

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/Rio Muni/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 subs spécifique de *tullbergi*, et (2) que la population de Bioko, décrite sous le nom subs spécifique 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 "unspckled 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 "unspckled" 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 M¹ 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 M² 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 "unspckled" 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 "unspckled 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 "unspckled 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 "unspotted 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 museums 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 museums 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 - Switzerland);
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 Ogoué;
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	Balandó	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	Djoliimpoum	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.

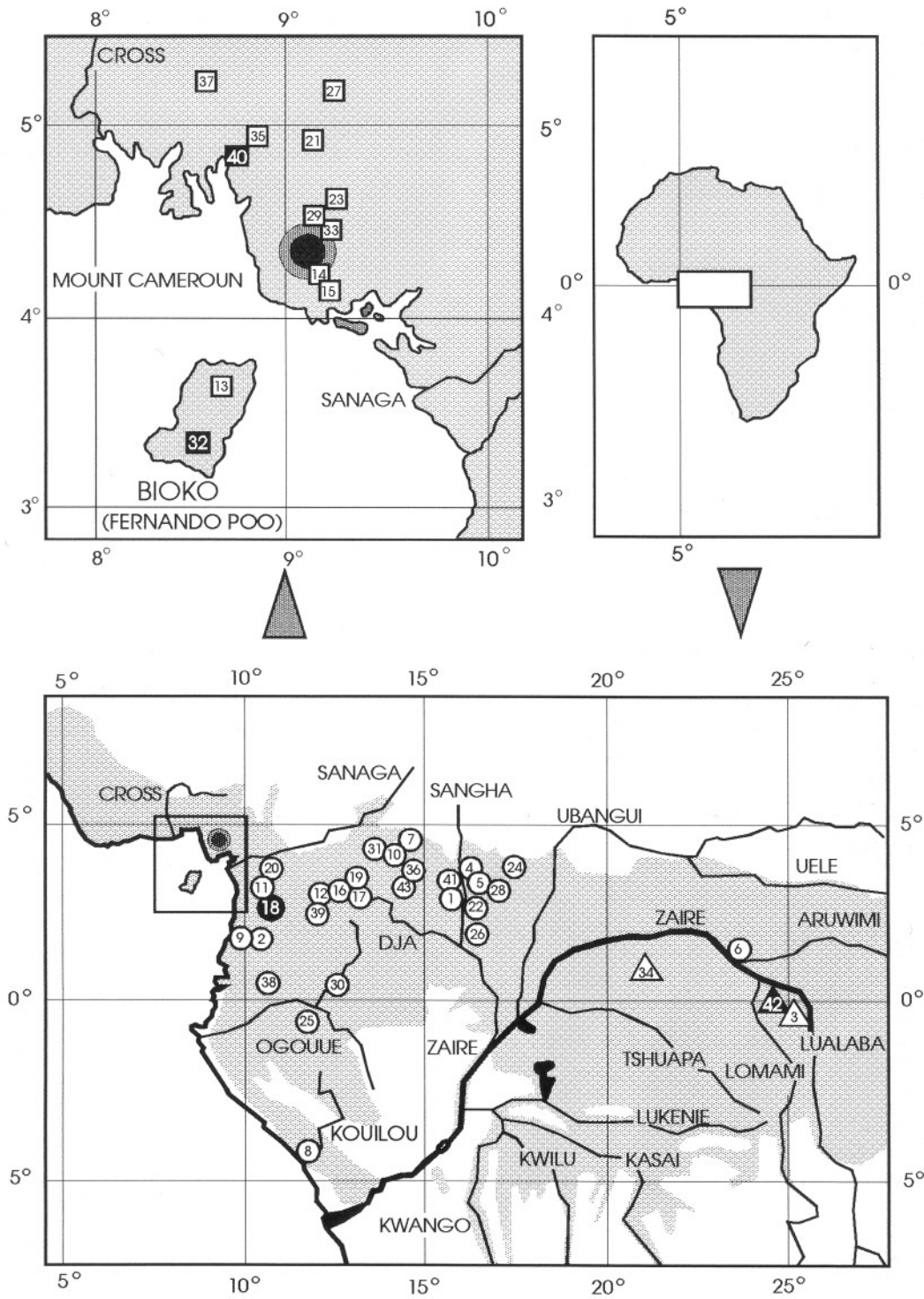


Fig. 1. – The geographical distribution of the *Lophuromys nudicaudus* species-complex. The following symbols characterize the collecting localities of

○ *Lophuromys nudicaudus nudicaudus* HELLER 1911;

□ *Lophuromys nudicaudus tullbergi* MATSCHIE 1911;

△ *Lophuromys hutereaui* VERHEYEN, COLYN & HULSELMAANS 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: M³ not yet fully erupted;
- cl. 1: all cheekteeth fresh but fully erupted; M¹ and M²: dentine-surface of 2nd cusp-row not continuous;
- cl. 2: light wear; M¹ and M²: 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 t₅;
- cl. 3: obvious wear; M¹: in occlusal view dentine-surface of t₅ > than remaining enamel-surface; dentine surface of 1st row of cusps not continuous with dentine surface of 2nd row;
- cl. 4: wear extensive; M¹: much flattened cusps; 1st and 2nd, or 2nd and 3rd cusp-row communicating; M²: 1st, 2nd and 3rd cusp-row communicating;
- cl. 5: wear severe; M¹: very heavily eroded, concave and all rows communicating; M²: 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

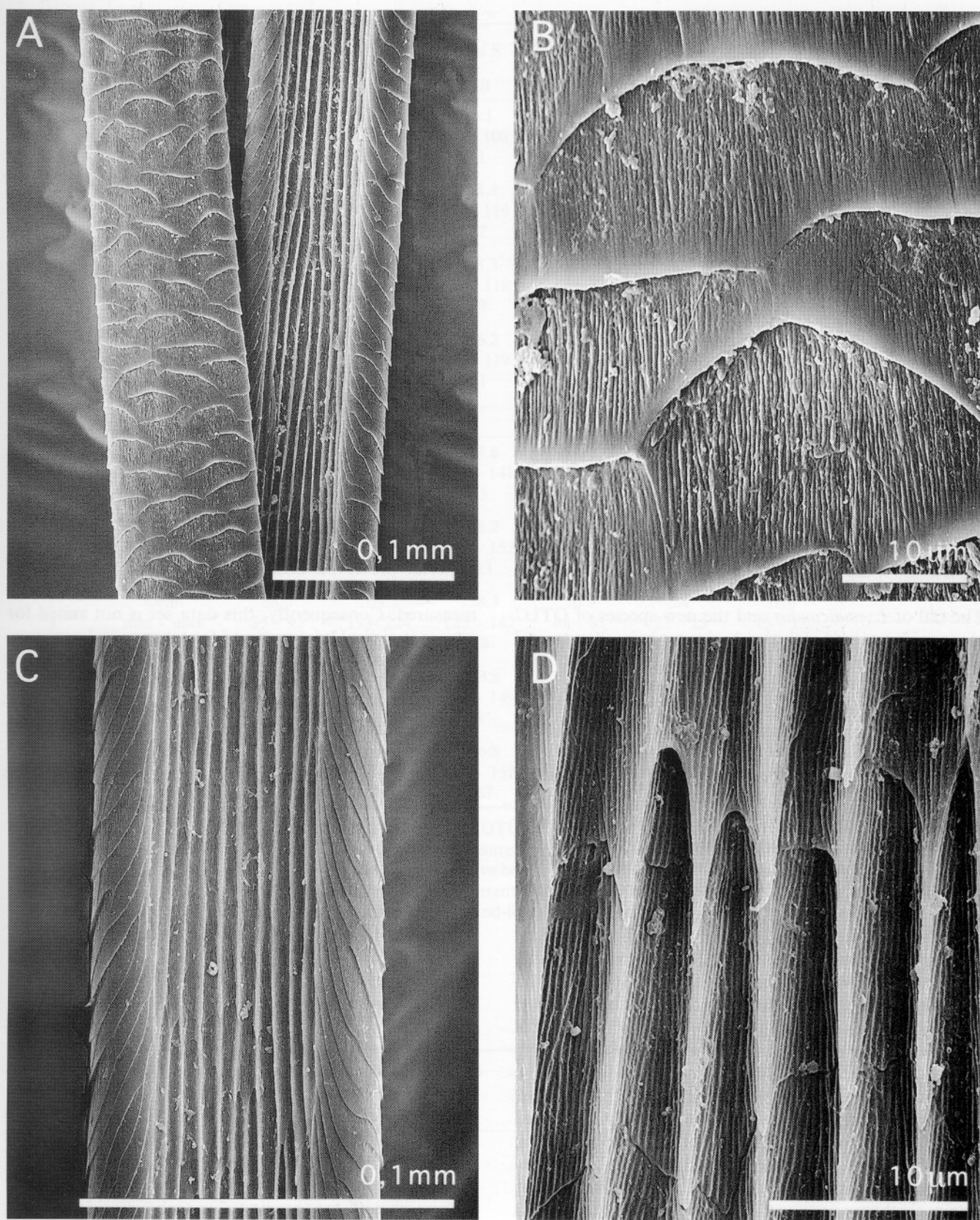


Fig. 2. – Scanning electron micrographs of dorsal hair morphology of *Lophuromys nudicaudus* UUZM 348D (syntype of *tullbergi*). A. General aspect of grooved and ungrooved side of hair. B. Detail of cuticular scaling pattern of ungrooved side. – *Lophuromys hutleri* RUCA Z1.774 (type). C. General aspect 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 brilliant 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-population 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 table 1 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 + bodylength 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		NUDICAUDUS					
(M + F)		W	Tol	HB	TI	HF	EL
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; TI: 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.

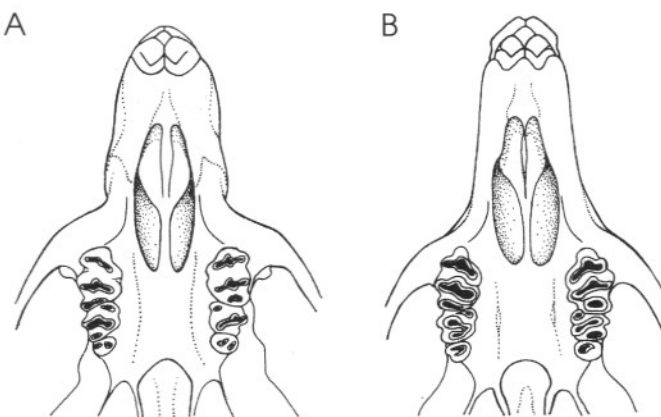


Fig. 3. – Schematic views of the ventral side of the rostra of adult crania of A. *Lophuromys hutcheri* (RUCA - Z6619) and B. *Lophuromys nudicaudus* (RUCA - R16029). The skulls are aligned on the anterior borders of the first molars.

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 tooththrow 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

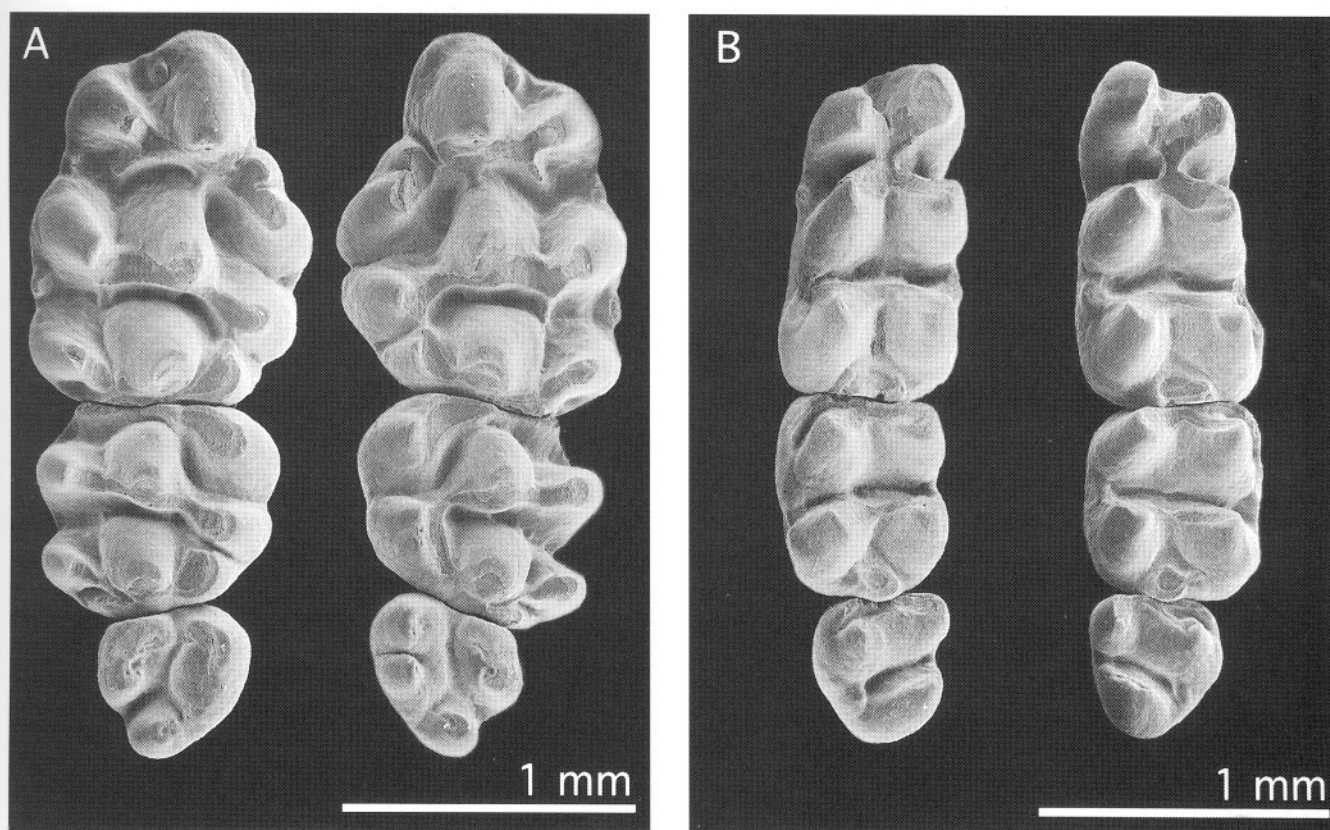


Fig. 4. – Scanning electron micrographs of the upper (A) and lower (B) tooththrows of a typical *Lophuromys nudicaudus* specimen (RUCA-R16023). The left and right series are shown to underline the amount of variation in cuspidation that can be observed in one animal.

conclude that *L. naso* falls well within the variational range observed in *Lophuromys nudicaudus*.

Finally, the maxillary tooththrows 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 M¹) 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 ($p < 0.01$ to $p < 0.001$) 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 ($p < 0.05$ to $p < 0.01$) 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.

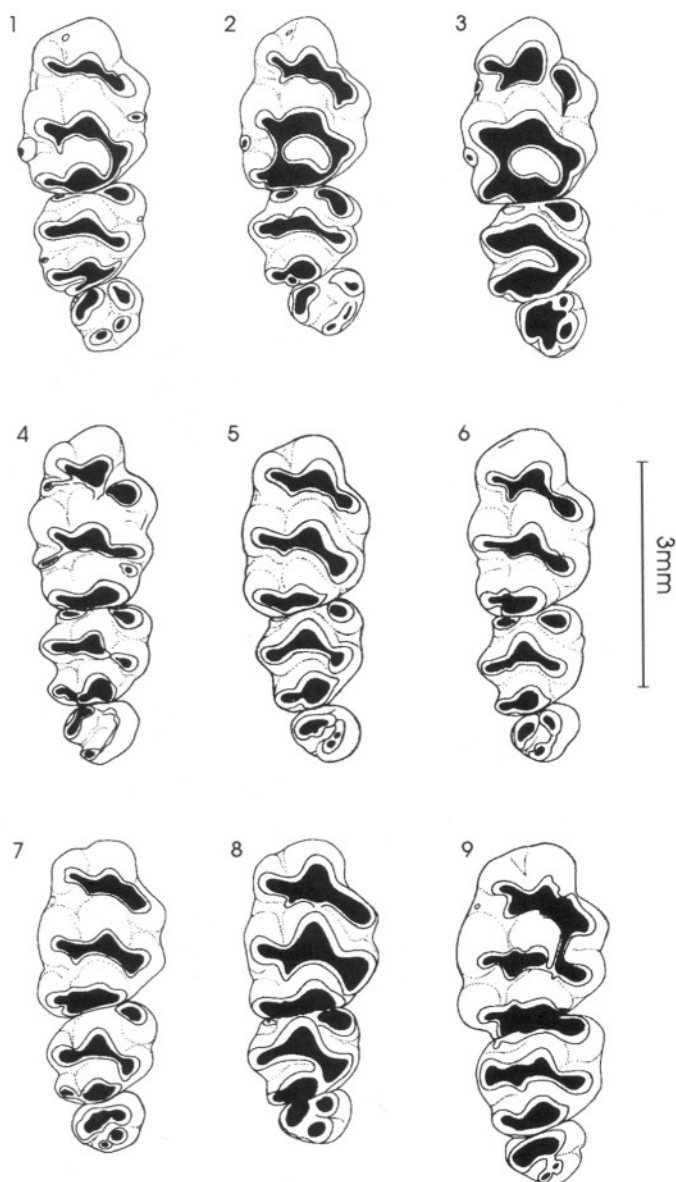


Fig. 5. – Comparative drawings of the right maxillary teeth of *Lophuromys nudicaudus* (1-5) and *Lophuromys huttereri* (6-9).

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).

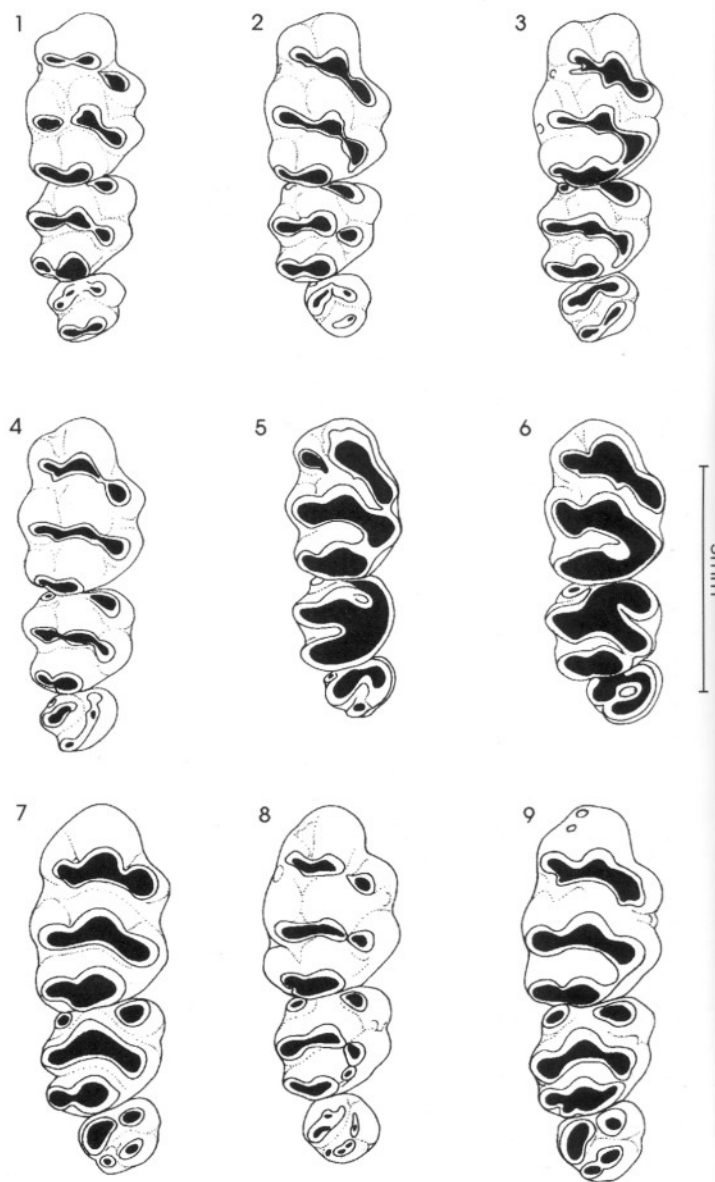


Fig. 6. – Comparative drawings of the right maxillary teeth of *Lophuromys nudicaudus* (1-6) and some type-specimens representative for the *Lophuromys sikapusi* species complex (7-9).

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).

<i>L. nudicaudus</i> (OTU 1)							<i>L. nudicaudus</i> (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

<i>L. nudicaudus</i> (OTU 4)							<i>L. hutterereri</i> 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 hutterereri* (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.

<i>L. nudicaudus</i> ANOVA (OTU's 1 - 3 - 4)							<i>L. nudicaudus</i> and <i>L. huttereri</i> 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 step-wise 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 (Zaire).

TYPE LOCALITY

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

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 "unspotted 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

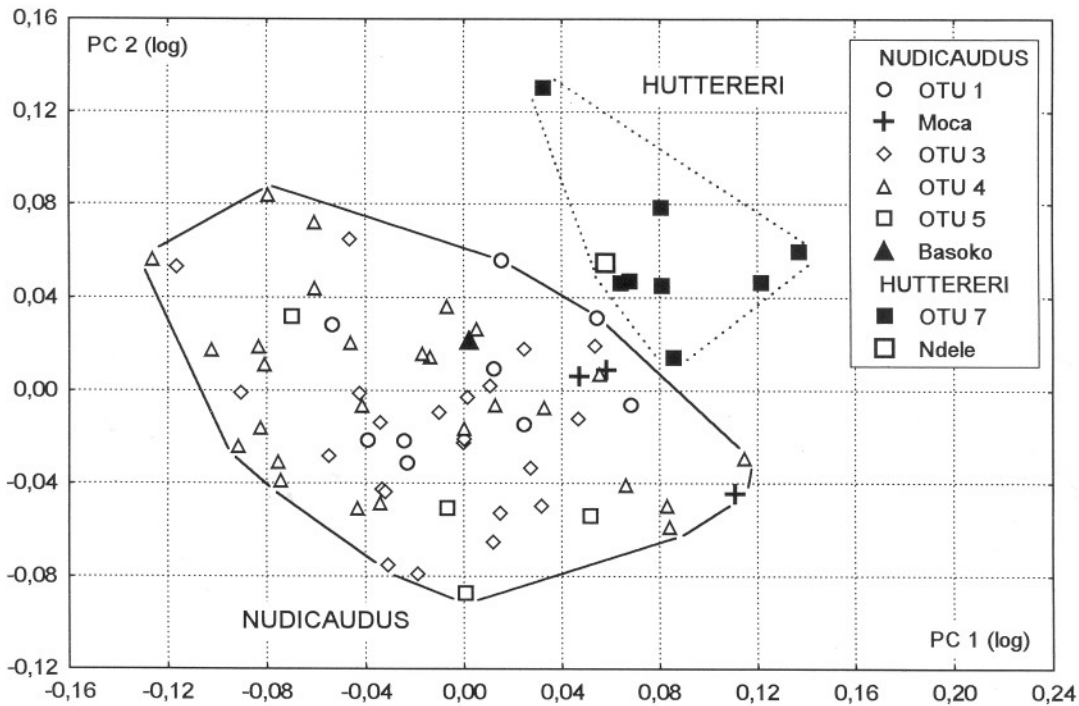
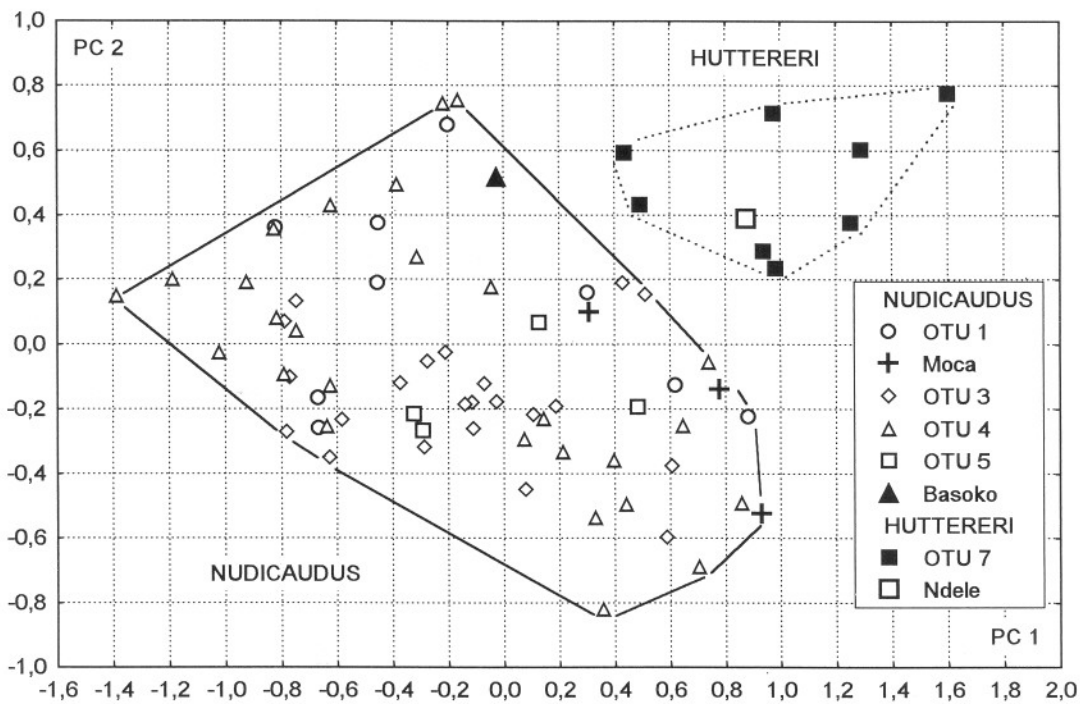


Fig. 7. – Principal component analyses on a data-set of 11 selected craniometrical measurements of *Lophuromys nudicaudus* and *Lophuromys huttereri*.

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 characte-

rizing the "South-Central" faunal region such as *Pan paniscus* SCHWARZ, 1929, *Cercocebus atterimus* (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*

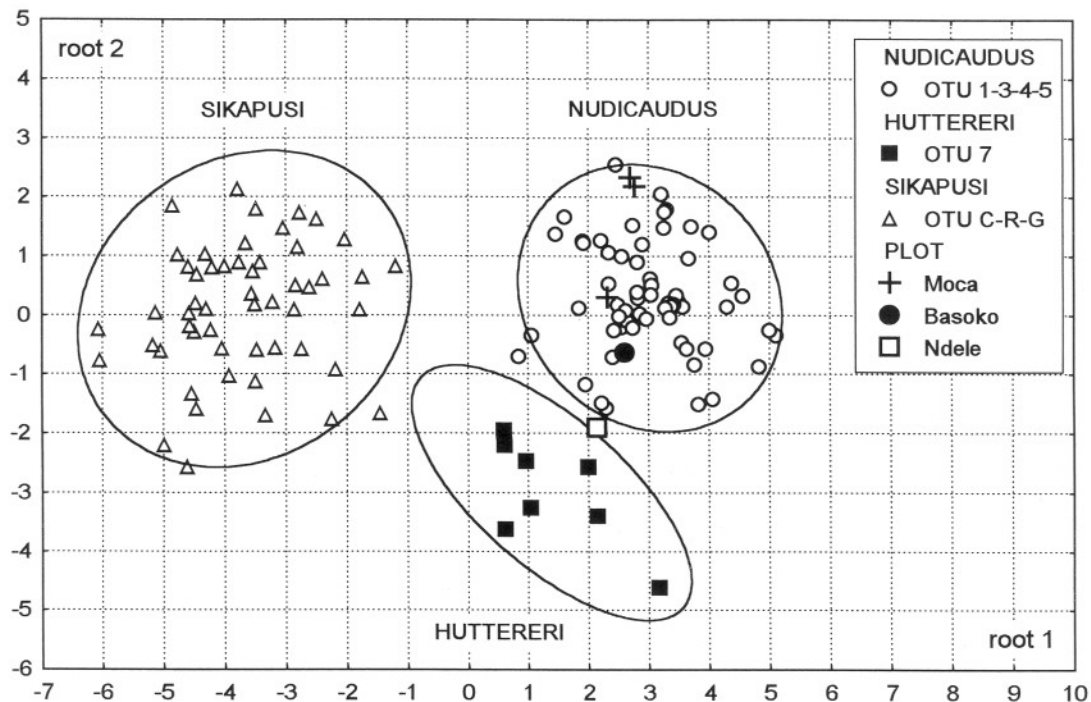
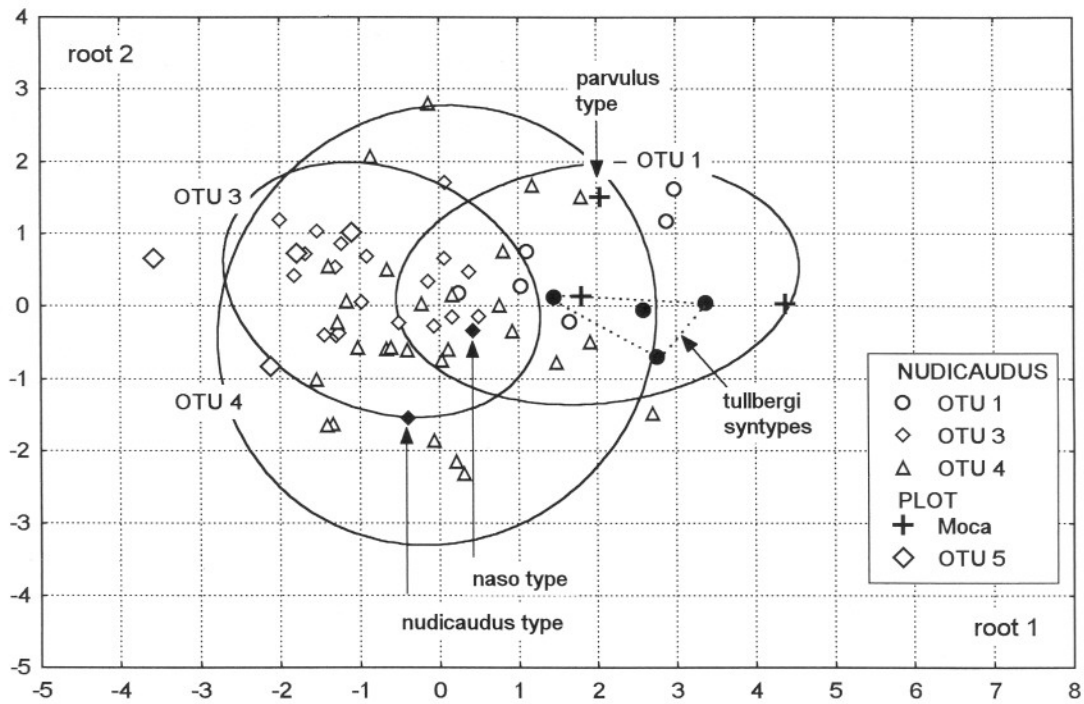


Fig. 8. – Canonical analyses on a selected craniometrical data-set of

8.1. *Lophuromys nudicaudus* s.s. and the relevant type-specimens.

8.2. *Lophuromys nudicaudus* s.s., *Lophuromys hutterereri* 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 occurring 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. Subspecifically 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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