonomic review of the "living Rodents" places *Lophuromys nudicaudus* and *Lophuromys naso* as separate species in an extended *sikapusi*-group and considers *tullbergi* and *afer* to be both synonyms of *L. sikapusi sikapusi*.

MALBRANT & MACLATCHY (1949) give evidence that *Lophuromys nudicaudus* exists in French Equatorial Africa and consider *Lophuromys naso* to be a different species.

PERRET & AELLEN (1956) decide that *L.nudicaudus* cannot be a valid species since in their opinion "les caractères invoqués nous semblent trop variables...". They propose however to retain *nudicaudus* as a subspecies of *L. sikapusi* until more material comes to hand.

VERHEYEN (1964) describes *Lophuromys rahmi*, an "unspeckled short-tailed" species, from the mountainous Kivu region (Zaire). In pelage coloration it resembles strongly young specimens from the *L. sikapusi-ansorgei*-complex but it can easily be characterized by its very short rostrum and small external measurements.

EISENTRAUT (1965) adds from Bioko (= Fernando Poo) the subspecies *parvulus* which at first he considers to belong to the species *Lophuromys sikapusi*. ROSEVEAR (1969) in his "Rodents of West Africa" comes to the conclusion that this subspecies, which he wrongly quoted as being described under the name of *poensis*, should probably be considered to be a subspecies of *L. nudicaudus*. EISENTRAUT (1973) accepts this view, but adds that more material has to be obtained before deciding whether *parvulus* should be retained as a valid subspecies of *nudicaudus*.

PETTER (1967) mentions *nudicaudus* as a subspecies of *sikapusi*.

ROSEVEAR (1969) considers *tullbergi* to be a synonym of *L. nudicaudus* and reviews the diagnostic value of the dental and craniological characters typical for *Lophuromys nudicaudus*. In view of this, it is amazing that MISONNE (1974), while recognizing *L. rahmi* as a valid species, lumps all the other "unspeckled short-tailed" forms into the

species *L. sikapusi* thus ignoring ROSEVEAR's analysis and merely stating that "this species includes markedly different forms, all in need of revision". DIETERLEN (1976), in his general review of the genus *Lophuromys* PETERS 1874, goes into details re-evaluating ROSEVEAR's findings. DIETERLEN (1978) describes the taxon *eisentrauti* from Mount Lefo (Bamenda-Cameroon) which he considers to be a small montane subspecies of *Lophuromys sikapusi*. In order to have a background to evaluate the relationship of this new taxon he simultaneously reviews nearly all the *nudicaudus* material available at that time (about 30 specimens). However, HUTTERER et al. (1992), after comparison with representatives of *L. sikapusi* from the Cameroon region, comes to the conclusion that *eisentrauti* should be accorded full species rank.

VERHEYEN and VAN DER STRAETEN (1980) publish the caryotype of *Lophuromys nudicaudus* and show that it is specifically different from a.o. *Lophuromys sikapusi*. GRANJON (1991) recognizes explicitly that *L. sikapusi* and *L. nudicaudus* are different species.

MUSSER and CARLETON (1993), in their attempt to clarify and update the taxonomy of the murids of the World, recognize *Lophuromys nudicaudus* as a good species and follow DIETERLEN (1978) in his conclusion to synonymise *L. naso* with it; they also include *L. parvulus* in *L. nudicaudus*, without mentioning this explicitly but by including Bioko in the geographical distribution of *nudicaudus*. On the other hand, they continue to consider *L. tullbergi* and *L. eisentrauti* to be synonyms of *L. sikapusi*, thus rejecting for *eisentrauti* the conclusion of HUTTERER et al. (1992).

This review, spanning more than a century, shows that, over the years, no consensus has been achieved regarding the systematic status of all the taxa of "unspeckled and short-tailed" *Lophuromys* involved. Part of this persisting confusion is due to the lack of adequate material. Notwithstanding, we can conclude that it is now firmly established that *Lophuromys nudicaudus* is a good species, clearly differentiated from *L. sikapusi* and *L. rahmi*. It is also evident that the status of *parvulus, tullbergi* and *eisentrauti* remains for the moment questionable.

Material and methods

When visiting the most important musea of the United States and of Europe we had the opportunity to study the main *Lophuromys* collections and all the relevant type specimens. This, together with the African murid collections we gathered over the last decades, allows us to discuss the status of all the taxa involved, to refine the description of *Lophuromys nudicaudus* and to describe a new species from Zaïre.

The material available for study has grown significantly since the reviews by DIETERLEN (1976, 1978). The number of specimens has tripled and the known geographical distribution has been extended considerably eastward. Nearly half of this augmentation is the result of the collecting efforts of Marc COLYN and his research team.

In App. 1.1. and 1.2. the most important data on the specimens examined are recorded. The following acronyms identify the musea and scientific institutions.

ACET	Asociacion Centro de Estudios Tropicales (Sevilla-Spain);
AMNH	American Museum of Natural History (New York - USA);
BMNH	British Museum of Natural History (London - U.K.);
KMMA	Koninklijk Museum voor Midden-Afrika (Tervuren- Belgium);
MHNP	Muséum National d'Histoire Naturelle (Paris - France);
NHMB	Naturhistorisches Museum (Basel - Switserland);
RUCA	(Rijks)Universitair Centrum Antwerpen (Antwerpen - Belgium) (collections to be incorporated in the KMMA);
SMNS	Staatliches Museum für Naturkunde (Stuttgart - Germany);
USNM	United States National Museum (Washington D.C. - USA);
UUZM	Uppsala Universitets Zoologiska Museum (Uppsala - Sweden);
ZFMK	Zoologisches Forschungsinstitut und Museum Alexander Koenig (Bonn - Germany);
ZMHB	Zoologisches Museum der Humboldt-Universität (Berlin - Germany).

Fig. 1 gives an overall view of the geographical distribution of the specimens and types studied. Appendix 3 summarizes the co-ordinates of the collecting sites, as well as the approximate altitudes; in a separate column the collecting localities are grouped in OTU's as used in our statistical analyses. The following operational taxonomical units are based on zoogeographical considerations.

OTU 1:	localities between the Cross and Sanaga rivers;
OTU 2:	localities on Bioko Island;
OTU 3:	localities situated in the coastal river systems of the Nyong, Ntem and Ogouué;
OTU 4:	localities situated in the Sangha and Dja river-systems draining into the Zaire;
OTU 5 :	localities of the Kouilou basin;
OTU 6 :	locality in Zaire on the north bank of the Zaire River;
OTU 7:	localities situated between the south bank of the Zaire-Lualaba and the Lomami River;
OTU 8:	locality in the region of the south bank of the Zaire and the westbank of the Lomami River.

Craniodental and other morphological data will be used in our descriptions and discussions; where necessary, drawings and photographs will complete the description. However, we will emphasize the statistical use of craniometrical data.

REF.NR.	LOCALITY	CO-ORDINATES	ALT.	OTU
1	Adibori	03.10N-16.03E	350	4
2	Alen (Parque Nac., Mt Alen)	01.39N-10.20E	600	3
3	Amadjabe	00.04S-25.17E	450	7
4	Balando	03.58N-16.45E	450	4
5	Bambio	03.57N-16.58E	450	4
6	Basoko	01.13N-23.35E	450	6
7	Batouri	04.26N-14.27E	600	4
8	Bena	04.02S-11.50E	50	5
9	Benito (riv. 15 mi. from mouth)	01.40N-09.45E	50	3
10	Bimba	04.10N-14.07E	600	4
11	Bipindi	03.06N-10.30E	200	3
12	Bitye	03.10N-12.20E	600	4
13	Bonyoma	03.36N-08.45E	450	2
14	Buea	04.09N-09.13E	1000	1
15	Buea (5 km. S.E. of)	04.06N-09.15E	600	1
16	Djolimpoum	03.20N-12.52E	650	4
17	Djomedjo	03.05N-13.36E	550	4
18	Efulen	02.47N-10.32E	500	3
19	Ekom	03.20N-13.03E	650	4
20	Eseka (5 km. S.E. of)	03.37N-10.45E	400	3
21	Kitta	04.56N-09.05E	100	1
22	Kongana	02.47N-16.25E	350	4
23	Koto Barombi	04.28N-09.15E	100	1
24	La Maboke	04.00N-17.53E	450	4
25	La Makande	00.41S-11.55E	200	3
26	Lidjimbo (upper Sangha)	01/02N-16/17E	450	4
27	Lobe	05.09N-09.10E	500	1
28	Londo	03.37N-17.04E	450	4
29	Mbonge	04.35N-09.10E	100	1
30	Menzale (16 km. W. of Makokou)	00.34N-12.40E	600	3
31	Mieri	04.14N-13.58E	600	4
32	Mocatal (Fernando Poo-Bioko)	03.20N-08.40E	1200	2
33	Mueli (Mt. Cameroun-N. side)	04.23N-09.07E	600	1
34	Ndele	00.51N-21.05E	300	8
35	N'Dian	04.57N-08.52E	50	1
36	Obala	03.30N-14.15E	650	4
37	Oban (14m.S.of)	05.15N-08.33E	100	1
38	Ogouma (riv. Nkam)	00.38N-10.50E	300	3
39	Olounou	02.49N-12.08E	550	4
40	Rio del Rey	04.45N-08.40E	50	1
41	Salo 2	03.11N-16.06E	350	4
42	Yaenero	00.12N-24.47E	450	7
43	Yokadouma	03.25N-14.08E	600	4

Appendix 3. – Alphabetical gazetteer of the collecting localities of the specimens of *Lophuromys nudicaudus* and *Lophuromys huttereri* included in this study. The localities are followed by their co-ordinates and approximate altitudes (m). The numbers preceding the localities refer to fig. 1 illustrating the geographical distribution of the *Lophuromys nudicaudus* species-complex. The numbers in the last column refer to the OTU in which each locality falls.

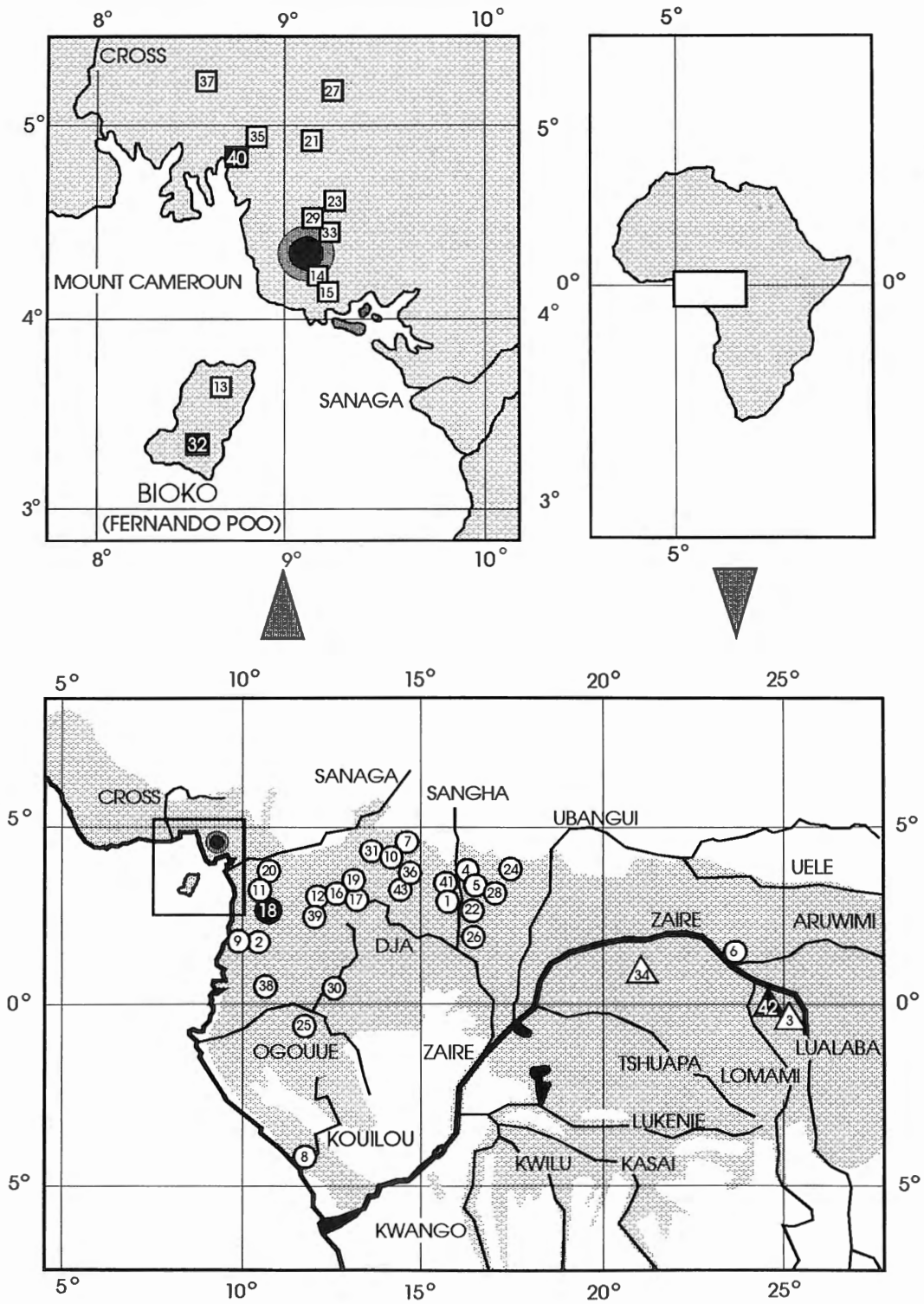


Fig. 1. – The geographical distribution of the *Lophuromys nudicaudus* species-complex. The following symbols characterize the collecting localities of

○ *Lophuromys nudicaudus nudicaudus* HELLER 1911;

□ *Lophuromys nudicaudus tullbergi* MATSCHIE 1911;

△ *Lophuromys huttereri* VERHEYEN, COLYN & HULSELMANS 1996.

The numbers refer to the co-ordinates and altitudes of the localities as described on the opposite page. The symbols filled in with black indicate the type localities.

All specimens and crania are age-classified using stage of tooth eruption and toothwear patterns as described below:

cl. 0: M^3 not yet fully erupted;
cl. 1: all cheekteeth fresh but fully erupted; M^1 and M^2: dentine-surface of 2nd cusp-row not continuous;
cl. 2: light wear; M^1 and M^2: dentine-surface of 2nd cusp-row continuous but in vertical occlusal view width of dentine-surface smaller than or equal to the width of enamel-surface of t_5;
cl. 3: obvious wear; M^1: in occlusal view dentine-surface of t_5 > than remaining enamel-surface; dentine surface of 1st row of cusps not continuous with dentine surface of 2nd row;
cl. 4: wear extensive; M^1: much flattened cusps; 1st and 2nd, or 2nd and 3rd cusp-row communicating; M^2: 1st, 2nd and 3rd cusp-row communicating;
cl. 5: wear severe; M^1: very heavily eroded, concave and all rows communicating; M^2: continuous dentine wear surface.

Taking into account the important morphological variability observed in the cheekteeth of *L. nudicaudus* s.l. (figs. 4, 5, 6), this age-classifying method with its well documented theoretical and practical limitations, becomes even less reliable and can at best be used to give only a general impression. The age-classification was cross-checked by an evaluation of the degree of ossification of the cranial sutures.

In Appendices 4.1. and 4.2. the definition of the 24 craniometrical, dental and 5 external measures is given as well as their acronyms. Our selection of twenty-four craniometrical measurements samples in our opinion rather well the variability of the cranium as a whole and is potentially informative of inter- and intraspecific differences. However, we deliberately gave, for reasons of frequent damage, little attention to the mandibula and it is possible that by doing so we did overlook some valuable metrical information. For the total "skull length" we took some alternative measurements so that skulls slightly damaged at their rostral ends, could still be incorporated in our statistical analyses. All craniometrical measurements were taken with calipers with digital reading graduated to hundreds of millimeters but the measurements were recorded with a precision of 0,05 mm.

The relative scarcity of the available specimens limits our statistical possibilities. Indeed, we have no sufficient sample from one locality permitting a serious evaluation of sexual dimorphism and growth in *Lophuromys nudicaudus*. We have to rely on our experience with other *Lophuromys* species, for which we have examined large samples (*L. sikapusi, L. flavopunctatus* and *L. woosnami*). We usually observed that, where taxonomic studies are concerned, age-classes 0 and 5 should be excluded and sexual dimorphism has only a minor impact. Consequently, since we found that females and males of *L.nudicaudus* are of approximately equal body size and show no clear sexual dimorphism in craniodental morphometry and morphology, we decided to lump male and female specimens.

Basic Statistics, Student-t tests, One-way Analysis of Variance, Student-Newman-Keuls a posteriori test (SOKAL & ROHLF, 1969) and Multiple Discriminant Analysis were performed on a PC with the statistical package STATISTICA 5.0 from StatSoft, Inc. The Principal Component Analysis (MORRISON (1976)) program was originally written in FORTAN by F. Hebrant, and adapted for personal computer by W.Wendelen and J.Hulselmans.

When performing basic statistics and ANOVA-tests we used the whole set of available data except for specimens of age classes cl. 0, cl. 1 and cl. 5. For the multivariate craniometrical analyses we selected our informative sets (age-classes 1 + 2 + 3 + 4) by using only the measurements that we also could retrieve from the type skulls of *L. nudicaudus*, *L. naso*, *L. tullbergi* and *L. parvulus*. Redundant measurements (e.g. of total skull-length) were not included in the analyses.

All the basic data on the studied voucher-specimens, including those of the type-specimens, are grouped in App. 1.1., 1.2., 2.1. and 2.2. The complete listing of the craniometrical data is given in App. 5.1., 5.2., 6.1. and 6.2.

Finally, anyone engaged in revisory activities and describing new species, cannot ignore the theoretical discussions on the different "species"-concepts actually in use. We choose to follow the "cohesion" species-concept as a theoretical background for our studies; for a full discussion and definition of this concept we refer to TEMPLETON (1989).

In the absence of adequate genetical information it is obvious that we will continue to focus our attention on diagnosable morphological and morphometrical divergences between taxa. We are well aware that certain genetical differences or identities within the genus *Lophuromys* will remain undiscovered and consequently that species-diversity will respectively be under- or overestimated.

Results

EXTERNAL MORPHOLOGY AND MORPHOMETRY

DIETERLEN (1976, 1978) and ROSEVEAR (1969) discussed in extenso the external characters differentiating *L. nudicaudus* and *L. sikapusi*.

The relative stiffhairedness of the dorsal region, which is rather typical for most *Lophuromys* species, is pronounced in *L. nudicaudus* and is an excellent character to distinguish it from most forms of the softer haired *sikapusi* species-group. The type specimens of *L. naso*, *L. tullbergi* and *L. parvulus* are as bristly as *nudicaudus*. The difference in hairstiffness between these species-groups is due to a relative difference in hair diameter; for equal length, the hair width in *L. nudicaudus* is about double that in *L. sikapusi*.

The colour of the dorsal pelage of *L. nudicaudus* closely resembles young *sikapusi* and is brownish with a reddish tinge and without speckling. The dorsal coloration of the

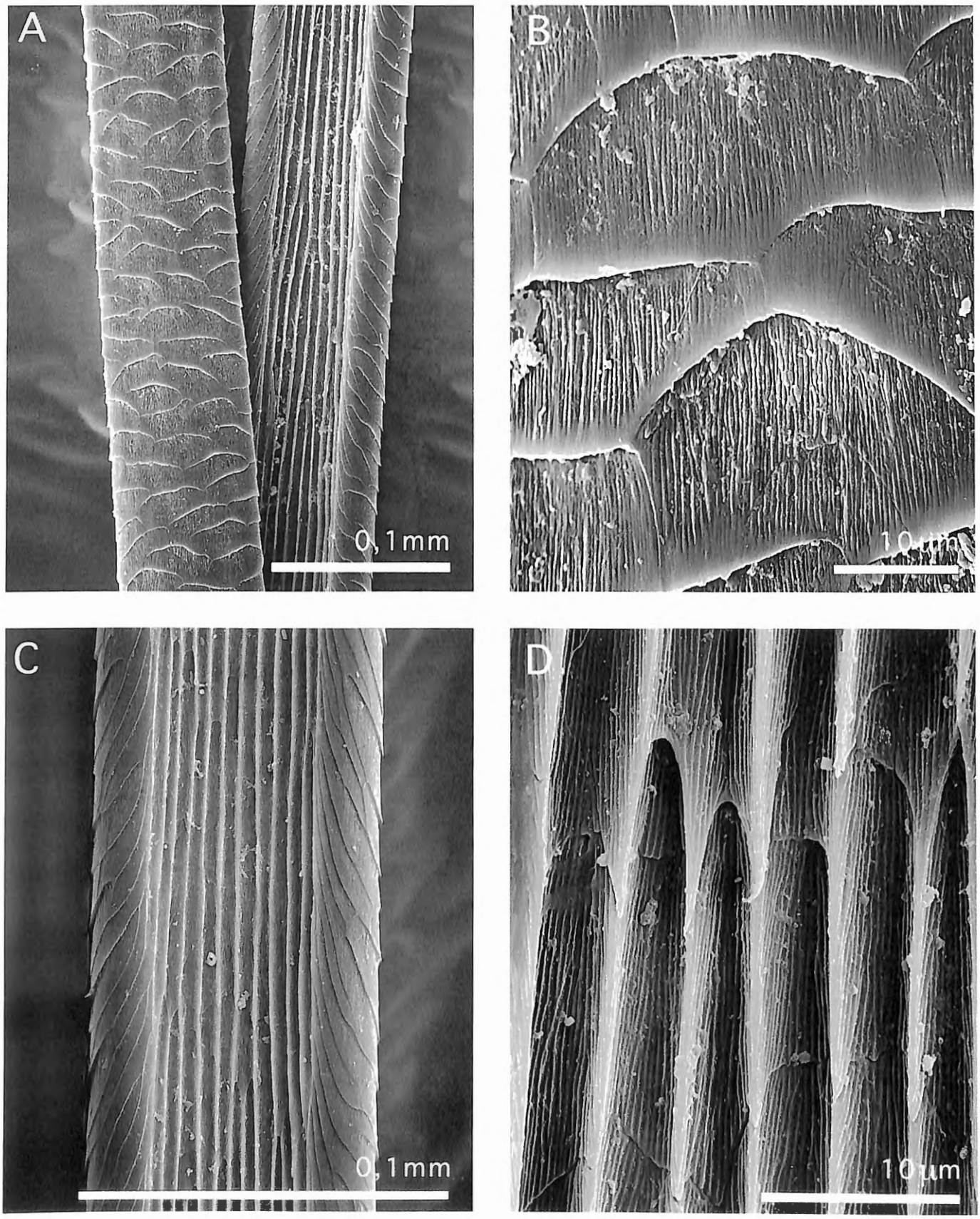


Fig. 2. – Scanning electron micrographs of dorsal hair morphology of *Lophuromys nudicaudus* UUZM 348D (syntype of *tullbergi*). A. General aspect of grooved and ungrooved side of hair. B. Detail of cuticular scaling pattern of ungrooved side. – *Lophuromys huttereri* RUCA Z1.774 (type). C. General aspect of grooved side of hair. D. Detail of cuticular scaling of grooved side.

type-specimen of *naso* is a little clearer, probably due to bleaching, but falls within the observed range of typical *nudicaudus*. The syntype specimens of *L. tullbergi* are very bleached and have lost much of their coloration; from the original description (MATSCHIE 1911) we know that the dorsal pelage was dark brown with an olive brown tone and the ventral side red-yellow. Adult specimens of *L. parvulus* from Bioko seem to be a little darker than the mainland representatives of *nudicaudus* as DIETERLEN (1978) already remarked.

The pelage of the throat, chest and belly of adult *L. nudicaudus* (incl. *parvulus, naso, tullbergi*) is of a striking brillant yellow-red such as often encountered in young *L. sikapusi*, but contrasts rather strongly with the duller coloration of these parts in adult *L. sikapusi*.

The specimens of the type-series of our new species (OTU7) are as stiff-haired as typical *nudicaudus* but the pelage coloration cannot be described since all the specimens were submerged for more than a year in a rusty formaline solution. They have been so thoroughly impregnated that hairs, skin, body-tissues, skull and skeleton have all taken a deep rusty coloration. Fortunately, there is also the well preserved spirit-specimen from Ndele (BMNH 89.441) which shows that the pelage coloration of the specimens of OTU7 is probably similar to typical *nudicaudus*.

The tail of *L. nudicaudus* and the new species of OTU7 is sparingly covered with clearly shorter hairs than typical for representatives of the *sikapusi* species-complex. This "naked" aspect has been noticed since the original description of *nudicaudus* by HELLER (1911) and clearly inspired him when searching for an appropriate name for his new species.

A set of scanning electron micrographs (fig. 2.) illustrates the general structure as well as the cuticular scaling patterns of the dorsal hairs of *Lophuromys nudicaudus* and the OTU7-form. These hairs are characterized by a longitudinal groove with, at its bottom, a series of overlapping coronal scales bearing sets of longitudinal crests closely applied to each other along the longitudinal axis of the hair. On the ungrooved side, the surface of the hair is covered by coronal scales typically shorter than wide and with their irregular angular edges slightly tilted; on the sides of the groove the coronal scales are deflected at angle towards the hair-tip. The coronal scales of both dorsal and ventral sides of the hairs are characterized by a dense longitudinal striation; the striation density on the ungrooved side seems to be a rather variable character. The general morphology of the dorsal hair of *L. sikapusi* corresponds to this description; however, the individual hairs of *L. sikapusi* being narrower, the number of coronal scales across the ungrooved side and the number of longitudinal crests across the grooved side is smaller than what we encountered in *L. nudicaudus* and the OTU7-population.

When compared to the cuticular scaling patterns of African Murids published by KEOGH (1985) we found that *L. nudicaudus*, the OTU7-population and *L. sikapusi* have a hair-morphology resembling most the spiny mice *Acomys spinosissimus* PETERS, 1852 and *Acomys subspinosus* (WATERHOUSE, 1838).

All ten nursing female specimens of the *nudicaudus* species-complex, that we were able to investigate, show 2 pairs of pectoral and 1 pair of inguinal nipples. (*Lophuromys nudicaudus* RUCA JCR412-R.13387-R.13531-R.13633-R.13651; OTU7-populatoin RUCA Z.1665-Z.6616-Z.6764-Z.6889; BMNH 89.441).

According to ROSEVEAR (1969), the female of *L. sikapusi* has 4 nipples (1 abdominal and 1 inguinal pair); potentially this seems to be a good taxonomical character to distinguish between *sikapusi* and *nudicaudus*. Unfortunately, when examining a number of lactating *sikapusi*-specimens from the Cameroon-Gabon-R.C.A.-regions, we noted invariably the same configuration as in *nudicaudus*.

We did not detect, in our spirit-preserved specimens, any further striking morphological differences in hindfoot, forefoot, ear, rhinarium, penis, either within the *nudicaudus*-species complex, or between *nudicaudus* and *sikapusi*.

Concerning the external corporal measurements (table 1) we have to point out primarily that the available data-set is rather limited; secondly, that the external measurements have been taken in the field by different collectors or on material preserved under widely different conditions; thirdly, that ears and tails are often too damaged to be measured. Consequently, this data set is not suited for proper statistical treatment and for taxonomical purposes. Nevertheless, as was to be expected, we can conclude from table1 that weight, total length, head + bodylength increase with age whereas hindfootlength is only slightly influenced by age.

When comparing (table 2) adult specimens of *L. nudicaudus*, the OTU7-specimens and *L.sikapusi,* we see that the minimal values of hindfoot length, head + body-length and weight are higher in *sikapusi* than the maximum values obtained for the other two species. Finally, the corporal measurements of the *L. nudicaudus* species-complex are somewhat bigger than the mountain-dwelling *L. rahmi* from the Kivu-region characterized by the following scores (in mm): for age-classes 2 + 3 + 4 and n = 25; W = 34,1 (28-41); TOL = 155 (143-171); HB = 103 (95-115); TL = 53 (48-62); HF (-n) = 17,2 (15-20); EL = 12,4 (11-15).

CRANIODENTAL MORPHOLOGY

In the past nearly all authors have emphasized that *L. nudicaudus* is a somewhat smaller species than *L. sikapusi*. Several have indicated that not only the size of the skull is important but that there are also some characters with taxonomic value to be considered such as the general profile of the muzzle and zygoma-root. We found that *L. nudicaudus* differs clearly from the *L. sikapusi-ansorgei* species group for the following craniological characters: (1) in every aspect, its rostrum is slenderer; (2) the zygomatic plate is narrower and its anterior border more strongly reclining; (3) the zygomatic

TOOTH-WEAR CLASSES (M + F)		W	Tol	HB	Tl	HF	EL
		NUDICAUDUS					
1	mean	34.5	154.6	96.1	58.8	18.2	13.2
	min - max	30 - 39	143 - 172	87 - 108	51 - 70	17 - 20	11 - 15
	n	2	10	11	10	15	13
2	mean	37.8	167	104.4	62.9	18.7	14.3
	min - max	29 - 52	143 - 185	89 - 119	53 - 74	16,3 - 21	10 - 17
	n	13	19	22	19	22	21
3 + 4	mean	41.7	166.5	108.3	60.2	18.6	14.9
	min - max	35 - 52	145 - 179	90 - 118	47 - 69	17,5 - 20	12,9 - 18
	n	10	14	19	14	22	19
2 + 3 + 4	mean	39.5	166.8	106.2	61.8	18.6	14.6
	min - max	29 - 52	143 - 185	89 - 119	47 - 74	16,3 - 21	10 - 18
	n	23	33	41	33	44	40
		SIKAPUSI					
1	mean	52	189.1	124.6	64.4	23.6	15.6
	min - max	36 - 75	161 - 220	105 - 141	55 - 79	22 - 25	14 - 18
	n	75	55	75	55	62	55
2	mean	68.2	204.6	136.2	68.8	23.9	16.1
	min - max	50 - 89	189 - 223	122 - 152	60 - 81	22 - 25	15 - 18
	n	121	86	123	86	96	85
3	mean	68.5	209.3	138.3	70.9	24	16.4
	min - max	55 - 95	193- 224	125 - 147	63 - 81	23 - 25	15 - 18
	n	38	26	38	26	31	22
4	mean	70.1	213.5	139.8	72.3	24	16.4
	min - max	57 - 80	205 - 231	135 - 149	63 - 82	23 - 25	16 - 17
	n	8	6	8	6	7	5
2 + 3 + 4	mean	68.5	206	136.8	69.5	23.9	16.2
	min - max	50 - 95	189 - 231	122 - 152	60 - 82	22 - 25	15 - 18
	n	165	116	167	116	132	112

Table 1. – External measurements of *Lophuromys nudicaudus* (OTU's 1 + 3 + 4 + 5), compared to *Lophuromys sikapusi* (Mopoyem - Ivory Coast). Only the measurements of specimens of known tooth-wear categories were retained. No statistical analyses have been attempted because of the discrepancies observed in the measuring techniques used by different collectors. (W: weight; Tol: total length; HB: head + body length; Tl: tail length; HF: hind-foot length (- nail); EL: ear length).

TOOTH-WEAR CLASSES	NUDICAUDUS	HUTTERERI	SIKAPUSI
2 + 3 + 4	n = 33 to 44	n = 8 to 11	n = 112 to 167
TOTAL LENGTH	143 - 185	152 - 175	189 - 231
HEAD + BODY LENGTH	89 - 119	93 - 114	122 - 152
HIND-FOOT LENGTH	16,3 - 21,0	18,0 - 20,0	22,0 - 25,0
CLASS 1	17,0 - 20,0	–	22,0 - 25,0

Table 2. – Minimal and maximal values of the external measurements as diagnostic characters to differentiate between *L. nudicaudus* and *L. huttereri* on the one hand and *L. sikapusi* on the other. Only specimens from adult tooth-wear categories (cl. 2-3-4) have been retained except for HF (-n) where we show separately also the values for age cl.1.

process of the maxilla is clearly narrower and (4) the base of the rostrum in its frontal region is more laterally inflated. In these aspects *nudicaudus* even resembles, as already suggested by HATT (1940), the *Lophuromys woosnami-luteogaster* species-complex that inhabits respectively the mountain and lowland forests of Eastern Zaire.

Our new species OTU7 is craniologically related to *nudicaudus* but can easily be characterized by its wider and heavier rostrum and the more proximal implantation of the zygoma-roots on the rostrum (see fig. 3).

The species *L. rahmi* has also a short zygoma-root but is easily differentiated by its very short rostrum. The *L. eisentrauti* type skull has a rostrum and zygoma-root characteristic for the *flavopunctatus* species-complex and is craniologically not related to the *L. nudicaudus* or *L. sikapusi* species-complexes.

Before attempting a short comparative description of the dentition of *L.nudicaudus* s.l. we quote several statements that ELLERMAN (1941) formulated concerning the dentition of the genus *Lophuromys* and that we can endorse fully:

"The cheekteeth are strongly cuspidate, and very variable in both elements and appearance of pattern. This variation seems to be an individual character rather than a specific or racial one."
"... teeth tending to vary in detail individually to a larger extent than in any other genus seen."
"Dentitions characteristic of other genera seem covered by specimens in this genus to a bewildering degree."
"The dentition appears too variable a character on which to base even species in this genus."

This extreme variation exists also in the *L. nudicaudus* species-complex, as is shown by the series of schematic drawings of a number of selected upper dentitions that we group in figs. 5 and 6. The scanning micrographs (fig. 4) of the occlusal surface of the right upper and lower dental row of a young and typical *nudicaudus* specimen will help to visualize this variability better.

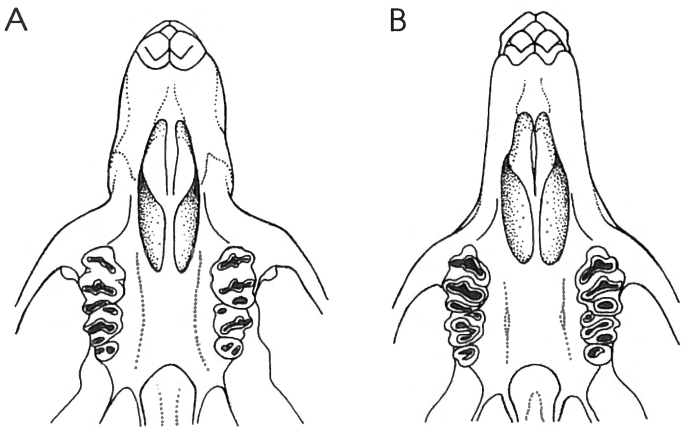


Fig. 3. – Schematic views of the ventral side of the rostra of adult crania of A. *Lophuromys huttereri* (RUCA - Z6619) and B. *Lophuromys nudicaudus* (RUCA - R16029). The skulls are aligned on the anterior borders of the first molars.

Figs. 6.7, 6.8 and 6.9 show that the dental morphology of the type specimens of *L. sikapusi, L. afer* and *L. ansorgei* are of the same general structure. The *L.afer* type is of rather young "dental wear" age, which explains the relatively small skull; there can be no doubt that, on craniodental grounds, *afer* is to be considered synonym of *L. sikapusi*. We draw also attention to the relative importance of t_3 on M^2 in the *sikapusi*-complex in contrast to what we encounter normally in the *nudicaudus-tullbergi-naso-parvulus*-group.

Figs. 5.1 and 5.2 exhibit the maxillary tooth pattern of *Lophuromys nudicaudus* typical for specimens of the OTU's 3-4-5. The molars present the following characters:

M^1: between cusps t_1 and t_2 often a small additional cusp; between cusps t_4 and t_8 a more or less pronounced ridge (t_7); often t_1, t_2, t_3, t_4, t_6 with a more or less pronounced posterior ridge; often additional tubercles between t_1-t_4, t_3-t_6, t_6-t_9 and t_2-t_3;
M^2: t_3 rather reduced and often a more or less pronounced posterior cingulum or cusp;
M^3: very rarely a slight indication of a t_3.

The occlusal surface of the molars of *L. tullbergi* (OTU 1 - figs. 6.1-6.2-6.3) and *L. parvulus* (OTU 2 - figs. 6.4-6.5-6.6) corresponds rather closely to this description except for the lack of additional tubercles on the rim of M^1 and the less pronounced posterior ridges on its main cusps. Compared with specimens of the OTU's 3-4-5 the M^1 of *tullbergi* (OTU 1) and *parvulus* (OTU 2) have a more slender appearance.

The molars of the OTU7-specimens (figs. 5.7-5.8-5.9) compared with typical *L. nudicaudus* are characterized by their slightly heavier and wider build and the nearly or complete absence of a t_3 on M^2. We also draw attention to the very thin enamel ridge forming the posterior side of the t_8 of M^1; this peculiarity, together with the absence of a t_3 on M^2, results, in adult specimens, in the formation of a more or less continuous dental abrasion-surface between M^1 and M^2.

Some of the dentitions in figs. 5 and 6 reveal the variation in a number of more unusual cusp-patterns such as an isolated t_1 in M^1 (fig. 5.3-5.4-6.1); an isolated t_3 in M^1 (fig. 6.5); an isolated t_6 in M^1 (fig.6.1); an isolated t_4 in M^2 (figs. 5.4 and 6.2); a rather well developed t_3 in M^2 (figs. 5.2-5.4-5.6); a strong crista between t_1 and t_4 in M^1 (fig. 5.9); t_3 totally absent on M^2 (figs. 5.5-5.7-6.1).

When Thomas (1911) described *Lophuromys naso*, he stressed the peculiarly cuspidate first molars of his new species. Fig. 5.4 represents a schematic drawing of the right maxillary toothrow of the type-specimen. It is clear that its M^1 combines a rather unique set of unusual traits such as: t_1 isolated from t_2; isolated tubercle (t_7) between t_4 and t_8; accessory tubercles between t_3-t_6 and t_6-t_9 linked to the posterior ridges of respectively t_3 and t_6. Concerning its M^2 we remark that its t_3 is rather well developed and that t_4 is isolated from t_5. However, despite its unique combination of dental characters, we

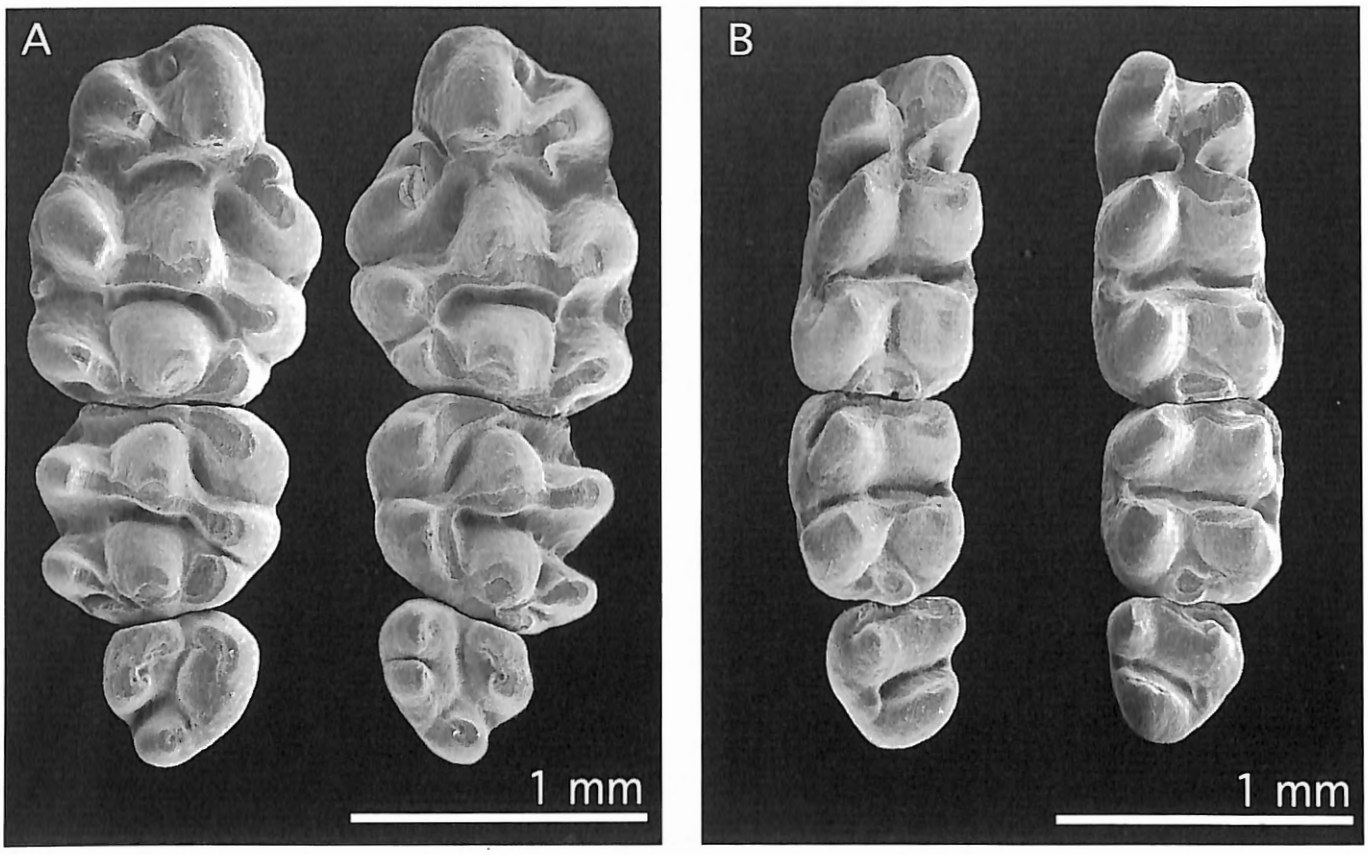


Fig. 4. – Scanning electron micrographs of the upper (A) and lower (B) toothrows of a typical *Lophuromys nudicaudus* specimen (RUCA-R16023). The left and right series are shown to underline the amount of variation in cuspidation that can be observed in one animal.

conclude that *L.naso* falls well within the variational range observed in *Lophuromys nudicaudus*.
Finally, the maxillary toothrows as depicted in figs. 5.5 and 5.6 from respectively Basoko (KMMA 6.251) and Ndele (BMNH 89.441) both in Zaire, seem to be somewhat closer to typical *nudicaudus* than to OTU7; therefore we put them respectively in OTU6 and 8 so that we can plot them as separate entities in our multivariate analyses.

CRANIOMETRICAL ANALYSES
Univariate approach (ANOVA and Basic Statistics)

(Tables 3 and 4)

One-way ANOVA's and SNK-a posteriori tests (details not shown) were calculated on the complete set of untransformed data, excluding age classes 0,1 and 5, and lumping sexes.
When comparing OTU's 1-3-4 only three measurements show a significant difference: skull length (M1) and length of the nasals (M16) each oppose OTU3 to OTU4, while M13 (width of M^1) differentiates OTU3 from OTU1 and M16 (length of nasals) OTU4 from OTU1. Because of the very small number of specimens of OTU1 we hesitate to interpret these results.

On the other hand we see from the data in table 4, summarizing the results on the OTU's 1-3-4-7 and from the SNK-tests, that OTU7 (population between the Lomami and Lualaba) is significantly larger (p h 0.01 to p h 0.001) than the OTU's 1-3-4 for a large number of measurements (M2, M5, M8, M9, M12, M15, M22, M23, M24). Moreover, OTU7 is differentiated from OTU's 3-4 (p h .05 to ph.01) by some other measurements (M1, M4, M10, M21); OTU7 differs only from OTU4 for M6 and M18, M13 also differentiates OTU1 from OTU3 and OTU7 and M16 opposes OTU4 to the others.
In conclusion, it is clearly shown that for most measurements OTU7 differs significantly from the other OTU's. This is an important argument in favour of the description of a new species.

CRANIOMETRICAL ANALYSES
Multivariate approach

In order to maximize the number of specimens and to include the often damaged skulls of the type-specimens of the *nudicaudus* species-complex we limited our original data-set to the following 11 measurements: M4, M6, M8, M11, M13, M14, M15, M17, M21, M22, M23. We also excluded age classes 0 and 5, and specimens with missing data; the original data-set of 100 was thus reduced to 72 specimens.

PRINCIPAL COMPONENT ANALYSIS

(Table 5; figs. 7.1 and 7.2)

To evaluate geographical variation, we executed principal component analyses on (1) the raw untransformed metrical data and (2) the log-transformed metrical data thus reducing size-dependency. OTU's are projected in the planes PC1/PC2 (figs. 7.1 and 7.2.). The overall results for raw data or log-transformed data are identical.

Table 5 summarizes the main results of the principal component analysis. Eigenvalues 1 and 2 account for 70.5% for the raw data and for 59.1% for the log- transformed data. The first principal component shows positive coefficients in eigenvector 1 of both analyses and is positively correlated with the original variables, thus reflecting a size component (REYMENT et al. 1984).
In PCA(raw), PC1 is mostly correlated with M6, M4, M15, M22 and M8. In PCA(log), PC1 is mostly influenced by M14, M15, M4, M6 and M21. Both sets of variables reflect rostrum dimensions.

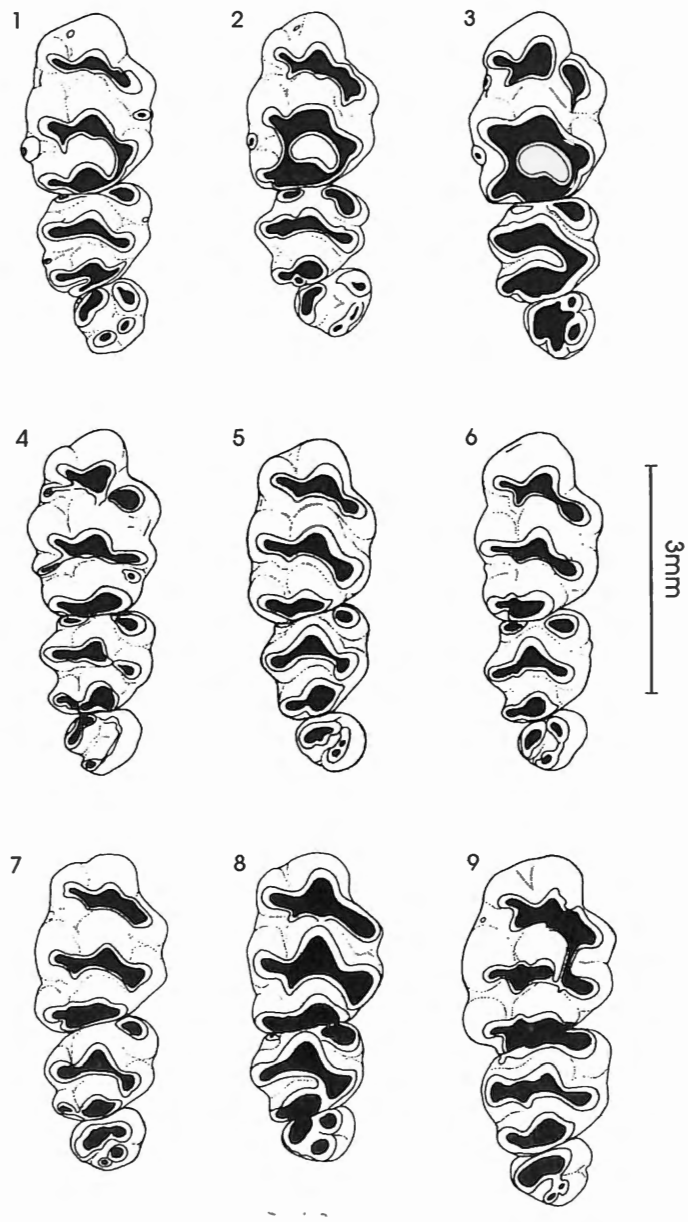


Fig. 5. – Comparative drawings of the right maxillary teeth of *Lophuromys nudicaudus* (1-5) and *Lophuromys huttereri* (6-9).
1. *nudicaudus* RUCA JCR 514; 2. *nudicaudus* RUCA R12416. 3. *nudicaudus* RUCA JCR 508. 4. *naso* BMNH 7.1.1.85 (type); 5. *nudicaudus* KMMA 6.251 (Basoko); 6.*huttereri* BMNH 89.441 (Ndele); 7. *huttereri* RUCA Z1774 (type); 8.*huttereri* RUCA Z6764 (paratype); 9.*huttereri* RUCA Z6889 (paratype).

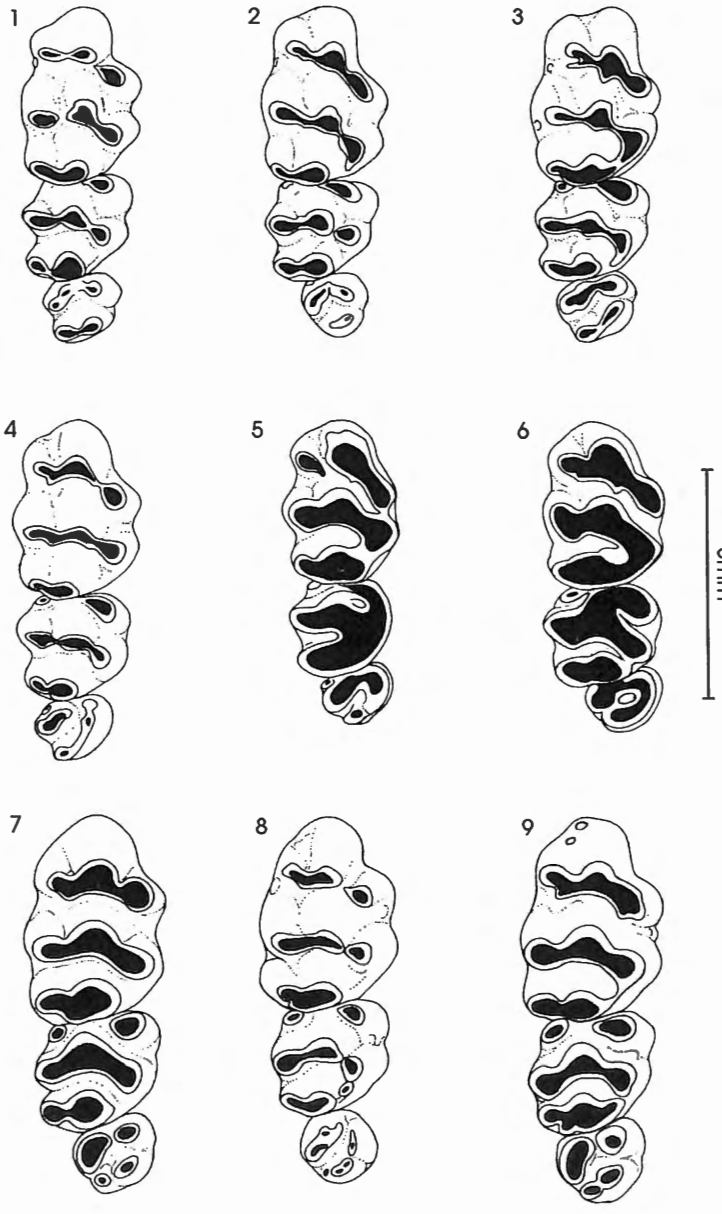


Fig. 6. – Comparative drawings of the right maxillary teeth of *Lophuromys nudicaudus* (1-6) and some type-specimens representative for the *Lophuromys sikapusi* species complex (7-9).
1. *tullbergi* UUZM 348M (syntype); 2. *tullbergi* UUZM 348K (syntype); 3.*tullbergi* UUZM 348L (syntype); 4.*parvulus* MAKB 64481 (paratype); 5.*parvulus* MAKB 64.482 (paratype); 6.*parvulus* (left row in reverse) MAKB 63669 (type); 7.*sikapusi* NHML 25.734 (syntype); 8.*afer* NHMB 4868 (type); 9.*ansorgei* BMNH 96.5.81 (type).

L. nudicaudus (OTU 1)						*L. nudicaudus* (OTU 3)					
VAR	N	MEAN	MIN	MAX	STD	CV%	N	MEAN	MIN	MAX	STD	CV%
M1	3	28,47	27,80	29,25	0,73	2,6	13	28,18	27,60	28,75	0,39	1,4
M2	5	25,94	24,05	27,45	1,23	4,7	14	26,36	25,65	27,10	0,47	1,8
M3	5	22,23	20,80	23,30	0,99	4,5	13	22,43	21,80	23,35	0,49	2,2
M4	5	11,32	10,50	12,05	0,65	5,8	16	11,37	11,00	11,95	0,26	2,3
M5	6	5,42	4,80	5,70	0,33	6,0	15	5,54	5,05	6,20	0,32	5,7
M6	6	7,21	6,60	7,90	0,47	6,5	16	7,09	6,65	7,60	0,27	3,8
M7	6	8,62	8,05	9,45	0,60	7,0	15	8,50	8,10	9,10	0,28	3,3
M8	6	5,98	5,80	6,10	0,14	2,3	15	5,92	5,65	6,10	0,14	2,4
M9	5	13,45	12,30	14,00	0,68	5,0	13	13,45	12,90	14,20	0,42	3,1
M10	6	3,48	3,20	3,75	0,20	5,8	14	3,20	2,90	3,65	0,26	8,0
M11	6	4,34	4,10	4,55	0,19	4,4	16	4,48	4,30	4,70	0,11	2,5
M12	5	6,69	6,50	6,95	0,16	2,4	13	6,85	6,55	7,05	0,12	1,8
M13	6	1,66	1,60	1,75	0,05	3,0	16	1,78	1,65	1,90	0,08	4,5
M14	6	1,78	1,60	2,00	0,15	8,3	16	1,73	1,30	1,90	0,15	8,5
M15	6	2,64	2,35	2,85	0,19	7,3	16	2,58	2,25	2,90	0,18	6,9
M16	5	12,01	11,30	13,00	0,65	5,4	15	11,61	11,00	12,35	0,40	3,4
M17	6	4,26	4,15	4,40	0,10	2,3	16	4,16	3,90	4,45	0,14	3,4
M18	4	1,54	1,25	1,75	0,22	14,1	10	1,41	1,10	1,65	0,20	13,9
M19	5	4,70	4,20	5,30	0,42	9,0	15	4,70	4,25	5,10	0,22	4,6
M20	5	12,15	11,70	12,60	0,34	2,8	15	12,23	11,65	12,65	0,27	2,2
M21	6	1,11	0,90	1,30	0,13	11,6	16	1,02	0,90	1,20	0,08	8,0
M22	6	5,25	4,90	5,70	0,28	5,3	15	5,19	4,95	5,60	0,16	3,2
M23	6	4,50	4,10	4,85	0,28	6,2	15	4,35	3,95	4,90	0,24	5,5
M24	5	6,81	5,80	7,40	0,66	9,7	14	6,83	6,35	7,45	0,34	5,0

L. nudicaudus (OTU 4)						*L. huttereri n. sp.* (OTU 7)					
VAR	N	MEAN	MIN	MAX	STD	CV%	N	MEAN	MIN	MAX	STD	CV%
M1	18	27,64	26,50	29,20	0,77	2,8	7	28,76	28,00	29,90	0,71	2,5
M2	23	25,91	24,60	27,35	0,85	3,3	9	27,18	26,35	28,45	0,71	2,6
M3	21	22,10	20,80	23,30	0,75	3,4	9	22,79	21,90	24,40	0,79	3,5
M4	23	11,25	10,35	12,10	0,50	4,4	10	11,73	11,30	12,05	0,25	2,1
M5	24	5,45	4,95	6,30	0,31	5,6	10	6,15	5,85	6,55	0,22	3,7
M6	24	7,03	6,35	7,65	0,40	5,7	10	7,43	7,05	8,05	0,29	4,0
M7	24	8,43	7,70	9,35	0,43	5,1	10	8,84	8,30	9,55	0,35	4,0
M8	25	5,94	5,65	6,25	0,17	2,8	10	6,28	6,05	6,70	0,20	3,2
M9	25	13,38	12,20	14,10	0,53	4,0	10	14,38	13,70	15,20	0,44	3,1
M10	25	3,21	2,70	3,75	0,26	8,3	10	3,45	3,20	3,75	0,18	5,4
M11	25	4,38	3,90	5,00	0,25	5,7	10	4,44	4,15	4,75	0,19	4,4
M12	24	6,74	6,35	7,05	0,18	2,7	10	7,11	6,75	7,40	0,21	3,0
M13	25	1,72	1,50	1,90	0,09	5,4	10	1,80	1,65	2,00	0,11	6,1
M14	25	1,64	1,25	2,05	0,19	11,8	10	1,76	1,45	1,90	0,13	7,3
M15	24	2,54	2,25	2,90	0,18	7,0	10	2,95	2,75	3,15	0,13	4,3
M16	19	11,22	10,35	12,75	0,62	5,5	8	11,81	11,50	12,40	0,27	2,3
M17	25	4,11	3,65	4,85	0,26	6,3	8	4,25	3,90	4,50	0,22	5,1
M18	24	1,40	1,05	2,05	0,29	20,6	10	1,67	1,40	2,10	0,20	11,8
M19	24	4,64	4,00	5,00	0,21	4,6	10	4,52	4,35	4,70	0,11	2,5
M20	25	12,21	11,65	13,00	0,33	2,7	10	12,14	11,40	12,65	0,37	3,0
M21	25	1,02	0,85	1,25	0,09	9,1	10	1,12	1,05	1,20	0,05	4,3
M22	24	5,16	4,80	5,75	0,25	4,9	10	5,86	5,60	6,15	0,16	2,7
M23	24	4,44	4,05	5,40	0,32	7,1	10	5,14	4,80	5,45	0,22	4,4
M24	21	6,89	6,15	7,50	0,33	4,7	8	7,59	7,20	8,00	0,29	3,9

Table 3. – Basic statistics of *Lophuromys nudicaudus* (OTU 1; OTU 3; OTU 4) and of *Lophuromys huttereri* (OTU 7) for age classes (2 + 3 + 4). The complete set of metrical data can be consulted in App. 5.1. - 5.2. - 6.1. - 6.2. For the definition of the OTU's we refer to Material and Methods and App. 1.1. and 1.2.

	L. nudicaudus ANOVA (OTU's 1 - 3 - 4)							*L. nudicaudus and L. huttereri* n. sp. ANOVA (OTU's 1 - 3 - 4 - 7)						
VAR.	MSB	DF	MSW	DF	F	P	hHOTU	MSB	DF	MSW	DF	F	P	hHOTU
M1	16155,13	2	4184,96	31	3,860	0,032	3hH4	24406,77	3	4315,01	37	5,656	0,003	4hH3,7
M2	9392,58	2	6317,67	39	1,487	0,239		37134,30	3	6090,20	47	6,097	0,001	7hH-
M3	4368,15	2	5067,90	36	0,862	0,431		10504,85	3	5273,49	44	1,992	0,129	
M4	625,24	2	2002,91	41	0,312	0,734		5244,30	3	1754,64	50	2,989	0,040	7hH4,3
M5	438,75	2	979,82	42	0,448	0,642		12657,35	3	896,13	51	14,124	0,000	7hH--
M6	790,87	2	1357,10	43	0,583	0,563		3956,84	3	1271,45	52	3,112	0,034	7hH4
M7	865,24	2	1707,08	42	0,507	0,606		4057,04	3	1626,47	51	2,494	0,070	
M8	96,29	2	242,25	43	0,397	0,674		3173,02	3	269,79	52	11,761	0,000	7hH--
M9	262,39	2	2696,68	40	0,097	0,907		25274,10	3	2556,73	49	9,885	0,000	7hH--
M10	1880,14	2	653,27	42	2,878	0,067		2374,85	3	598,24	51	3,970	0,013	7hH3,4
M11	695,02	2	428,56	44	1,622	0,209		487,04	3	419,75	53	1,160	0,334	
M12	659,41	2	264,25	39	2,495	0,096		3543,21	3	300,58	48	11,788	0,000	7hH--
M13	340,02	2	72,17	44	4,712	0,014	1hH3	346,25	3	80,67	53	4,292	0,009	1hH3,7
M14	643,73	2	304,23	44	2,116	0,133		555,37	3	280,35	53	1,981	0,128	
M15	246,85	2	323,96	43	0,762	0,473		4127,43	3	295,77	52	13,955	0,000	7hH--
M16	14772,69	2	3008,07	36	4,911	0,013	4hH1,3	12342,67	3	2634,01	43	4,686	0,006	4hH--
M17	520,05	2	445,63	44	1,167	0,321		584,38	3	450,15	51	1,298	0,285	
M18	336,28	2	685,22	35	0,491	0,616		1929,51	3	624,83	44	3,088	0,037	7hH4
M19	245,67	2	586,52	41	0,419	0,661		742,01	3	504,15	50	1,472	0,233	
M20	132,56	2	973,79	42	0,136	0,873		237,27	3	1039,25	51	0,228	0,876	
M21	204,25	2	88,93	44	2,297	0,113		325,90	3	77,65	53	4,197	0,010	7hH3,4 1hH4
M22	222,19	2	525,61	42	0,423	0,658		12574,26	3	477,41	51	26,338	0,000	7hH--
M23	593,75	2	830,06	42	0,715	0,495		14468,64	3	771,86	51	18,745	0,000	7hH--
M24	214,35	2	1446,79	37	0,148	0,863		11904,15	3	1353,84	44	8,793	0,000	7hH--

Table 4. – Results of ANOVA (one way) analyses performed on 24 craniodental measurements of age classes (2 + 3 + 4) of *Lophuromys nudicaudus* (OTU's 1 - 3 - 4) and *L.huttereri* (OTU7). OTU's 2, 5, 6 and 8 are not included because their sample-sizes are too small. A posteriori tests (Student, Newman, Keuls) are used to evaluate the differences between OTU's (SOKAL & ROHLF, 1969), indicated by the column h H.

In PCA(raw), PC2 is most positively correlated with M23 and M22 but negatively with M11, M17, M13 and M4, thus opposing rostrum dimensions to tooth-row length. In PCA(log), there is a clear opposition in PC2 between M15, M22 and M23 on the one hand and M14, M11, M13 and M17 on the other hand, thus opposing rostrum dimensions to teeth dimensions.

In conclusion, when evaluating figs 7.1. and 7.2., it is clear (1) that there is no difference between OTU's 1 through 5, (2) that the type specimens of *L. parvulus,* (+Mocatal) do not differentiate from *L. nudicaudus*, (3) that the Basoko specimen coincides with these OTU's and is thus considered to be *L. nudicaudus*. Finally, specimens of OTU7 as well as the Ndele specimen can easily be differentiated from all the others, which underlines the necessity to consider these specimens as belonging to a new species.

DISCRIMINANT ANALYSIS

Analysis of L. nudicaudus (OTU's 1, 3 and 4)

(Table 6.1 and fig. 8.1)

A set of 11 variables and 57 specimens (OTU1 = 9; OTU3 = 21; OTU4 = 27) was analysed, using stepwise forward analysis and finally retaining only the variables M13, M14, M17 and M23 in the discriminant function.

As table 6.1. shows, 93.5% of the total variation is expressed in root 1; Wilks' Lambda (= .526) is rather high; both indicate poor discrimination between OTU's. Looking at fig 8.1 we see that OTU4 is widely dispersed in the plane of root 1 / root 2, which is mainly due to some specimens with high positive scores on root 2. OTU3, including the type specimens of *nudicaudus* and *naso,* completely coincides with OTU4; so, mostly, does OTU5 (Bena) plotted on this graph.

In spite of its small number of specimens, OTU1 (containing the type specimens of *tullbergi)* again tends, as in ANOVA, to differentiate from OTU's 3 and 4 along root 1, opposing M13 (width of M^1) to the other measurements. Also the Mahalanobis distances between OTU1 and OTU's 3 and 4 are significant. This tendency of OTU1 to differentiate from typical *nudicaudus* needs further investigation with e.g. biochemical data, before deciding whether to synonymize *tullbergi* with *nudicaudus* or not. The *parvulus* type specimens, plotted on this graph, fall within the range of OTU1.

DISCRIMINANT ANALYSIS

Analysis of L. sikapusi (OTU C-R-G), L. nudicaudus (OTU's 1-3-4-5) and the OTU7-population

(Table 6.2 and fig. 8.2)

A sample of *L.sikapusi* (n = 53), from the same Cameroon - R.C.Africaine - Gabon region as our *L.nudicaudus* series was included in this analysis in order to evaluate the position of OTU7 relative to both other species. In the stepwise analysis, variable M21 was not retained.
Table 6.2 summarizes the results of this analysis. 94.3% of the total variance is expressed in root 1. Wilks' Lambda (= .051) is close to zero, indicating a highly significant difference between the mean vectors. Mahalanobis' D^2 values are much higher than in the foregoing analysis and are all highly significant; *L. sikapusi* is far more distant from both other species. Fig. 8.2. shows *L. sikapusi* to differ clearly from *nudicaudus* and our new species along the first axis, while the latter differentiates from both *nudicaudus* and *sikapusi* along the second axis. Plotting the Basoko specimen and the *parvulus* types (OTU2) clearly situates them within *nudicaudus* while the Ndele specimen falls between our new species (OTU7) and *nudicaudus.*

DESCRIPTION OF *LOPHUROMYS HUTTERERI* sp.nov.

HOLOTYPE

RUCA Z1774; adult male; specimen in alcohol; pelage and skin strongly coloured by rust; skull complete and also rust-impregnated; collected by Marc COLYN in the first week of January 1984 in Yaenero - Zaire (00°12'N - 24°47'E).

PARATYPES

RUCA Z1665; Z6613; Z6614; Z6616; Z6619; Z6764; Z6766; Z6889; Z6890; 5 adult females and 4 adult males; specimens in alcohol (all deeply impregnated with rust and in rather poor condition); skulls rusty coloured; collected by Marc COLYN between January and April 1984 in Yaenero (Zaïre).

TYPE LOCALITY

The holotype and paratypes were collected in equatorial forest, alt. 450m, near the village Yaenero in Zaïre.

ETYMOLOGY

We dedicate this new species to our colleague and friend Rainer HUTTERER of the Zoologisches Forschungsinstitut und Museum Alexander Koenig in Bonn (Germany) to show our appreciation for his contributions to the taxonomy and zoogeography of the small mammal fauna of Central Africa.

DIAGNOSIS

This new species is morphologically well differentiated from *L. nudicaudus* by its clearly wider and higher rostrum, by the more rostrally situated zygomatic plate when compared to the implantation of its M^1 and by the nearly always totally absent t_3 on its M^2.
Can easily be characterized craniometrically by multivariate statistics (see principal component and canonical analyses - tables 5 and 6; figs. 7 and 8.2.).

DISCUSSION

L. huttereri is a new species of "unspeckled and short-tailed" *Lophuromys*, more related to *L.nudicaudus* than to representatives of the *L. sikapusi* species-complex. This is not only suggested by the general corporal measurements and pelage characters but can easily be demonstrated by a number of craniological, odontological and craniometrical arguments. It is also morphologically very different from *Lophuromys rahmi*, a somewhat smaller specialized species from the mountainous Kivu region and from *Lophuromys eisentrauti*, a *flavopunctatus*-related species endemic to Mount Lefo in the Cameroon highlands.
Comparison of the type specimens with the relevant museum material led us to put *L. naso* in synonymy with *L. nudicaudus*, a conclusion already formerly reached by DIETERLEN (1978) and MUSSER & CARLETON (1993).
The characteristics of pelage, teeth and skull situates *L. huttereri* in the vicinity of *L. nudicaudus* with which it forms a species-complex. The morphological differences between both taxa exceed clearly the level of intraspecific variability as it is observed within comparable situations in small African mammal taxonomy.

Principal Component Analysis (partim)					
	PCA (raw)			PCA (log)	
	PC1	PC2		PC1	PC2
root	0,432	0,134	root	0,00367	0,00185
%	53,8	16,7	%	39,3	19,8
Normalized Eigenvectors					
	PC1	PC2		PC1	PC2
M4	0,6669	−0,3926	M4	0,2158	0,0654
M6	0,5351	−0,0000	M6	0,2701	0,1895
M8	0,2216	0,0506	M8	0,1326	0,1267
M11	0,0390	−0,3217	M11	0,1030	−0,2449
M13	0,0117	−0,1120	M13	0,0580	−0,2740
M14	0,1254	−0,1411	M14	0,6429	−0,6101
M15	0,2249	0,1178	M15	0,4122	0,3884
M17	0,0562	−0,2543	M17	0,1345	−0,1534
M21	0,0704	−0,0406	M21	0,4163	0,2086
M22	0,3246	0,4478	M22	0,2249	0,3270
M23	0,1952	0,6532	M23	0,1539	0,3341
Correlation Variable / Component					
	PC1	PC2		PC1	PC2
M4	0,921	−0,302	M4	0,717	0,154
M6	0,924	−0,000	M6	0,698	0,348
M8	0,672	0,085	M8	0,510	0,346
M11	0,121	−0,556	M11	0,302	−0,510
M13	0,069	−0,366	M13	0,126	−0,421
M14	0,438	−0,274	M14	0,779	−0,531
M15	0,709	0,207	M15	0,728	0,487
M17	0,176	−0,444	M17	0,375	−0,304
M21	0,518	−0,166	M21	0,675	0,240
M22	0,704	0,540	M22	0,557	0,575
M23	0,398	0,742	M23	0,307	0,472

Table 5. – Review of the main results of principal component analyses performed on a data-set of 11 selected craniometrical measurements (raw and log-transformed) of *Lophuromys nudicaudus* and *Lophuromys huttereri*.
For description of the measurements we refer to App. 4.1. and 4.2. and for discussion to the text.

Zoogeographical discussion

The present craniological and craniometrical study of the *Lophuromys nudicaudus* species-complex and the ensuing description of *L. huttereri* provide us with some new information concerning the zoogeography of the lowland rainforest of Central Africa.
The resultant distributional patterns (fig. 1) cover three of the five classical zoogeographical faunal divisions as are currently recognized in Central Africa, namely the "South-Central", "West-Central" and "Cameroon"-regions (COLYN et al., 1991). *L. huttereri* and *L. nudicaudus* occur respectively in the "South-Central" and the "West-Central" - "Cameroon"-regions.
L. huttereri has a known geographical distribution limited to the rainforest situated between the Lomami and Lualaba rivers. The specimen from Ndele (BMNH.89.441) belongs to the new species but, for certain tooth

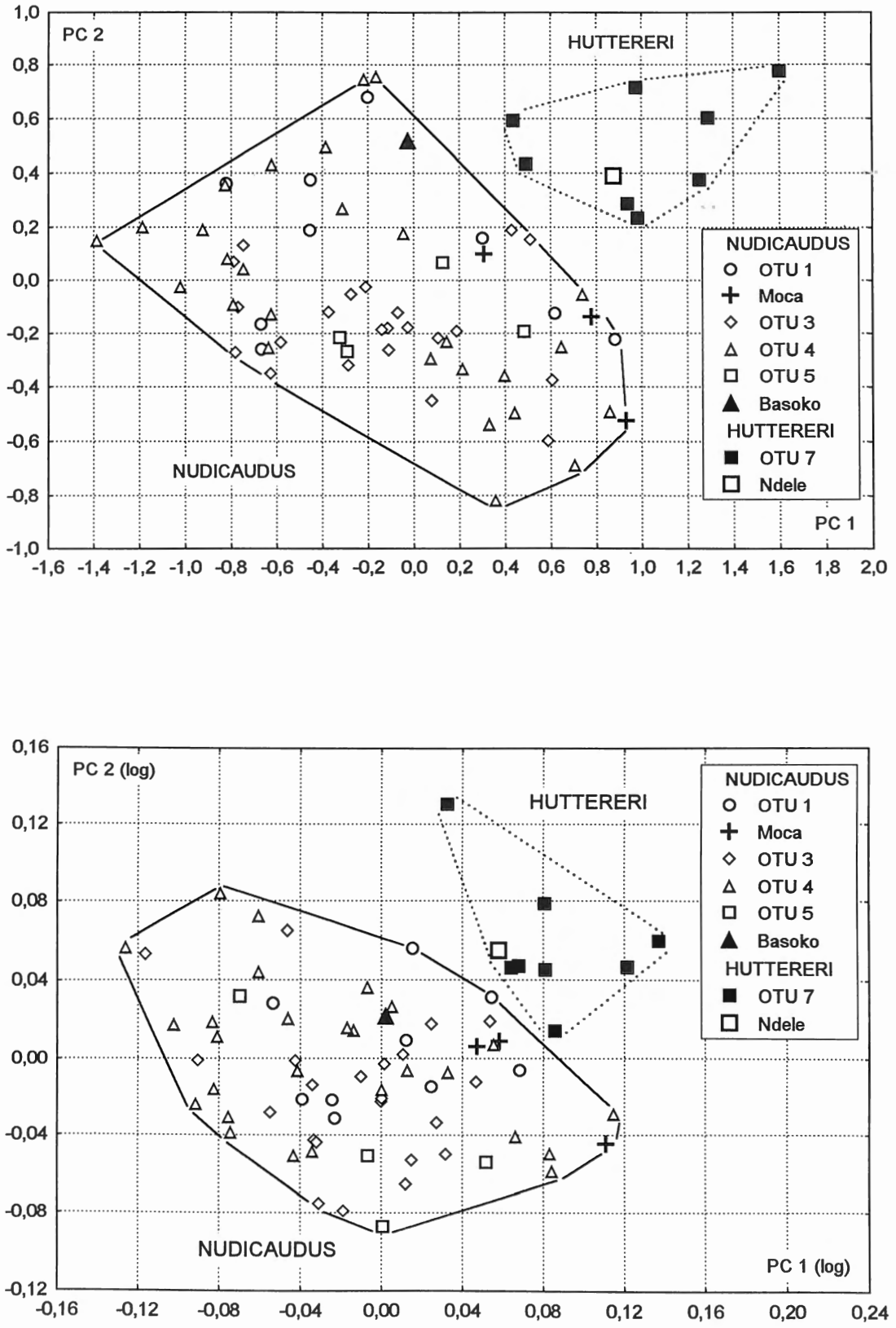


Fig. 7. – Principal component analyses on a data-set of 11 selected craniometrical measurements of *Lophuromys nudicaudus* and *Lophuromys huttereri*.
7.1. Graphical representation based on non-transformed data.
7.2. Graphical representation based on log-transformed data.
For description of the OTU's, see Material and Methods.

Wilks' Lambda: 0,52614

F (8,102) = 4,8276 p < 0,0000 / N = 57

Squared Mahalanobis Distances

GROUP	OTU 1	OTU 3	OTU 4
OTU 1	0,00000	7,209586	4,262228
OTU 3	7,209586	0,000000	0,677931
OTU 4	4,262228	0,677931	0,000000

F-values; df = 4,51 / p-levels

GROUP	OTU 1	OTU 3	OTU 4
OTU 1	-----	9,727219	6,156552
OTU 3	0,000006	-----	1,809454
OTU 4	0,000403	0,141370	-----

Raw Coefficients for Canonical Variables

VARIABLE	ROOT 1	ROOT 2
M13	−0,142661	0,0061
M17	0,030045	0,0295
M23	0,015711	−0,0002
M14	0,018252	0,0307
Constant	2,254870	−18,4174
Eigenval	0,801406	0,0551
Cum.prop	0,935691	1,0000

Wilks' Lambda: 0,05113

F (20,220) = 37,647 p < 0,0000 / N = 122

GROUP	OTU Σ	OTU 7	OTU 9
OTU 1	0,00000	13,90987	45,91427
OTU 7	13,90987	0,00000	36,13828
OTU 9	45,91427	36,13828	0,00000

F-values; df = 10,110 / p-levels

GROUP	OTU Σ	OTU 7	OTU 9
OTU 1	-----	8,06015	118,2306
OTU 7	0,00000	-----	20,6093
OTU 9	0,00000	0,00000	-----

Raw Coefficients for Canonical Variables

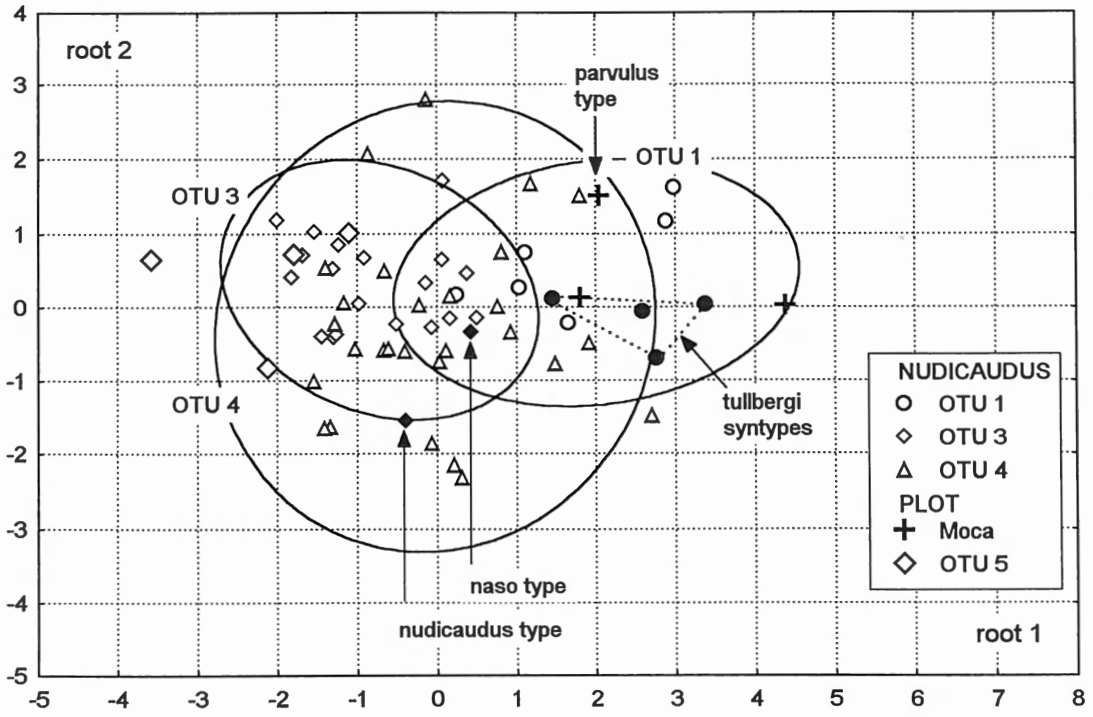
VARIABLE	ROOT 1	ROOT 2
M14	−0,01834	0,02930
M22	−0,03669	−0,00942
M6	0,01363	−0,00605
M11	−0,02407	0,00835
M15	0,00096	−0,03772
M23	−0,00214	−0,01519
M13	0,03600	−0,02511
M8	0,01335	−0,01241
M17	−0,01373	−0,00349
M4	0,00219	0,01011
Constant	15,97607	18,80955
Eigenval	10,80148	0,65723
Cum. prop	0,94264	1,00000

Table 6. – Summary of the main results of the discriminant function analyses on a selected craniometrical data-set.
6.1. *Lophuromys nudicaudus* (OTU's 1 - 3 - 4).
6.2. *Lophuromys huttereri* (OTU7), *Lophuromys nudicaudus* (OTU Σ sum of 1 + 3 + 4 + 5) and *Lophuromys sikapusi* (OTU9 = region Cameroon - RCA - Gabon).
For description of the measurements see table 3 and for discussion see text.

characteristics, it seems to be closer to typical *nudicaudus* than to *huttereri*. It remains possible that the *huttereri* population of the region between the western-bank of the Lomami and the Zaire River will prove to be different on the subspecific level from typical *huttereri*.

The taxonomic decision to recognize *huttereri* at the species-level has been solely based on the degree of observed morphological and craniometrical differences from its closest relative *L. nudicaudus*. However, this taxonomical decision is underpinned by an increasing number of well documented endemic species characterizing the "South-Central" faunal region such as *Pan paniscus* SCHWARZ, 1929, *Cercocebus aterrimus* (OUDEMANS, 1890), *Cercopithecus dryas* SCHWARZ, 1932, *Petrodromus tetradactylus* PETERS, 1846, *Crossarchus ansorgei* THOMAS, 1910, etc. (COLYN et al. 1991; COLYN and VAN ROMPAEY, 1994).

On the other hand typical *L. nudicaudus* has a geographical distribution encompassing probably all of the lowland rainforest between the Zaire, the Atlantic Coast and the Sanaga River, namely the "West-Central" region. The geographical distribution of *L. nudicaudus*



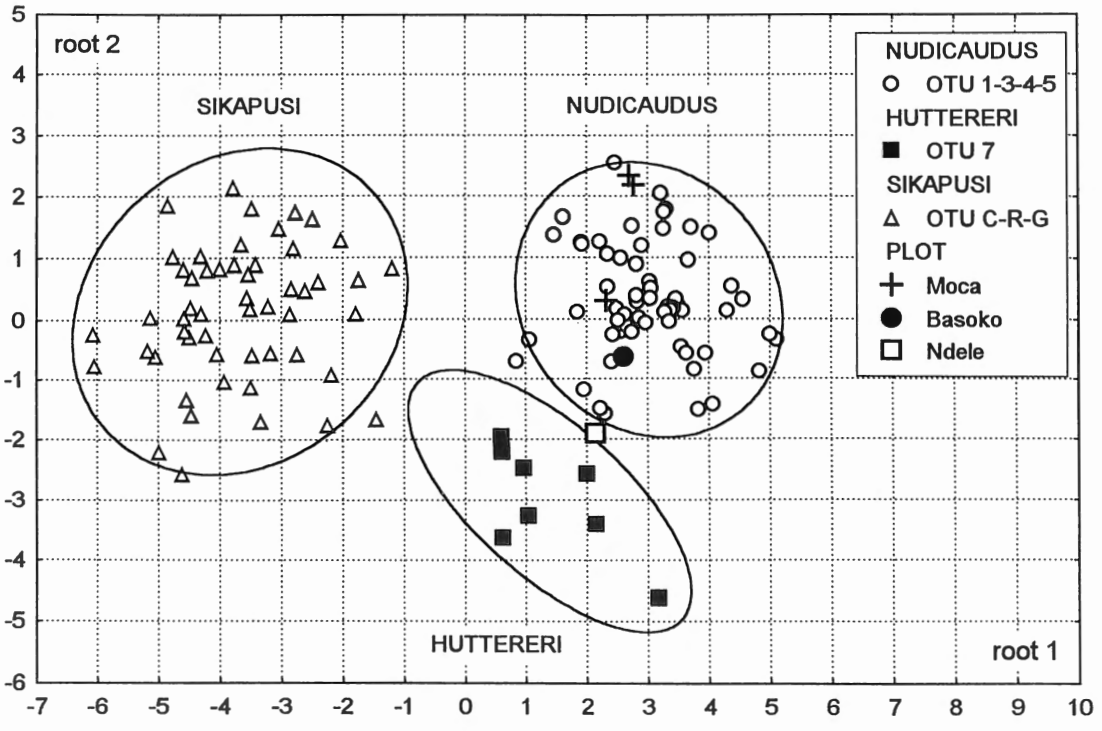


Fig. 8. – Canonical analyses on a selected craniometrical data-set of
8.1. *Lophuromys nudicaudus* s.s. and the relevant type-specimens.
8.2. *Lophuromys nudicaudus* s.s., *Lophuromys huttereri* sp.nov. and *Lophuromys sikapusi* (of the Cameroon - R.C.Africaine - Gabon region).
For description of the OTU's involved, see table 3.

within this region shows similarities with what is known for wide ranging polytypical primate species such as *Cercopithecus cephus* (LINNAEUS, 1758) and *Cercopithecus pogonias* BENNETT, 1833. Craniometrical analyses have not allowed us to show within the "West-Central" region any differentiation between the populations of the coastal region (OTU 3 + 5) and those from the continental basin of the Zaire-Congo system (OTU 4). It is possible that our failure to show any geographical differentiation is due to inadequate sampling, but we conclude that the subspecies *L.n.nudicaudus* occurs in most of the lowland rainforests of the "West-Central" region. The skull of specimen KMMA 6225 collected at Basoko falls morphologically and craniometrically well within the variation of typical *L. nudicaudus,* demonstrating that this species is also present in the lowland rainforests on the right bank of the Zaire between the Aruwimi and the Ubangui rivers. Notwithstanding intensive collecting by M. COLYN on the right bank of the Zaire, between Kisangani and the mouth of the Aruwimi River, this species was never encountered further to the south. This type of distribution on the right bank of the Zaire east of the Ubangui River is already well established for polytypical primate species with wide distributions [*Cercopithecus pogonias, Cercopithecus nictitans* (LINNAEUS, 1766), *Gorilla gorilla* (SAVAGE and WYMAN, 1847) etc.]. Our results clearly indicate that the *nudicaudus* populations living in the lowland rainforest between the Sanaga and the Cross rivers are sufficiently differentiated by morphological and craniometrical characters to justify subspecific distinction as *L. n. tullbergi.* Thus, to the west, the subspecies *tullbergi* characterizes the faunal region "Cameroon" in a similar way as do subspecies of the wide ranging polytypical primate species occuring in the "West-Central" region. To our knowledge no *nudicaudus* specimens were collected further to the west beyond the Cross River.

As to the taxonomic status of the *L. nudicaudus* population of Bioko our data force us to synonymize the subspecific name *parvulus* with *tullbergi.* However, we draw attention to the unusually high altitude of the type locality on Bioko Island (Mocatal - 1200 m) in contrast to all the collecting localities on the continent that are all situated below 700 m altitude with the exception of Buea (1000 m alt) (SMNS 53.385). Since both localities are situated on mountain sides, the possibility remains that these specimens were actually collected in lower regions than indicated by the collectors.

Conclusions

Summarizing, *L. nudicaudus* and *huttereri* are sister-taxa well characterized by craniometrical and craniological characters and with an allopatric distribution. *L. nudicaudus* has a geographical distribution encompassing probably the whole of the lowland rainforest between the right bank of the Zaire and the coast. Subspecificially recognizable within this region are the populations between the Cross and Sanaga rivers including Bioko Island (*tullbergi*). To the east, *L. nudicaudus* is present on the right bank of the Aruwimi; it is unlikely that it will be found further to the east in rainforests situated above 700 m (it was never collected in Epulu etc.). However, it probably exists westward along the Zaire River up to the Ubangui. *L. huttereri* on the other hand is probably distributed through the whole lowland rainforest on the left bank of the Zaire River and it is possible that the populations between the left bank of the Lomami River and the left bank of the Zaire River will prove to be subspecifically distinct.

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OTU	LOCALITY	MUSEUM	NUMBER	SEX	AGE	CR	P	AL
1	BUEA (5km S.E. of)	AMNH	241319	M	2	X	X	–
1	BUEA	SMNS	5338	F	2	X	X	–
1	KOTO BAROMBI	SMNS	6488	F	1	X	X	–
1	LOBE	BMNH	66.69	F	2	X	X	–
1	MUELI	SMNS	6489	M	4	X	X	–
1	N'DIAN	BMNH	61.1105	F	0	X	X	–
1	N'DIAN	BMNH	61.1300	M	1	X	X	–
1	N'DIAN	BMNH	61.1301	M	0	X	X	–
1	N'DIAN	BMNH	61.1302	M	3	X	X	–
1	N'DIAN	BMNH	94.1.3.1	F	0	X	–	X
1	OBAN	USNM	377521	M	5	X	X	–
1	RIO DEL REY	UUZM	348G=348	?	1	X	X	–
1	RIO DEL REY	UUZM	348H=348B	?	0	X	–	X
1	RIO DEL REY	UUZM	348I=348C	F	0	X	–	X
1	RIO DEL REY	UUZM	348J=348D	M	1	X	–	X
1	RIO DEL REY	UUZM	348K=348E	?	1	X	–	X
1	RIO DEL REY	UUZM	348L=348F	M	2	X	–	X
2	BONYOMA	ZFMK	69303	M	0	X	X	–
2	MOCATAL	ZFMK	63669	F	3	X	X	–
2	MOCATAL	ZFMK	64481	F	1	X	X	–
2	MOCATAL	ZFMK	64482	F	3	X	X	–
2	MOCATAL	ZFMK	64483	M	0	X	X	–
3	ALEN (Aconangui)	ACET	862	M	0	X	X	–
3	ALEN (Mbut)	ACET	878	F	5	X	X	–
3	BENITO	BMNH	98.10.7.12	?	0	X	–	X
3	BIPINDI	ZMHB	58904	F	1	X	X	–
3	BIPINDI	ZMHB	83978	F	0	X	X	–
3	BIPINDI	ZMHB	83981	M	1	X	X	–
3	BIPINDI	ZMHB	83983	M	2	X	X	–
3	BIPINDI	ZMHB	83984	M	0	X	X	–
3	BIPINDI	AMNH	89609	F	2	X	X	–
3	EFULEN	USNM	125436	M	1	X	X	–
3	EFULEN	BMNH	3.2.4.17	M	3	X	X	–
3	EFULEN	BMNH	3.2.4.18	F	4	X	X	–
3	ESEKA	AMNH	236458	M	3	X	X	–
3	ESEKA	AMNH	236459	M	1	X	X	–
3	ESEKA	AMNH	236460	F	4	X	X	–
3	ESEKA	AMNH	236462	M	0	X	X	–
3	GABON	BMNH	7.1.1.85	?	2	X	X	–
3	LA MAKANDE	RUCA	R16023	M	1	X	–	X
3	LA MAKANDE	RUCA	R16029	F	3	X	–	X
3	LA MAKANDE	RUCA	R16037	M	1	X	–	X
3	LA MAKANDE	RUCA	R16120	F	3	X	–	X
3	LA MAKANDE	RUCA	R16131	M	2	X	–	X
3	LA MAKANDE	RUCA	R16141	M	2	X	–	X
3	LA MAKANDE	RUCA	R16154	?	2	X	–	X
3	LA MAKANDE	RUCA	R16216	?	2	X	–	X
3	LA MAKANDE	RUCA	R16287	F	2	X	–	X
3	LA MAKANDE	RUCA	R16292	F	3	X	–	X
3	MENZALE	MHNP	1982.590	M	2	X	X	–
3	OGOUMA	USNM	220742	F	3	X	X	–
3	OGOUMA	USMN	220763	M	3	X	X	–
3	OGOUMA	USNM	220764	M	5	X	X	–

Appendix 1.1. – Listing of the specimens of the *Lophuromys nudicaudus* species-complex that have been included in this study (OTU's 1-2-3). For the definition of the OTU's, the acronymes of the Institutions and Musea, and the age-classes we refer to the text (material and methods). For the co-ordinates of the localities see App. 3. (cr = cranium; p = skin; al = in spirit; F = female; M = male).

OTU	LOCALITY	MUSEUM	NUMBER	SEX	AGE	CR	P	AL
4	ADIBORI	RUCA	R13531	F	2	X	–	X
4	ADIBORI	RUCA	R13633	F	2	X	–	X
4	ADIBORI	RUCA	R13649	M	3	X	–	X
4	ADIBORI	RUCA	R13651	F	3	X	–	X
4	BALANDO	RUCA	R12218	M	3	X	–	X
4	BALANDO	RUCA	R12242	M	2	X	–	X
4	BAMBIO	RUCA	R13 A	M	1	X	–	X
4	BAMBIO	RUCA	R13906	M	1	X	–	X
4	BATOURI	NHMB	8703	M	2	X	X	–
4	BIMBA	KMMA	76.14.M.5	F	3	X	X	–
4	BIMBA	KMMA	76.65.M.2	F	1	X	X	–
4	BITYE	BMNH	14.1.24.22	F	2	X	X	–
4	BITYE	BMNH	19.11.1.13	?	3	X	X	–
4	BITYE	BMNH	23.1.22.54	F	3	X	?	–
4	BITYE	BMNH	9.10.2.44	F	2	X	X	–
4	DJOLIMPOUM	RUCA	R14475	F	2	X	–	X
4	DJOMEDJO	RUCA	R14384	F	3	X	–	X
4	EKOM	RUCA	R14186	F	3	X	–	X
4	EKOM	RUCA	R14479	F	3	X	–	X
4	KONGANA	RUCA	JCR412	F	2	X	–	X
4	KONGANA	RUCA	JCR508	?	3	X	–	–
4	KONGANA	RUCA	JCR514	?	2	X	–	–
4	LA MABOKE	MHNP	1967.1590	M	1	X	X	–
4	LIDJIMBO	MHNP	1961.303	F	2	X	X	–
4	LONDO	RUCA	R12416	M	2	X	–	X
4	LONDO	RUCA	R12419	F	0	X	–	X
4	MIERI	KMMA	76.65.M.1	M	3	X	X	–
4	OBALA	BMNH	36.10.28.11	F	?	?	X	–
4	OLOUNOU	KMMA	73.16.M.140	F	3	X	X	–
4	SALO 2	RUCA	R13192	M	2	X	–	X
4	SALO 2	RUCA	R13387	F	2	X	–	X
4	YOKADOUMA	MHNP	474	F	0	X	X	–
5	BENA	MHNP	1991.75	F	2	X	X	–
5	BENA	MHNP	1991.76	M	4	X	X	–
5	BENA	MHNP	1991.81	M	3	X	X	–
5	BENA	MHNP	1991.82	M	2	X	X	–
6	BASOKO	KMMA	6251	?	2	X	X	–
7	AMADJABE	RUCA	Z584	M	3	X	–	X
7	KISANGANI 5 (left bank Zaire)	RUCA	Z.A	?	3	X	–	
7	KISANGANI 5 (left bank Zaire)	RUCA	Z.B	?	3	X	–	
7	YAENERO	RUCA	Z1774	M	2	X	–	X
7	YAENERO	RUCA	Z1665	F	2	X	–	X
7	YAENERO	RUCA	Z6613	M	2	X	–	X
7	YAENERO	RUCA	Z6614	M	4	X	–	X
7	YAENERO	RUCA	Z6616	F	3	X	–	X
7	YAENERO	RUCA	Z6619	M	2	X	–	X
7	YAENERO	RUCA	Z6764	F	3	X	–	X
7	YAENERO	RUCA	Z6766	F	2	X	–	X
7	YAENERO	RUCA	Z6889	F	2	X	–	X
7	YAENERO	RUCA	Z6890	M	3	X	–	X
8	NDELE	BMNH	89.441	F	2	X	–	X

Appendix 1.2. – Listing of the specimens of *Lophuromys nudicaudus* (OTU's 4-5-6) and *L. huttereri* sp. nov. (OTU's 7-8) included in this study. See legend of App. 1.1. for abbreviations.

OTU	MUSEUM	NUMBER	W	TOL	HB	TL	HF	EL	REMARKS
1	AMNH	241319	44	175	110	65	210	160	
1	SMNS	5338	30	156	93	63	186	170	HF+N=195
1	SMNS	6488	39	172	102	70	170	130	
1	BMNH	66.69	29	143	90	53	200	100	
1	SMNS	6489	50	178	115	63	200	150	
1	BMNH	61.1105	0	150	95	55	180	130	
1	BMNH	61.1300	0	0	108	0	190	140	
1	BMNH	61.1301	0	127	85	42	180	110	
1	BMNH	61.1302	0	179	116	63	180	180	
1	BMNH	94.1.3.1	0	0	0	50	190	110	
1	USNM	377521	58	170	107	63	180	150	
1	UUZM	348G=348	0	0	0	56	170	0	Syntype L. tullbergi
1	UUZM	348H=348B	0	0	0	0	0	0	Syntype L. tullbergi
1	UUZM	348I=348C	0	136	87	49	180	0	Syntype L. tullbergi, HF+N=200
1	UUZM	348J=348D	0	148	90	58	190	130	Syntype L. tullbergi, HF+N=205
1	UUZM	348K=348E	0	0	0	0	185	0	Syntype L. tullbergi
1	UUZM	348L=348F	0	150	89	61	185	125	Syntype L. tullbergi
2	ZFMK	69303	12	113	72	41	170	120	
2	ZFMK	63669	51	174	112	62	190	150	Type L. sikapusi parvulus
2	ZFMK	64481	41	154	101	53	180	150	Paratype L. sikapusi parvulus
2	ZFMK	64482	51	0	118	0	180	150	Paratype L. sikapusi parvulus
2	ZFMK	64483	31	152	96	56	180	150	Paratype L. sikapusi parvulus
3	ACET	862	0	0	76	0	160	130	
3	ACET	878	64	0	100	0	180	150	
3	BMNH	98.10.7.12	0	0	0	0	0		
3	ZMHB	58904	0	155	95	60	170	110	
3	ZMHB	83978	11	107	60	47	170	110	HF+N=185
3	ZMHB	83981	0	149	87	62	185	110	HF+N=200
3	ZMHB	83983	32	170	104	66	190	110	HF+N=210
3	ZMHB	83984	0	116	70	46	160	120	HF+N=170
3	AMNH	89609	0	180	106	74	180	100	
3	USNM	125436	0	166	0	0	180	150	Type L. nudicaudus
3	BMNH	3.2.4.17	0	169	116	53	180	140	
3	BMNH	3.2.4.18	0	175	118	57	180	150	
3	AMNH	236458	42	177	112	65	200	150	
3	AMNH	236459	30	156	99	57	200	150	
3	AMNH	236460	35	0	0	0	190	150	
3	AMNH	236462	27	143	87	56	200	140	
3	BMNH	7.1.1.85	0	0	0	0	190	150	Type L. naso
3	RUCA	R16023	0	153	92	61	189	116	
3	RUCA	R16029	0	0	107	0	181	143	
3	RUCA	R16037	0	156	98	58	189	115	
3	RUCA	R16120	0	168	106	62	185	129	
3	RUCA	R16131	0	0	112	0	179	126	
3	RUCA	R16141	0	170	107	63	184	134	
3	RUCA	R16154	22	160	94	66	0	125	
3	RUCA	R16216	57	0	0	0	133	0	
3	RUCA	R16287	43	176	104	72	194	153	
3	RUCA	R16292	43	174	112	62	185	143	
3	MHNP	1982.590	0	168	105	63	200	140	
3	USNM	220742	0	172	106	66	180	0	
3	USMN	220763	0	0	110	0	200	0	
3	USNM	220764	0	0	100	0	190	0	

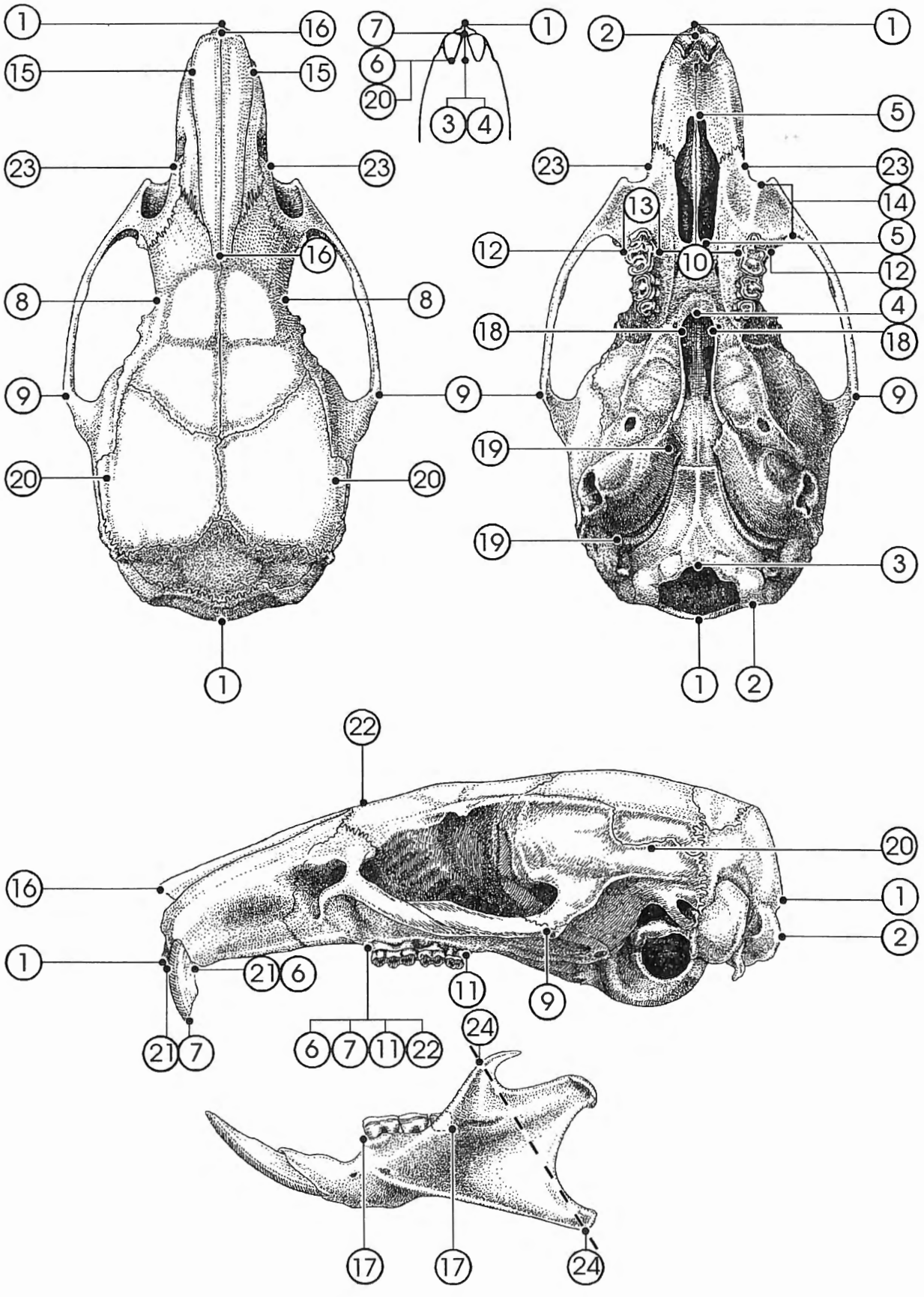
Appendix 2.1. – Additional data on the specimens of *Lophuromys nudicaudus* (OTU's 1-2-3). See App. 1.1. for other basic data. (W = weight; TOL = total length; HB = head + body length; Tl = tail length; HF = hindfootlength-nail).

OTU	MUSEUM	NUMMER	W	TOL	HB	TL	HF	EL	REMARKS
4	RUCA	R13531	52	185	119	66	172	144	
4	RUCA	R13633	42	161	99	62	186	151	
4	RUCA	R13649	40	0	103	0	185	140	
4	RUCA	R13651	52	149	98	51	179	151	
4	RUCA	R12218	38	152	105	47	180	130	
4	RUCA	R12242	32	150	89	61	175	140	
4	RUCA	R13 A	0	0	101	0	180	135	
4	RUCA	R13906	0	148	97	51	177	143	
4	NHMB	8703	0	0	0	0	0	0	Skin NHMB 4757
4	KMMA	76.14.M.5	0	0	0	0	184	146	HF+N=198
4	KMMA	76.65.M.2	0	0	0	0	181	138	HF+N=196
4	BMNH	14.1.24.22	0	172	110	62	180	155	
4	BMNH	19.11.1.13	0	173	110	63	180	160	
4	BMNH	23.1.22.54	0	0	0	0	0	0	Skin not found
4	BMNH	9.10.2.44	0	181	117	64	190	170	
4	RUCA	R14475	0	170	110	60	191	0	
4	RUCA	R14384	43	172	103	69	188	148	
4	RUCA	R14186	40	171	109	62	186	150	
4	RUCA	R14479	0	145	111	34	177	139	
4	RUCA	JCR412	43	178	115	63	200	170	
4	RUCA	JCR508	0	0	0	0	0	0	
4	RUCA	JCR514	0	0	0	0	0	0	
4	MHNP	1967.1590	0	143	88	55	180	150	
4	MHNP	1961.303	0	0	100	0	200	150	
4	RUCA	R12416	34	160	101	59	0	0	
4	RUCA	R12419	18	120	74	46	155	125	
4	KMMA	76.65.M.1	0	151	90	61	185	149	HF+N=209
4	BMNH	36.10.28.11	0	0	0	0	0	0	Skull not found
4	KMMA	73.16.M.140	0	0	0	61	175	0	HF+N=195
4	RUCA	R13192	42	0	107	0	168	150	
4	RUCA	R13387	30	158	96	62	163	132	
4	MHNP	474	0	150	85	65	190	150	
5	MHNP	1991.75	40	170	107	63	175	160	HF+N=195
5	MHNP	1991.76	37	0	113	0	200	170	HF+N=220
5	MHNP	1991.81	40	0	109	0	190	160	HF+N=205
5	MHNP	1991.82	41	176	111	65	200	170	HF+N=220
6	KMMA	6251	0	0	0	0	0	0	
7	RUCA	Z584	0	0	0	0	0	0	
7	RUCA	Z.A	0	0	0	0	0	0	
7	RUCA	Z.B	0	0	0	0	0	0	
7	RUCA	Z1774	0	155	96	59	180	130	Type L. huttereri, HF+N=200
7	RUCA	Z1665	0	0	0	59	198	140	Paratype L. huttereri, HF+N=215
7	RUCA	Z6613	0	155	93	62	195	139	Paratype L. huttereri, HF+N=216
7	RUCA	Z6614	0	175	110	65	195	130	Paratype L. huttereri, HF+N=206
7	RUCA	Z6616	0	0	114	0	196	0	Paratype L. huttereri, HF+N=210
7	RUCA	Z6619	0	164	105	59	196	0	Paratype L. huttereri, HF+N=214
7	RUCA	Z6764	0	164	105	59	199	0	Paratype L. huttereri, HF+N=210
7	RUCA	Z6766	0	152	93	59	195	135	Paratype L. huttereri, HF+N=215
7	RUCA	Z6889	0	0	0	55	200	0	Paratype L. huttereri, HF+N=225
7	RUCA	Z6890	0	165	104	61	185	140	Paratype L. huttereri, HF+N=208
8	BMNH	89.441	42	175	113	62	186	138	Paratype L. huttereri, HF+N=200

Appendix 2.2. – Additional data on the specimens of *Lophuromys nudicaudus* (OTU's 4-5-6) and of *Lophuromys huttereri* sp.nov. (OTU's 7-8). See App. 1.2. for basic data and App. 2.1. for abbreviations.

SYMBOL	MORPHOMETRICAL CHARACTERS
HB	head and body length
TL	length of tail
HF-fe-N*	length of hind-foot (-nail)
EL*	length of ear
GRLS (1)	greatest length of skull
PRCO (2)*	condylobasal length
HEBA (3)*	henselion-basion
HEPA (4)	henselion-palation
PAFL (5)*	length of palatal incisive foramen (= palatal foramen)
DIA1 (6)*	length of diastema: distance between the anterior border of the alveolus of M^1 and the posterior border of the alveolus of the upper incisor
DIA2 (7)*	distance between the anterior border of the alveolus of M^1 and the foremost edge of the upper incisor
INTE (8)	smallest interorbital breadth
ZYGO (9)	zygomatic breadth on the zygomatic process of the squamosal
PALA (10)	smallest palatal breadth between first upper molars
UPTE (11)*	length of upper cheekteeth:distance between the anterior border of the alveolus of M^1 and the posterior border of the alveolus of M^3
UPDA (12)	breadth of upper dental arch: greatest breadth across first upper molars
M^1BR (13)*	greatest breadth of first upper molar
ZYPL (14)*	smallest breadth of zygomatic plate: distance taken in a plane parallel to the occlusal surface of the upper molar-row
BNAS (15)	greatest breadth of nasals
LNAS (16)*	greatest length of nasals
LOTE (17)*	length of lower cheekteeth: distance between the anterior border of the alveolus of M_1 and the posterior border of the alveolus of M_3
CHOB (18)	greatest breadth of the choanae
BULL (19)*	length of auditory bulla (- the protruding part of the bony Eustachian tube)
BRCA (20)	greatest breadth of braincase
DINC (21)*	depth of upper incisors (perpendicular on length axis of tooth)
ROHE (22)	mediosagittal projection of rostrum heigth at anterior border of first upper molars
ROBR (23)	greatest rostrum breadth (in front of zygomatic plates)
PCPA (24)*	distance between the extreme points of the coronoid and the angular processes of the mandibula

Appendix 4.1. – Recapitulation and short description of the measurements as used in this study. The measurements marked with * were preferably taken on the left side of the skull or the animal. The numbers following the acronyms indicate the craniometrical reference points (Appendix 4.2.).



Appendix 4.2. – Drawings of a *Lophuromys* skull showing the craniometrical points used in the morphometrical study; the numbers refer to the position of the two points of the caliper when taking the corresponding measure as described in App. 4.1.

OTU	MUSEUM	NUMBER	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12
1	AMNH	241319	2835	2615	2285	1135	540	720	840	610	1390	345	415	665
1	SMNS	5338	0	2625	2250	1185	555	725	850	585	1350	360	455	670
1	SMNS	6488	0	0	0	0	0	700	790	0	0	0	0	0
1	BMNH	66.69	0	2405	2080	1085	540	680	805	580	1230	320	435	650
1	SMNS	6489	0	0	0	0	570	790	945	610	0	355	435	0
1	BMNH	61.1105	2480	2310	2025	1005	485	590	695	560	1235	295	425	620
1	BMNH	61.1300	2705	2540	2175	1085	495	650	775	595	1260	275	450	625
1	BMNH	61.1301	0	0	0	0	0	0	0	0	0	0	0	0
1	BMNH	61.1302	2925	2745	2330	1205	565	750	925	610	1400	375	455	695
1	BMNH	94.1.3.1	2595	2370	2020	1045	515	650	725	595	1280	315	455	650
1	USNM	377521	0	0	0	1165	555	760	880	605	0	330	415	665
1	UUZM	348G	2785	2600	2205	1080	520	685	810	605	1340	335	430	640
1	UUZM	348H	2635	2420	2060	995	450	615	745	590	1280	270	440	625
1	UUZM	348I	2520	2285	1895	945	415	585	710	560	1200	300	410	615
1	UUZM	348J	2760	2580	2175	1080	450	700	820	560	1310	310	430	625
1	UUZM	348K	2885	2645	2225	1075	520	690	810	610	1370	320	440	655
1	UUZM	348L	2780	2580	2170	1050	480	660	805	595	1355	330	410	665
2	ZFMK	69303	0	0	0	0	0	0	0	0	0	0	0	0
2	ZFMK	63669	0	2705	2340	1225	530	740	910	610	1330	355	440	685
2	ZFMK	64481	2880	2655	2250	1165	545	695	825	595	1365	310	440	650
2	ZFMK	64482	2860	2695	2390	1225	550	730	870	575	1330	375	415	665
2	ZFMK	64483	0	0	0	0	0	0	0	0	0	0	0	0
3	ACET	862	2510	2280	1930	0	485	590	685	530	1175	0	475	0
3	ACET	878	2850	2680	2310	1150	515	695	820	615	1355	280	470	690
3	BMNH	98.10.7.12	0	0	0	0	0	0	0	0	0	0	0	0
3	ZMHB	58904	2650	2490	2100	1075	500	650	825	575	0	280	455	680
3	ZMHB	83978	0	0	0	0	0	0	0	0	0	0	0	0
3	ZMHB	83981	0	0	0	1075	555	655	790	585	0	265	455	650
3	ZMHB	83983	0	0	0	1120	505	705	835	0	0	0	450	0
3	ZMHB	83984	0	0	0	0	0	0	0	0	0	0	0	0
3	AMNH	89609	2800	2620	0	1195	535	730	840	610	1300	360	470	690
3	USNM	125436	0	0	0	1070	565	675	785	620	0	290	425	615
3	BMNH	3.2.4.17	2775	2605	2220	1115	0	710	860	590	0	315	455	655
3	BMNH	3.2.4.18	2760	2680	2315	1140	605	760	910	595	1330	360	435	685
3	AMNH	236458	2865	2710	2335	1170	565	760	875	580	1375	300	440	695
3	AMNH	236459	2715	2560	2195	1085	595	665	820	570	1300	300	460	670
3	AMNH	236460	2775	2605	2200	1120	555	710	835	565	1295	315	435	675
3	AMNH	236462	0	0	0	0	0	0	0	0	0	0	0	0
3	BMNH	7.1.1.85	0	0	0	1155	540	705	0	605	0	0	460	0
3	RUCA	R16023	2750	2490	2110	1095	540	635	775	560	1260	280	470	695
3	RUCA	R16029	2865	2700	2315	1170	570	720	890	585	1375	340	430	705
3	RUCA	R16037	2750	2570	2175	1100	575	665	840	560	1290	300	470	675
3	RUCA	R16120	2840	2705	2250	1100	565	700	845	600	1420	295	445	690
3	RUCA	R16131	2825	2630	2240	1130	620	670	840	570	1365	300	440	680
3	RUCA	R16141	2845	2645	2250	1125	530	705	835	590	1305	310	465	685
3	RUCA	R16154	0	2600	2200	1120	520	695	850	580	1385	305	450	675
3	RUCA	R16216	0	0	0	0	0	0	0	0	0	0	0	0
3	RUCA	R16287	2875	2650	2235	1145	580	730	880	610	1350	305	450	695
3	RUCA	R16292	2780	2605	2200	1140	520	705	830	610	1385	290	455	685
3	MHNP	1982.590	2825	2565	2180	1105	550	665	810	595	1290	320	455	685
3	USNM	220742	2805	2590	2225	1140	545	680	810	590	1315	365	440	0
3	USMN	220763	0	0	0	1140	600	695	840	600	0	340	455	0
3	USNM	220764	0	0	0	0	0	720	825	0	0	0	440	0

Appendix 5.1. – Craniometrical data-set (M_1 to M_{12}) of *Lophuromys nudicaudus* specimens and types (OTU's 1-2-3). For details on the origins of the individual specimens see App. 1.1., 1.2., 2.1., 2.2. and 3. For the description of the measurements see App. 4.1. and 4.2.

OTU	MUSEUM	NUMBER	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12
4	RUCA	R13531	2760	2630	2235	1100	515	685	835	590	1385	310	410	680
4	RUCA	R13633	2675	2490	2090	1035	500	645	770	575	1325	275	415	645
4	RUCA	R13649	2725	2545	2150	1070	495	685	820	590	1335	340	425	670
4	RUCA	R13651	2795	2625	2210	1125	565	720	875	580	1335	320	420	690
4	RUCA	R12218	2735	2545	2150	1095	515	690	830	600	1390	360	390	680
4	RUCA	R12242	2650	2475	2105	1095	530	635	785	580	1335	315	435	660
4	RUCA	R13 A	2740	2510	2095	1080	540	660	790	570	1250	280	455	635
4	RUCA	R13906	2590	2420	2030	1035	480	625	750	540	1195	255	405	600
4	NHMB	8703	2920	2700	2330	1170	575	750	885	610	1410	340	435	690
4	KMMA	76.14.M.5	0	2570	0	1075	550	705	825	585	1240	330	430	670
4	KMMA	76.65.M.2	2725	2545	2125	1055	565	665	820	555	1275	290	455	650
4	BMNH	14.1.24.22	2755	2585	2215	1160	550	705	850	615	1365	340	500	0
4	BMNH	19.11.1.13	2820	2625	2230	1185	565	765	885	610	1395	350	465	675
4	BMNH	23.1.22.54	0	0	0	1150	545	720	830	605	1340	340	445	650
4	BMNH	9.10.2.44	2775	2505	2250	1165	550	725	865	605	1340	375	485	705
4	RUCA	R14475	0	2700	2260	1175	580	710	850	610	1370	285	470	670
4	RUCA	R14384	0	2610	2215	1165	590	715	870	580	1330	320	420	670
4	RUCA	R14186	0	2695	2285	1160	535	740	895	625	1395	320	460	690
4	RUCA	R14479	2865	2735	2320	1210	540	755	935	625	1395	330	440	700
4	RUCA	JCR412	2870	2670	2275	1190	570	760	895	605	1395	355	425	700
4	RUCA	JCR508	2855	2670	2275	1165	630	690	825	580	1320	295	450	665
4	RUCA	JCR514	2735	2535	2160	1100	530	665	800	570	1320	310	450	685
4	MHNP	1967.1590	0	0	0	1100	510	635	780	600	1305	285	470	645
4	MHNP	1961.303	0	0	0	0	0	0	0	575	1285	270	430	635
4	RUCA	R12416	2695	2495	2105	1085	545	660	775	585	1355	290	430	660
4	RUCA	R12419	0	0	0	0	0	0	0	0	0	0	0	0
4	KMMA	76.65.M.1	0	2660	2280	0	550	760	890	590	1220	330	430	685
4	BMNH	36.10.28.11	0	0	0	0	0	0	0	0	0	0	0	0
4	KMMA	73.16.M.140	2715	2460	0	1060	520	640	800	600	1230	310	460	675
4	RUCA	R13192	2740	2605	2200	1085	510	695	845	595	1365	320	410	670
4	RUCA	R13387	2660	2465	2080	1065	535	655	800	565	1280	295	420	650
4	MHNP	474	0	0	0	0	0	590	710	0	0	0	445	0
5	MHNP	1991.75	2735	2595	2210	1115	490	675	790	565	1375	300	485	705
5	MHNP	1991.76	2965	2750	2325	1155	595	720	870	650	1390	335	470	705
5	MHNP	1991.81	2770	2625	2235	1135	545	720	885	605	1370	330	435	705
5	MHNP	1991.82	2855	2650	2250	1120	465	680	835	580	1395	305	470	685
6	KMMA	6251	0	0	0	1105	550	705	860	605	1395	320	425	665
7	RUCA	Z584	0	2740	2335	1180	585	765	875	635	1370	370	455	735
7	RUCA	Z.A	0	0	0	1175	625	740	905	670	1430	320	435	705
7	RUCA	Z.B	2800	2650	2200	1190	615	725	875	610	1425	330	445	710
7	RUCA	Z1665	0	0	0	0	0	0	0	0	0	0	0	0
7	RUCA	Z1774	2870	2710	2280	1170	615	750	890	625	1425	335	415	685
7	RUCA	Z6613	2880	2690	2245	1160	610	750	895	640	1470	335	470	720
7	RUCA	Z6614	2990	2845	2440	1205	615	805	955	610	1520	375	420	740
7	RUCA	Z6616	0	0	0	0	0	0	0	0	0	0	0	0
7	RUCA	Z6619	2805	2650	2215	1130	595	725	835	630	1400	330	435	695
7	RUCA	Z6764	2945	2785	2305	1180	645	755	880	640	1470	360	440	730
7	RUCA	Z6766	2840	2635	2190	1135	590	705	830	605	1400	340	450	675
7	RUCA	Z6889	0	2760	2300	1200	655	710	895	610	1465	350	475	710
7	RUCA	Z6890	0	0	0	0	0	0	0	0	0	0	0	0
8	BMNH	89.441	2785	2630	2250	1190	545	725	850	615	1430	365	435	695

Appendix 5.2. – Craniometrical data-set (M_1 to M_{12}) of *Lophuromys nudicaudus* specimens (OTU's 4-5-6) and *Lophuromys huttereri* (OTU's 7-8) types and specimens. See legend of App. 5.1.

OTU	MUSEUM	NUMBER	M13	M14	M15	M16	M17	M18	M19	M20	M21	M22	M23	M24
1	AMNH	241319	160	160	275	1215	420	0	530	1205	110	570	425	740
1	SMNS	5338	175	170	285	1130	420	125	490	1205	115	535	460	0
1	SMNS	6488	160	205	285	1265	0	0	0	0	105	445	0	0
1	BMNH	66.69	165	170	235	0	425	165	420	1170	110	490	410	580
1	SMNS	6489	165	200	280	1300	440	0	0	0	130	535	470	720
1	BMNH	61.1105	170	135	245	995	430	165	460	1170	105	470	430	620
1	BMNH	61.1300	170	175	265	1170	435	135	470	1185	120	485	435	605
1	BMNH	61.1301	0	0	0	0	0	0	0	0	0	0	0	0
1	BMNH	61.1302	165	190	260	1200	435	175	465	1260	110	510	485	715
1	BMNH	94.1.3.1	180	185	270	1035	425	160	455	1215	115	455	410	625
1	USNM	377521	170	165	260	1290	375	0	0	0	140	550	445	695
1	UUZM	348G	150	180	235	1180	410	135	475	1240	95	525	440	0
1	UUZM	348H	175	145	245	1100	425	125	460	1215	95	505	455	625
1	UUZM	348I	150	150	240	1015	395	150	395	1165	85	455	430	0
1	UUZM	348J	155	155	250	1150	410	120	450	1170	95	510	475	640
1	UUZM	348K	160	180	250	1215	405	140	450	1220	100	560	490	685
1	UUZM	348L	165	175	250	1160	415	150	445	1235	90	510	450	650
2	ZFMK	69303	0	0	0	0	0	0	0	0	0	0	0	0
2	ZFMK	63669	165	220	265	0	415	0	475	1200	115	520	435	720
2	ZFMK	64481	165	185	265	1245	405	115	475	1220	110	525	480	0
2	ZFMK	64482	145	195	250	1290	395	130	470	1185	115	520	470	760
2	ZFMK	64483	0	0	0	0	0	0	0	0	0	0	0	0
3	ACET	862	175	135	215	990	445	0	415	1135	90	445	0	545
3	ACET	878	170	180	235	1160	415	160	450	1235	95	510	440	660
3	BMNH	98.10.7.12	0	0	0	0	0	0	0	0	0	0	0	0
3	ZMHB	58904	185	140	225	1060	445	140	455	1170	100	505	460	655
3	ZMHB	83978	0	0	0	0	0	0	0	0	0	0	0	0
3	ZMHB	83981	175	165	245	1070	410	130	0	0	90	490	465	645
3	ZMHB	83983	165	175	250	1145	400	0	0	0	100	0	0	660
3	ZMHB	83984	0	0	0	0	0	0	0	0	0	0	0	0
3	AMNH	89609	170	185	270	1140	415	0	425	1225	95	515	415	680
3	USNM	125436	165	125	240	1065	410	0	0	1255	105	490	400	0
3	BMNH	3.2.4.17	170	165	265	1120	415	155	460	1165	120	525	425	635
3	BMNH	3.2.4.18	180	180	290	1120	390	155	460	1225	105	535	455	735
3	AMNH	236458	180	180	265	1170	420	0	490	1210	110	560	395	720
3	AMNH	236459	180	185	250	1115	455	0	460	1185	105	510	410	670
3	AMNH	236460	175	170	280	1150	400	0	460	1180	100	530	400	655
3	AMNH	236462	0	0	0	0	0	0	0	0	0	0	0	0
3	BMNH	7.1.1.85	170	130	265	1205	445	0	505	1230	115	495	425	660
3	RUCA	R16023	195	175	240	1105	445	150	450	1220	95	490	445	670
3	RUCA	R16029	180	175	250	1235	400	145	460	1240	100	530	490	0
3	RUCA	R16037	185	165	240	1165	440	135	425	1185	100	495	445	655
3	RUCA	R16120	190	190	250	1210	425	160	455	1240	105	510	450	715
3	RUCA	R16131	170	170	250	1190	410	150	465	1245	105	510	450	745
3	RUCA	R16141	175	190	250	1115	415	165	470	1210	95	525	435	650
3	RUCA	R16154	185	185	225	0	425	125	480	1250	95	500	430	660
3	RUCA	R16216	0	0	0	0	0	0	0	0	0	0	0	0
3	RUCA	R16287	190	170	230	1175	425	115	490	1265	90	505	455	695
3	RUCA	R16292	190	170	265	110	435	110	470	1250	95	510	445	670
3	MHNP	1982.590	175	175	280	1190	420	130	510	1215	95	510	430	0
3	USNM	220742	180	155	245	1150	415	0	455	1200	100	525	425	685
3	USMN	220763	190	160	250	1215	375	0	0	0	100	505	420	705
3	USNM	220764	170	145	240	1200	385	0	0	0	125	515	440	725

Appendix 6.1. – Craniometrical data-set (M_{13} to M_{24}) of *Lophuromys nudicaudus* specimens and types (OTU's 1-2-3). See App. 5.1.

OTU	MUSEUM	NUMBER	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12
4	RUCA	R13531	175	165	255	1040	400	125	460	1225	105	525	450	715
4	RUCA	R13633	170	145	245	1080	385	125	500	1220	105	510	405	660
4	RUCA	R13649	160	150	235	1095	365	130	465	1165	85	520	450	750
4	RUCA	R13651	175	145	260	1080	385	150	475	1230	95	510	455	700
4	RUCA	R12218	150	150	260	1090	390	145	440	1245	90	565	470	690
4	RUCA	R12242	165	125	240	1035	400	130	445	1200	100	500	440	630
4	RUCA	R13 A	180	140	230	1150	425	125	420	1190	105	505	450	650
4	RUCA	R13906	165	185	250	1030	380	125	435	1190	100	480	420	615
4	NHMB	8703	170	180	275	1240	430	185	480	1245	110	545	420	690
4	KMMA	76.14.M.5	165	165	260	0	405	120	460	1235	100	535	510	710
4	KMMA	76.65.M.2	175	160	245	1055	425	160	435	1205	100	490	495	0
4	BMNH	14.1.24.22	190	195	290	1175	455	200	470	1235	125	535	430	0
4	BMNH	19.11.1.13	170	205	240	1275	435	160	465	1205	120	525	405	695
4	BMNH	23.1.22.54	170	200	265	1140	435	185	0	1165	110	485	450	695
4	BMNH	9.10.2.44	190	190	285	1165	485	205	480	1230	115	480	425	0
4	RUCA	R14475	180	165	270	0	435	140	480	1290	105	505	425	725
4	RUCA	R14384	175	150	250	0	415	115	495	1220	100	505	435	695
4	RUCA	R14186	170	155	250	0	410	115	465	1300	105	530	410	700
4	RUCA	R14479	185	175	275	1120	425	155	460	1260	100	505	435	695
4	RUCA	JCR412	170	165	250	1160	395	125	435	1225	105	530	455	705
4	RUCA	JCR508	175	170	240	1140	415	125	470	1195	110	515	440	685
4	RUCA	JCR514	180	170	240	1120	415	120	440	1195	95	490	425	670
4	MHNP	1967.1590	175	150	250	1085	440	0	0	1175	85	510	440	630
4	MHNP	1961.303	170	170	0	0	400	0	470	1195	105	0	0	0
4	RUCA	R12416	175	160	230	1065	390	105	455	1195	95	495	415	635
4	RUCA	R12419	0	0	0	0	0	0	0	0	0	0	0	0
4	KMMA	76.65.M.1	170	155	275	0	405	115	465	1225	95	575	540	725
4	BMNH	36.10.28.11	0	0	0	0	0	0	0	0	0	0	0	0
4	KMMA	73.16.M.140	185	160	230	1085	415	130	400	1230	90	485	475	0
4	RUCA	R13192	160	135	260	1125	375	110	485	1200	100	525	455	615
4	RUCA	R13387	165	155	225	1085	420	115	465	1185	95	480	430	685
4	MHNP	474	170	160	235	970	440	0	0	0	85	0	0	0
5	MHNP	1991.75	200	190	235	1165	410	125	460	1220	95	525	440	645
5	MHNP	1991.76	185	200	260	1260	415	115	480	1275	95	540	440	675
5	MHNP	1991.81	185	140	240	1180	415	105	460	1220	95	540	445	660
5	MHNP	1991.82	190	175	245	1215	430	115	475	1220	100	500	445	715
6	KMMA	6251	165	170	245	1150	410	125	0	1210	105	535	495	715
7	RUCA	Z584	175	190	315	0	430	140	460	1140	110	590	495	750
7	RUCA	Z.A	190	170	295	1175	0	165	450	1195	110	580	540	0
7	RUCA	Z.B	190	180	300	1175	0	210	450	1175	110	590	545	0
7	RUCA	Z1665	0	0	0	0	0	0	0	0	0	0	0	0
7	RUCA	Z1774	170	145	310	1165	415	155	435	1200	110	570	520	725
7	RUCA	Z6613	185	170	275	1170	435	155	435	1230	120	595	480	780
7	RUCA	Z6614	180	175	290	1240	390	170	450	1220	105	615	525	800
7	RUCA	Z6616	0	0	0	0	0	0	0	0	0	0	0	0
7	RUCA	Z6619	170	175	290	1150	430	165	455	1265	110	560	485	745
7	RUCA	Z6764	175	190	305	1180	450	150	465	1235	120	600	525	790
7	RUCA	Z6766	165	180	290	1190	400	180	450	1245	110	575	500	720
7	RUCA	Z6889	200	180	280	0	450	180	470	1230	110	580	520	760
7	RUCA	Z6890	0	0	0	0	0	0	0	0	0	0	0	0
8	BMNH	89.441	165	175	290	1085	410	145	455	1250	105	555	510	720

Appendix 6.2. – Craniometrical data-set (M_{13} to M_{24}) of *Lophuromys nudicaudus* specimens and *Lophuromys huttereri* (OTU's 7-8) types and specimens. See also legend of App. 5.1.