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)

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Abstract

In an attempt to properly identify *Dasymys* specimens that were collected during the last decades 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. naudiges* and to describe three new taxa. Subsequent genetic analysis (cytochrome b) allowed us to provide a genetic 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 incités à entreprendre une révision de ce genre. Alors que nous avions décidé initialement de nous limiter aux *Dasymys* de ces régions, nos observations nous ont forcé à inclure dans notre étude des espèces comparatives des régions limitrophes.

Nous avons réalisé cette révision génétique en nous basant sur des données métriques d'une vingtaine d'UTO's groupant un millier de crânes.

L'observation que la composition variable (âge et sexe) d'une UTO ne semble qu'avoir un impact négligeable sur l'aspect des arbres phylogéniques obtenus, nous a permis d'entreprendre un «screening» des *Dasymys* de l'Afrique orientale.

Grâce à cette approche quantitative nous avons pu évaluer la qualité des formes déjà décrites, de sélectionner un néotype pour *D. naudiges* et de décrire trois nouvelles formes de *Dasymys*.

Des analyses génétiques subséquentes (cytochrome b) nous ont permis 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*, taxonomie, 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 us 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 water parts of floodplains and even highland bogs (Davis, 1962; Rosevear, 1966; Smithers, 1971; Shippee, 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; Cob, 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, 1970) it is not easily captured (Meister, 1976; Corbet & Hill, 1980; De Graaf, 1981; Raubenach 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 speculation (Avity, 1991; Gordon, 1991).

*Dasymys* are rats that are well characterized by their thick-set heavy habits, 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 dusky 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-scently haired and have five digits (Nowak, 1995).

Dasyurus 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 Dasyurus 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 (1959) was the first to synomise some of the described taxa and retained 10 species for the genus Dasyurus. 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 Dasyurus must be monotypic, inexactis 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 Dasyurus 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, 1963; Rosevear, 1969; Misonne, 1974; Delany, 1975; De Graaff, 1981; Honacki et al., 1992; Meister et al., 1986; Corbet & Hill, 1996; Haasfio, 1967). Except for Roberts (1951) and Crawford-Cabral (1983, 1985), who accepted D. nudipes as a second species, all the other classifications recognize only one species D. inexactis (Sundevall, 1847). However, Crawford-Cabral & Pacheco (1989: 11) published a craniometric study on Angolan Dasyurus, 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 Dasyurus based upon cranialdental morphometric variation among west African populations concluded that (p. 415) “Two morphological kinds can be discerned in this region and that the degree of craniodental differentiation between these two phyla matches that documented for other geographically narrow murid species inhabiting parts of west Africa” has convincingly shown that continuing to consider Dasyurus to be monotypic is most certainly not a realistic option (Carleton & Martinez, 1991). This view was maintained by Misser & Carlton (1993), who recognize five species in sub-Saharan Africa in their classification of the genus Dasyurus: D. fusi in Jos plateau, Nigeria; D. refus in West-Africa; D. montanus at high altitudes in the Rwenzori Mt of Uganda; D. nudipes in southwestern Angola; D. inexactis for the rest of its geographical range), they also recognize 14 synonyms within D. inexactis. Another study confirms that at least two taxa and possibly three - «specimens» are present in central Angola, stressing again that it is very probable that the monotypic approach to Dasyurus is outdated (Crawford-Cabral, 1998).

Recently, the wide distribution range for D. inexactis - as proposed by Misser & Carlton (1993) (from Sudans to Ethiopia, and then south to the southern coast of South Africa) is questioned (Mullin et al., 2002). She suggests (p. 583): “It seems more likely that the currently listed distribution range of D. inexactis 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 Dasyurus inexactis populations from the Kwa-Zulu-Natal and Northern Province strongly indicates that two separate subspecies or even species exist within D. i. inexactis (ibidem, p. 395).

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 Dasyurus, 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-
A cranometric and genetic approach to the systematics of the genus Dasyurus, 1975

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 Instinct 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 Museum national d’Histoire naturelle (Paris).

Fig. 1. Map showing the geographical position of the type localities of the different taxa of the Dasyurus genus. For the co-ordinates we refer to Appendix B (p. XIII) of Hall and Moreau (1970).

1. Inornatus Sundevall, 1849
2. sanguinolentus Peters, 1870
3. guineensis Peters, 1875
4. heterael Thoms, 1892
5. fasciatus De Winton, 1895
6. regalis Miller, 1900
7. meiurus Thomas, 1908
8. moschatus Thomas, 1908
9. helvitus Heller, 1910
10. oritis Heller, 1911
11. advenus Heller, 1911
12. fori Thomas, 1912
13. migratus Hollister, 1915
14. hawaii Kershaw, 1924
15. advenus Ratt, 1954
16. gracilis Crickmore, 1936
17. capensis Roberts, 1936
18. atheri Lawrence & Loveridge, 1933
19. palumbi Setzer, 1956
20. tarsipes Enderlein, 1953
Fig. 2. The geographical distribution of the OTU's of the genus Dorymys 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 & MOBBIN (1970).

1. Mupoyeni 11. Vinaags
1-1 Mt Coffee 11-1 Uwinka
1-2 Mt Nkobi 12. Bakuwa
1-3 Serefo 12-1 Rungwe Mt.
2. Luvu 12-2 Mwemba
3. Pumma 12-3 Uluba
4. Punyam 12-4 Mafinga
5. Kafu 13. Luwimbwosi
10-1 Balove
10-2 Albertville
15. Chitau
16. Hula
17. Okavango
18. Hove
19. Kaungu
20. Nyeveli

Paris (France) we would 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 lists all the relevant data concerning the type specimens of Dorymys (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 museums and institutions where these specimens are housed, we refer to VERHEYEN 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.
CRANIOLOGY

To evaluate the impact of ageing on the size and shape of the *Dasyurus* skulls, we grouped all the available crania into age-classes using the tooth-eruption and tooth-wear patterns as described in Vessey et al. (1996, p. 240). 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 (asymmetry in Vessey et al. 1996). The measurements were taken with callipers (digital reading) graduated to hundreds of millimeters, 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 *Dasyurus* 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 metric data of our OTU's (see Appendix 2) cannot be fully published here but can be obtained through Email (naked@unica.ac.it).

To enhance the clarity of the results depicted in our multi-group graphs, we only show the 95% equivalent 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 & SOEKAL, 1973); this method accounts for 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 maximized OTU's either by eliminating some measures responsible for excluding other specimens complete skulls (plotting of incomplete type skulls) or by substituting missing data by means.

Finally, most of our OTU's are homogeneous as to the geographical origin of the included specimens. Only to form OTU9 (Kiautsch). OTU10 (Kasavity) and OTU6 (Fianarantsoa) 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 *Dasyurus* species. We added two sequences from species identified as *Dasyurus inexpectatus* and *nigricans* (respectively EMBL accession number AF141121 and AF141216) and taken from the literature (TUCKER et al. 2001). All our groups we included three African marine sequences from LUNDURGAN et al. (2002) we used *Mastomys

hildebrandti* (AY057818) and *Nonomys minimus* (AY057815), *Hylomyscus parvus* (AY051830) was taken from LCOMFRE et al. (2002). Given the geographic area covered by this study we assume that our sample is sufficient to anchor the taxonomic diversity of the Central and East African *Dasyurus*.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Total DNA was extracted from frozen or ethanol preserved muscle or liver tissues using the QIAamp 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 25ul reaction volumes containing 10μM of each primer. 200μM dNTPs, 10mM Tris-HCl, 1.5 mM MgCl2, 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, extension 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 extension 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 L15108 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 cyt sequences are of mitochondrial origin, the corresponding amino acid sequences were screened for the presence of stop codons, deletions or insertions 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 calculation of a molecular clock based upon the presumed time divergence between the *Mus* and *Rattus* lineages (JACKER et al. 1999) we included the *Rattus rattus* sequence (SUZUKI et al. 2000) from the literature. Two trees 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 *Dasyurus* (Graph 1, 1.2; Appendix 5.1.5.2)

Before stating our canonical and other multivariate technique 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. rufius and D. incaucus s. l. (beetleyae).

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; OTU2: Garamba) to allow each analysis. OTU1 contains 58 skulls that were collected in the nineteen sixties in the savannah of Mopoyem near Adipodoumé (Ivory Coast). OTU2 is equally important and contains 100 skulls mainly collected in the nineteen fifties in the savannah of Nalama 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 2.1 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 1/4 a larger skull than the females (M1, M2, M3), 27/ a heavier developed rostrum and upper incisor (M4, M5, M6, M21, M22, M23), 37/ a higher ramus of the mandible (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 2.2). The sexual dimorphism shows an increase in age-class 2 and the skulls of the males are 27/ longer (M1, M2, M3, M6), 27/ a heavier ramus (M22, M23) and 37/ a higher ramus of the mandible (M24).

Since the observed craniofacial differences between the sexes range between 2 - 3% 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 sex and age may have on our data series, 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 1.1 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 (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 craniofacial measures appears to cover adequately the cranial variation present in our OTU's, even covering allometric differences due to age and sex. This leads us to the conviction that the observed craniofacial 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 Lapithonymia flavicarinata species complex (VERHEYEN et al. 2002).

2. The taxonomic status of the type specimen of the Dasyoma taxa

(Graph 2.1, 2.2, 3.1, 3.2; Appendix 1.1, 1.2)

We have examined 17 out of the 20 described Dasyoma 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 nudes Pernet (1870), Dasyoma nudes Pernet 1870, Dasyoma nudes capensis Roberts (1936). Especially the absence in our data-base of the nudes-type, discovered in the 1978 fire which devastated the 'Musee Beige' part of the Science Building of the University of Lisbon (Eds CRAWFORD-CAMAL, proved to be such a hindrance to reach a satisfying taxonomical solution that we decided to create a new and a new-paratype. Furthermore of both specimens are included in appendix 1.1 and 1.2; the description itself can be continued further in this paper.

A canonical analysis based upon a selection of six OTU's hopefully represents the actual craniofacial variation of Dasyoma in southern Africa (graph 2.1). The first observation is that we can discern in the selection three clearly differentiated groupings. If we plot according to these additional normal small series of more southern situated localities (Mimica - Harare - Nyasaland - Vatseiveri) as well as the bigger OTU9 (Kinsasa) we see that they all coincide with OTU's 13, 14, 15, 19 and that there is neither an overlap with OTU16 (Huila) typical for Dasyoma nudes nor with OTU17 (Okavango).

Another number of southern series we see that the type-specimen of D. incomus coincides perfectly with our set of OTU's 13, 14, 15, 19. This suggests that all of the Dasyoma 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) situated itself within the clines characterization incomus.

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

Another analysis compares a number of OTU'srepresentative for the two African regions (OTU1, 2, 3, 4) with a set of OTU's that we consider to contain the variation of the central African region inclusive of Ethiopia (OTU's 5, 7, 9) (graph 2.2.). It becomes immediately clear that OTU1 (Mopossem) 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 (Kinsasa) that in a way bridges the gap between OTU1 (Mopossem) and the other OTU's. It should however be mentioned that the geographical origin of the specimens composing OTU9 (Kinsasa) is rather diverse, which may explain its more elongated 95% equiprobable ellipse. Also the plotting of the series from Serada (OTU1-3) reveals that it coincides completely with OTU9 (Kinsasa).
Graph 2.1. Graphic representation of a forward canonical analysis performed on a set of six Dasyurus-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 Dasyurus-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 *edensii* HATT 1934.
Graph 3.1: Graphic representation of a forward canonical analysis performed on a set of five Dasyonyx populations representing the observed geographical variation in the eastern region of the distribution of Dasyonyx in order to allocate by plotting the type specimens originating from this region and some small but important OTUs (there 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 OTUs representing the western-central rift region and providing the background to allocate by plotting the relevant type specimens and some smaller but important OTUs. 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 monstrosus THOMAS 1906.
Even after the exclusion of OTU1 (Mpopoyi) from the analysis, a very important overlap remains between all the OTUs indicating that craniometrically there is no good argument to suggest the existence of important taxonomical differences (except maybe for the slightly different OTU15). It is reassuring that the relevant type-specimens fit rather well with their geographically related OTUs: that *longipilosa* and *edoni* fall within OTU9 (Kimhassa) and that the *raflus* type and paratypes more or less correspond with OTU1 (Mpopoyi). We conclude the discussion of graph 2.2 by accepting in western, central and northeastern Africa the existence of two craniometrically well differentiated species (*D. rafius* and *D. incontus*). There remains however some doubt whether OTU1 (Mpopoyi) can be considered to represent typical *raflus*. Indeed, 1° the topotypical locality of *raflus* (Mt. Coffee) is situated about 500 km to the west of Mpopoyi (locality in a forest enclosed savannah); 2° the *raflus* type series plots also closely with OTU9 (Kimhassa) and clusters more or less with the central African types of *longipilosa* and *edoni*. Both arguments suggest that OTU1 (Mpopoyni) might represent a new taxon that is different from (but related to) *raflus*. In this case typical *raflus* would be 'close' to OTU9 (Kimhassa) that we consider to represent *D. bendeyae* (together with OTU7 (Garana)).

In graph 3.1, we compare populations that represent eastern and central Africa (OTU's 7, 8, 10, 12) with OTU13 (Lubumbashi) that characterizes the south-eastern region and in our view representative of typical *D. incontus* (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 Rwandian OTU11 (Vinanga) because of the poor condition of the montanus type skull (see graph 3.2).

Apart from the fact that none of the *Dasyopus* types coincides with OTU12 (Dakawa), making this OTU a good candidate for taxonomical recognition, we find that the type of *D. alleni* (type locality: BCI, Mt. Ruwenzori, Tanzania) plots well inside the equiprobable ellipse of OTU10 (Tshibati-Kiwi). This rather surprising finding is confirmed by the plotting of the equiprobable ellipse of OTU12-4 (grouping respectively a few specimens from Mt. Ruwenzori and from Mutindi, Tanzania). The other small Tansanian OTU's (12-2, 12-3) as well as all the *Dasyopus* types of the eastern African region (Sudan-Ethiopia-Kenya-Congo-Zimbabwe) fall well grouped inside the equiprobable ellipse 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, 1-1) 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 (Vinanga), 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 (Uwinaka) situates clearly within OTU11 (Vinanga); 2° OTU10-1 (Bukawa) and OTU10-2 (Alvotri) 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 (*bendeyae, incontus, medius, montanus*) are to be found within the range of OTU7 and OTU7-1.

Finally we draw attention to the specimen IZEA 2716 of Rushab (Burundi) which clusters readily within the range of OTU10 (Tshibati). This specimen is particularly interesting because it has been hermatyped (MAIDALENA et al., 1989).

Summarized, the following conclusions can be drawn concerning the taxonomical position of the studied *Dasyopus* type-specimens:

- all our analyses suggest that *incontus* (SUNDENELL, 1845) is to be considered the *Dasyopus* with the widest geographical range: *bendeyae, medius, montanus, kelukus, orthus, tanganus, nigrigula, shavi, edoni, girielfons, poliastes, longipilosa* are possibly all synonyms of *incontus*, which in our present analysis can be best represented by OTU13 (Lubumbashi);
- the types *foss, Thomas* (1912) *alleni* LAUENRODGE & LOVERIDGE (1953), respectively represented by OTU4 (Kayaram-topotypical) and OTU10 (Tshibati) are sufficiently differentiated from *incontus* to be considered separate taxa;
- *rafius* MILLER (1900) can, with certain limits (see discussion) be represented by OTU1 (Mpopoyi);
- we will select in OTU16 (Huilu) a neotype and synonymous type to replace the lost type-specimen of *D. medius*.

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

In order to visualize the important craniometric variation discussed in the preceding paragraphs, we performed a canonical analysis (including as many OTU's as are 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 Darynya-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 incensus s. l. species complex.

Graph 4.2. UPGMA dendrogram based upon the craniometric comparison of 11 OTU's using a minimum of 16 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 incensus s. l. species complex.
of measure) 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 chap. 2). When we reduce the number of OTU's in the so called "inconclus" 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 (Huala) are easily identified as representatives of respectively the west African D. rufulus and the Angolan D. nudipes. Each 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 coincident with the Mt Coffee population (geographical 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 "inconclus" s.1. species group has by far the biggest geographical distribution of the OTU represented in graph 4.1. Within this group OTU10 (Tshibati) and OTU34 (Pelmia-Panyam) - representing respectively alleni and fosil - are clearly differentiated from the other OTU's. The rest of the grouping splits up into a bentleyae branch that encompasses OTU9 (Kimpasa), OTU7 (Garamba), OTU2 (Lamto), OTU19 (Kassanga) and an even more widely distributed inconclus s. s., here represented by OTU3 (Kalua), OTU8 (Kamoué), OTU18 (Haran), OTU13 (Lubumbashi), OTU14 (Daloa), OTU15 (Chiluba) and OTU17-1 (Dawenzendo Mt.). In graph 4.2 the differences between inconclus s. s. and bentleyae are somewhat enhanced and clearer with fosil (OTU34+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- (OTU7 and 9), the "inconclus"- (OTU8, 13, 14, 15, 18) and the fosil-populations (OTU3 and 4) represent craniometrically slightly different branches, but probably not important enough to justify taxononomic recognition.

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

4. Selecting a neotype for Dasynus 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 Philip Bradley Expedition (13 November 1932) in Humta (15.01S - 13.21E; alt. 6300 ft), collecting number 453.

**Neo-paratype**
ISCED 1987; adult male, skin and skull; collected by Simoes P. and C. (19 December 1965) in Humta (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 Humta (15.01S - 13.33E) of the original type-specimen of *Dasynus nudipes* Peters (1870) is situated about 25 km to the South East of Humta, the collecting locality of the neotype and neo-paratype. We choose for this solution since we could not locate an adequate specimen from Humta itself. Both localities are situated somewhat to the South of Sâ da Bandeira in the Sierra da Chela at a rather high altitude (6300 ft).

Hoping to locate and subsequently study the important type specimen of *Dasynus nudipes* we contacted our colleague John Crawford-Carrel who has been studying the Angolan murid collections conserved in the most important museums and scientific institutions (see publication of 1998).

He replied: The material studied by Bocage (including *Dasynus 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 Sciences Faculty of the University of Lisbon, a building that was largely was by a fire in 1978. Unhappily,
all collections in 'Museu Bocage' were lost then'. Since we know that the type specimen of nudipes has been destroyed and we have osteometric proof of the existence of a D. nudipes and an 'inconclus' 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 osteometrically through discriminant functions, respectively between OTU16 (Huila), OTU13 (Luambashi) 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 inconclus (OTU13) and the Okavango (OTU17) population to be described as a new taxon.

Appendix 5.3. compares through univariate analysis OTU16 (Huila) with OTU13 (Luambashi) and shows that nudipes-skulls are very significantly bigger than inconclus-skulls 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 acceptable for all the teeth measures M11 (OPTE), M12 (LPOA), M13 (M1ER) and M17 (LOTE) where we record important differenti (between 10.2 and 12.6%) and we find similar and even higher differences in measures which are strongly influenced by growth such as M1 (GLRS), M6 (DIA1), M16 (LANAS), 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 Dasypus through univariate 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 inconclus (Bunduwall, 1846) and of our newly described taxon. The general morphology of the teeth, more especially for nudipes and inconclus, is very similar.

5. Description of Dasypus cabralii 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 (Onatuka Junction) - Great Fontem District, S. W. Africa (17.565 - 20.25E; alt.: ± 1080 m); collecting number 7.129.

PARATYPES
14 specimens from the same Capriv district as the type specimen all collected by G. C. Shortridge between 26 and 27 June 1929. Onatuka Junction (alt.: ± 1080 m)

BMNH
35.9.1.660 (ad male; skull + skin; coll. nr. 77910)
35.9.1.667 (ad fem.; skull + skin; coll. nr. 76905)
35.9.1.658 (ad fem.; skull + skin; coll. nr. 78708)
35.9.1.670 (ad male; skull + skin; coll. nr. 77374)
35.9.1.672 (ad male; skull + skin; coll. nr. 78150)
60.220 (ad fem.; skull + skin; coll. nr. 71111)
60.221 (ad male; skull + skin; coll. nr. 71114)
60.222 (ad male; skull + skin; coll. nr. 73324)
60.224 (ad male; skull + skin; coll. nr. 73325)
60.236 (ad male; skull + skin; coll. nr. 74484)
60.238 (ad male; skull + skin; coll. nr. 73444)
60.239 (ad male; skull + skin; coll. nr. 74164)
60.240 (ad fem.; skull + skin; coll. nr. 74564)
60.241 (ad fem.; skull + skin; coll. nr. 78151)

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 Capriv strip.

Amba (18.068 - 21.286; alt.: ± 1068 m), 30 July 1929
BMNH 35.9.1.651 (ad male; skull + skin; coll. nr. 75483)
25.9.1.652 (ad fem.; skull + skin; coll. nr. 75484)
Manianghi drift (alt.: ± 1026 m), 11 August 1929
BMNH 35.9.1.653 (ad male; skull + skin; coll. nr. 77607)
35.9.1.654 (ad fem.; skull + skin; coll. nr. 77605)
25.9.1.655 (ad fem.; skull + skin; coll. nr. 77601)
25.9.1.656 (ad fem.; skull + skin; coll. nr. 77602)
25.9.1.657 (ad fem.; skull + skin; coll. nr. 77603)

Djebu (near Bagani Drift; alt.: ± 1026 m), 02 September 1929
BMNH 66.242 (ad male; skin + skull; coll. nr. 78005)
35.9.1.658 (ad male; skull + skin; coll. nr. 79344)
35.9.1.659 (ad male; skull + skin; coll. nr. 79407 - 01/IV 1929)
Garaungate (alt.: ± 1026 m), 28 November 1929
BMNH 35.9.1.657 (ad fem.; skull + skin; coll. nr. 8025)

As can be deduced from the collecting dates, the altitudes of the localities and the collecting numbers, the collecting localities are probably situated rather around or at a short distance to the east of Amba in the Capriv 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 Dasypus 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 published in his publication on the Angolan Murids (1988) when discussing the distribution of Dasypus 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. cabralii by a osteometric description based upon univariate and multivariate comparisons with populations of different taxa but of the same general geographical region. This comparison involves OTU13 (Luambashi) 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. núcpes versus a population OTU13 (Lubumbashi) that we consider to be representative for the species incanus. The coefficients for the canonical transformation are also represented.

Graph 5.2.
Graphic representation of the discriminant function (backward analysis) allowing the characterization of D. cebrai n.sp. (OTU7) versus our OTU16 (Hula) that we consider to represent D. radix. The four skull measurements needed for the craniometric diagnosis of our new taxon cebrai are also available.

Graph 5.3.
Graphic representation of the discriminant function (forward) permitting the definition of D. cebrai n.sp. (OTU7) versus OTU13 (Lubumbashi) that we consider to be representative for D. incanus. The coefficients for the canonical transformation, necessary for the diagnosis of the new taxon are also available.
species inconfusus and OTU16 (Huiia) typical for the species nudipes.

In appendix 5.3, we show cranioetric data that allow us to discuss the differences between OTU17 (Okavango) typical for cabrali and respectively OTU15 (Huiia) and OTU13 (Lupumbashi). This univariate approach reveals that cabrali is \(1^\text{st}\) for nearly all skull-dimensions respectively smaller than nudipes and bigger than inconfusus and \(2^\text{nd}\) 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 inconfusus. 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 inconfusus and cabrali (graph 5.3.) a forward analysis requires only 15 measures to realise 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.5) it is slightly different from nudipes and inconfusus, but this variation has in our opinion no taxonomic value.

6. Description of Damysye su a n. sp.

(Graph 6.1, 6.2; Appendix 1, 4, 5.4, 6)

HOLOTYPE

KMMA 96-037-M-3143; ad. female; skull and alcoholic specimen collected by Marcel Michiels (16 September 1986) in Mbata (65,525.37.41D) near Morogoro (Tanzania) on the flanks of the Uluguru-range at ±1500 m altitude (Kitutu forest); collecting number 2339.

PARATYPES

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

Mtwara (Choma-Kinwava forest): 05.528.37.46E alt. ±1540 m.

KMMA 96-037-M-3144; ad. male; skull + alcoholic specimen number 2771.

Main (05.588.37.38E; alt. ±600 m)

KMMA 96-037-M-3146; ad. female; skull + alcoholic specimen number 2669.

3137 (ad. male; skull + alcoholic specimen number 2666.

3138 (ad. male; skull + alcoholic specimen number 2659.

3139 (ad. female; skull + alcoholic specimen number 2612.

3140 (ad. male; skull + alcoholic specimen number 2140.

3141 (ad. female; skull + alcoholic specimen number 2140.

Mgena (07.058.37.35E; alt. ±1690 m)

KMMA 96-037-M-3133; ad. male; skull + alcoholic specimen number 622.

Kigoma (07.105.37.33E; alt. ±1500 m)

3142 (ad. male; skull + alcoholic specimen number 3423.

Dalat (55.285.37.46E; alt. ±400 m)

KMMA 96-037-M-4601; ad. male; skull + alcoholic specimen number 3980.

3461 (ad. male; skull + alcoholic specimen number 2099.

4068 (ad. male; skull + alcoholic specimen number 3949.

RICA 5432 (ad. female; skull + alcoholic specimen number 3432.

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 Redmi collection of the Redmi Pest Control Centre of the Sokolne University of Agriculture (Morogoro-Tanzania).

Dakawa (06.165.37.34E; alt. ±420 m)

KMMA 96-036-M-4632; ad. female; skull + alcoholic specimen number 5771.

4638 (ad. male; skull + alcoholic specimen number 5710.

Both specimens collected by Marc Colyn on 03 September 1987.

Memetery (near University Campus SUA in Morogoro): 06.525.37.34E; alt. ±420 m.

KMMA 96-057-M-3150 (ad. female; skull + alcoholic specimen number 2300).

3151 (ad. male; skull + alcoholic specimen number 1202.

Both specimens collected by Ivens DE GOYR on 04 and 06 October 1994.

Morneyasa (06.518.37.40E; alt. ±2150 m)

RUCA T9958; ad. female; skull; coll. number T9958.

Tangra Estate (06.408.37.38E; alt. ±000 m)

RUCA T7293; ad. male; skull; coll. number T7293.

Morogoro (SUAS campus): 06.525.37.35E; alt. ±600 m.

RUCA T1177 (ad. male; skull; coll. number T1177).

T1816 (ad. male; skull + alcoholic specimen number 2709).

T1402 (ad. female; skull + alcoholic specimen number T1402).

T12319 (ad. female; skull + alcoholic specimen number T12319).

T4377 (ad. male; skull + alcoholic specimen number T4377).

T14711 (ad. male; skull + alcoholic specimen number T14711).

The specimens from Morneyasa-Tangra-Morogoro were collected by Tieford (DANIDA, Redmi 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 morphological data of the type and the paratypes we refer to appendix 1, 4, and for the genetic characterisation to appendix 6.

ETYMOLOGY

This new species is named after the autonym SUA of the Sokolne University of Agriculture in Morogoro (Tanzania) where the Research Group of Evolutionary Biology of the University of Antwerp (Belgium) started in 1984 the Redmi Research Centre.

DIAGNOSIS

Our new taxon will be characterized by comparing it cranioetrically to OTU1 (Mopeyem) representing the rufidus-species and OTU7 (Garamba) that we consider to be close to the kepsleya-taxon of the inconfusus-complex. Appendix 5.4, describes through univariate analysis our typical series of su a. We conclude in the first place that su a has about the same cranial size as OTU7 (Garamba) but scores overall a little bigger than OTU1 (Mopeyem). Secondly we see that su a is smaller than both comparative OTU's (1 and 7) for M8 (INTE), M14 (ZYGP), M13 (CHOP) and bigger for M7 (DIAZ). Lastly su a is clearly bigger than OTU1 (Mopeyem) for M14 (ZYGP), M13 (CHOP) and M24 (FCPA).

In graph 6.1, we see that the population of our new taxon su a (OTU12) differentiates easily through a backward discriminant function from rufidus (OTU1: Mopeyem) 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. rufus n.sp. (OTU12) versus our OTU1 (Mopoyen) that we consider to represent D. rufus together with the canonical coefficients.

Graph 6.2.
Graphic representation of the discriminant function (forward analysis) characterizing between D. rufus n. sp. versus the Garamba-population (OTU7) that we consider to represent D. bertlesiene making part of the inconstans 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) differentiating between OTU10 (Tshibesti) that we consider to be representing alleni and our new taxon invarunci n.sp. (OTU11: Vinunga), the canonical coefficients permitting a correct diagnosis are also represented.
Graph 7.1.
Graphic representation of the discriminant function (backward analysis) allowing the characterization of our new species *D. n. sp.* versus OTU7 (Garumna) that we consider to represent *D. bentleyae* (part of the *incomptus*-species complex). The coefficients needed for the canonical transformation are also available.

Graph 7.2.
Graphic representation of the discriminant function (forward analysis) differentiating between OTU10 (Tshibata) that we consider to represent *D. affinis* and OTU7 (Garumna) which we accept to be *bentleyae* (part of the *incomptus*-species complex). The coefficients needed for the canonical transformation are also available.

Graph 7.3.
Graphic representation of the discriminant function (backward analysis) characterizing OTU1 (Mopoyem) that we consider to represent *D. rugulatus* versus *fossi* (OTU3 + 4) which makes part of the *incomptus*-species complex. The coefficients for the canonical transformation are also shown. We plotted next to the type specimens of *rugulatus* and *fossi* also the sequenced specimen AKB470 from Mopoyem (see text).
Graph 8.1.
Graphic representation of the discriminant function (backward analysis) characterizing OTU1 (Mepycem) versus OTU2 (Lamto). The type specimen of bentleyae and refusae are plotted as well as the sequenced specimen AKB479 from Mepycem (see text).

Graph 8.2.
Graphic representation of the discriminant function (backward analysis) differentiating cosmoterritorially 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 (Paracypris) demonstrating that fossi can easily be differentiated cosmoterritorially from bentleyae.
tioned in our univariate approach. To differentiate between
the OTU12 and OTU2 (Garamba) representing *beleleyae*,
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 *raa* with a repre-
sentative skull of *inermis* 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 nasus height; 4° smaller bullae;
and 5° finer and more pro-odont upper incisors.

As to the upper molars (fig 2) we see that the teeth are some-
what smaller than the average *inermis* molars.

7. Description of *Dasygnathus rwandae* n. sp.
(Graph 6.3, 7.1; Appendix 1.5, 5.4, 5.5, 5)

HOLOTYPE
KMMA 96-038-M-2270: ad male; skull and alcoholic speci-
men; collected by Walter Verheyen (04 June 1982) in Kingi,
Rwanda (01.265º55 39.6E, alt. 2250 m); collecting number
2934.

PARATYPES
24 specimens from Kingi, 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 2199)
2214 (ad fem.; skull + alc. sp.; coll. nr 2200)
2215 (ad male; skull + alc. sp.; coll. nr 2249)
2216 (ad male; skull + alc. sp.; coll. nr 2273)
2217 (ad male; skull + alc. sp.; coll. nr 2290)
2218 (ad male; skull + alc. sp.; coll. nr 2290)
2219 (ad male; skull + alc. sp.; coll. nr 2277)
2220 (ad male; skull + alc. sp.; coll. nr 2279)
2221 (ad male; skull + alc. sp.; coll. nr 2295)
2222 (ad male; skull + alc. sp.; coll. nr 2321)
2223 (ad male; skull + alc. sp.; coll. nr 2333)
2224 (ad male; skull + alc. sp.; coll. nr 2370)
2225 (ad male; skull + alc. sp.; coll. nr 2377)
2226 (ad fem.; skull + alc. sp.; coll. nr 3108)
2227 (ad male; skull + alc. sp.; coll. nr 3209)
2228 (ad male; skull + alc. sp.; coll. nr 3247)
2229 (ad fem.; skull + alc. sp.; coll. nr 3255)
2230 (ad fem.; skull + alc. sp.; coll. nr 3260)
2231 (ad fem.; skull + alc. sp.; coll. nr 3267)
2232 (ad fem.; skull + alc. sp.; coll. nr 3277)

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

KMMA 96-038-M-2227 (ad fem.; skull + alc. sp.; coll. nr 3084)
2228 (ad fem.; skull + alc. sp.; coll. nr 3085)

For the meristic data of the type and paratypes we refer to
Appendix 1.5 and for generic characterization to appendix 6.

ADDITIONAL SPECIMENS

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

- *Gisonge Volcano* (E1:2425-39.08) in grid 36, collected by E. van der Straeten, 31-38 June 1982
- KMMA 96-038-M-
  2247 (ad male; skull + alc. sp.; coll. nr 4003)
  2248 (ad male; skull + alc. sp.; coll. nr 4003)
  2249 (ad male; skull + alc. sp.; coll. nr 4057)
  2250 (ad male; skull + alc. sp.; coll. nr 4093)
  2251 (ad male; skull + alc. sp.; coll. nr 5960)
  2252 (ad male; skull + alc. sp.; coll. nr 5972)
  2253 (ad male; skull + alc. sp.; coll. nr 5973)
  2254 (ad male; skull + alc. sp.; coll. nr 5973)
  2255 (ad male; skull + alc. sp.; coll. nr 5981)
  2256 (ad male; skull + alc. sp.; coll. nr 5981)
  2257 (ad male; skull + alc. sp.; coll. nr 5989)
  2258 (ad male; skull + alc. sp.; coll. nr 5990)
  2259 (ad male; skull + alc. sp.; coll. nr 5991)
  2260 (ad male; skull + alc. sp.; coll. nr 5991)
  2261 (ad male; skull + alc. sp.; coll. nr 5991)
  2262 (ad male; skull + alc. sp.; coll. nr 5991)
  2263 (ad male; skull + alc. sp.; coll. nr 5991)
  2264 (ad male; skull + alc. sp.; coll. nr 5991)
  2265 (ad male; skull + alc. sp.; coll. nr 5991)
  2266 (ad male; skull + alc. sp.; coll. nr 5991)
  2267 (ad male; skull + alc. sp.; coll. nr 5991)

- *Gisonge Volcano* (E1:2354-29.40B), collected by E. Van der Straeten, 23 June -
04 July 1982 (grids 27-39)
  2270 (ad fem.; skull + alc. sp.; coll. nr 4549)
  2271 (ad fem.; skull + alc. sp.; coll. nr 5196)
  2272 (ad fem.; skull + alc. sp.; coll. nr 5215)

- KMMA 96-038-M-2227 (ad fem.; skull + alc. sp.; coll. nr 5915)
  2273 (ad fem.; skull + alc. sp.; coll. nr 5915)
  2274 (ad fem.; skull + alc. sp.; coll. nr 5915)
  2275 (ad fem.; skull + alc. sp.; coll. nr 5915)
  2276 (ad fem.; skull + alc. sp.; coll. nr 5915)
  2277 (ad fem.; skull + alc. sp.; coll. nr 5915)

- *Kigali Volcano* (01.235-29.39B) collected by E. Van der Straeten, 13 July 1982
  KMMA 96-038-M-2227 (ad fem.; skull + alc. sp.; coll. nr 5915)

ETYMOLOGY

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

DIAGNOSIS

This new species will be compared craniometrically with
two clearly differentiated taxa of the *inermis* clade 1° OTU7
(Garamba) that we consider to be close to the
*beleleyae* taxon and 2° OTU10 (Tshibati) that we identified
with the type specimen of *altera*.

In appendix 5.4 and 5.5, we situate through univariate analy-
sis our new taxon *rwandae*. In the first place we see that it is
significantly smaller (between 3% to 20%) for all body
to the more inclusive OTU's (we except these results but underline also that a certain caution is
needed when comparing external measurements recorded by
different collecting teams). When comparing the cranio-
metric data we found that overall our new taxon *rwandae* has
about the same skull size as OTU7 (Garamba) but is clearly
smaller than OTU10 (Tshibati) (23 out of 2d measurements).
On the one hand *rwandae* is markedly smaller than OTU7
and OTU10 for MES (INTE), M14 (ZYGO), 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
measure 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 K* 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).

- Mus iridogaster
- *AF518330
- Mastomys hildebrandtii *AY057318
- Dasymys SENEGAL *AF142126
- Dasymys AKB470 RCI
- Dasymys G10137 Franceville GABON
- Dasymys G10138 Franceville GABON
- Dasymys R22204 MbM CONGO BRAZZA
- Dasymys R22518 MbM CONGO BRAZZA
- Dasymys TM4200 SOUTH AFRICA
- Dasymys WR3915 V isoke RWANDA
- Dasymys 64790 Bumba TANZANIA
- Dasymys 6405 Sume TANZANIA
- Dasymys 13752 Musze TANZANIA
- Dasymys 13119 Mbi TANZANIA
- Dasymys 13155 Mbi TANZANIA
- Dasymys 13575 Chingoza TANZANIA
- Dasymys 10524 Wifendii TANZANIA
- Dasymys Berega TANZANIA *AF142127
- Dasymys 2148 Mbi TANZANIA
- Dasymys 5715 Dakawa TANZANIA
- Dasymys 3242 Kidege TANZANIA
- Dasymys 3828 Mbi TANZANIA
- Dasymys 3771 Mbele TANZANIA
- Dasymys 552 Mbele TANZANIA
- Dasymys 12676 Morongoro TANZANIA
- Dasymys 2839 Mbele TANZANIA
- Dasymys 5711 Dakawa TANZANIA

Outgroups
- cf. rufulus
- bentleyae
- incontitus
- rwandae
- alleni
- species complex
- incontitus species complex
- su

Ritzing our new taxon (graph 6.3.),
A backward discriminant function between su and OTU7 (bentleyae) selects next to the already known taxonomically important measures (M1, 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 cranial 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, weak upper incisors and somewhat shorter maxillae.
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 alignment 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 observed 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 insertions (Kumar et al., 2001), and 21 of the 380 amino acids are variable, and 10 are informative under the parsimony criterion. The saturation curve reveals that transitions of the first and second codon positions, and transversions at the third 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. Uncorrected sequence divergences (%) among conspecific Dasynys taxa.

<table>
<thead>
<tr>
<th>TAXON</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
</tr>
</thead>
<tbody>
<tr>
<td>(1) n. rubida</td>
<td>7.5-7.8</td>
<td>8.9</td>
<td>8.2-8.3</td>
<td>7.9-8.3</td>
<td>7.9-8.3</td>
<td>8.0-8.1</td>
<td>7.0-8.1</td>
</tr>
<tr>
<td>(2) rubida</td>
<td>5.5-5.7</td>
<td>4.9-5.1</td>
<td>4.9-5.2</td>
<td>4.9-5.2</td>
<td>4.4-6.0</td>
<td>4.9-6.0</td>
<td>6.4-6.0</td>
</tr>
<tr>
<td>(3) i. inconst</td>
<td>3.3</td>
<td>3.3</td>
<td>3.3</td>
<td>4.4</td>
<td>4.4</td>
<td>3.3</td>
<td>3.3</td>
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<tr>
<td>(4) inconst</td>
<td>1.0</td>
<td>2.0</td>
<td>1.0</td>
<td>2.0</td>
<td>1.0</td>
<td>2.0</td>
<td></td>
</tr>
<tr>
<td>(5) alleni</td>
<td>1.5-1.6</td>
<td>1.5-1.6</td>
<td>1.5-1.6</td>
<td>1.5-1.6</td>
<td>1.5-1.6</td>
<td>1.5-1.6</td>
<td>1.5-1.6</td>
</tr>
<tr>
<td>(6) medius</td>
<td>3.6-4.1</td>
<td>3.6-4.1</td>
<td>3.6-4.1</td>
<td>3.6-4.1</td>
<td>3.6-4.1</td>
<td>3.6-4.1</td>
<td>3.6-4.1</td>
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<tr>
<td>(7) <em>species</em></td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
</tr>
<tr>
<td>(8) n.</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
<td>1.5-1.8</td>
</tr>
</tbody>
</table>

Table 2. Times since divergence among the sequenced was estimated using the molecular clock as described in the material and methods section and the preeminent age of the splitting of the *Mis-Rana* lineages 12 Myr ago (Ladiges et al., 1986).

<table>
<thead>
<tr>
<th>TAXA</th>
<th>TIME SINCE DIVERGENCE</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Nar</em> versus <em>Dasynys</em></td>
<td>12-13 Myr</td>
</tr>
<tr>
<td><em>Dasynys</em> rubida (Senegal/RCA)</td>
<td>1.0 Myr</td>
</tr>
<tr>
<td><em>rubida/beneyi</em></td>
<td>1.0-2.0 Myr</td>
</tr>
<tr>
<td><em>rubida/inconst</em> sp. complex</td>
<td>2.0-3.0 Myr</td>
</tr>
<tr>
<td><em>inconst/inconst</em></td>
<td>± 300,000 yrs</td>
</tr>
<tr>
<td><em>inconst/alleni</em></td>
<td>± 250,000 yrs</td>
</tr>
<tr>
<td><em>rubida/alleni</em></td>
<td>± 250,000 yrs</td>
</tr>
<tr>
<td><em>rubida/inconst</em></td>
<td>± 100,000 yrs</td>
</tr>
</tbody>
</table>

Sequences used in this study were submitted to EMBL and accession numbers will be provided as soon as they will be available (enr. verheyen@natural sciences.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 623, Cl=0.723 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 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 *Dasynys* (represented by specimens from Senegal and Ivory Coast (BKO), followed by *D. beneyi* (from Gabon and Congo-Brazzaville) and the existence of a relatively younger *Dasynys* species group (see further) that not only contains *inconst* (South Africa) but also *beneyi, medius, 'species' and the new taxa *rubidae* and *n.*

Age estimates

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

Discussion and Conclusions

The cranio metric methodology that we introduced in our study of the *Lepidopus flavinaculatus* species complex (Verheyen et al., 2002) proved to be also the case of the genus *Dasynys* a valuable tool to straighten 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 cranio metric variation we conclude...
that Dasygnys is certainly polytypic and contains a series of morphometrically well-defined taxa. Translated into a geographical distribution we observe that D. incomitus s.s. has the widest range covering ggs: 17: the moist woodlands of western, northern, and northeastern Africa. 2. The moist woodlands of both northern and eastern parts of southern Africa and 3. Practically the whole half of the inland of Kenya and Tanzania (shown in the table below as fossi 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 analysis even suggest that representatives of this species are present in the fringes of the eastern 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. rufus, probably restricted to the forest-enclosed savannas of western Africa;
- D. natalis: restricted to the highland region of Hambro in southwestern Angola;
- D. cabrari: distribution restricted to the Okavango basin (Caprivi, Namibia);
- D. allenii: restricted to the eastern part of the eastern Arc (Mt. Runywa) and also to the mountain ranges of the western rim of the rift (Tshibati, Bukavu, Albertville);
- D. rwandaense: restricted to certain mountain ranges on the eastern rim of the rift (Nyungu Volcanoes, Nyungwe Forest);
- D. saa: possibly restricted to eastern Tanzania.

We have however to underline that while it is easy to characterize through canonical and discriminant analysis the species with restricted ranges such as rufus, natalis, cabrari, alleni, rwandaens and saa, the same cannot be achieved when trying to define thin that versus bentleyae. Indeed, we have always found an important morphometric 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 incomitus as well-defined taxa, then we have to consider fossi 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 the discussion a conservative attitude and continue to recognize for the moment incomitus, bentleyae and fossi as separate species.

When we combine in a next step these results with the limited genetic tree of Dasygnys 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 specimens AKB470 (collected in Mopoyen, Ivory Coast, in 2002) forms together with the specimens AF141316 from Senegal (EMBL, determined as D. rufus by VOLSOGEN et al., 2000) a clearly separated clade from all other sequenced Dasygnys 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 (Mopoyen) that we used to represent rufus, neither with our fossi and bentleyae populations. We may explain this by the following hypothesis. During the 35 years separating the collecting of OTU1 (Mopoyen) by our colleague L. Bellier and the sequenced specimen AKB470, the formerly closed savannas of Mopoyen has been opened up through extensive deforestation resulting in an influx of savannah-dwelling rodent species of the V. Entroué (OTU2, Lambi). This may have resulted either in the disappearance of the original rufus population or in a hybridisation process which strongly influenced the craniodontic morphology of the Dasygnys occurring in Mopoyen.

When we link this finding to the rather important genetic distances that we detected between both of rufus representatives; 2. the craniodontic resemblance (graph 8.2) that we found between OTU2 (Lambi) and bentleyae (OTU7, Garamba) and 3. the caryological variation detected in West African Dasygnys populations from the Adiopodouné and Lambi regions (Mattey, 1958; TANIER & GAUTUN, 1970) it is obvious that the taxonomy of the western African "forest" Dasygnys is still not fully resolved.

For the moment we tend to believe that 17 D. rufus has a distribution range more or less limited to the enclosed savannas near the coast, 2. the Dasygnys inhabiting the fringes of the rainforest and the adjacent guinean savannas may be a new taxon related to the bentleyae group and 3. the Dasygnys living more to the north in the Guinean and Sudanese savannas should probably all be referred to the fossi taxon (incomitus s.l.).

CENTRAL AFRICA

In fig. 4 we accept that the sequenced specimens of Francaville and Mbomo pertain to bentleyae because caryologically 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 if the Dasygnys of North-East Congo (Garamba: OTU7) are genetically related to populations of Uganda Sudan and of Gabon-Cameroon and 2. if the Dasygnys west of lake Malawi (Kasangu, OTU19) relate genetically to bentleyae (Kinshasa, OTU9) and to incomitus (Luhumbishi, OTU13).

However, notwithstanding the sparsity of our genetic data, we can conclude that the "forest-linked" African Dasygnys 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 Dasygnys incomitus s.l. species complex, but also that the taxa we could discern by craniometry (saa, rwandaense, alleni, medusa) can also be genetically characterized (appendix 6).
Another interesting point is that the Dasyurus of the rift region and the southern part of the Eastern Arc form a separate clade when compared to the Dasyurus from the lower plains of Tanzania (type). We mention also that the single specimen that we could sequence from Mudawi (Ungawasa) and that proved to be clonetically near to allys (topotype locality being Mt. Runge), seems to be genetically sufficiently differentiated to justify specific taxonomic recognition.

SOUTHERN AFRICA

The only South African Dasyurus specimen available to us for sequencing (Vaalwater - TM02000) was assigned to inconexus. We reached this conclusion by directly comparing its skull to the type skull of D. inconexus (Sundevald 1846) and its placement on graph 2.1. For as much as we can evaluate, the absence of sequences from specimens representing sympagala, catazus and Dasyurus from other South African regions - we conclude that the Central African forest-populations (bengalese) are basal to all inconexus and its related East African taxa like rufus, moenni and allys.

Finally, the obtained phylogeny (fig. 4), when viewed in a contextual context, is revealing as to the possible evolutionary trajectories of the members of this genus. The well documented habitat preferences of Dasyurus (permanent moist conditions such as riverbanks, swampy edges of ponds, brooks and marshy areas etc.) (Davie, 1962; Rosevear, 1969; Sheepe, 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 Miocene, 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 Dasyurus survived these severe climate changes by finding shelter in the few forest refugia in Central and West Africa (Mayr and O’Hara, 1964) from where descendants of the surviving lineages (colonized the rest of Sub-Saharan Africa 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 concept. Because the evaluation of the observed morphological diversity is unrealistic as 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 cranial data with genetic data to detect the real patterns of biodiversity in often difficult to identify mammalian species. We recognize that this approach has its limitations. Indeed, not all cranometric differences that we may observe, 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 discrete 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 taxonomic units that we consider to be good species (see elsewhere for arguments to that effect, Ferugline et al. 2002, Verheyen et al. 2002). Although we agree that the decision whether or not a taxon should be elevated to the species status is not resolved by our combined morphological and genetic 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 taxonomic 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 Dasyurus and other African mammals that are currently plagued with too many taxonomic 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 cranometric and genetic variation in the East African Dasyurus 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 Dasyurus from Natal and Kwazulu demonstrates how a detailed multi-disciplinary approach (karyology, cranometry and genetics) may reveal how previously unobserved diversification processes within 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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We also acknowledge the important assistance we received from colleagues who sent us critical specimens (skulls or tissue) to help clarify some aspects of our study. Here we mention our colleagues J. Crawford-Cabral (Lisbon, Portugal), P. Catzeflis (Montpellier, France) and P. Vogel (Lausanne, Switzerland). We are grateful for the work of T. Dillen who carried out the DNA sequencing in the molecular laboratory of the Koninklijk Belgisch Instituur voor Natuurwetenschappen, Brussels.

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