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A craniometric and genetic approach to the systematics of the genus *Dasymys* PETERS, 1875, selection of a neotype and description of three new taxa (Rodentia, Muridae, Africa)

by Walter N. VERHEYEN, Jan L. J. HULSELMANS, Theo DIERCKX, Marc COLYN, Herwig LEIRS & Erik VERHEYEN

Abstract

In an attempt to properly identify *Dasymys* specimens that were collected during the last decennia in the East-African region (Rwanda-Tanzania) we undertook a revision of this genus. Although we initially limited our study area to central and eastern Africa, we were forced to include specimens for comparison from other areas, including western Africa, Angola and Zimbabwe-Zambia. This revision was realized using craniometric data of nearly 1000 skulls grouped in 20 operational taxonomical units (OTU's) mainly occurring in the central and eastern part of the African continent.
The observation that differences in age and sex composition of the OTU's are of no or little consequence for the branching of the obtained phenetic trees, allowed us to undertake the screening of the genus *Dasymys* of the central and eastern African region. This approach enabled us to evaluate already described taxa, to select a neotype for *D. nudipes* and to describe three new taxa. Subsequent genetic analysis (cytochrome *b*) allowed us to provide a genetical characterization of two of the new species and several other taxa. Our phylogenetic analysis suggests that the genus *Dasymys* originated in the west African forest block before spreading in a first step to the forest of the central African region and then in a second step to the savannahs of southern, eastern and possibly also western Africa.

Keywords: Rodentia, Africa, *Dasymys*, taxonomy, craniometry, phylogeny, cytochrome *b*

Résumé

Les difficultés d'ordre taxinomique que nous rencontrions en essayant de déterminer les *Dasymys* collectés par nos équipes de terrain pendant ces dernières décennies en Afrique orientale (Rwanda – Tanzanie) nous ont incitées a entreprendre une révision de ce genre. Alors que nous avions décidé initialement de nous limiter aux *Dasymys* de ces régions, nos observations nous ont forcées à inclure dans notre étude des séries comparatives des régions limitrophes.
Nous avons réalisé cette révision générique en nous basant sur des données métriques d'une vingtaine d'UTO's groupant un millier de crânes.
L'observation que la composition variable (sexe et âge) d'une UTO ne semble qu'avoir un impact négligeable sur l'aspect des arbres phénétiques obtenus, nous a permise d'entreprendre un «screening» des *Dasymys* de l'Afrique orientale.
Grâce à cette approche quantitative nous avons pu évaluer la qualité des formes déja décrites, de sélectionner un néotype pour *D. nudipes* et de décrire trois nouvelles formes de *Dasymys*.
Des analyses génétiques subséquentes (cytochrome *b*) nous ont permises de caractériser deux de nos nouvelles espèces ainsi que plusieurs taxa décrits depuis longtemps.
Nos analyses génétiques suggèrent en outre que le genre *Dasymys* est originaire de l'Afrique occidentale, avant de se répandre d'abord dans la région de l'Afrique centrale, ensuite dans les savanes de l'Afrique australe, orientales et probablement aussi occidentales.

Mots-clés: Rodentia, Afrique, *Dasymys*, taxinomie, craniométrie, phylogénie, cytochrome *b*.

INTRODUCTION

The so-called 'marsh', 'swamp', 'water', 'shaggy-furred' or even 'shaggy swamp' rats of the genus *Dasymys* are widely distributed over most of the sub-Saharan part of the African continent. Its distribution is, for as much as is actually known, strongly linked to biotopes characterized by permanent moist conditions such as riverbanks, swampy edges of ponds and brooks, marshy areas with reedbeds, sedges and semi-aquatic grasses, the wetter parts of flood plains and even highland bogs (DAVIS, 1962; ROSEVEAR, 1969; SMITHERS, 1971; SHEPPE, 1972; KINGDON, 1974). Also the presence of a dense ground cover that allows protected runways and nesting facilities seems to be of great importance. Shaggy-furred rats appear to be mostly terrestrial and nocturnal; however, semi-aquatic and limited diurnal behaviour has also been described. Their diet consists mainly of green vegetable matter but occasionally insect parts have been identified in stomach contents (THOMAS, 1912; ROBERTS, 1951; HANNEY, 1965; SMITHERS, 1971; COE, 1975; DE GRAAF, 1981).
Many authors have stressed that although *Dasymys* is rather common in its preferred wetland habitat (WALKER, 1964; ROSEVEAR, 1969; DELANY & HAPPOLD, 1979) it is not easily captured (MEESTER, 1976; CORBET & HILL, 1980; DE GRAAF, 1981; RAUTENBACH et al., 1981; GORDON, 1991). As a consequence *Dasymys* is not so well represented in museum-collections. It is noteworthy that this habitat preference is likely to make populations of swamp rats sensitive to habitat-fragmentation and thus theoretically prone to speciation (AVERY, 1991; GORDON, 1991).
Dasymys are rats that are well characterized by their thick-set heavy habitus, entirely due to their fur which varies consid-

erably from long-soft-straight and silky to loose-coarse and shaggy. Moreover, also their dorsal pelage colour varies strikingly over its geographical range; from olive-brown over yellowish-brown to brown mixed with black and slaty black, whereas their underparts are described as being grayish-white over whitish to pale buff and olive buff. Their tail – which is almost naked and dark-brown, sometimes slightly paler below - is somewhat shorter than the head and body lengths combined. Their ears are rather small and rounded with a fringe of short hairs on their rims. Both the hands and feet are usually light brownish scantily haired and have five digits (NOWAK, 1995).

Dasymys has a taxonomical history which is typical for most of the African small mammal genera. Whereas initially (at the end of the 19th and the first half of the 20th century) there was a tendency to describe many taxa, later on the number of nominal taxa was significantly reduced by putting many of these taxa in synonymy. The tendencies to split and lump respectively resulted in an over- and underestimate of the taxonomical diversity of Africa's small mammals. We argue that this is largely due to the fact that the observed morphological variation could not be properly assessed as the result of the relative sparsity of voucher-specimens. However, during the last quarter of the 20th century an increased collecting effort has been made and now statistically important series of African small mammals have become available in the major European, North American and South African Museums, so that this problem does no longer exist.

In the specific case of *Dasymys* we see that since the description of the genus by PETERS (1875), some twenty taxa were named throughout the whole of sub-Saharan Africa. By far the greater part was described before 1940 and most - if not all - of those descriptions were solely based upon colour differences in pelage and on some morphological and metrical differences. However, in most cases the real justification for the description of these new taxa was «geographically» inspired; indeed, it was generally accepted that geographical distances between populations imply the existence of biological differences important enough to justify taxonomic recognition.

ALLEN (1939) was the first to synonymise some of the described taxa and retained 10 species for the genus *Dasymys*. A few years later ELLERMAN (1941) further reduced the number of species to two, whereas MISONNE (1974) and KINGDON (1974) even went as far as to decide that the genus *Dasymys* must be monotypic, *incomtus* being the type species. Without presenting any evidence KINGDON (1974) even suggested that all the previously described taxa represented only individual variations in pelage colour and (or) body size, and were therefore not even good subspecies.

A review of the literature concerning the systematics of the genus *Dasymys* prior to 1989 illustrates that little or no research was carried out to test the validity of the above described lumping of taxa (ELLERMAN et al., 1953; HANNEY, 1965; ROSEVEAR, 1969; MISONNE, 1974, DELANY, 1975, DE GRAAFF, 1981; HONACKI et al., 1982; MEESTER et al., 1986; CORBET & HILL, 1986; HAPPOLD, 1987). Except for ROBERTS (1951) and CRAWFORD-CABRAL (1983, 1986), who accepted *D. nudipes* as a second species, all the other classifications recognize only one species *D. incomtus* (SUNDEVALL, 1847). However, CRAWFORD-CABRAL & PACHECO (1989: 11) published a craniometric study on Angolan *Dasymys*, unfortunately on very limited material, reaching the conclusion that 'at least the two central Angolan forms (*D. nudipes* and *D. i. aff. bentleyae*) are not conspecific'.

A first bigger scale attempt to revise the genus *Dasymys* based upon craniodental morphometric variation among west African populations concluded that (p. 419) 'Two morphological kinds can be discerned in this region' and that '... the degree of craniodental differentiation between these two phena matches that documented for other congeneric pairs of murid species inhabiting parts of west Africa' has convincingly shown that continuing to consider *Dasymys* to be monotypic is most certainly not a realistic option (CARLETON & MARTINEZ (1991).This view was maintained by MUSSER & CARLETON (1993), who recognize five species in sub-Saharan Africa in their classification of the genus *Dasymys*: (*D. foxi* in Jos Plateau, Nigeria; *D. rufulus* in West-Africa; *D. montanus* at high altitudes in the Ruwenzori Mt of Uganda; *D. nudipes* in southwestern Angola; *D. incomtus* for the rest of its geographical range); they also recognize 14 synonyms within *D. incomtus*. Another study confirms that at least two taxa and possibly three «allospecies» are present in central Angola, stressing again that it is very probable that the monotypic approach to *Dasymys* is outdated (CRAWFORD-CABRAL, 1998).

Recently, the wide distribution range for *D. incomtus* – as proposed by MUSSER & CARLTON (1993) [from Sudan to Ethiopia, and then south to the southern coast of South Africa] is questioned (MULLIN et al., 2002). She suggests (p. 383): 'It seems more likely that the currently listed distribution range of *D. incomtus* is a remnant of the time when all of Africa was supposedly inhabited by this one known species (CARLETON & MARTINEZ, 1991)'. In addition her study on *Dasymys incomtus* populations from the Kwa-Zulu-Natal and Northern Province strongly indicates that two separate subspecies or even species exist within *D. i. incomtus* (ibidem, p. 399).

It is in the context of this debate that we have initiated the present study. We intend to describe the morphometric variation in populations of the East African 'shaggy-furred' rats by using craniometric methods, and where possible add information provided by mitochondrial cytochrome *b* sequences. Our final objective is to define some of the taxonomical problems concerning the genus *Dasymys*, while also describing some populations that we consider to be new taxa.

We will use the same methods as described in VERHEYEN et al. (2002) which aims at discussing the status of the described taxa by comparing quantitative characters of the type specimens with sufficiently large samples (OTU's = Operational Taxonomical Units) of measurable skulls from animals collected from the whole geographical range of the studied genus (in total 20 OTU's were used). Essential to this approach is that we attempt, through specific multivariate analyses and subsequent plotting of the type-skulls, to evaluate the status of the described taxa and to eventually identify OTU's which can be considered to represent these taxa. The results of this metrical and statistical approach will be com-

plemented with a molecular phylogenetic analysis of the mitochondrial cytochrome *b* sequences (see VERHEYEN et al., 2002).

MATERIAL AND METHODS

Morphological and metrical methods

THE SPECIMENS

This study is largely based on the rodent specimen collections made by the Research group on African Rodents (RUCA, Department of Biology, University of Antwerp, Belgium), the collections of the Koninklijk Museum voor Midden-Afrika (Tervuren, Belgium) and the Koninklijk Belgisch Instituut voor Natuurwetenschappen (Brussels, Belgium). All of the specimens collected by the research group of RUCA were prepared for study at the University of Antwerp before being deposited at the Koninklijk Museum voor Midden-Afrika (Tervuren, Belgium). However, without the important input of collections from the Smithsonian Institution (Washington), the American Museum of Natural History (New York), the British Museum (Natural History) (London) and the Muséum national d'Histoire naturelle de

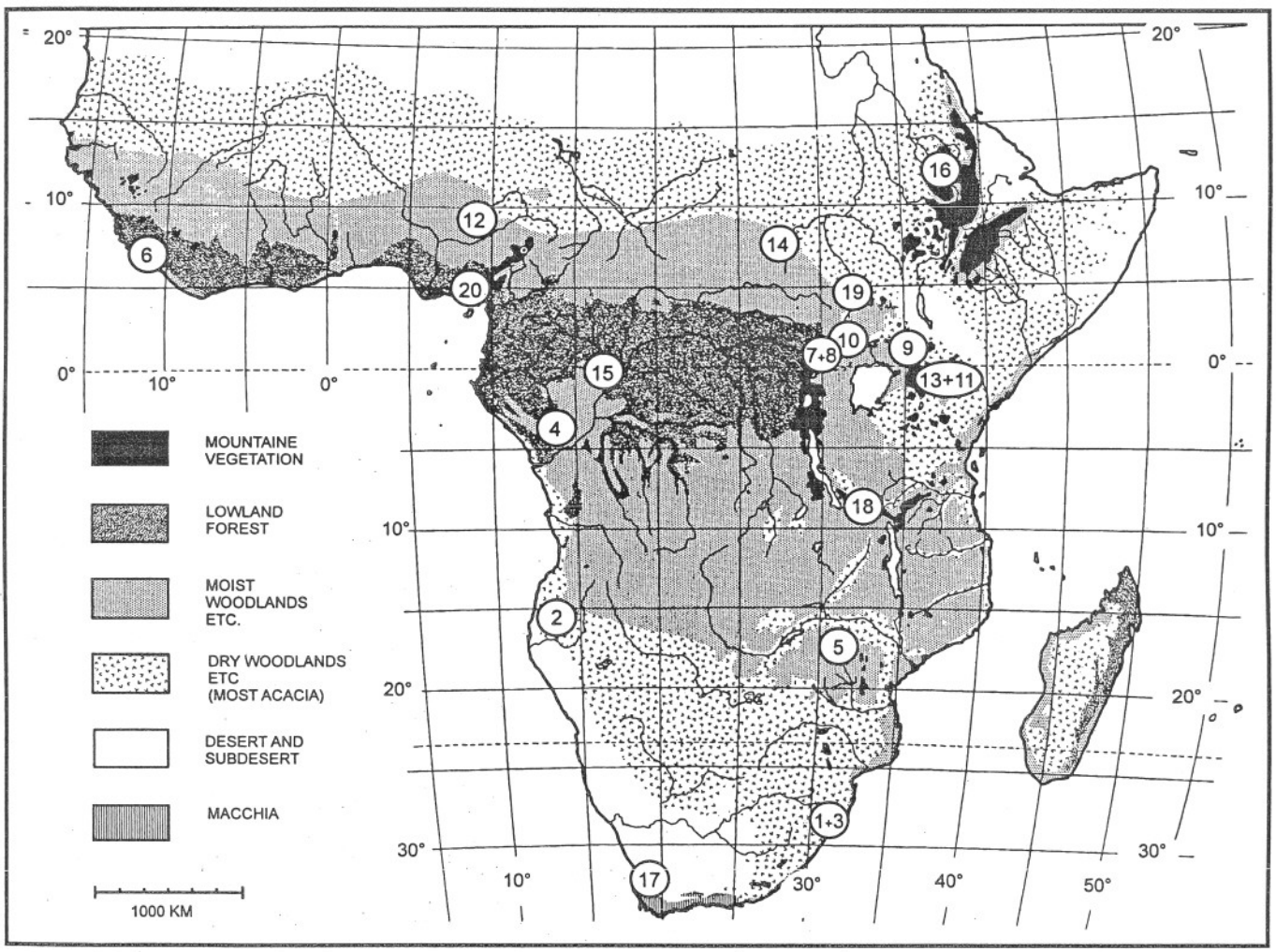


Fig.1. Map showing the geographical position of the type localities of the different taxa of the *Dasymys* genus. For the co-ordinates we refer to Appendix 3. Based on Map B (p. XIII) of HALL and MOREAU (1970).

1. *incomtus* SUNDEVALL, 1846
2. *nudipes* PETERS, 1870
3. *gueinzii* PETERS, 1875
4. *bentleyae* THOMAS, 1892
5. *fuscus* DE WINTON, 1896
6. *rufulus* MILLER, 1900
7. *medius* THOMAS, 1906
8. *montanus* THOMAS, 1906
9. *helukus* HELLER, 1910
10. *orthos* HELLER, 1911
11. *savannus* HELLER, 1911
12. *foxi* THOMAS, 1912
13. *nigridius* HOLLISTER, 1916
14. *shawi* KERSHAW, 1924
15. *edsoni* HATT, 1934
16. *griseifrons* OSGOOD, 1936
17. *capensis* ROBERTS, 1936
18. *alleni* LAWRENCE & LOVERIDGE, 1953
19. *palustris* SETZER, 1956
20. *longipilosus* EISENTRAUT, 1963

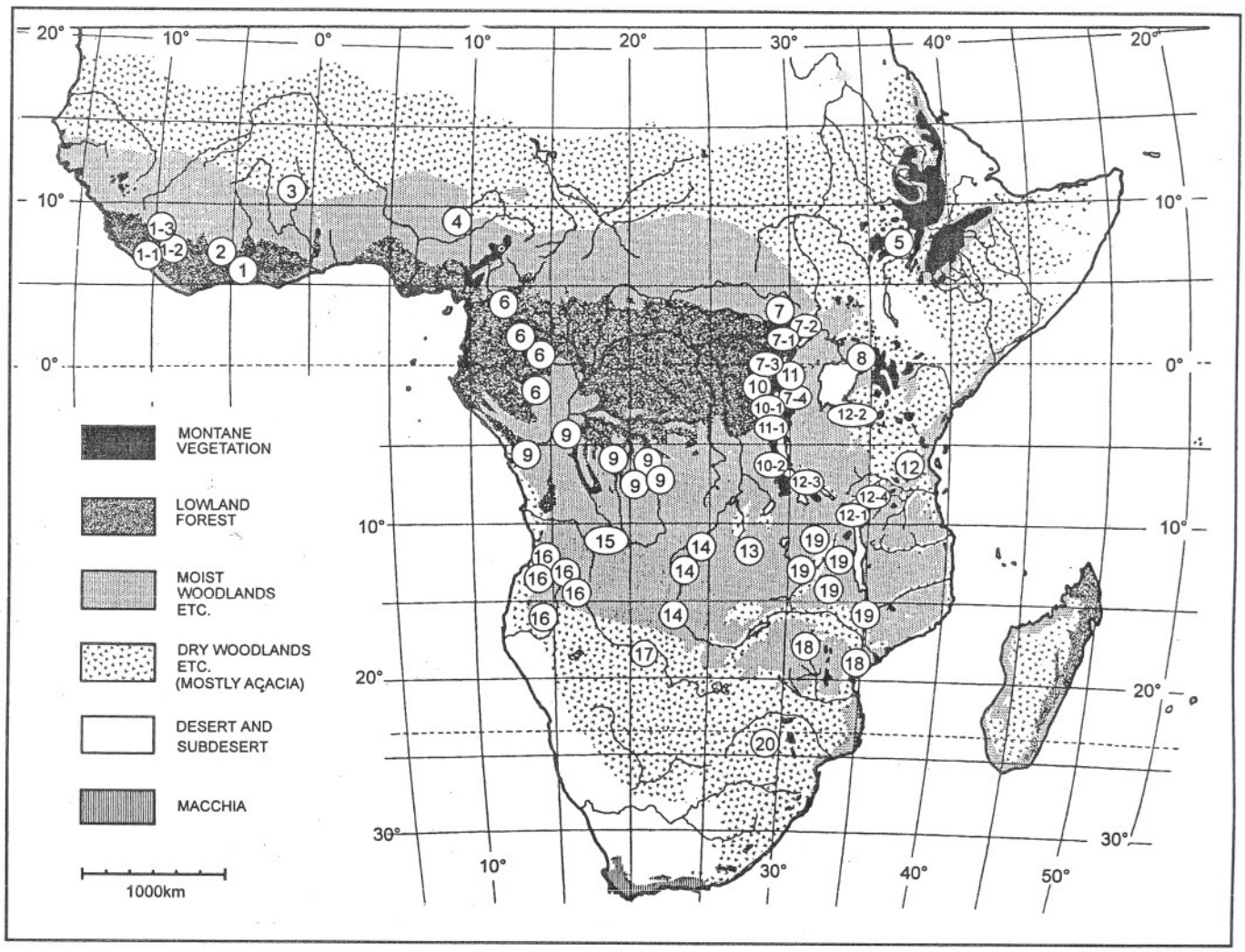


Fig.2. The geographical distribution of the OTU's of the genus *Dasymys* used in this study. For the exact content of each OTU, we refer to Appendix 2 and for the co-ordinates of the collecting localities, see Appendix 3. Based on Map B (p. XIII) of HALL & MOREAU (1970).

1. Mopoyem
1-1 Mt Coffee
1-2 Mt Nimba
1-3 Seredou
2. Lamto
3. Pulima
4. Panyam
5. Kaffa
6. Franceville
7. Garamba
7-1 Ruwenzori Mt
7-2 Blukwa
7-3 Butembo
7-4 Astrida
8. Kaimosi
9. Kinshasa
10. Tshibati
10-1 Bukavu
10-2 Albertville
11. Virunga
11-1 Uwinka
12. Dakawa
12-1 Rungwe Mt.
12-2 Mwanza
12-3 Ufipa
12-4 Mufindi
13. Lubumbashi
14. Balovale
15. Chitau
16. Huila
17. Okavango
18. Harare
19. Kasungu
20. Nylsvlei

Paris (France) we would not have been able to carry out this revision. Our results are based on information from 1059 skulls, of which 981 were suited for our analyses.

Appendix 1.1 lists all the relevant data concerning the type specimens of *Dasymys* (type-localities, geographical co-ordinates etc...) and Appendix 1.2 summarizes the skull-measurements of the type-specimens, as measured by us. Fig.1 depicts the geographical distribution of the type localities across Africa.

Appendix 2 groups all the measured specimens per OTU. For each OTU the number of specimens, classified by sex and age, is provided. For the description of the acronyms that identify the musea and institutions where these specimens are curated, we refer toVERHEYEN et al. (1996).

Appendix 3 is an alphabetical listing of the collecting localities, followed by their geographical co-ordinates; between brackets we provide the OTU number into which the locality is included. Fig.2 visualizes the geographical distribution of the OTU's.

CRANIOMETRY

To evaluate the impact of ageing on the size and shape of the *Dasymys* skulls we grouped all the available crania into age-classes using the tooth-eruption and tooth-wear patterns as described in VERHEYEN et al. (1996, p. 246). We are aware that this method has its limitations, and that the use of this approach results in at best approximate age estimates.

We use the cranial and external measurements as described elsewhere (acronyms as in VERHEYEN et al. 1996). The measurements were taken with callipers (digital reading) graduated to hundreds of millimetres, but recorded with a precision of 0,05 mm. Appendices 4.1. and 4.2. supply a full description of our measurements accompanied by drawings of a *Dasymys* skull with the exact localisation of our measuring points.

Basic statistics, Student-t-tests, Multiple Discriminant or Canonical Analysis were performed on a PC with the statistical package Statistica 5.5. from StatSoft Inc (1995). All statistical analyses used the whole data set regardless of sex, but excluding data from specimens of age-classes 0 and 5. The original metrical data of our OTU's (see Appendix 2) cannot be fully published here but can be obtained through E-mail (hulsel@ruca.ua.ac.be).

To enhance the clarity of the results depicted in our multi-group graphs, we only show the 95% equiprobable ellipses instead of the individual scores. In certain cases, especially when comparing a great number of OTU's, we opted for the construction of tree-diagrams, based on the Mahalanobis squared distances between the centroids, using the Unweighted Pair Groups Arithmetic Average Method (SNEATH & SOKAL, 1973); this method accounts for all the relevant axes in the canonical hyperspace. In some occasions we replaced missing data by the means .

Each of our OTU's comprises only fully adult and complete skulls and contains a sufficient number of specimens to make statistically valid analyses. In only a few isolated cases we maximalized OTU's either by eliminating some measures responsible for excluding some otherwise complete skulls (plotting of incomplete type skulls) or by substituting missing data by means.

Finally, most of our OTU's are homogenous as to the geographical origin of the included specimens. Only to form OTU9 (Kinshasa), OTU10 (Kasungu) and OTU6 (Franceville) we had to group specimens from a rather widespread geographical origin.

DNA-METHODS

TAXONOMIC SAMPLING

Twenty three sequences were made for this study to represent the currently recognized *Dasymys* species. We added two sequences from specimens identified as *Dasymys incomtus* and *rufulus* (respectively EMBL accession number AF141217 and AF141216) and taken from the literature (DUCROZ et al., 2001). As outgroups we included three African murine sequences: from LUNDRIGAN et al. (2002) we used *Mastomys hildebrandti* (AY057818) and *Nannomys minutoides* (AY057816), *Hylomyscus parvus* (AF518330) was taken from LECOMPTE et al. (2002). Given the geographic area covered by this study we assume that our sampling is sufficient to assume that it covers a significant proportion of the taxonomic diversity of the Central and East African *Dasymys*.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total DNA was extracted from frozen or ethanol preserved muscle or liver tissues using the QuiaAmp DNA Minikit. The complete mitochondrial cytochrome *b* sequences (1140 bp) were amplified using primers L14723 and H15915 (DUCROZ et al., 1998). Double stranded PCR amplifications were carried out in 25µl reaction volumes containing 10µM of each primer, 200 µmol dNTPs, 10mM Tris-HCl, 1.5 mM $MgCl_2$, 50 mM KCl (pH 8.3), and 1 unit Taq polymerase. We used one cycle of denaturation at 94°C for 4 minutes, annealing at 52°C for 2 minutes, extention at 72°C for 2 minutes, followed by 30 cycles of denaturing at 94°C for 1 minute, annealing at 52°C for 1 minute, and extention at 72°C for 10 minutes. Double stranded PCR products were cleaned using the GFX PCR DNA and Gel band Purification Kit (Amersham Biosciences). Dye terminator cycle sequencing was performed following the manufacturer's instructions. The used primers included L14723, H15915 and two additional primers L15408 and H15553 (DUCROZ et al., 1998). The reaction products were either run on an ABI 373 sequencer in the lab of the RBINS or at the VIB sequencing facility at the University of Antwerp. To ensure that the obtained cytb sequences are of mitochondrial origin, the corresponding amino acid sequences were screened for the presence of stop codons, deletions or inserts using MEGA2.0 (KUMAR et al., 2001).

DATA ANALYSES

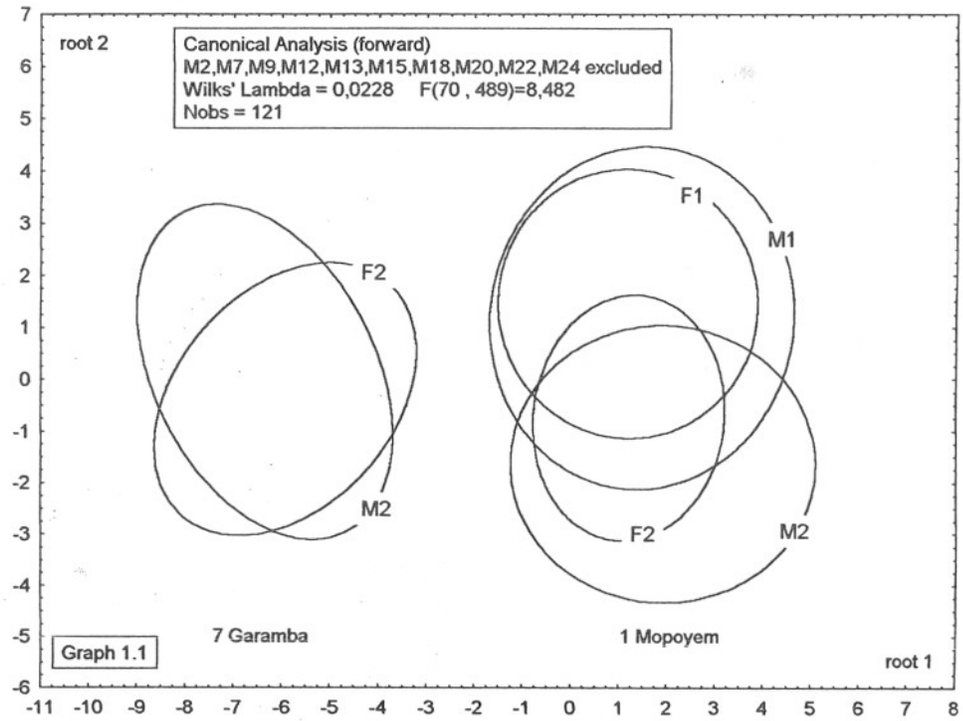
The sequences were visually aligned using the 1140 bp sequence of *Mus musculus* (BIBB et al. 1981). Parsimony (MP), distance (NJ) methods were implemented using PAUP version 4.0b10 with settings as described in the results. For the calibration of a molecular clock based upon the presumed time divergence between the *Mus* and *Rattus* lineages (JAEGER et al., 1986) we included one *Rattus rattus* sequence (SUZUKI et al., 2000) from the literature. Time estimates were computed from distances based on 3rd base position transversions following DUCROZ et al. (1998).

RESULTS

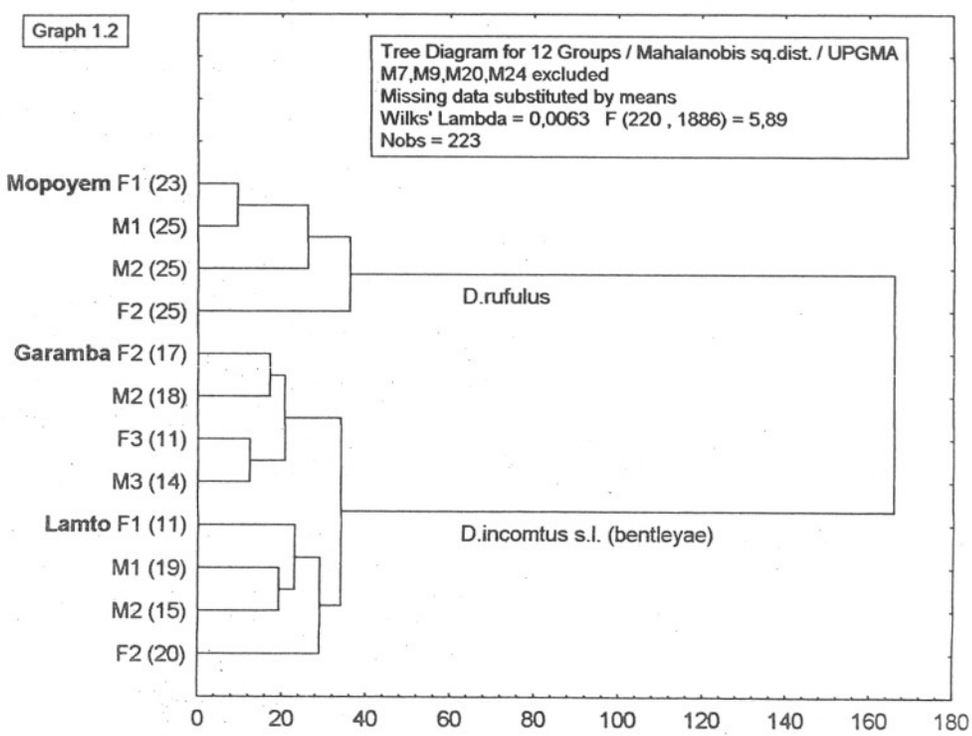
1. Sexual dimorphism and growth in the skull of *Dasymys*

(Graph1.1, 1.2; Appendix 5.1,5.2)

Before starting our canonical and other multivariate techniques we evaluated whether the age-sex composition of the compared OTU's is likely to influence the obtained results. Only two series of skulls at our disposal are large enough



Graph 1.1. Graphic representation of a forward canonical analysis comparing some sex-age groups of OTU1 (Mopoyem) and OTU7 (Garamba) in order to evaluate the influence of sex and (or) age on the morphometric differences between *D. rufulus* and *D. incomtus* s. l. (*bentleyae*).



Graph 1.2. Phenetic tree based upon the Mahalanobis squared distances between the different sex-age groups of the OTU's Mopoyem (OTU1), Garamba (OTU7) and Lamto (OTU2).

(OTU1: Mopoyem; OTU7: Garamba) to allow such analyses. OTU1 contains 98 skulls that were collected in the nineteen sixties in the savannah of Mopoyem near Adiopodoumé (Ivory Coast). OTU7 is equally important, and contains 100 skulls mainly collected in the nineteen fifties in the savannahs of the National Garamba Park of the former Belgian Congo. Unfortunately, the latter series is much less appropriate to evaluate sexual dimorphism since the sex of an important number of specimens is unknown.

Appendix 5.1. demonstrates that we cannot detect a significant sexual dimorphism in the external and cranial dimensions in age-class 1 of OTU1. However, in age class 2 we observe that the males are significantly bigger than the females; males have indeed 1°/ a larger skull than the females (M1, M2, M3), 2°/ a heavier developed rostrum and upper-incisor (M5, M15, M21, M22, M23), 3°/ a higher ramus of the mandibula (M24). Our data suggest that this sexual dimorphism increases with age but since we do not have the adequate cranial series we have no statistical support for this finding.

Also in age-class 2 of OTU7 (Garamba) the males are slightly bigger than the females (M13, M14, M15, M23) (appendix 5.2). The sexual dimorphism shows an increase in age-class 3 and the skulls of the males are 1°/ longer (M1, M2, M3, M6), 2°/ have a heavier rostrum (M22, M23) and 3°/ have a slightly higher ramus of the mandible (M24).

Since the observed craniometrical differences between the sexes range between 2 - 5% it would appear to be logical to take into consideration the age-sex composition of our OTU's. However, in order to evaluate directly the impact that sexual differences could eventually have on our results, we performed some preliminary canonical analyses. The comparison of the sex-age groups for the two OTU's not only reveals that the age-sex groups clearly overlap within an OTU, but also that taxonomical or geographical differences between OTU's do not seem to be influenced significantly by sex or age (graph 1.1.).

Graph 1.2. represents a phenetic tree based upon the Mahalanobis squared distances between 3 OTU's (two OTU's geographically very distant but pertaining to the same taxon and one OTU of a taxonomically different population). Also here we conclude that the age and sex composition of the compared OTU's has little or no influence on the branching of the tree. To test the robustness of the method we even included some subgroups consisting of too few specimens (see the number of specimens mentioned after the subgroups of each OTU). Even in this statistically unreliable situation the obtained branching remained remarkably stable.

We cannot but conclude that our set of craniometric measures appears to cover adequately the cranial variation present in our OTU's, even covering allometric interferences due to age and (or) sex. This leads us to the conviction that the observed craniometric differences - as revealed by our canonical analyses - should be considered highly relevant in a taxonomic context. We underline that we came to the same conclusion when revising the *Lophuromys flavopunctatus* species complex (VERHEYEN et al 2002).

2. The taxonomical status of the type specimens of the *Dasymys* taxa

(Graph2.1, 2.2, 3.1, 3.2; Appendix1.1, 1.2)

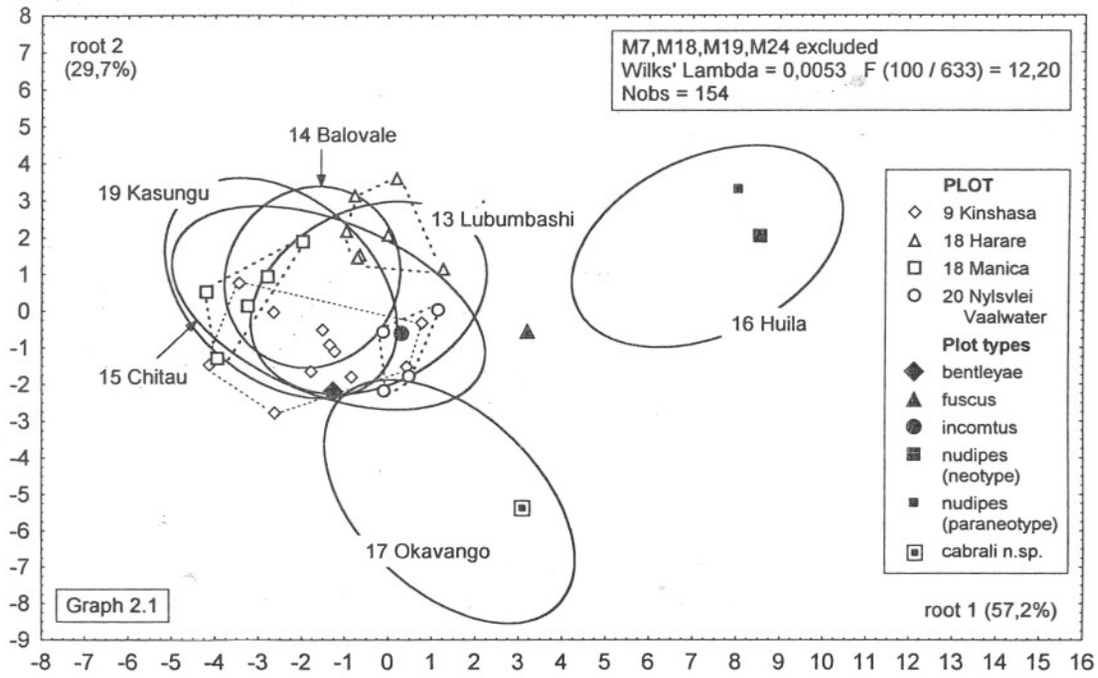
We have examined 17 out of the 20 described *Dasymys* taxa and appendix 1.1 groups all relevant data concerning the type specimens. The skulls were measured by us and the resulting data presented in appendix 1.2. We were not able to examine and measure the types of *Mus nudipes* PETERS (1870), *Dasymys gueinzii* PETERS (1870) and *Dasymys incomtus capensis* ROBERTS (1936). Especially the absence in our data-base of the *nudipes*-type, destroyed in the 1978 fire which devastated the 'Museu Bocage' part of the Science Building of the University of Lisbon (fide CRAWFORD-CABRAL), proved to be such a hindrance to reach a satisfying taxonomical solution that we decided to create a neotype and a neo-paratype. Particulars of both specimens are included in appendices 1.1 and 1.2 ; the description itself can be consulted further in this paper.

A canonical analysis based upon a selection of six OTU's hopefully represents the actual craniometrical variation of *Dasymys* in southern Africa (graph 2.1). The first observation is that we can discern in the selection three clearly differentiated groupings. If we plot on this background some additional small series of more southern situated localities (Manica - Harare - Nylsvlei - Vaalwater) as well as the bigger OTU9 (Kinshasa) we see that they all coincide with our OTU's 13, 14, 15, 19 and that there is neither an overlap with OTU16 (Huila) typical for *Dasymys nudipes* or with OTU17 (Okavango).

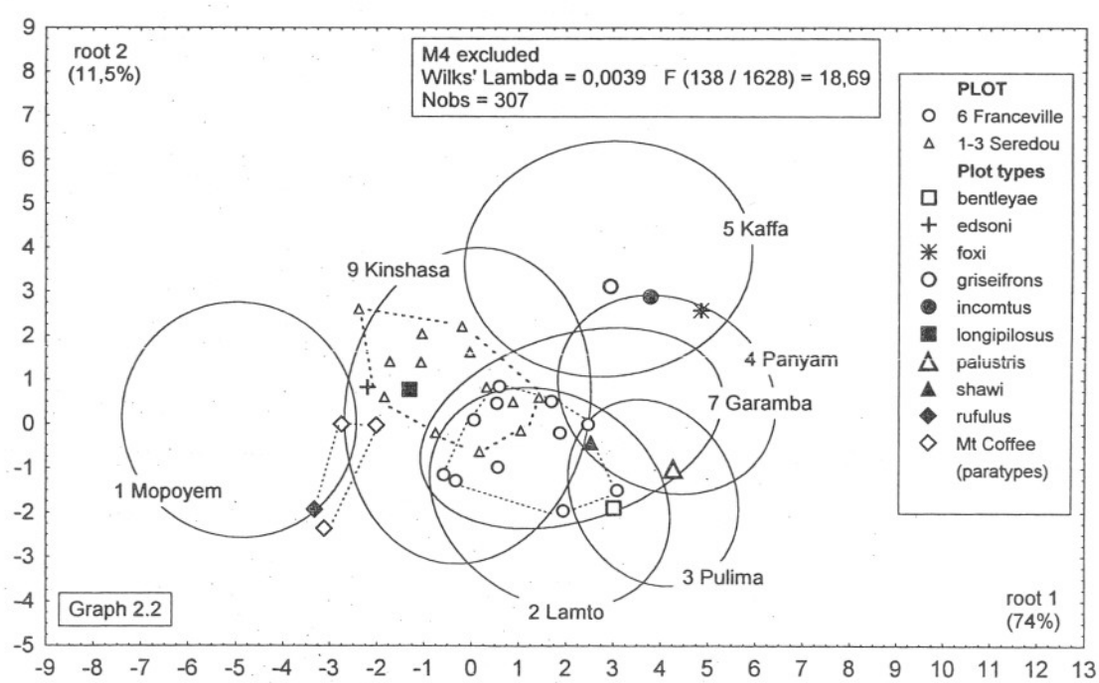
After adding a number of southern types we see that the type specimen of *D. incomtus* coincides perfectly with our set of OTU's 13, 14, 15, 19. This suggests that all of the *Dasymys* from western central Angola over southern Shaba, through Zambia-Malawi-Zimbabwe-Mozambique till south eastern S. Africa pertain to that species. Also the type of *bentleyae* (lower Congo) situates itself within the ellipses characterizing *incomtus*.

On the other hand, the type-specimen of *D. fuscus* clearly falls outside the *D. incomtus* group between the OTU's 16 and 17 suggesting that *fuscus* might represent another taxon or an eastern representative of either *nudipes* (characterized by OTU16) or of the new taxon that we will describe for the Okavango region (OTU17).

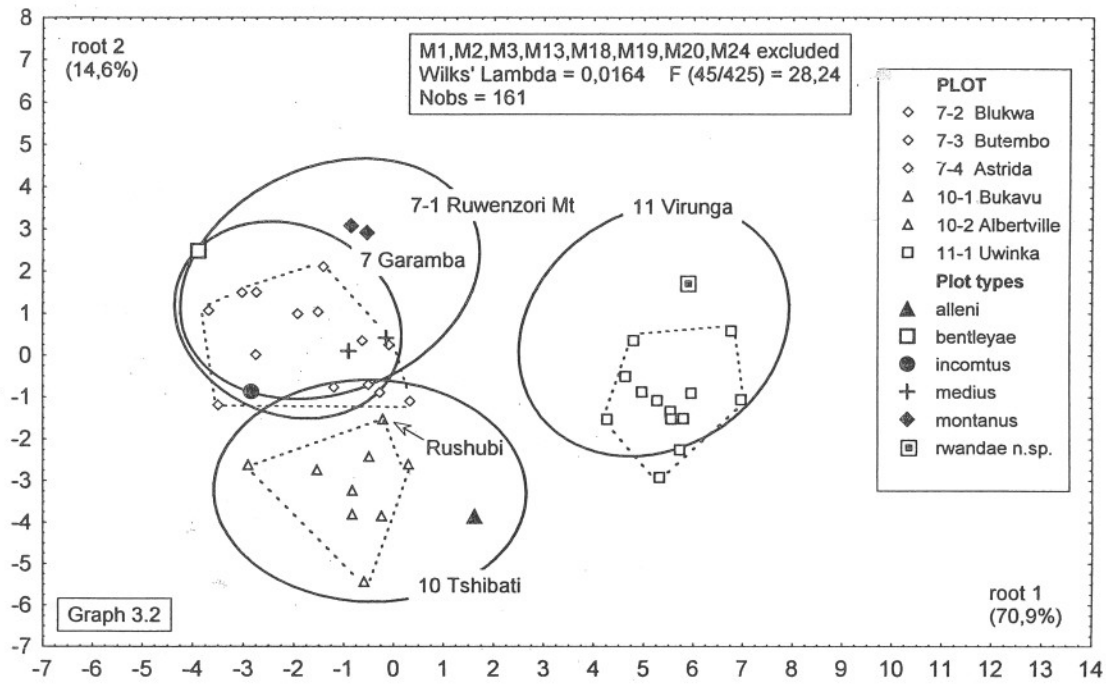
Another analysis compares a number of OTU's representative for the west African region (OTU1, 2, 3, 4) with a set of OTU's that we consider to cover the variation of the central African region inclusive of Ethiopia (OTU's 5, 7, 9) (graph 2.2.). It becomes immediately clear that OTU1 (Mopoyem) of West Africa is manifestly separated from all other OTU's and also that OTU5 (Kaffa) is somewhat differentiated. Plotting OTU6 (Franceville) into this analysis situates these specimens well within OTU7 (Garamba) and OTU9 (Kinshasa) that in a way bridges the gap between OTU1 (Mopoyem) and the other OTU's. It should however be mentioned that the geographical origin of the specimens composing OTU9 (Kinshasa) is rather diverse, which may explain its more elongated 95% equiprobable ellipse. Also the plotting of the series from Seredou (OTU1-3) reveals that it coincides completely with OTU9 (Kinshasa).



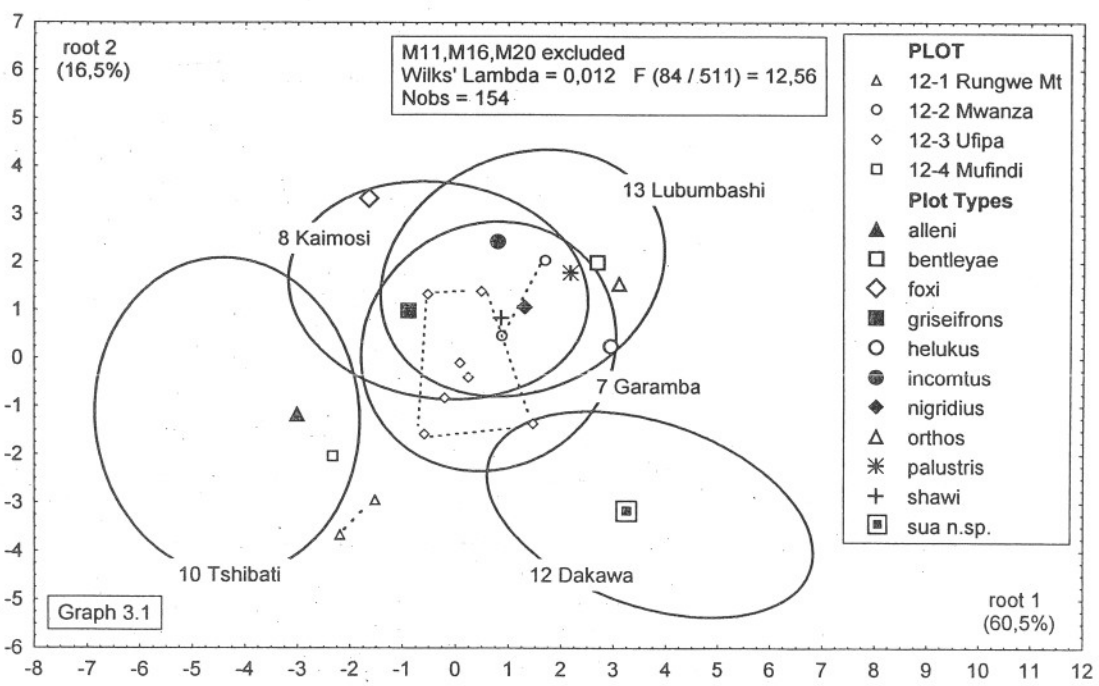
Graph 2.1. Graphic representation of a forward canonical analysis performed on a set of six *Dasymys*-populations representing more or less the cranial variability present in the southern regions of its distribution providing the background to situate by plotting some of the important south African type-specimens and some small crucial OTU's. Some cranial measures were excluded to maximize numerically some of the OTU's.



Graph 2.2. Graphic representation of a forward canonical analysis performed on a set of seven *Dasymys*-populations providing the background to allocate by plotting the type-specimens of the northern area of its geographical distribution and some small but important OTU's. M4 (HEPA) was excluded in order to be able to plot the type specimen of *edsoni* HATT 1934.



Graph 3.1. Graphic representation of a forward canonical analysis performed on a set of five *Dasymys*-populations representing the observed geographical variation in the eastern region of the distribution of *Dasymys* in order to allocate by plotting the type-specimens originating from this region and some small but important OTU's (here also some measures were excluded in order to allow the plotting of the relevant type specimens).



Graph 3.2. Graphic representation of a forward canonical analysis performed on a set of four OTU's representing the western-central rift region and providing the background to allocate by plotting the relevant type specimens and some smaller but important OTU's. In this analysis we had to reduce the number of measures by one third in order to enable a plotting of the important but seriously damaged type-skull of *montanus* THOMAS 1906.

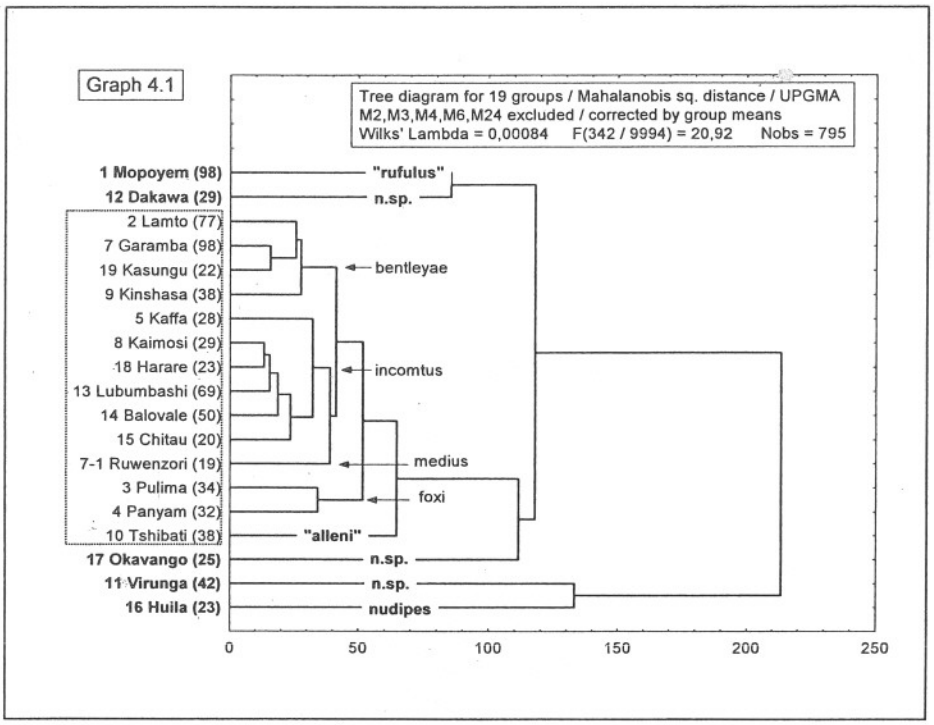
Even after the exclusion of OTU1 (Mopoyem) from the analysis, a very important overlap remains between all the OTU's indicating that craniometrically there is no good argument to suggest the existence of important taxonomical differences (except maybe for the slightly different OTU5).
It is reassuring that the relevant type-specimens fit rather well with their geographically related OTU's; that *longipilosus* and *edsoni* fall within OTU9 (Kinshasa) and that only the *rufulus* type and paratypes more or less correspond with OTU1 (Mopoyem).
We conclude the dicussion of graph 2.2 by accepting in western, central and northeastern Africa the existence of two craniometrically well differentiated species (*D. rufulus* and *D. incomtus*). There remains however some doubt whether OTU1 (Mopoyem) can be considered to represent typical *rufulus*. Indeed, 1°/ the topotypical locality of *rufulus* (Mt Coffee) is situated about 500 km to the west of Mopoyem (locality in a by forest enclosed savannah); 2°/ the *rufulus*-type series plots also closely with OTU9 (Kinshasa) and clusters more or less with the central African types of *longipilosus* and *edsoni*.
Both arguments suggest that OTU1 (Mopoyem) might represent a new taxon that is different from (but related to) *rufulus*. In this case typical *rufulus* would be 'close' to OTU9 (Kinshasa) that we consider to represent *D. bentleyae* [together with OTU7 (Garamba)].
In graph 3.1. we compare populations that represent eastern and central eastern Africa (OTU's 7, 8, 10, 12) with OTU13 (Lubumbashi) that characterizes the south-eastern region and in our view representative of typical *D. incomtus* (see graph 2. 1.). This graph was conceived to clarify the taxonomical position of OTU12 (Dakawa) against a background of east African populations and type specimens. In this analysis we did not include the strongly differentiated Rwandan OTU11 (Virunga) because of the poor condition of the *montanus* type skull (see graph 3.2.).
Apart from the fact that none of the *Dasymys* types coincides with OTU12 (Dakawa), making this OTU a good candidate for taxonomical recognition, we see that the type of *D. alleni* (type locality: Ilolo, Mt. Rungwe, Tanzania) plots well inside the equiprobable ellipse of OTU10 (Tshibati-Kivu). This rather surprising finding is confirmed by the plotting of the small OTU12-1 and OTU12-4 (grouping respectively a few specimens from Mt Rungwe and from Mufindi, Tanzania).
The other small Tanzanian OTU's (12-2, 12-3) as well as all the *Dasymys* types of the eastern African region (Sudan-Ethiopia-Kenya-Congo-Zimbabwe) fall well grouped inside the equiprobable ellipses of OTU8 (Kaimosi), OTU7 (Garamba) and OTU13 (Lubumbashi).
As indicated above, we created graph 3.2. to evaluate 1°/ the taxonomical position of the *montanus* type-specimen which has a very damaged skull and 2°/ to determine the taxonomical position of some of the small OTU's (7-2, 7-3, 7-4, 10-1, 10-2, 11-1) of the rift-region. The first conclusion we can draw is that the *D. montanus* type falls well within the topotypical OTU7-1 (Ruwenzori Mt) and that it in our opinion should be considered to be synonymous with *D. medius* (both types were measured twice with about 10 years interval). Next we can conclude that OTU10 (Tshibati) is well differentiated from OTU11 (Virunga), from OTU7 (Garamba) and from OTU7-1 (Ruwenzori Mt).
Furthermore, it is clear that the smaller OTU's pertain to one of the three taxa represented in this graph: 1°/ OTU11-1 (Uwinka) situates clearly within OTU11 (Virunga); 2°/ OTU10-1 (Bukavu) and OTU10-2 (Albertville) coincide with OTU10 (Tshibati) as well as the type- and topotypical specimens of *alleni* and 3°/ the small OTU's (7-2, 7-3, 7-4 and 7-5) of Kivu, Rwanda and Burundi fall for the greater part within the equiprobable ellipses of OTU7 (Garamba) and OTU7-1 (Ruwenzori Mt). All the other plotted types (*bentleyae, incomtus, medius, montanus*) are to be found within the range of OTU7 and OTU7-1.

Finally we draw attention to the specimen IZEA 2716 of Rushubi (Burundi) which clusters neatly within the range of OTU10 (Tshibati). This specimen is particularly interesting because it has been caryotyped (MADDALENA et al., 1989).
Summarized, the following conclusions can be drawn concerning the taxonomical position of the studied *Dasymys* type-specimens:

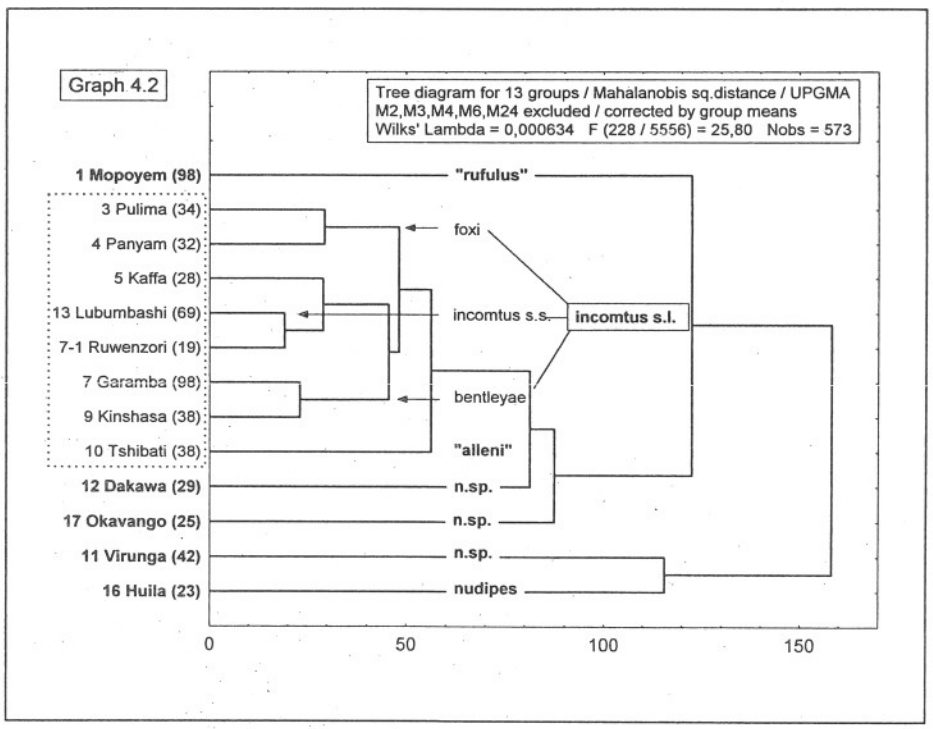
- all our analyses suggest that *incomtus* (SUNDEVALL, 1846) is to be considered the *Dasymys* taxon with the widest geographical range; *bentleyae, medius, montanus, helukus, orthos, savannus, nigridius, shawi, edsoni, griseifrons, palustris, longipilosus* are possibly all synonyms of *incomtus*, which in our present analysis can be best represented by OTU13 (Lubumbashi);
- the types *foxi* THOMAS (1912) *alleni* LAWRENCE & LOVERIDGE (1953), respectively represented by OTU4 (Panyam-topotypical) and OTU 10 (Tshibati) are sufficiently differentiated from *incomtus* to be considered separate taxa;
- *rufulus* MILLER (1900) can, within certain limits (see discussion) be represented by OTU1 (Mopoyem);
- we will select in OTU16 (Huila) a neotype and neoparatype to replace the lost type-specimen of *D. nudipes*.

3. The craniometric variation within the genus *Dasymys*
(Graph 4.1, 4.2)

In order to visualize the important craniometric variation disclosed in the preceding paragraphs, we performed a canonical analysis including as many OTU's as available to us (19) and covering most of the geographical range of the genus. We present the results by a tree-diagram based upon the Mahalanobis squared distances between the obtained centroids (UPGMA) (graph 4.1.). In a second analysis we reduced the number of OTU's to 13 (graph 4.2.).
Before discussing both graphs we want to point out the methodological limitations of this approach. Its reliability is limited by the size of the OTU's (numbers of skulls) in comparison to the number of cranial variables (measurements) taken per skull. The number of observations per OTU has to be preferably greater than the number of variables (i.e. measurements) per skull, otherwise the matrix of within variation of the concerned OTU tends to be singular.
In graph 4.1. we show a phenetic tree based upon an UPGMA analysis of 19 OTU's. We underline that similar analyses (based upon a varying set of OTU's and (or) varying number



Graph 4.1. UPGMA dendrogram based upon the craniometric comparison of 19 OTU's of *Dasymys*-populations using a minimum of 19 skull-measurements. The OTU's representing craniometrically clearly defined taxa are printed in bold characters. The remaining OTU's (rectangle) group the taxa we consider to form the *incomtus* s. l. species complex.



Graph 4.2. UPGMA dendrogram based upon the craniometric comparison of 13 OTU's using a minimum of 19 skull-measurements. By reducing the number of OTU's by nearly half we intended to clarify the craniometric position of the new taxa represented by OTU12 (Dakawa) and OTU17 (Okavango) versus the *incomtus* s. l. species complex.

of measures) always give comparable results. To facilitate the discussion we identified OTU's on the graph that we could link to some of the described taxa (see chapt. 2). When we reduce the number of OTU's in the so called '*incomtus*' species clade to the eight taxonomically most important, we obtain graph 4.2. where the phenetic tree is based upon only 13 OTU's.

A comparison between both graphs shows that the branching at a high linkage level (above 100) expresses only phenetic relations and has no phylogenetic meaning whatsoever. This is clearly demonstrated by the position of OTU12 (Dakawa) which is closest to OTU1 (Mopoyem) in graph 4. 1. and shifts to OTU17 (Okavango) in graph 4.2.

In graphs 4.1. and 4.2., OTU1 (Mopoyem) and OTU16 (Huila) are easily identified as representatives of respectively the west African *D. rufulus* and the Angolan *D. nudipes*. Both are craniometrically well differentiated taxa and easy to characterize. We formulate here, however some reservation (see graph 2.2.) as to whether the Mopoyem population is truly concordant with the Mt Coffee population (topotypical locality of *rufulus*). It remains possible that the Mopoyem population represents a different taxon, be it close to true *rufulus*. Unfortunately we could not obtain a statistically valid skull-series of the Mount Coffee area to test this hypothesis.

OTU11 (Virunga), OTU12 (Dakawa) and OTU17 (Okavango) are the three new taxa that we will describe. These three OTU's are craniometrically strongly differentiated from each other and do not identify with any of the known taxa (see also graphs 2.1., 3.1., 3.2.).

The *incomtus* s.l. species group has by far the biggest geographical distribution of the OTU's represented in graph 4. 1. Within this group OTU10 (Tshibati) and OTU3+4 (Pulima + Panyam) - representing respectively *alleni* and *foxi* - are clearly differentiated from the other OTU's. The rest of the grouping splits up into a *bentleyae* branch that encompasses OTU9 (Kinshasa), OTU7 (Garamba), OTU2 (Lamto), OTU19 (Kasungu) and an even more widely distributed *incomtus s. s.*, here represented by OTU5 (Kaffa), OTU8 (Kaimosi), OTU18 (Harare), OTU13 (Lubumbashi), OTU14 (Balovale), OTU15 (Chitau) and OTU7-1 (Ruwenzori Mt).

In graph 4. 2 the differences between *incomtus s. s.* and *bentleyae* are somewhat enhanced and cluster with *foxi* (OTU3+4), while *alleni* (OTU10, Tshibati) represents a valid taxon.

Combining the evidence from both graphs we conclude that:

- the Tshibati-population (OTU10) represents a clearly differentiated taxon that we identified with the type specimen of *alleni*;
- the *bentleyae*- (OTU's 7 and 9), the *incomtus*- (OTU8, 13, 14, 15, 18) and the *foxi*-populations (OTU's 3 and 4) represent craniometrically slightly different branches, but probably not important enough to justify taxonomic recognition.

Summarizing, we conclude that we can identify craniometrically three *Dasymys*-populations OTU12 (Dakawa), OTU17 (Okavango) and OTU11 (Virunga), which we will formally describe below.

4. Selecting a neotype for *Dasymys nudipes* (PETERS, 1870)

(Graph 2.1, 5.1, 5.2; Appendix 1.1, 1.2, 5.3)

NEOTYPE

AMNH.87.744; adult male; skin and skull; collected by the Phipps Bradley Expedition (13 November 1932) in Humpata (15. 01S - 13. 21E; alt. 6300 ft); collecting number 463.

NEO-PARATYPE

ISCED 1987; adult male; skin and skull; collected by Simoes P. and C. (19 December 1966) in Humpata (15.01S - 13.21E) collecting number 572.

For the craniometrical and other relevant data of the neotype and neo-paratype we refer to Appendix 1.1 and 1.2.

TYPE LOCALITY

The collecting locality Huilla (15.04S - 13.33E) of the original type-specimen of *Mus (Isomys) nudipes* PETERS (1870) is situated about 25 km to the South East of Humpata, the collecting locality of the neotype and neo-paratype. We choose for this solution since we could not locate an adequate specimen from Huilla itself. Both localities are situated somewhat to the South of Sá da Bandeira in the Serra da Chela at a rather high altitude (6.300 ft).

Hoping to locate and subsequently study the important type specimen of *Dasymys nudipes* we contacted our colleague João CRAWFORD-CABRAL who has been studying the Angolan murid collections conserved in the most important musea and scientific institutions (see publication of 1998). He replied: 'The material studied by Bocage (including *Dasymys nudipes*) was stored in the Zoological Department of the National Museum of Natural History. Such a department, known as 'Museu Bocage', occupied part of the huge building of the Science Faculty of the University of Lisboa, a building that was largely wasted by a fire in 1978. Unhappily,

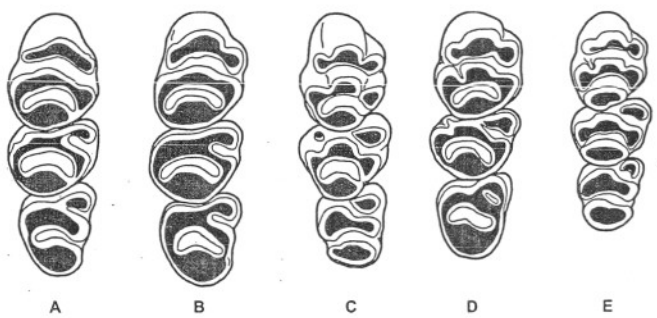


Fig. 3. Comparative drawings of the right maxillary teeth of

A. *Dasymys incomtus* (Sundevall, 1846) type Stockholm M.N.H. A64.1211
B. *Dasymys nudipes* (ISCED 1987) neo-paratype
C. *Dasymys cabrali* (BMNH 35.9.1.648)
D. *Dasymys rwandae* (KMMA 96-038-M-2270) type
E. *Dasymys sua* (KMMA 96-037-M-3143) type

all collections in 'Museu Bocage' were lost then '. Since we know that the type specimen of *nudipes* has been destroyed and we have craniometric proof of the existence of a '*nudipes*' and an '*incomtus*' taxon in Angola, we decided to select a neotype for *nudipes*, in order to facilitate the description of a third new taxon of the Okavango-region.
Graph 2.1. indicates the exact position of the specimens we selected as neotype and neo-paratype inside OTU16 (Huila). Also in graphs 5.1. and 5.2., in which we characterize the craniometrical differences through discriminant functions, respectively between OTU16 (Huila), OTU13 (Lubumbashi) and OTU17 (Okavango), we have indicated the positions of the neotype and neo-paratype of *nudipes*. The raw coefficients for canonical variables printed in both graphs allow to characterize easily *nudipes* specimens versus populations of *incomtus* (OTU13) and the Okavango (OTU17) population to be described as a new taxon.
Appendix 5.3. compares through univariate analysis OTU16 (Huila) with OTU13 (Lubumbashi) and shows that *nudipes*-skulls are very significantly bigger than *incomtus* crania except for M10 (PALA) where the observed difference in mean, although substantial, is not significant due to its very high coefficient of variation (CV). This is very noticeable for all the teeth measures M11 (UPTE), M12 (UPDA), M13 (M1BR) and M17 (LOTE) where we record important 'growth independent' differences (between 10.2 and 12.6%); we find similar and even higher differences in measures which are strongly influenced by growth such as M1 (GRLS), M6 (DIA1), M16 (LNAS), M23 (ROBR). For M18 (CHOB) the difference reaches even 20% but it has to be reminded that this measure is highly variable (CV = 9.5%).
We can safely conclude that *D. nudipes* has by far the biggest skull of all the taxa we were able to investigate and is easy to distinguish from other *Dasymys* through uni- and multivariate analyses.
In fig. 3 we compare the right maxillary teeth of the neo-paratype of *D.nudipes* with those of the type specimen of *incomtus* (Sundevall, 1846) and of our newly described taxa. The general morphology of the teeth, more especially for *nudipes* and *incomtus,* is very similar.

5. Description of *Dasymys cabrali* n. sp.
(Graph 5.2, 5.3; Appendix 1.3, 5.3)

HOLOTYPE

BMNH 35.9.1.662; adult male; skin and skull; collected by Shortridge G. C. (26 June 1929) near the Okavango river (Omatoka Junction) - Groot Fontein District, S. W. Africa (17.56S - 20.25E; alt.± 1080 m); collecting number 7.129.

PARATYPES

14 specimens from the same Caprivi region as the type specimen all collected by G. C. Shortridge between 26 and 27 June 1929.
Omatoka Junction (alt. ± 1080 m)

BMNH

35.9.1.660 (ad.male; skull + skin; coll. nr 7109)
35.9.1.667 (ad.fem.; skull + skin; coll. nr 7096)
35.9.1.668 (ad.fem.; skull + skin; coll. nr 7106)
35.9.1.670 (ad.fem.; skull + skin; coll. nr 7137)
35.9.1.672 (ad.fem.; skull + skin; coll. nr 7154)
66.220 (ad.fem.; skull + skin; coll. nr 7112)
66.221 (ad.fem.; skull + skin; coll. nr 7114)
66.222 (ad.fem.; skull + skin; coll. nr 7119)
66.224 (ad.male; skull + skin; coll. nr 7132)
66.226 (ad.male; skull + skin; coll. nr 7140)
66.228 (ad.male; skull + skin; coll. nr 7144)
66.229 (ad.male; skull + skin; coll. nr 7146)
66.230 (ad.fem.; skull + skin; coll. nr 7156)
66.231 (ad.fem.; skull + skin; coll. nr 7157)

For the metrical data of the type and the paratypes we refer to appendix 1.3.

ADDITIONAL SPECIMENS

To characterize our new taxon, we included in our analyses the following specimens also collected by G. C. Shortridge, a little later in the year 1929, but all from the Caprivi strip.

Andara (18. 04S - 21. 29E; alt. ± 1060 m) - 30 July 1929
BMNH 35.9.1.651 (ad. male; skull + skin; coll. nr 7543)
35.9.1.652 (ad. fem.; skull + skin; coll. nr 7544)
Mahango drift (alt. ± 1020 m) - 11 August 1929
BMNH 35.9.1.648 (ad. male; skull + skin; coll. nr 7703)
35.9.1.650 (ad. fem.; skull + skin; coll. nr 7704)
66.239 (ad. fem.; skull + skin; coll. nr 7705)
Diwai (near Bagane Drift) (alt. ± 1022 m) - 02 September 1929
BMNH 66.242 (ad. fem.; skull + skin; coll. nr 7901)
35.9.1.653 (ad. fem.; skull + skin; coll. nr 7902)
35.9.1.654 (ad. fem.; skull + skin; coll. nr 7914) - 03/10/ 1929
Gangongo (alt. ± 1020 m) - 28 September 1929
BMNH 35.9.1.657 (ad. fem.; skull + skin; coll. nr 8035)

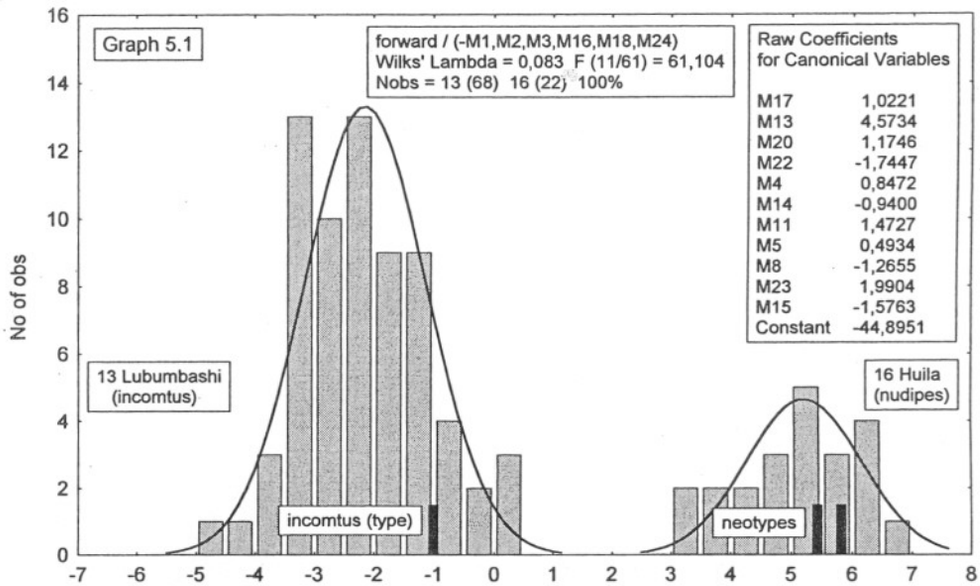
As can be deduced from the collecting dates, the altitudes of the localities and the collecting numbers, the collecting localities are probably situated either around or at a short distance to the east of Andara in the Caprivi-strip. We decided not to include these specimens as paratypes since their collecting localities are more than 100 km to the east of the topotypical locality.

ETYMOLOGY

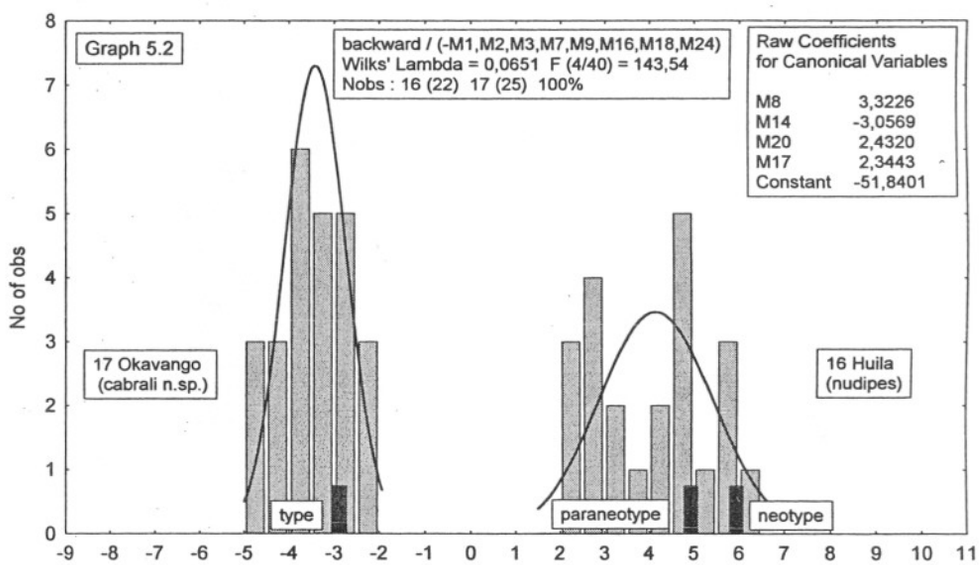
We have the pleasure to dedicate this new species of *Dasymys* to our colleague J. CRAWFORD-CABRAL in recognition of his contributions to the scientific knowledge of African mammals. In this context we mention that he remarked in his publication on the Angolan Murids (1998) when discussing the distribution of *Dasymys nudipes* 'It is possible that the specimens from Okavango and adjacent countries of Zambia and Angola represent a different subspecies' (p. 64).

DIAGNOSIS

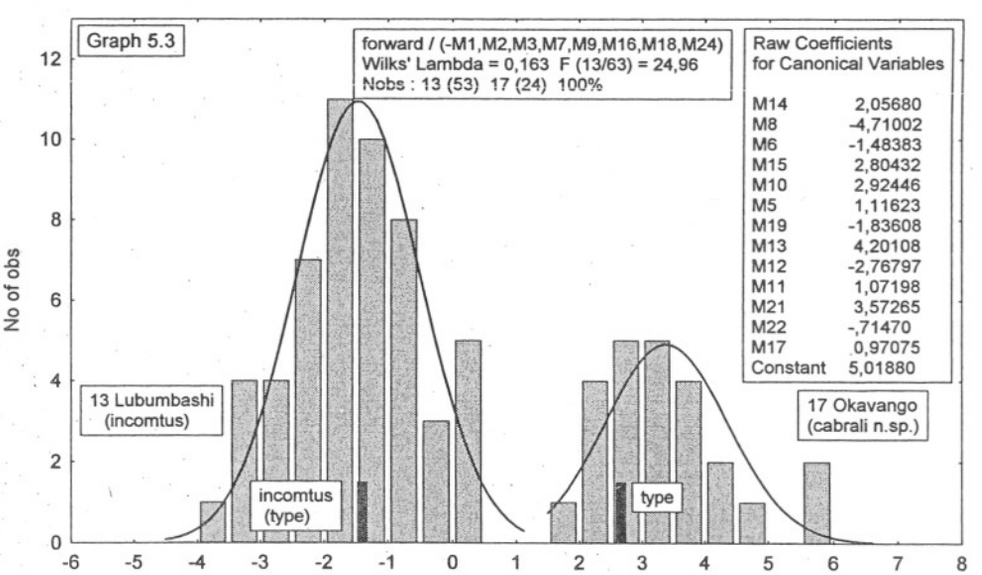
We will characterize *D. cabrali* by a craniometric description based upon univariate and multivariate comparisons with populations of different taxa but of the same general geographical region. This comparison involves OTU13 (Lubumbashi) that we consider to be representative for the



Graph 5.1.
Graphic representation of the discriminant function (forward analysis) allowing the characterization of the species *D. nudipes* versus a population OTU13 (Lubumbashi) that we consider to be representative for the species *incomtus*. Are also represented the coefficients for the canonical transformation.



Graph 5.2.
Graphic representation of the discriminant function (backward analysis) allowing the characterization of *D. cabrali* n.sp. (OTU17) versus our OTU16 (Huila) that we consider to represent *D. nudipes*. The four skull measurements needed for the craniometric diagnosis of our new taxon *cabrali* are also available.



Graph 5.3.
Graphic representation of the discriminant function (forward) permitting the definition of *D. cabrali* n.sp. (OTU17) versus OTU13 (Lubumbashi) that we consider to be representative for *D. incomtus*. The coefficients for the canonical transformation, necessary for the diagnosis of the new taxon are also available.

species *incomtus* and OTU16 (Huila) typical for the species *nudipes*.
In appendix 5. 3. we show craniometric data that allow us to discuss the differences between OTU17 (Okavango) typical for *cabrali* and respectively OTU16 (Huila) and OTU13 (Lubumbashi). This univariate approach reveals that *cabrali* is 1°/ for nearly all skull-dimensions respectively smaller than *nudipes* and bigger than *incomtus* and 2°/ strikingly different from both species for M8 (INTE) and M14 (ZYGP).
Also in the multivariate analyses (graphs 5.2. and 5.3.) we see that *cabrali* can easily be distinguished from *nudipes* and *incomtus*. The difference between *nudipes* and *cabrali* is so important that a backward discriminant analysis needs only four measures (M8, M14, M20, M17) to allow 100% correct classification (graph 5.2.). To differentiate between *incomtus* and *cabrali* (graph 5.3.) a forward analysis requires only 13 measures to realize 100% correct diagnosis. In both graphs we publish all the necessary data to permit a diagnosis through discriminant analysis. Finally we underline that also in both multivariate analyses the measures M8 (INTE) and M14 (ZYGP) make a very important contribution, which explains why the skull of *cabrali* can easily be described by its extremely narrow interorbital region combined with its strongly developed zygomatic plate.
As to the morphology of the maxillary teeth (fig.3) it is slightly different from *nudipes* and *incomtus*, but this variation has in our opinion no taxonomic value.

6. Description of *Dasymys sua* n. sp.

(Graph 6.1, 6.2; Appendix 1.4, 5.4, 6)

HOLOTYPE

KMMA 96-037-M-3143; ad. female; skull and alcohol specimen; collected by Marcel Michiels (16 September 1986) in Mbete (06.52S - 37.41E) near Morogoro (Tanzania) on the flanks of the Uluguru-range at ±1540 m altitude (Kitundu forest); collecting number 2339.

PARATYPES

26 specimens collected in the surroundings of Morogoro (Tanzania).

Mbete (Choma-Kitundu-forest; 06. 52S - 37. 41E; alt. ±1540 m).
KMMA 96-037-m-3144 (ad. male; skull + alc. sp.; coll. nr 2771).
Mlali (06. 58S-37. 33E; alt. ± 600 m)
KMMA 96-037-M-3136 (ad. fem.; skull + alc. sp.; coll. nr 2064)
3137 (ad. male; skull + alc. sp.; coll. nr 2066)
3138 (ad. fem.; skull + alc. sp.; coll. nr 2068)
3139 (ad. fem.; skull + alc. sp.; coll. nr 2112)
3140 (ad. male; skull + alc. sp.; coll. nr 2146)
3141 (ad. fem.; skull + alc. sp.; coll. nr 2149)
Mgeta (07. 03S-37. 35E; alt. ± 1600 m)
KMMA 96-037-M-3133 (ad. fem.; skull + alc. sp.; coll. nr 652)
Kidege (07. 10S-37. 50E; alt. ± 1500 m)
KMMA 96-037-M-3145 (ad. male; skull + alc. sp.; coll. nr 3423)
3146 (ad. fem.; skull + alc. sp.; coll. nr 3424)
Dakawa (06. 26S-37. 34E; alt. ± 400 m)
KMMA 96-036-M-4630 (ad. male; skull + alc. sp.; coll. nr 1998)
4631 (ad. fem.; skull + alc. sp.; coll. nr 2009)
4906 (ad. male; skull + skin; coll. nr 9449)
RUCA 8432 (ad. fem.; skull + skin; coll. nr 8432

All the above mentioned specimens were collected by Marcel Michiels between 12 June 1986 and 18 August 1988. Specimen RUCA 8432 was sent to the Rodent collection of the Rodent Pest Control Centre of the Sokoine University of Agriculture (Morogoro-Tanzania).

Dakawa (06.26S-37.34E; alt. ± 400 m)
KMMA 96-036-M-4632 (ad. fem.; skull + alc. sp.; coll. nr 5711)
4633 (ad. male; skull + alc. sp.; coll. nr 5714)
Both specimens collected by Marc Colyn on 03 September 1987.
Mindu (near University Campus SUA in Morogoro: 06. 52S-37. 36E; alt. ± 600 m)
KMMA 96-037-M-3150 (ad. fem.; skull + alc. sp.; coll. nr 12306)
3151 (ad. male; skull + alc. sp.; coll. nr 12329)
Both specimens collected by Sven DE VOCHT respectively on 04 and 06 October 1994.
Morningside (06.53S-37.40E; alt. ± 1550 m)
RUCA T0938 (ad. fem.; skull; coll. nr T0938)
Tungi Estate (06. 49S-37. 38E; alt. ± 500 m)
RUCA T7293 (ad. male; skull; coll. nr T7293)
Morogoro (SUA-campus: 06.52S-37.39E; alt. ± 600 m)
RUCA T1177 (ad. male; skull; coll. nr T1177)
T2806 (ad. male; skull + skin; coll. nr T2806)
T5442 (ad. fem.; skull + skin; coll. nr T5442)
T12319 (ad. fem.; skull + skin; coll. nr T12319)
T14377 (ad. male; skull + skin; coll. nr T14377)
T14710 (ad. male; skull + skin; coll. nr T14710)

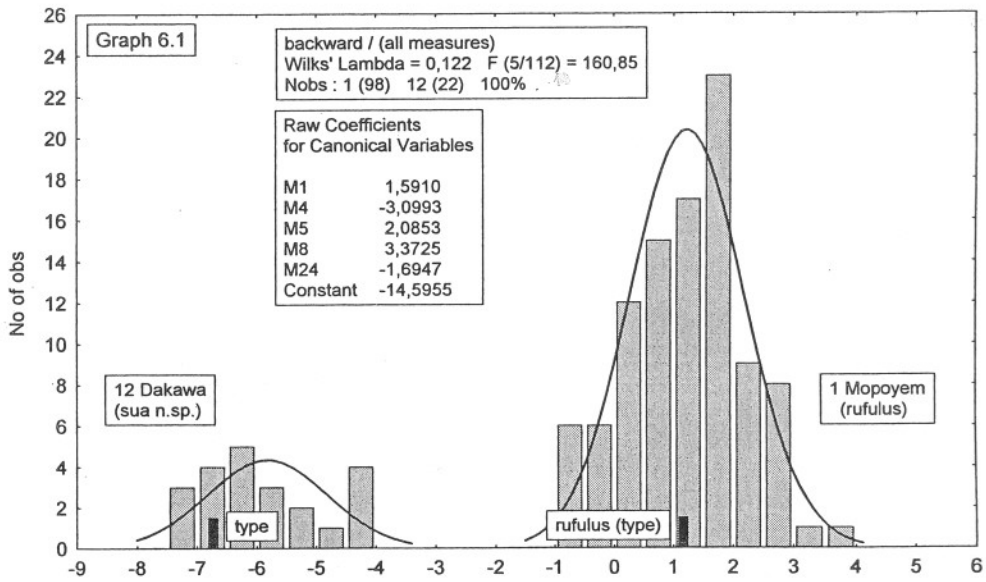
The specimens from Morningside-Tungi-Morogoro were collected by Telford (DANIDA, Rodent Centre, Ministry of Agriculture, Morogoro) between 03 March 1982 and 20 February 1985 and will be registered in the collections of the Koninklijk Museum voor Midden-Afrika (Tervuren).
For the metrical data of the type and the paratypical series we refer to appendix 1.4. and for the genetic characterisation to appendix 6.

ETYMOLOGY

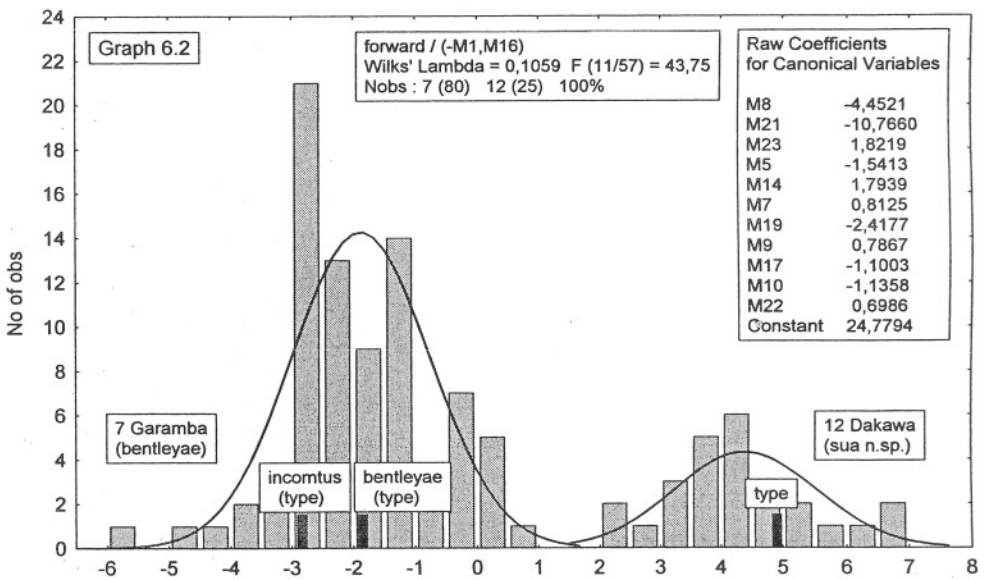
This new species is named after the acronym SUA of the **S**okoine **U**niversity of **A**griculture in Morogoro (Tanzania) where the Research Group of Evolutionary Biology of the University of Antwerp (Belgium) started in 1984 the Rodent Research Centre.

DIAGNOSIS

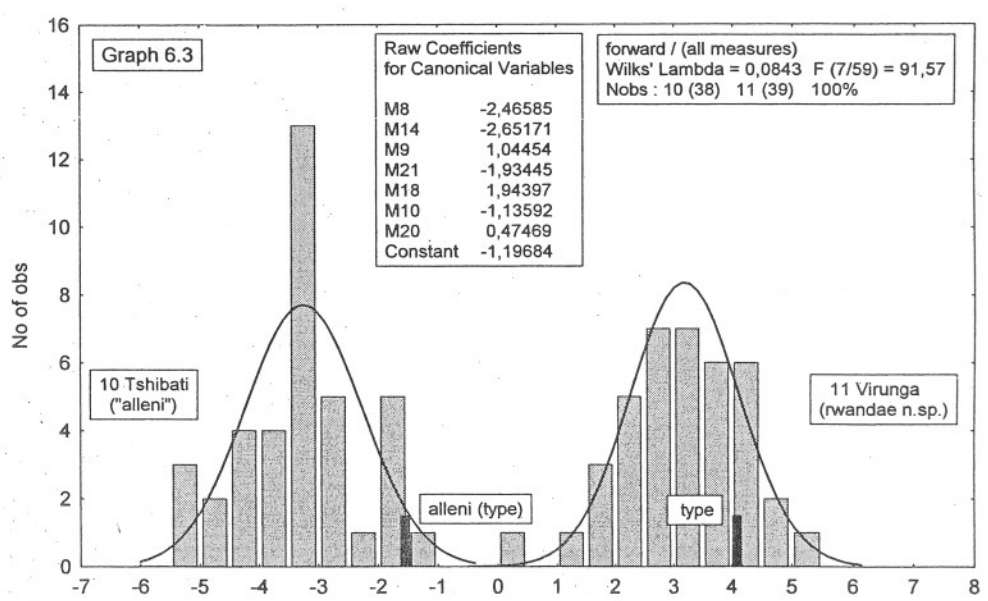
Our new taxon will be characterized by comparing it craniometrically to OTU1 (Mopoyem) representing the *rufulus*-species and OTU7 (Garamba) that we consider to be close to the *bentleyae*-taxon of the *incomtus* - complex.
Appendix 5.4. describes through univariate analysis our typical series of *sua*. We conclude in the first place that *sua* has about the same cranial size as OTU7 (Garamba) but scores overall a little bigger than OTU1 (Mopoyem). Secondly we see that *sua* is smaller than both comparative OTU's (1 and 7) for M8 (INTE), M5 (PAFL), M13 (M1Br) and bigger for M7 (DIA2). Lastly *sua* is clearly bigger than OTU1 (Mopoyem) for M14 (ZYGP), M18 (CHOB) and M24 (PCPA).
In graph 6.1. we see that the population of our new taxon *sua* (OTU12) differentiates easily through a backward discriminant function from *rufulus* (OTU1: Mopoyem) and selects five measures to do so; these measures were already men-



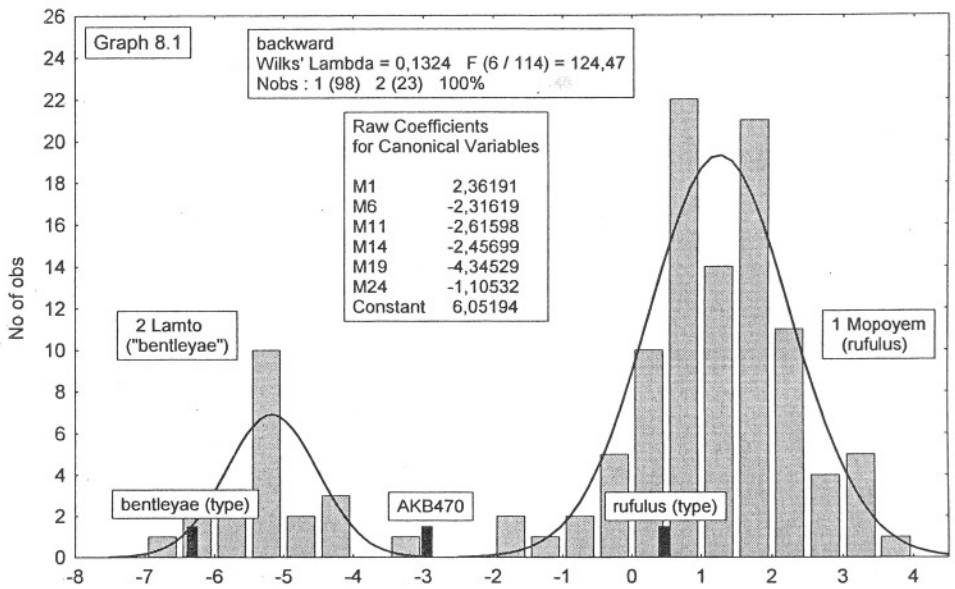
Graph 6.1.
Graphic representation of the discriminant function (backward analysis) allowing the characterization of D. *sua* n.sp. (OTU12) versus our OTU1 (Mopoyem) that we consider to represent *D. rufulus* together with the canonical coefficients.



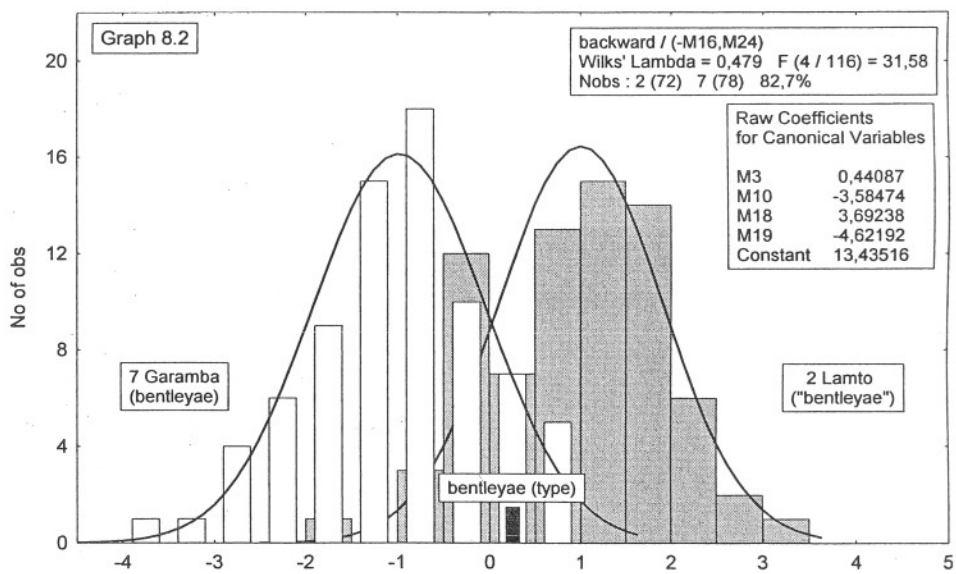
Graph 6.2.
Graphic representation of the discriminant function (forward analysis) characterizing between *D. sua* n. sp. versus the Garamba-population (OTU7) that we consider to represent *D. bentleyae* making part of the *incomtus*-species complex. The coefficients for the canonical transformation, needed for the diagnosis are also available.



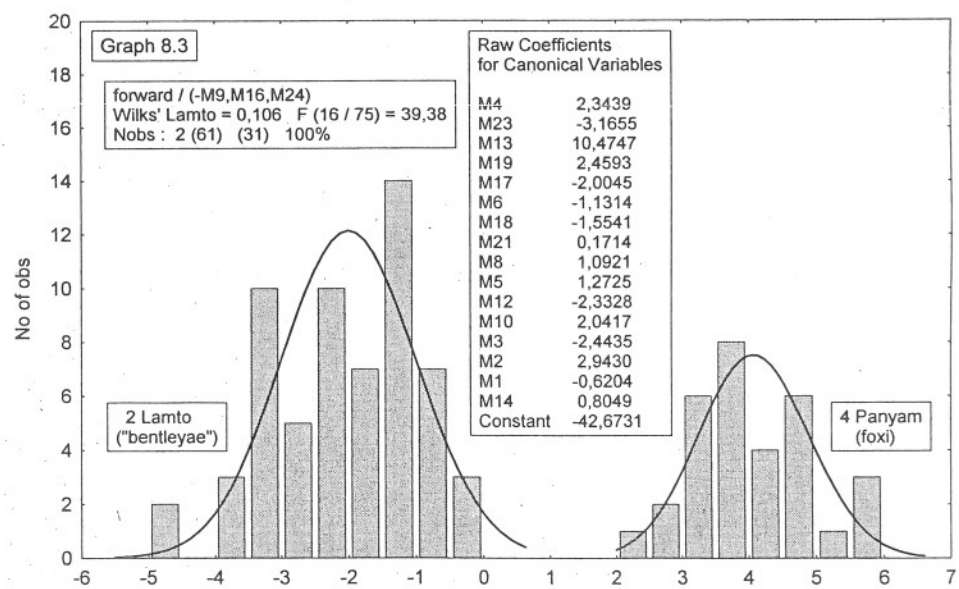
Graph 6.3.
Graphic representation of the discriminant function (forward analysis) differentating between OTU10 (Tshibati) that we consider to be representing *alleni* and our new taxon *rwandae* n.sp.(OTU11: Virunga); the canonical coefficients permitting a correct diagnosis are also represented.



Graph 8.1.
Graphic representation of the discriminant function (backward analysis) characterizing OTU1 (Mopoyem) versus OTU2 (Lamto). The type specimens of *bentleyae* and *rufulus* are plotted as well as the sequenced specimen AKB470 from Mopoyem (see text).



Graph 8.2.
Graphic representation of the discriminant function (backward analysis) differentiating craniometrically between OTU7 (Garamba) versus OTU2 (Lamto) and visualizing the very important overlapping between both groups, as well as the intermediate position of the type specimen of *bentleyae*.



Graph 8.3.
Graphic representation of the discriminant function (forward analysis) between OTU2 (Lamto) and OTU4 (Panyam) demonstrating that *foxi* can easily be differentiated craniometrically from «*bentleyae*».

tioned in our univariate approach. To differentiate between *sua* (OTU12) and OTU7 (Garamba) representing *bentleyae*, we performed a forward discriminant analysis (graph 6.2.) and also here the level of 100% exact allocation is easily reached.
When we attempt to compare the skull of *sua* with a representative skull of *incomtus* we notice that 1°/ it has a heavier rostrum, a larger zygomatic plate and a larger zygomatic width; 2°/ a narrower interorbital breadth and a narrower palatal width; 3°/ a lower ramus height; (4) smaller bullae and (5) finer and more pro-odont upper incisors.
As to the upper molars (fig.3) we see that the teeth are somewhat smaller than the average *incomtus* molars.

7. Description of *Dasymys rwandae* n. sp.
(Graph 6.3, 7.1; Appendix 1.5, 5.4, 5.5, 6)

HOLOTYPE

KMMA 96-038-M-2270: ad. male; skull and alcoholic specimen; collected by Walter Verheyen (04 June 1982) in Kinigi, Rwanda (01. 26S-29. 36E; alt. 2250 m); collecting number 2934.

PARATYPES

24 specimens from Kinigi, the same locality as the holotype, collected by Walter Verheyen between 01 June and 10 July 1982.

KMMA 96-038-M-
2213 (ad. fem.; skull + alc. sp.; coll. nr 2399)
2214 (ad. fem.; skull + alc. sp.; coll. nr 2402)
2215 (ad. male; skull + alc. sp.; coll. nr 2445)
2217 (ad. male; skull + alc. sp.; coll. nr 2675)
2218 (ad. male; skull + alc. sp.; coll. nr 2676)
2219 (ad. male; skull + alc. sp.; coll. nr 2677)
2220 (ad. male; skull + alc. sp.; coll. nr 2679)
2221 (ad. male; skull + alc. sp.; coll. nr 2806)
2224 (ad. male; skull + alc. sp.; coll. nr 2932)
2225 (ad. male; skull + alc. sp.; coll. nr 2933)
2229 (ad. male; skull + alc. sp.; coll. nr 3770)
2230 (ad. fem.; skull + alc. sp.; coll. nr 3808)
2231 (ad. male; skull + alc. sp.; coll. nr 3809)
2234 (ad. male; skull + alc. sp.; coll. nr 3847)
2235 (ad. fem.; skull + alc. sp.; coll. nr 3848)
2236 (ad. fem.; skull + alc. sp.; coll. nr 3853)
2237 (ad. fem.; skull + alc. sp.; coll. nr 3894)
2267 (ad. fem.; skull + alc. sp.; coll. nr 2400)
2268 (ad. fem.; skull + alc. sp.; coll. nr 2401)
2269 (ad. male; skull + alc. sp.; coll. nr 2804)
2271 (ad. fem.; skull + alc. sp.; coll. nr 3763)
2272 (ad. male; skull + alc. sp.; coll. nr 3837)

Two specimens from Kinigi collected by E. Van der Straeten on 08 June 1982

KMMA 96-038-M-2227 (ad. fem.; skull + alc. sp.; coll. nr 3088)
2228 (ad. fem.; skull + alc. sp.; coll. nr 3089)

For the metrical data of the type and paratypes we refer to appendix 1.5. and for genetic characterisation to appendix 6.

ADDITIONAL SPECIMENS

In order to characterize craniometrically our new taxon we included in our analyses:

Gahinga Volcano (01:24S-29.40E) in grid 26, collected by E.Van der Straeten, 21-28.June.1982

KMMA 96-038-M-
2247 (ad. male; skull + alc. sp.; coll. nr 4891)
2249 (ad. fem.; skull + alc. sp.; coll. nr 4933)
2251 (ad. fem.; skull + alc. sp.; coll. nr 4957)
2252 (ad. fem.; skull + alc. sp.; coll. nr 5035)
2254 (ad. fem.; skull + alc. sp.; coll. nr 5064)
2257 (ad. male; skull + alc. sp.; coll. nr 5072)
2258 (ad. male; skull + alc. sp.; coll. nr 5073)
2260 (ad. ?; skull + alc. sp.; coll. nr 5111)
2263 (ad. ?; skull + alc. sp.; coll. nr 5148)
2264 (ad. ?; skull + alc. sp.; coll. nr 5149)
2265 (ad. ?; skull + alc. sp.; coll. nr 5150)
2276 (ad. ?; skull + alc. sp.; coll. nr 5110)

Gasiza Volcano (01.25S-29.40E), collected by E. Van der Straeten, 23 June - 04 July1982 (grids 27-39).
2250 (ad. fem.; skull + alc. sp.; coll. nr 4949)
2278 (ad. fem.; skull + alc. sp.; coll. nr 5196)
2279 (ad. fem.; skull + alc. sp.; coll. nr 5215)

Visoke Volcano (01.27S-29.30E), collected by W. Verheyen,12 July 1982
KMMA-96-038-M2238 (ad. male; skull + alc. sp.; coll. nr 3915)
Kidaho (01. 23S-29. 47E) collected by E. Van der Straeten, 16 July 1982
KMMA-96-038-M2246 (ad. fem.; skull + alc. sp.; coll. nr 4666).

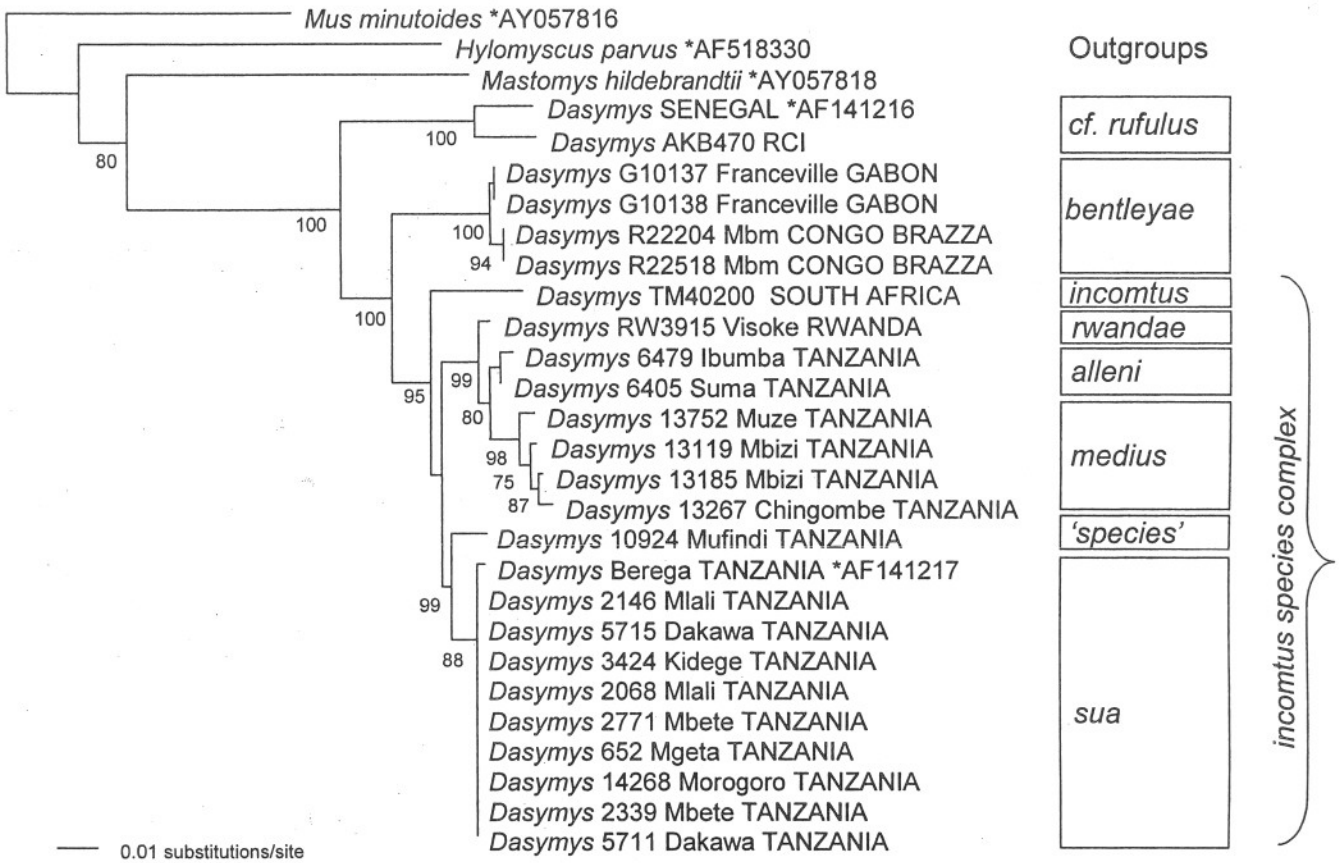
ETYMOLOGY

We decided to name this new taxon after Rwanda, the country were it was collected and also because we think that its geographical range will prove to be restricted to the mountainous region forming the eastern rim of the rift valley.

DIAGNOSIS

This new species will be compared craniometrically with two clearly differentiated taxa of the *incomtus* clade 1°/ OTU7 (Garamba) that we consider to be close to the *bentleyae* taxon and 2°/ OTU10 (Tshibati) that we identified with the type specimen of *alleni*.
In appendix 5.4. and 5.5. we situate through univariate analyses our new taxon *rwandae*. In the first place we see that it is significantly smaller (between 5% to 20%) for all body measurements than both comparative OTU's (we accept these results but underline also that a certain caution is needed when comparing external measurements recorded by different collecting teams). When comparing the craniometric data we find that overall our new taxon *rwandae* has about the same skull size as OTU7 (Garamba) but is clearly smaller than OTU10 (Tshibati) (22 out of 24 measurements). On the one hand *rwandae* is markedly smaller than OTU7 and OTU10 for M8 (INTE), M14 (ZYGP), M16 (LNAS), M21 (DINC) but on the other hand bigger for M18 (CHOB) and M10 (PALA).
A forward discriminant function between *rwandae* and OTU10 (Tshibati) shows that next to the already mentioned measures in the univariate analysis also M9 (ZYGO) and M20 (BRCA) appear to play an important role in characte-

Fig. 4. Neighbor-joining tree based on K2p distances with bootstrap replicates obtained after 1000 replications. Shown branches are supported by bootstrap values > 50, values> 75 are given. Sequences with an asterisk were taken from the literature (see text)



rizing our new taxon (graph 6.3.).
A backward discriminant function between *sua* and OTU7 (*bentleyae*) selects next to the already known taxonomically important measures (M8, M14, M20, M21) also two skull-length measures (M2 (PRCO) and M3 (HEBA)) (graph 7.1.). In both discriminant functions 100% correct classification is reached. When we compare de visu a skull of *rwandae* with representative crania of the other populations we observe that it has a somewhat wider skull (palate and choanae; zygomatic breadth-braincase breadth) combined with a narrower interorbital region, a weaker zygomatic plate, weaker upper incisors and somewhat shorter nasals.
We did not find any morphological structure in the maxillary teeth that could be used to characterize *rwandae* taxonomically (fig.3).

REMARK

The few specimens that we could measure from the mountains of western Burundi (Tora) identify neither with *rwandae*, nor with *alleni*, but with OTU7 (Garamba) (*bentleyae*).

8. Mitochondrial DNA data
(Table 1a, 1b, 2; Fig 4)

SEQUENCE ANALYSIS

The entire cytochrome *b* gene was sequenced in twenty three *Dasymys* specimens. The alignement of the complete data set does not require indels and reveals no stop codons using the translation table for vertebrate mitochondrial sequences as in MEGA 2.0 (KUMAR et al., 2001). Average nucleotide composition in the obtained sequences [T (7.3%) C (29.8%) A (30.5%) and G (12.4%)] is typical for what has been reported in other studies on murine cytochrome *b* (LUNDRIGAN et al., 2002; DUCROZ et al., 2001; LECOMPTE et al., 2002). For the ingroup comparisons, we observe a total of 168 variable sites, 118 of which are informative under the parsimony criterion. Due to some missing data in some sequences, only 104 of these are shown in the appendix 6. The corresponding amino acid sequences do not reveal stop codons, deletions or inserts (KUMAR et al. 2001), and 21 of the 380 amino acids are variable, and 10 are informative under the parsimony criterion. The saturation curves reveal that transitions of the first and second codon positions, and transversions at the three codon positions are not saturated (results not shown). The genetic distances range among the studied representatives of the genus *Dasymys* range between 8.9% (*rufulus* ver-

Table 1 a.
Upper triangle are uncorrected sequence divergences (%) among the studied *Dasymys* taxa.

TAXON	2	3	4	5	6	7	8
(1) cf. *rufulus*	7.5-7.8	8.9	8.2-8.3	7.9-8.3	7.9-8.8	8.0-8.1	7.0-8.1
(2) *bentleyae*		5.5-5.7	4.9-5.1	4.9-5.3	5.4-6.0	4.6-4.8	4.2-4.5
(3) *incomtus*			3.3	3.2-3.5	4.1-4.4	3.3	3.1-3.4
(4) *rwandae*				1.0-1.2	1.5-1.9	2.7	2.0-2.3
(5) *alleni*					1.3-1.6	2.8-3.2	2.1-2.5
(6) *medius*						3.6-4.1	2.7-4.1
(7) *'species'*							1.5-1.8
(8) *sua*							

Table 1 b. Uncorrected sequence divergences (%) among conspecific Dasymys.

TAXON	(%)	COMPARED TAXA/POPULATIONS
rufulus	3.0	Senegal/RCI
bentleyae	0.0 0.4	from one locality Gabon/Congo Brazza
incomtus *rawandae* *alleni* *medius* *'species'* *sua*	*n.a.* *n.a.* 0.4 0.4-0.8 *n.a.* 0.0	one specimen one specimen Ibumba/Suma Muze/Mbisi/Chingombe one specimen alle except one specimen from Berega [differs from others by 0,4%]

Table 2. Times since divergence among the sequenced were estimated using the molecular clock as described in the material and methods section and the presumed age of the splitting of the *Mus / Rattus* lineages 12 Myrs ago (JAEGER et al., 1986).

TAXA	TIME SINCE DIVERGENCE	
Mus versus *Dasymys*	12-13	Myrs/yrs
Dasymys		
rufukus (Senegal/RCI)	1.0	Myrs
rufulus/bentleyae	2.1-1.6	Myrs
rufulus/incomtus sp. complex	2.0-1.6	Myrs
incomtus/rwandae	± 190,000	yrs
incomtus/alleni	± 250,000	yrs
incomtus/medius	± 250,000	yrs
incomtus/'species'	± 250,000	yrs
incomtus/sua	> 100,000	yrs

sus *incomtus*) to 1.0-1.2% (*rwandae* versus *alleni*) (table 1a). Within most species the observed uncorrected % divergence was 3.0% (*D. rufulus*), but mostly considerably lower (0.4-0.8%) (table 1b).

SEQUENCE AVAILABILITY

Sequences used in this study were submitted to EMBL and accession numbers will be provided as soon as they will be available (erik.verheyen@naturalsciences.be)

PHYLOGENETIC ANALYSES

Under the parsimony criterion, using unweighted characters, stepwise taxon addition is random with 10 replicates and the TBR branch swapping option we obtained 3 MP trees with length 633, CI=0.733 and RC=0.559 with a topology identical to the NJ tree (SAITOU and NEI 1987) obtained using the K2p distances (fig.4). Bootstrap support for the major branches exceeds values required to infer the reliability of the obtained branching pattern (FELSENSTEIN 1985). Overall, the obtained phylogeny corresponds well with taxonomic groups inferred on morphological and biogeographic data. The inferred phylogeny supports the basal position of *D.*cf.*rufulus* (represented by specimens from Senegal and Ivory Coast (RCI), followed by *D. bentleyae* (from Gabon and Congo-Brazzaville) and the existence of a relatively younger *D. incomtus* species group (see further) that not only contains *incomtus* (South Africa) but also *alleni*, *medius*, *'species'* and the new taxa *rwandae* and *sua*.

AGE ESTIMATES

In agreement with the branch lenghts in the different clades in the shown tree (fig.4), we observe that the times since divergence are highest (2.1-1.0 Myrs) among and between West and Central *Dasymys* (table 2). The remaining taxa in Central, East and South Africa, that predominantly belong to the considerably younger *incomtus* species complex, diverged less than 250,000 yrs ago from a common ancestor.

DISCUSSION AND CONCLUSIONS

The craniometric methodology that we introduced in our study on the *Lophuromys flavopunctatus* species complex (VERHEYEN et al., 2002) proved to be also in the case of the genus *Dasymys* a valuable tool to straighthen out some of the intricacies of its taxonomy. For a discussion of the limitations of this quantitative methodology we refer to the above mentioned publication.

When we combine our results concerning the type-specimens with the observed craniometric variation we conclude

that *Dasymys* is certainly polytypical and contains a series of morphometrically well defined taxa. Translated into a geographical distribution we observe that *D. incomtus* s.s. has the widest range covering grosso modo 1°/ the moist woodlands of western, northcentral and northeastern Africa, 2°/ the moist woodlands of the north western and eastern part of southern Africa and 3°/ approximately the western half of the inland of Kenya and Tanzania (see the discussion below on *foxi* as well) .

Also *D. bentleyae* occurs over a big area, consisting mainly of the fringes of the lowland rain forest between the Atlantic coast and the western rift; certain analyses even suggest that representatives of this species are also present in the fringes of the western forest block and in the region adjacent to the highlands of the western flank of Lake Malawi.

All the other taxa appear to have much more restricted ranges:

- *D. rufulus*: probably restricted to the forest-enclosed savannahs of western Africa;
- *D. nudipes*: restricted to the highland region of Huambo in southwestern Angola;
- *D. cabrali*: distribution restricted to the Okavango basin (Caprivi, Namibia);
- *D. alleni*: restricted to the southern part of the eastern Arc (Mt Rungwe) and also to the mountain regions of the western rim of the rift (Tshibati, Bukavu, Albertville).
- *D. rwandae*: restricted to certain mountain ranges on the eastern rim of the rift (Virunga Volcanoes, Nyungwe Forest);
- *D. sua:* possibly restricted to eastern Tanzania.

We have however to underline that while it is easy to characterize through canonical and discriminant analyses the species with restricted ranges such as *rufulus*, *nudipes*, *cabrali*, *alleni*, *rwandae* and *sua,* the same cannot be achieved when trying to define *incomtus* versus *bentleyae*. Indeed, we always found an important morphometrical overlap between populations of both taxa. This situation is best visualized and summarized by graphs 4.1 and 4.2 where we see that the linkage distances are in both instances very low and around the value of 50. Moreover, if we recognize *bentleyae* and *incomtus* as well defined taxa, then we have to consider *foxi* to represent a valid taxon as well (graph 8.3).

Since it is obvious that our craniometric approach alone will not solve this taxonomical problem we will adopt at this point of the discussion a conservative attitude and continue to recognize for the moment *incomtus*, *bentleyae* and *foxi* as separate species.

When we combine in a next step these results with the limited genetic tree of *Dasymys* we could construct (fig.4) we see that some of these problems can be solved, but also that new questions arise. In order to facilitate the discussion we will group the argumentation region by region.

WESTERN AFRICA

The specimen AKB470 (collected in Mopoyem, Ivory Coast in 2002) forms together with the specimens AF141316 from Senegal (EMBL, determined as *D. rufulus* by VOLOBOUEV et al., 2000) a clearly separated clade from all other sequenced *Dasymys* specimens. However, when we plot its skull (graphs 7.3 and 8.1) we see that it does not identify itself at all with OTU1 (Mopoyem) that we used to represent *rufulus*, neither with our *foxi* and *bentleyae* populations. We may explain this by the following hypothesis. During the 35 years separating the collecting of OTU1 (Mopoyem) by our colleague L. BELLIER and the sequenced specimen AKB470, the formerly enclosed savannah of Mopoyem has been opened up through extensive deforestation resulting in an influx of savannah-dwelling rodent species of the V. Baoulé (OTU2, Lamto). This may have resulted either in the disappearance of the original *rufulus* population or in a hybridisation process which strongly influenced the craniometric morphology of the *Dasymys* occurring in Mopoyem.

When we link this finding to 1°/ the rather important genetic distances that we detected between both 'cf *rufulus*' representatives; 2°/ the craniometric resemblance (graph 8.2) that we found between OTU2 (Lamto) and *bentleyae* (OTU7, Garamba) and 3°/ the caryological variation detected in West African *Dasymys* populations from the Adiopodoumé and Lamto regions (MATTHEY, 1958; TRANIER & GAUTUN, 1979) it is obvious that the taxonomy of the west African "forest" *Dasymys* is still not fully resolved..

For the moment we tend to believe that 1°/ *D.rufulus* has a distribution range more or less limited to the enclosed savannahs near the coast; 2°/ the *Dasymys* inhabiting the fringes of the rainforest and the adjacent guinean savannahs may be a new taxon related to the *bentleyae* group and 3°/ the *Dasymys* living more to the north in the Guinean and Sudanese savannahs should probably all be referred to the *foxi* taxon *(incomtus* s.l.).

CENTRAL AFRICA

In fig.4 we accept that the sequenced specimens of Franceville and Mbomo pertain to *bentleyae* because craniometrically they plot within OTU9 (Kinshasa). We are however aware that more detailed research, such as caryological and sequencing of topotypical specimens of *bentleyae* will be needed to evaluate the correctness of our position.

Similar research will also help ascertain the eastern limits of the range of *bentleyae* and to find out 1°/ how the *Dasymys* of North East Congo (Garamba: OTU7) are genetically related to populations of Uganda-Sudan and of Gabon-Cameroon and 2°/ how the *Dasymys* west of lake Malawi (Kasungu , OTU19) relate genetically to *bentleyae* (Kinshasa , OTU9) and to *incomtus* (Lubumbashi, OTU13) .

However, notwithstanding the sparsity of our genetic data, we can conclude that the «forest-linked» African *Dasymys* descend from the ancestral stock situated in western Africa and from which all other taxa of the continent seem to have evolved.

EAST AFRICA

Fig.4 shows that the swamp rats from the East African region all belong to what we call the *Dasymys incomtus* s.l. species complex, but also that the taxa we could discern by craniometry (*sua, rwandae, alleni, medius*) can also be genetically characterized (appendix 6).

that *Dasymys* is certainly polytypical and contains a series of morphometrically well defined taxa. Translated into a geographical distribution we observe that *D. incomtus* s.s. has the widest range covering grosso modo 1°/ the moist woodlands of western, northcentral and northeastern Africa, 2°/ the moist woodlands of the north western and eastern part of southern Africa and 3°/ approximately the western half of the inland of Kenya and Tanzania (see the discussion below on *foxi* as well) .

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- *D. rwandae*: restricted to certain mountain ranges on the eastern rim of the rift (Virunga Volcanoes, Nyungwe Forest);
- *D. sua:* possibly restricted to eastern Tanzania.

We have however to underline that while it is easy to characterize through canonical and discriminant analyses the species with restricted ranges such as *rufulus*, *nudipes*, *cabrali*, *alleni*, *rwandae* and *sua,* the same cannot be achieved when trying to define *incomtus* versus *bentleyae*. Indeed, we always found an important morphometrical overlap between populations of both taxa. This situation is best visualized and summarized by graphs 4.1 and 4.2 where we see that the linkage distances are in both instances very low and around the value of 50. Moreover, if we recognize *bentleyae* and *incomtus* as well defined taxa, then we have to consider *foxi* to represent a valid taxon as well (graph 8.3).

Since it is obvious that our craniometric approach alone will not solve this taxonomical problem we will adopt at this point of the discussion a conservative attitude and continue to recognize for the moment *incomtus*, *bentleyae* and *foxi* as separate species.

When we combine in a next step these results with the limited genetic tree of *Dasymys* we could construct (fig.4) we see that some of these problems can be solved, but also that new questions arise. In order to facilitate the discussion we will group the argumentation region by region.

WESTERN AFRICA

The specimen AKB470 (collected in Mopoyem, Ivory Coast in 2002) forms together with the specimens AF141316 from Senegal (EMBL, determined as *D. rufulus* by VOLOBOUEV et al., 2000) a clearly separated clade from all other sequenced *Dasymys* specimens. However, when we plot its skull (graphs 7.3 and 8.1) we see that it does not identify itself at all with OTU1 (Mopoyem) that we used to represent *rufulus*, neither with our *foxi* and *bentleyae* populations. We may explain this by the following hypothesis. During the 35 years separating the collecting of OTU1 (Mopoyem) by our colleague L. BELLIER and the sequenced specimen AKB470, the formerly enclosed savannah of Mopoyem has been opened up through extensive deforestation resulting in an influx of savannah-dwelling rodent species of the V. Baoulé (OTU2, Lamto). This may have resulted either in the disappearance of the original *rufulus* population or in a hybridisation process which strongly influenced the craniometric morphology of the *Dasymys* occurring in Mopoyem.

When we link this finding to 1°/ the rather important genetic distances that we detected between both 'cf *rufulus*' representatives; 2°/ the craniometric resemblance (graph 8.2) that we found between OTU2 (Lamto) and *bentleyae* (OTU7, Garamba) and 3°/ the caryological variation detected in West African *Dasymys* populations from the Adiopodoumé and Lamto regions (MATTHEY, 1958; TRANIER & GAUTUN, 1979) it is obvious that the taxonomy of the west African "forest" *Dasymys* is still not fully resolved..

For the moment we tend to believe that 1°/ *D.rufulus* has a distribution range more or less limited to the enclosed savannahs near the coast; 2°/ the *Dasymys* inhabiting the fringes of the rainforest and the adjacent guinean savannahs may be a new taxon related to the *bentleyae* group and 3°/ the *Dasymys* living more to the north in the Guinean and Sudanese savannahs should probably all be referred to the *foxi* taxon *(incomtus* s.l.).

CENTRAL AFRICA

In fig.4 we accept that the sequenced specimens of Franceville and Mbomo pertain to *bentleyae* because craniometrically they plot within OTU9 (Kinshasa). We are however aware that more detailed research, such as caryological and sequencing of topotypical specimens of *bentleyae* will be needed to evaluate the correctness of our position.

Similar research will also help ascertain the eastern limits of the range of *bentleyae* and to find out 1°/ how the *Dasymys* of North East Congo (Garamba: OTU7) are genetically related to populations of Uganda-Sudan and of Gabon-Cameroon and 2°/ how the *Dasymys* west of lake Malawi (Kasungu , OTU19) relate genetically to *bentleyae* (Kinshasa , OTU9) and to *incomtus* (Lubumbashi, OTU13) .

However, notwithstanding the sparsity of our genetic data, we can conclude that the «forest-linked» African *Dasymys* descend from the ancestral stock situated in western Africa and from which all other taxa of the continent seem to have evolved.

EAST AFRICA

Fig.4 shows that the swamp rats from the East African region all belong to what we call the *Dasymys incomtus* s.l. species complex, but also that the taxa we could discern by craniometry (*sua, rwandae, alleni, medius*) can also be genetically characterized (appendix 6).

Another interesting point is that the *Dasymys* of the rift region and the southern part of the Eastern Arc form a separate clade when compared to the *Dasymys* from the lower plains of Tanzania (*sua*). We mention also that the single specimen that we could sequence from Mufindi (Uzungwa) and that proved to be craniometrically near to *alleni* (topotype locality being Mt Rungwe), seems to be genetically sufficiently differentiated to justify possible taxonomic recognition.

SOUTHERN AFRICA

The only South African *Dasymys* specimen available to us for sequencing (Vaalwater – TM40200) we assigned to *incomtus*. We reached this conclusion by directly comparing its skull to the type skull of *D. incomtus* (SUNDEVALL 1846) and its placement on graph 2.1. For as much as we can evaluate – in the absence of sequences from specimens representing *nudipes, cabrali* and *Dasymys* from other South African regions - we conclude that the Central African forest populations (*bentleyae*) are basal to all *incomtus* and its related East African taxa like *sua, rwandae* and *alleni*.
Finally, the obtained phylogeny (fig. 4), when viewed in a continental context, is revealing as to the possible evolutionary trajectories of the members of this genus. The well documented habitat preferences of *Dasymys* (permanent moist conditions such as riverbanks, swampy edges of ponds, brooks and marshy areas etc.) (DAVIS, 1962; ROSEVEAR, 1969; SHEPPE, 1972; KINGDON, 1974) suggest that it is no coincidence that the most basal lineages of the genus are found in West and Central Africa. While during the Mio-Pliocene, sub-Saharan Africa was completely covered by tropical moist forests, the development of the African Rift modulated the regional effects of Quaternary climate changes (COPPENS, 1999). During the last 2 My, these cycles of climatic change resulted in the shrinking and expansion of forests in Central and West Africa, whereas in East Africa these events resulted in extremely arid conditions. It is likely that moisture dependent taxa such as *Dasymys* survived these severe climate changes by finding shelter in the few forest refugia in Central and West Africa (MAYR and O'HARA, 1986) from where descendants of the surviving lineages (re)colonized the rest of sub-Saharan African as the prevailing climate conditions gradually became more humid.

FINAL REMARKS

Until today species descriptions of mammals are largely based on morphological criteria and tend to follow a pragmatic typological species concept. Because the evaluation of the observed morphological diversity is unrealistic as far too many studies are based on relatively few specimens, this approach has led to unwarranted splitting and equally unjustified lumping. Our study methodology attempts to combine extensive craniometric data with genetic data to detect the real patterns of biodiversity in often difficult to identify mammal species. We recognize that this approach has its limitations. Indeed, not all craniometric differences that we may observe, not even when they are statistically very significant, are in themselves sufficient to decide whether or not the investigated populations should be attributed species rank. We are also aware that the genetic data that are added here do not provide an unambiguous answer to the taxonomic rank of the investigated taxa. There are obviously no rules as to how much sequence divergence is required for a population to belong to discreet biologically valid species. As has been shown before, this study shows that large differences may be observed between the degrees of morphological and genetical differentiation among taxonomical units that we consider to be good species (see elsewhere for arguments to that effect, FERGUSON et al. (2002), VERHEYEN et al. (2002)). Although we agree that the decision whether or not a taxon should be given species status is not resolved by our combined morphological and genetical approach, we argue that this approach is at least an attempt to capture the morphological and genetical diversity that exists in the studied genus, and to place it in a correct taxonomical context. The availability of such data is important as it provides a very different perspective on the meaning of the distribution ranges and patterns of *Dasymys* and other African murids that are currently plagued with too many taxonomical problems. After all it is obvious that reliable knowledge on the distribution ranges of well characterized species is of paramount importance for all studies that intend to study the ecology and the biodiversity of these small mammals.
Finally, we want to underline once more that our study started as an attempt to describe the craniometric and genetic variation in the East African *Dasymys* populations, but eventually it gave us the opportunity to recognize and evaluate some of the many problems that still surround the taxonomy of this genus. The recent publication of MULLIN et al. (2002) concerning the *Dasymys* from Natal and Kwazulu demonstrates how a detailed multi-disciplinary approach (karyology, craniometry and genetics) may reveal how previously undetected diversity still exists in this genus. Undoubtedly, when applied on a wider geographic and systematic scale, such an approach will allow us to better understand the problems that will face the taxonomy of small African mammals in the future.

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REFERENCES

ALLEN, G.M., 1939. A checklist of African Mammals. *Bulletin of the Museum of comparative Zoology at Harvard College*, 83, 763 pp.

AVERY, D.M., 1991. Late Quaternary incidence of some micromammalian species in Natal. *Durban Museum Novitates*, 16: 1-11.

BIBB, M.J., VAN EITEN, R.A., WRIGHT, C.T., WALBERG, M.W. & CLAYTON, D.A. 1981. Sequence and gene organisation of house mouse mitochondrial DNA. *Cell* 26: 167-180

CARLETON, M.D. & MARTINEZ, C., 1991. Morphometric differentiation among west African populations of the rodent genus *Dasymys* (Muridae, Murinae) and its taxonomic implications. *Proceedings of the biological Society of Washington*, 104: 419-435.

COE, M., 1975. Mammalian ecological studies on Mount Nimba, Liberia. *Mammalia*, 39: 523-588.

CORBET, G.B. & HILL, J.E., 1980. A world list of mammalian species. British Museum (Natural History), Comstock Publishing Associates, London.

CORBET, G.B. & HILL, J.E., 1986. A world list of mammalian species. Second edition. British Museum (Natural History), London, 254 pp.

COPPENS, Y., 1999. African Biogeography, climate change and Human evolution.. Oxford University Press.

CRAWFORD-CABRAL, J., 1983. Patterns of allopatric speciation in some Angolan Muridae. *Annales du Musée royal de l'Afrique centrale, Tervuren, Belgique, Ser. 8 (Sciences zoologiques)*, 237: 153-157.

CRAWFORD-CABRAL, J., 1986. A discussion of the taxa to be used in zoogeographical analysis as illustrated in Angolan Muridae. *Cimbebasia*, Ser. A8, 19: 162-166.

CRAWFORD-CABRAL, J., 1998. The Angolan Rodents of the superfamily Muroidea . An account of their distribution. Istituto de Investigaçao Cientifica Tropical, *Estudios, Ensaios e Documentos*, 161: 1-223.

CRAWFORD-CABRAL J. & PACHECO, A.P., 1989. A craniometrical study of some water rats of the genus *Dasymys* (Mammalia, Rodentia, Muridae). *Garcia de Orta, Seria de Zoologica*, 15: 11-24.

DAVIS, D.H.S., 1962. Distribution patterns of southern African Muridae, with notes on some of their fossil antecedants. *Annals of the Cape Provincial Museum*, 2: 56-76.

DE GRAAFF, G., 1981. The Rodents of South Africa. Butterworth and Company, Durban.

DE WINTON, W.E., 1896. On collections of Rodents made by Mr. J. ffolliott Darling in Mashunaland and Mr. F. C. Selous in Matabeleland, with short field-notes by the collectors. *Proceedings of the Zoological Society of London*, 1896: 798-808.

DELANY, M.J., 1975. The rodents of Uganda. *Trustees of the British Museum (Natural History), London*, 165 pp.

DELANY, M.J. & HAPPOLD, D.C.D., 1979. Ecology of African Mammals. *Longmans Group Ltd, London*, VIII + 434 pp

DUCROZ, J. F., VOLOBOUEV, V. & GRANJON, L., 2001. An assessment of the systematics of arvicanthine rodents using mitochondrial DNA sequences: evolutionary and biogeographical implications *Journal of Mammalian Evolution,* 8 (3): 173-206.

EISENTRAUT, M., 1963. Die Wirbeltiere des Kamerungebirges. Unter besonderen Berücksichtigung des Faunenwechsels in den verschiedenen Höhenstufen. Verlag Paul Parey, Hamburg, Berlin.

ELLERMAN, J.R., 1941. The families and genera of living rodents. Vol. II. Family Muridae. British Museum (Natural History), London, 690 pp.

ELLERMAN, J.R., MORRISON-SCOTT, T.C.S. & HAYMAN, R.W., 1953. Southern African Mammals 1758 to 1951: a reclassification. British Museum (Natural History), London, 363 pp.

FELSENSTEIN, J., 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution.* 39: 783-791.

FERGUSON, J.W.H., 2002. On the use of genetic divergence for identifying species. *Biological Journal of the Linnean Society*. 75: 509-516.

GORDON, D.H., 1991. Chromosomal variation in the water rat *Dasymys incomtus* (Rodentia, Muridae). *Journal of Mammalogy*, 72: 411-414.

HALL, B.P. & MOREAU, R.E., 1970. An Atlas of Speciation in African Passerine Birds. Trustees of the British Museum (Natural History), London, XV + 423 pp.

HANNEY, P., 1965. The Muridae of Malawi. *Journal of Zoology*, 146: 577-633.

HAPPOLD, D.C.D., 1987. The Mammals of Nigeria. Oxford University Press, New York, 402 pp.

HATT, R.T., 1934. Fourteen hitherto unrecognized African Rodents. *American Museum Novitates*, 708: 1-15.

HELLER, E., 1910. Five new Rodents from British East Africa. *Smithsonian Miscellaneous Collections*, 54. (1924): 1-4.

HELLER, E., 1911. New species of Rodents and Carnivores from Equatorial Africa. *Smithsonian Miscellaneous Collections*, 56. (17): 1-16.

HOLLISTER, N., 1916. Three new murine Rodents from Africa. *Smithsonian Miscellaneous Collections*, 66. (10): 1-3.

HONACKI, J.H., KINHAM, K.E. & KOEPPL, J.W. (eds)., 1982. Mammalian species of the world. A taxonomic and geographic reference. Allen Press Inc. and The Association of Systematic Collections, Lawrence, Kansas, 694 pp. .

JAEGER, J.-J., TONG, H. & DENYS, C., 1986. Age de la divergence *Mus-Rattus*: comparaison des données paléontologique et moléculaires. *Comptes rendus Académie Sciences, Paris,* (série II). 302: 917-922.

KERSHAW, P.S., 1924. On two collections of Mammals: (1) from Mongalla and Bahr-el-Ghazal, (2) from lake Tsana, Abyssinia. *Annals and Magazine of natural History*; (Ser. 9). 13: 19-29.

KINGDON, J., 1974. East African Mammals. Vol. IIB - Hares and Rodents. University of Chicago Press: 343-704.

KIMAR, S., TAMURA, K., JAKOBSEN, I.B. & NEI, M., 2001. MEGA 2.1: Molecular Evolutionary Genetics Analysis software, Arizona State University, Tempe, Arizona, USA.

LAWRENCE, B. & LOVERTIDGE, A., 1953. Zoological results of a fifth expedition to East Africa. I . Mammals from Nyasaland and Tete. With notes on the genus *Otomys*. *Bulletin of the Museum of comparative Zoology at Harvard College*, 110: 3-80.

LECOMPTE E., GRANJON, L., PETERHAN, J.K. & DENYS, C., 2002. Cytochrome *b*-based phylogeny of the *Praomys* group (Rodentia,Murinae): a new African radiation? *Comptes rendus. Biol.* 325 (7): 827-840 (2002).

LUNDRIGAN, B.L., JANSA, S.A. & TUCKER, P.K., 2002. Phylogenetic relationships in the genus *Mus*, based on paternally, maternally, and biparentally inherited characters. *Systematic Biology*, 51 (3): 410-431.

MADDALENA, T., VAN DER STRAETEN, E., NTANHUGA, L. & SPARTI, A., 1989. Nouvelles données et caryotypes des rongeurs du Burundi. *Revue Suisse de Zoologie*, 96: 939-948.

MATTHEY, R., 1958. Les chromosomes et la position systématique de quelques Murinae africains (Mammalia, Rodentia). *Acta tropica*, 15: 97-117.

MAYR, E. & O'HARA, R.J., 1986. The biogeographic evidence supporting the Pleistocene forest refugia hypothesis. *Evolution*. 40, 55-67.

MEESTER, J.A.J., 1976. South African Red Dayta Book. Small Mammals. *South African National Scientific Program Report*, n° 11, Pretoria.

MEESTER, J.A.J., RAUTENBACH, L.L., DIPPENAAR, N.J. & BAKER, C.M., 1986. Classification of southern African Mammals. *Transvaal Museum Monographs*, 5: 1-359.

MILLER, G.S.Jr., 1900. A collection of small Mammals from Mount Coffee, Liberia. *Proceedings of the Washington Academy of Science,* 2: 631-649.

MISONNE, X., 1974. Order Rodentia. in: Meester J. & H. W. Setzer. (eds). The Mammals of Africa: an identification manual. Smithsonian Institution Press. Washington, D. C., Part 6: 1-39.

MULLIN, S. K., PILLAY, N., TAYLOR, P.J. & CAMPBELL, G., 2002. Genetic and morphometric variation in populations of South African *Dasymys incomtus incomtus* (Rodentia, Muridae). Mammalia, 66. (3): 381 - 404.

MUSSER, G.G. & CARLETON, M.D., 1993 . Family Muridae. In: Wilson D. E. & D. A. M. Reeder (eds). Mammals species of the World. A taxonomic and geographic reference. 2nd edition. Smithsonian Institution Press. Washington, London: 501-755.

NOWAK, R. M., 1995. Walker's Mammals of the Worlds - Online. The John Hopkins University Press.

OSGOOD, W.K., 1936. New and imperfectly known small Mammals from Africa. *Publications of the Field Museum of natural History, Zoological Series,* 20: 217-256.

PETERS, W., 1870. Lista de Mammiferos das possessões Portuguezas da Africa occidental e diagnoses de algunas especies novas. *Jorn. Sci. Math., Phys. e Nat., Lisboa, Ser.* 1, 3: 123-127.

PETERS, W., 1875. Ueber *Dasymys*, eine neue Gattung von murinen Nagethieren aus Südafrika. *Monatsberichte Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1875: 12-14.

RAUTENBACH, J.L., NEL, J.A.J. & ROOT, G.A., 1981. Mammals of Itala Nature Reserve, Natal. *The Lammergeyer,* 31: 21-37.

ROBERTS, A., 1936. New South African Mammals. *Annals of the Transvaal Museum*, 18: 250 - 254.

ROBERTS, A., 1951. The mammals of South Africa. Trustees of The Mammals of South Africa Book Fund, Johannesburg, 700 pp.

ROSEVEAR, D.R., 1969. The Rodents of West Africa. British Museum (Natural History), London, 604 pp.

SAITOU, N. & NEI, M., 1987. The Neighbor-joining Method: A New Method for Reconstructing Phylogenetic Trees. *Molecular Biology and Evolution,* 4: 406-425.

SETZER, H.W., 1956. Mammals of the Anglo-Egyptian Sudan. *Proceedings of the United States national Museum*, 106 (3377): 447-587.

SHEPPE, W.A., 1972. The annual cycle of small mammal populations on a Zambian flood plain. *Journal of Mammalogy*, 53: 445-460.

SMITHERS, R.H.N., 1971. The Mammals of Botswana. Trustees of the National Museum of Rhodesia, Salisbury.

SNEATH, P.H.A. & SOKAL, R.R., 1973. Numerical Taxonomy. W.H. Freeman & Co. San Francisco.

STATSOFT, Inc., 1995. Statistica for Windows. Tulsa. OK.

SUNDEVALL, C. J., 1846. *Öfversigt af Kongl. Svenska Vet. -Akad. Förhandl.,* Stockholm, for 1846, 3 (4): 120 (1847).

SUZUKI, H., TSUCHIYA K. & TAKEZAKI, N., 2000. A molecular phylogenetic framework for the Ryukyu endemic rodents *Tokudaia osimensis* and *Diplothrix legata. Molecular Phylogenetics and Evolution,* 15 (1): 15-24 (2000).

THOMAS, O., 1892. Description of three new African Muridae. *Annals and Magazine of natural History*, Ser. 6, 10: 179-183.

THOMAS, O., 1906. Descriptions of new mammals from Mount Ruwenzori. *Annals and Magazine of natural History*, Ser. 7, 18: 136-147.

THOMAS, O., 1912. List of the third collection of Mammals from Panyam, N.Nigeria, presented by the rev. G.T. Fox. *Annals and Magazine of natural History*, Ser. 8, 9: 683-686.

TRANIER, M. & GAUTUN, J.C., 1979. Recherches caryologiques sur les rongeurs de Côte d'Ivoire: résultats préliminaires pour les milieux ouverts. *Mammalia*, 43: 252-254.

VERHEYEN, W.N., COLYN, M. & HULSELMANS, J., 1996. Re-evaluation of the *Lophuromys nudicaudus* HELLER 1911 species-complex with a description of a new species from Zaire (Muridae - Rodentia). *Bulletin van het Koninklijk Belgisch Instituut voor Natuurwetenschappen, Biologie,* 66: 241-273.

VERHEYEN, W.N, HULSELMANS, J.L., DIERCKX, T. & VERHEYEN, E., 2002. The *Lophuromys flavopunctatus* THOMAS 1888 s. l. species complex: a craniometric study, with the description and genetic characterization of two new species (Rodentia - Muridae - Africa). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Biologie*, 72: 141-182.

VOLOBOUEV V.T., SICARD, B., ANISKIN, V.M., GAUTUN, J.C. & GRANJON, L., 2000. Robertsonian polymorphism, B chromosomes variation and sex chromosomes heteromorphism in the African water rat *Dasymys* (Rodentia, Muridae). *Chromosome Research*. 2000 . 8 (8): 689-697.

WALKER, E.P., 1964. Mammals of the World. John Hopkins Press, Baltimore.

Walter N. VERHEYEN
Jan L. HULSELMANS
Theo DIERICKX
Herwig LEIRS
Universiteit Antwerpen
Departement Biologie
Onderzoeksgroep Evolutionaire Biologie
Groenenborgerlaan 171
B-2020 Antwerpen (Belgium)

Erik VERHEYEN
Koninklijk Belgisch Instituut voor Natuurwetenschappen
Vautierstraat 29 B-1000
Brussel (Belgium)

Marc COLYN
Université de Rennes 1
CNRS – UNRS 6552 Ethologie – Evolution- Ecologie
Station Biologique de Paimpont
F-3538 Paimpont [France]