

Skull size and shape of *Dasymys* (Rodentia, Muridae) from sub-Saharan Africa

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ABSTRACT

Three morphological datasets (traditional measurements, dorsal and ventral skull shape coordinates) were used to examine craniometric variation in the water rat *Dasymys*, a genus found throughout sub-Saharan Africa. This study is the first to examine the entire genus as well as to statistically compare taxa within the genus to the nominate species *D. incommutus*. Morphological data confirmed that the five species recognised by Musser & Carleton (1993); *D. incommutus*, *D. foxi*, *D. nudipes*, *D. montanus* and *D. rufulus*, represent valid morphological species although two of the species do not encompass the geographic areas presently assigned to them. *Dasymys rufulus* occupies a larger range and *D. incommutus* a much smaller range than previously suggested with *D. rufulus* appearing to be part of a species complex. Furthermore, we discerned six additional morphological species resulting from the elevation of four subspecies (*D. i. capensis*, *D. i. griseifrons*, *D. i. medius* and *D. i. longipilosus*) and the recognition of two *species novitates*: *D. shortridgei* (restricted to the Okavango Delta) and *D. robertsii* (occurring in the Limpopo and Mpumalanga Provinces of South Africa).

KEY WORDS

Taxonomy,
systematics,
morphometrics,
rodents,
Africa.

RÉSUMÉ

Taille et conformation du crâne des Dasymys (Rodentia, Muridae) d'Afrique Sub-Saharienne.

Trois jeux de données morphologiques (mesures traditionnelles, coordonnées dorsales et ventrales du crâne) ont été utilisés pour examiner les variations crâniennes pour les rats d'eau *Dasymys* présent en Afrique Sub-Saharienne. Cette étude est la première à examiner le genre entier ainsi qu'à comparer statistiquement les espèces dans le genre au nominate espèce, *D. incommutus*. Les données morphologiques confirment que les cinq espèces identifiées par Musser et Carleton (1993); *D. incommutus*, *D. foxi*, *D. montanus*, *D. nudipes* et *D. rufulus*, représentent des espèces morphologiques valides même si deux d'entre-elles n'occupent pas les zones géographiques qui leurs sont assignées actuellement. *Dasymys rufulus* occupe une zone plus grande et *D. incommutus* une zone beaucoup plus petite que celles précédemment suggérées, avec *D. rufulus* appartenant apparemment à un complexe d'espèces. De plus, nous discernons six espèces morphologiques supplémentaires à partir des quatre sous-espèces (*D. i. capensis*, *D. i. griseifrons*, *D. i. medius* et *D. i. longipilosus*) et mettons en évidence deux nouvelles espèces: *D. cf. shortridgei* (pour la seule zone du Delta d'Okavango) et *D. cf. robertsii* (pour les Provinces du Limpopo et de Mpumalanga en Afrique du Sud).

MOTS-CLÉS

Taxonomie,
systématique,
morphométrie,
rongeurs,
Afrique

INTRODUCTION

The water rat *Dasymys* is widespread throughout Sub-Saharan Africa. The genus is in immediate need of taxonomic revision (Kingdon 1997) with a history of up to 20 subspecies and 21 taxa named throughout Africa (Allen 1939; Ellerman *et al.* 1941; Rosevear 1969; Kingdon 1974; Carleton & Martinez 1991; Musser & Carleton 1993). Ellerman *et al.* (1941) decreased the number of species to two, which Misonne (1974) further reduced to one, naming *D. incommutus* as the type species. Despite cytogenetic evidence strongly suggesting otherwise (Matthey 1958; Tranier & Gautun 1979; Gautun *et al.* 1985; Maddalena *et al.* 1989), the genus was generally accepted to be monotypic until 1991 (Carleton & Martinez 1991). Currently, five species of *Dasymys* are listed for sub-Saharan Africa: *D. foxi* in Jos Plateau, Nigeria; *D. rufulus* in west Africa (ranging from Senegal to Nigeria); *D. montanus* at high altitudes in the Ruwenzori Mountains of Uganda; *D. nudipes* in southwestern Angola and

D. incommutus elsewhere (Musser & Carleton 1993).

Dasymys incommutus is currently distributed across 42 degrees of latitude and 28 degrees of longitude, with 15 synonyms recognised within the species (Musser & Carleton 1993).

Dasymys has been poorly studied, and information is available for only some species, particularly *D. incommutus*. Members of this genus have been implicated in crop damage (Bellier 1965; Misonne & Verschuren 1976; Delany & Happold 1979; Sodeinde 1995; Appiah & Attuquayetio 2000) as well as being zoonoses for diseases such as bilharzia (Schwetz 1956). *Dasymys* is primarily nocturnal, prefers marshy habitats (De Graaff 1981), and is an able swimmer (Duplantier & Bâ 2001). Recent behavioral studies indicate that members of this genus adopt a solitary lifestyle (Pillay 2003). This genus is listed in the IUCN Red Data List as Data Deficient (Hilton-Taylor 2000), while an assessment of *Dasymys* in South Africa listed this genus as Near Threatened (Friedmann *et al.* 2002). As *Dasymys* is a habitat specialist, with an ecology and behavior intimately linked with vlei/swamp

habitats (Hanney 1965), researchers have suggested that *Dasymys* is prone to habitat fragmentation and thus speciation (Avery 1991; Gordon 1991). It has been hypothesised that the distribution of *Dasymys* is not associated with a specific biome, as it is found in a wide variety of biomes, but rather, it is dependent on habitats with relatively wet ground and lush vegetation (Rosevear 1969; Smithers 1971; Rautenbach 1982; Carleton & Martinez 1991; Taylor 1998).

Although *Dasymys* is still widespread throughout Africa (Glass 1965; Sheppe & Osborne 1971), it was previously more widely distributed than is seen today (Lavocat 1956; De Graaff 1961; Misonne 1969; Kingdon 1971; Avery 1991; Duplantier *et al.* 1997; Avery 1998; Denys 1999). Its distribution is patchy and some populations have been regarded as relict (Davis 1962; De Graaff 1981; Gordon 1991; Duplantier *et al.* 1997; Lavrenchenko *et al.* 2000). Meester (1976) and Smithers (1986) predicted a declining trend in population size for this species, and Mugo *et al.* (1995) cited wetland destruction as being responsible for low *D. i. capensis* numbers in the Western Cape Province of South Africa.

The objectives of this study are to compare all five of the *Dasymys* species listed by Musser & Carleton (1993) and to discern possible morphological species or species groups (defined as a homogeneous cluster or phenon, separated from other such clusters, without invoking arbitrary distance thresholds) using traditional and geometric morphometric techniques. This study does not constitute a complete systematic revision of *Dasymys* due to the lack of other types of data available for this genus (e.g. DNA, genetic or behavioral data) but rather attempts to identify good morphological species or species complexes for these future studies and to indicate localities where genetic information is urgently needed. This is the first study to examine the skull morphometrics of the entire *Dasymys* genus, and represents the most widescale study of this genus to date. Kingdon (1997) stated that the four *Dasymys* species recently named by Carleton & Martinez (1991) and Musser & Carleton (1993) should remain provisional until they are compared to the

nominate species *D. incommutus* from the KwaZulu-Natal Province of South Africa. Previous morphometric studies on *Dasymys* included a comparison of *D. foxi* and *D. rufulus* in west Africa (Carleton & Martinez 1991), *D. incommutus* and *D. nudipes* from Angola, Zimbabwe and South Africa (Crawford-Cabral & Pacheco 1989; Crawford-Cabral 1998) and *D. i. incommutus* from South Africa (Mullin *et al.* 2001, 2002). The skull morphology of *D. rufulus*, *D. foxi* or *D. montanus* has not been statistically compared to that of *D. incommutus*.

MATERIALS AND METHODS

Data were analyzed starting at an individual level and progressing to localities and OTUs (Operational Taxonomic Units). At each stage, subsets were screened for outliers and tested for normality. Since the dataset examined in this study was large, the data were first examined in smaller subsets before the entire dataset was analyzed. The smallest geographical subsets included each separate country, followed by increasing larger subsets including neighboring countries. It was not possible to present all of these data in this submission, and only random phenograms or canonical variate plots were included from selected subsets for the purpose of clarifying ambiguous boundary limits. Data for any of the subsets are available from SKM.

Within South Africa, the Limpopo (combined with material from the Mpumalanga Province), Western Cape and KwaZulu-Natal Provinces were treated separately based on the results from a previous study suggesting that material from each province represents a separate group (Mullin *et al.* 2002). Southwestern Angola, northeastern Namibia (in particular the Caprivi Strip) and northern Botswana are referred to here as the Okavango Delta.

The data were examined at a locality level only once it was determined that each locality was represented by the same phenon. This was done in order to ascertain the inter-locality relationship on a more manageable scale and to decide whether or not neighboring localities could be pooled together for further analyses. Special attention was paid to certain localities where sympatry between

separate *Dasymys* species was recorded (e.g. Chitau, Angola; Musser & Carleton 1993; Luluabourg, Zaire; Crawford-Cabral 1986). Finally, after consulting vegetation, geology, soil, altitude and phytogeographic maps, the localities that were represented by less than three individuals were pooled into Operational Taxonomic Units (OTUs), while respecting geographical barriers such as mountain ranges and rivers, which represented geographically close localities found in the same biome type (after Taylor & Meester 1993; Table 1). If a locality consisted of less than 3 individuals and it was not possible to combine that locality into an OTU, the data were treated separately. In this case, the canonical scores of individuals were projected onto the scores of the OTUs to produce a comprehensive plot. Symbols were assigned to species, subspecies or areas of interest in the diagrams presented in the results section.

TRADITIONAL MORPHOMETRICS

Multivariate methods were employed on a dataset of 804 individuals. The character suite consisted of the following 13 cranial characters (see Mullin *et al.* 2002): GSL-Greatest skull length; UTR-Crown length of upper (maxillary) toothrow; PWM-Hard palate width; NAS-Nasal width; ZYN-Zygomatic arch width; FRO-Greatest internal diameter of zygomatic arch; IOB-Least breadth of interorbital constriction; FMW-Foramen magnum width; UMW-Least width of zygomatic arch; ZPW-Zygomatic plate width; GML-Greatest mandible length; MTR-Mandibular tooth row; GHS-Greatest height of skull. The dataset was normally distributed, non-kurtotic, non-skewed and homoscedastic.

Only two of the localities examined in this study (Limalunga, Zambia and Okavango-Omatako, Namibia) had a large number of unbroken skulls that could be used to examine non-geographic variation. A previous study of non-geographic variation (based on individuals from Limalunga, Zambia only) revealed that specimens from age-classes III, IV, V, VI represent adult *D. incommisus* individuals (Mullin *et al.* 2001) and that sexual dimorphism is negligible in *D. incommisus* populations (Mullin *et al.* 2001). The same analysis was completed on individuals from Okavango-Omatako,

Namibia and produced the same results. In addition, Carleton & Martinez showed that neither *D. foxi* nor *D. rufulus* exhibited sexual dimorphism and therefore the data for adult males and females were pooled in the analyses presented in this study. Standardised data were subjected to multivariate analyses, including a principal component analysis (PCA), a multi-group canonical variates analysis (CVA), which tested multivariate differences among OTUs and an unweighted pair-group means with averages (UPGMA) cluster analysis (CA) based on Euclidean distances. A CA was also used to produce a phenogram of the distinct morphological groups discerned in this study. The PCA and CVA plots and CA phenograms for each subgroup were all used to obviate bias possibly resulting from the use of only one approach. Since the different approaches provided similar results, we subjectively chose scatterplots and phenograms for the results section for ease of presentation. Although CA is considered an exploratory method, we included the phenograms since strong patterns were seen.

An Analysis of Variance (ANOVA) was completed on morphologically distinct groups (see results section) to determine significant differences in both cranial and external measurements. A Student Newman-Keuls (SNK) multiple range test was used to examine inter-group variation. These tests included the following additional characters to the ones mentioned above: BBC-braincase breadth, HB-head-body length (mm), TL-tail length (mm), HF-hind foot length (mm), E-ear length (mm), TOT-total body length (mm), M-Mass (g) and HB/TL-head-body/tail ratio (mm). These characters were not included in multivariate methods as one (BBC) was highly correlated with other characters used and others (HB, TL, HF, E, TOT, M and HB/TL) had a large number of missing values. All of the statistical analyses were undertaken using the program NTSYS-pc (Rohlf 1996), except for the ANOVA and Student Newman-Keuls multiple range test which were done using Statistica (StatSoft 2001).

GEOMETRIC MORPHOMETRICS

A 5mm Leica DC100 camera attached directly to a PC was used to capture images of the dorsal and

TABLE 1. – Locality and OTU names for the specimens examined. The species names follow Musser and Carleton (1993). Under the heading **OTU**, “-”, analyzed at an individual level only (not OTU); **2n**, diploid numbers of karyotyped populations; **TM**, Traditional Morphometrics; **GM**, Geometric Morphometrics; **n**, number of individuals. Localities and OTUs are plotted in Fig. 8.

Species or complex	Country	Locality	OTU Coordinates	2n	TM (n)	GM(n) Dorsal	GM(n) Ventral	Type locality
<i>D. rufulus</i>	Senega	Niayes	1 14°52'N, 15°41'W	36 ₁	3	2	2	
<i>D. rufulus</i>	Senegal	Lake Retba	2 14°50'N, 17°15'W	36 ₂	5	4	4	
<i>D. rufulus</i>	Senegal	Lake Mbaouane	2 14°40'N, 17°26'W		1	1	0	
<i>D. rufulus</i>	Mali	Kangaba	- 11°58'N, 8°24'W	36-39 ₁	2	0	0	
<i>D. rufulus</i>	Guinea	Macenta	3 8°33'N, 9°28'W		23	17	14	
<i>D. rufulus</i>	Guinea	Yalé	- 7°39'N, 8°30'W		2	2	2	
<i>D. rufulus</i>	Sierra Leone	Rokupr	- 8°40'N, 12°23'W		2	2	2	
<i>D. rufulus</i>	Liberia	Mount Nimba	4 7°44'N, 8°28'W		3	3	3	
<i>D. rufulus</i>	Liberia	Mount Coffee	5 6°30'N, 10°35'W		3	3	3	<i>D. rufulus</i>
<i>D. rufulus</i>	Liberia	Begwai	6 6°13'N, 10°06'W		2	1	1	
<i>D. rufulus</i>	Liberia	Harbel	6 6°19'N, 10°20'W		0	2	2	
<i>D. rufulus</i>	Ivory Coast	Sienso	7 9°25'N, 7°31'W		7	9	7	
<i>D. rufulus</i>	Ivory Coast	Tiegbe	8 9°42'N, 5°20'W		7	6	6	
<i>D. rufulus</i>	Ivory Coast	Kong	9 9°09'N, 4°37'W		5	5	5	
<i>D. rufulus</i>	Ivory Coast	Bolo	10 8°29'N, 7°34'W		10	8	11	
<i>D. rufulus</i>	Ivory Coast	Lamto	11 6°43'N, 5°15'W	36 _{1,3}	7	7	4	
<i>D. rufulus</i>	Ivory Coast	Bouaké	11 7°41'N, 5°02'W		2	3	3	
<i>D. rufulus</i>	Ivory Coast	IDERT	12 5°20'N, 4°07'W		9	9	7	
<i>D. rufulus</i>	Ivory Coast	Adiopodoumé	13 5°20'N, 4°07'W		7	7	6	
<i>D. rufulus</i>	Ivory Coast	Dabou	14 5°25'N, 4°33'W		12	12	8	
<i>D. rufulus</i>	Ivory Coast	Monpoyemé	15 5°18'N, 4°27'W		13	14	11	
<i>D. rufulus</i>	Burkina-Faso	Banfora	16 10°36'N, 4°45'W	36 ₄	6	4	4	
<i>D. rufulus</i>	Burkina-Faso	Bobo-Dioulasso	16 11°11'N, 4°18'W		1	1	1	
<i>D. rufulus</i>	Ghana	Pulima	17 10°51'N, 2°03'W		5	7	8	
<i>D. rufulus</i>	Ghana	Pirisi	18 10°07'N, 2°27'W		5	4	4	
<i>D. rufulus</i>	Ghana	Wenchi	19 7°42'N, 2°07'W		3	3	3	
<i>D. rufulus</i>	Togo	Padori	20 10°13'N, 0°25'E		6	6	6	
<i>D. rufulus</i>	Togo	Pewa	20 9°17'N, 1°14'E		1	1	1	
<i>D. rufulus</i>	Togo	Pagola	21 8°11'N, 0°58'E		3	2	2	
<i>D. rufulus</i>	Benin	Zizonkamé	22 7°55'N, 2°01'E		1	1	1	
<i>D. rufulus</i>	Benin	Kétou	22 7°21'N, 2°37'E		1	1	1	
<i>D. rufulus</i>	Benin	Nikki	22 9°56'N, 3°13'E		2	2	2	
<i>D. rufulus</i>	Nigeria	Dada	23 11°34'N, 4°29'E		7	8	7	
<i>D. rufulus</i>	Nigeria	Gudi	- 8°54'N, 8°17'E		2	2	2	
<i>D. rufulus</i>	Nigeria	Ibadan	24 7°17'N, 3°30'E		3	5	4	
<i>D. rufulus</i>	Nigeria	Lagos	24 6°27'N, 3°23'E		2	4	4	
<i>D. foxi</i>	Nigeria	Panyam	25 5°32'N, 7°29'E		11	10	9	<i>D. foxi</i>
<i>D. foxi</i>	Nigeria	Ugar Jabar	25 5°38'N, 6°24'E		2	3	2	
<i>D. rufulus</i>	Nigeria	Umuahia	26 9°27'N, 9°12'E		0	3	0	
<i>D. rufulus</i>	Nigeria	Ashaka	26 9°31'N, 8°23'E		1	1	0	
<i>D. incomtus</i>	Chad	Bekao	- 8°34'N, 16°05'E		2	0	1	
<i>D. incomtus</i>	Sudan	Mt Kinyeti	27 3°57'N, 32°54'E		1	1	1	
<i>D. incomtus</i>	Sudan	Torit	27 4°27'N, 32°31'E		2	1	1	<i>D. i. palustris</i>
<i>D. incomtus</i>	Sudan	Juba	28 4°52'N, 31°30'E		2	0	0	
<i>D. incomtus</i>	Sudan	Iwatoka	28 3°45'N, 30°38'E		1	0	0	
<i>D. incomtus</i>	Sudan	Kagelu	28 4°03'N, 30°37'E		1	0	0	
<i>D. incomtus</i>	Sudan	Raga	- 8°27'N, 25°35'E		1	1	0	
<i>D. incomtus</i>	Sudan	Mount Baginzi	- 7°46'N, 27°40'E		1	0	0	<i>D. i. shawi</i>
<i>D. incomtus</i>	Sudan	Jebel	- 8°35'N, 24°42'E		1	1	0	
<i>D. incomtus</i>	Ethiopia	Lake Tana	29 11°40'N, 37°20'E		4	3	3	<i>D. i. griseifrons</i>
<i>D. incomtus</i>	Ethiopia	Jigga	- 9°34'N, 35°20'E		1	1	1	
<i>D. incomtus</i>	Ethiopia	Jimma	30 7°39'N, 36°48'E		8	8	7	
<i>D. incomtus</i>	Ethiopia	Limu	30 7°45'N, 36°44'E		1	1	0	
<i>D. incomtus</i>	Ethiopia	Serbo	30 7°44'N, 37°04'E		1	1	1	

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<i>D. incomtus</i>	Ethiopia	Dorsey	-	6°16'N, 37°32'E	1	1	1	
<i>D. incomtus</i>	Cameroon	Miéri	31	4°14'N, 13°58'E	5	4	4	
<i>D. incomtus</i>	Cameroon	Yaoundé	32	3°52'N, 11°31'E	3	3	0	
<i>D. incomtus</i>	Cameroon	Mt Cameroon	33	4°12'N, 9°11'E	3	0	0	<i>D. i. longipilosus</i>
<i>D. incomtus</i>	Cameroon	Tongo	34	4°11'N, 16°14'E	0	3	3	
<i>D. incomtus</i>	C.A.R.	Bangui	35	4°22'N, 18°35'E	1	1	1	
<i>D. incomtus</i>	C.A.R.	La Maboké	35	3°54'N, 17°56'E	3	3	2	
<i>D. incomtus</i>	C.A.R.	Bambari	-	5°40'N, 20°37'E	0	2	2	
<i>D. incomtus</i>	Congo	M'boko	-	0°36'N, 14°53'E	1	0	0	
<i>D. incomtus</i>	Congo	Brazzaville	-	4s14'N, 15°14'E	1	1	1	
<i>D. incomtus</i>	DRC	Bagbele	36	4°21'N, 29°17'E	6	6	4	
<i>D. incomtus</i>	DRC	Faradje	36	3°44'N, 29°43'E	2	4	3	
<i>D. incomtus</i>	DRC	Nambira	37	4°20'N, 29°16'E	10	10	8	
<i>D. incomtus</i>	DRC	Nambirima	37	ca. 4°20'N, 29°16'E	2	2	1	
<i>D. incomtus</i>	DRC	Medje	38	2°25'N, 27°18'E	6	5	2	
<i>D. incomtus</i>	DRC	Niangara	38	3°42'N, 27°52'E	0	0	1	
<i>D. incomtus</i>	DRC	Likouala	-	1°37'N, 18°04'E	1	1	1	
<i>D. incomtus</i>	DRC	Lukolela	-	1°10'S, 17°11'E	1	0	0	<i>D. b. edsoni</i>
<i>D. incomtus</i>	DRC	Lubero	39	0°09'S, 29°13'E	3	4	3	
<i>D. incomtus</i>	DRC	Rutshuru	39	1°11'S, 29°28'E	3	4	3	
<i>D. incomtus</i>	DRC	Buhengeri	40	1°30'S, 29°38'E	3	3	3	
<i>D. incomtus</i>	DRC	Kalehe	40	2°06'S, 28°55'E	1	1	1	
<i>D. incomtus</i>	DRC	Kahungu	40	2°07'S, 28°55'E	1	2	2	
<i>D. incomtus</i>	DRC	Lushala	40	2°13'S, 28°49'E	1	1	1	
<i>D. incomtus</i>	DRC	Muganzo	40	2°22'S, 28°53'E	2	4	3	
<i>D. incomtus</i>	DRC	Ngombe	-	6°40'S, 20°57'E	1	0	0	<i>D. i. bentleyae</i>
<i>D. incomtus</i>	DRC	Nawenga Reserve	41	8°42'S, 36°43'E	4	4		
<i>D. incomtus</i>	DRC	Katobwe	42	8°54'S, 26°05'E	3	3	2	
<i>D. incomtus</i>	DRC	Lumbumbashi	43	11°40'S, 27°28'E	4	4	3	
<i>D. incomtus</i>	DRC	Kinshasha	44	4°17'S, 15°18'E	4	4	3	
<i>D. incomtus</i>	DRC	Luluabourg	-	5°54'S, 22°25'E	0	1	0	
<i>D. incomtus</i>	DRC	Bukarabwa	-		1	2	1	
<i>D. incomtus</i>	Uganda	Butiaba	-	1°49'N, 31°19'E	1	0	0	<i>D. i. orthos</i>
<i>D. incomtus</i>	Uganda	Minunga	45	0°20'N, 30°03'E	1	2	2	
<i>D. incomtus</i>	Uganda	Kalonge Village	45	0°20'N, 29°48'E	8	8	6	
<i>D. incomtus</i>	Uganda	Kampala	46	0°19'N, 32°34'E	4	6	5	
<i>D. incomtus</i>	Uganda	Kanaba	47	0°16'N, 31°37'E	3	3	3	
<i>D. montanus</i>	Uganda	John Mate Camp	48	0°15'N, 29°55'E	3	3	3	<i>D. montanus</i>
<i>D. incomtus</i>	Uganda	Mabuku Valley	-	0°21'N, 29°55'E	1	0	0	<i>D. i. medius</i>
<i>D. incomtus</i>	Uganda	Masaka Rakai	49	0°20'S, 31°44'E	3	3	3	
<i>D. incomtus</i>	Uganda	Kirima Kanunga	50	0°50'S, 29°50'E	3	3	4	
<i>D. incomtus</i>	Uganda	Impenetrable Forest	50	0°53'S, 29°43'E	1	1	1	
<i>D. incomtus</i>	Uganda	Bunkinda	51	1°10'S, 30°01'E	4	4	3	
<i>D. incomtus</i>	Uganda	Rubanda	52	1°14'S, 29°48'E	4	4	4	
<i>D. incomtus</i>	Uganda	Lake Bunyoni	-	1°15'S, 29°59'E	1	1	1	
<i>D. incomtus</i>	Uganda	Behungi	-	1°30'S, 29°15'E	1	1	1	
<i>D. incomtus</i>	Kenya	Kitale	-	1°02'N, 35°00'E	1	1	1	
<i>D. incomtus</i>	Kenya	Fort Hall	-	0°43'N, 37°09'E	1	0	0	<i>D. i. savannus</i>
<i>D. incomtus</i>	Kenya	Sirgoit	-	0°40'N, 35°22'E	1	0	0	<i>D. i. helukus</i>
<i>D. incomtus</i>	Kenya	Kaimosi	53	0°12'N, 34°57'E	8	8	7	
<i>D. incomtus</i>	Kenya	Yala River	53	0°06'N, 34°31'E	1	1	1	
<i>D. incomtus</i>	Kenya	Rift Valley	-	0°17'S, 36°04'E	1	1	1	
<i>D. incomtus</i>	Kenya	Naivasha	54	0°43'S, 36°26'E	8	6	5	<i>D. i. nigridius</i>
<i>D. incomtus</i>	Kenya	Kangaita	55	0°25'S, 37°15'E	2	2	2	
<i>D. incomtus</i>	Kenya	Kiambu	55	1°13'S, 36°33'E	1	1	0	
<i>D. incomtus</i>	Kenya	Nairobi	55	1°17'S, 36°49'E	5	5	5	
<i>D. incomtus</i>	Kenya	Queen's Falls	-	ca. 0°25'S, 36°57'E	0	1	0	
<i>D. incomtus</i>	Rwanda	Routabansougera	56	2°26'S, 29°11'E	7	6	7	
<i>D. incomtus</i>	Rwanda	Butare	56	2°35'S, 29°44'E	1	0	0	
<i>D. incomtus</i>	Rwanda	Kinigi	57	1°26'S, 29°36'E	4	3	5	
<i>D. incomtus</i>	Rwanda	Gahinga	58	1°24'S, 29°40'E	4	4	4	

<i>D. incomtus</i>	Burundi	Ntentamaza	59	ca. 3°41'S, 29°33'E	7	8	8
<i>D. incomtus</i>	Burundi	Tora	60	3°41'S, 29°33'E	12	10	11
<i>D. incomtus</i>	Tanzania	Usuhilo	-	6°24'S, 33°57'E	2	1	1
<i>D. incomtus</i>	Tanzania	Mlali	61	6°58'S, 37°33'E	6	6	6
<i>D. incomtus</i>	Tanzania	Dabaga, Uzungwe	-	8°07'S, 35°55'E	1	1	1
<i>D. incomtus</i>	Tanzania	Igale	-	9°04'S, 33°23'E	1	1	1
<i>D. incomtus</i>	Tanzania	Iloilo	-	9°10'S, 33°36'E	1	0	0
<i>D. incomtus</i>	Angola	Duque du Braganca	62	9°06'S, 15°57'E	5	5	5
<i>D. incomtus</i>	Angola	Dundo	-	8°58'S, 21°36'E	2	1	1
<i>D. incomtus</i>	Angola	Chitau	63	11°25'S, 17°09'E	7	7	7
<i>D. incomtus</i>	Angola	Dondi	63	12°31'S, 16°25'E	0	2	0
<i>D. incomtus</i>	Angola	Alto Chicapa	-	10°56'S, 19°09'E	0	1	0
<i>D. nudipes</i>	Angola	Humpata	64	15°02'S, 13°24'E	5	6	5
<i>D. nudipes</i>	Angola	Huíla	65	15°04'S, 13°33'E	4	4	4
<i>D. incomtus</i>	Angola	Mombolo	-	11°35'S, 14°25'E	1	0	0
<i>D. incomtus</i>	Angola	Luiana Camp	-	17°23'S, 23°03'E	1	1	1
<i>D. incomtus</i>	Zambia	Mayau	66	14°55'S, 27°40'E	3	0	0
<i>D. incomtus</i>	Zambia	Kasama	67	10°13'S, 31°10'E	15	6	4
<i>D. incomtus</i>	Zambia	Fort Rosebery	68	11°11'S, 28°53'E	1	0	0
<i>D. incomtus</i>	Zambia	Lake Chiyaya	68	11°15'S, 29°45'E	3	3	0
<i>D. incomtus</i>	Zambia	Ntambo's Area	69	11°44'S, 24°26'E	5	4	3
<i>D. incomtus</i>	Zambia	Mpika	70	11°52'S, 31°26'E	4	3	3
<i>D. incomtus</i>	Zambia	Solwezi Boma	71	12°10'S, 26°24'E	12	13	6
<i>D. incomtus</i>	Zambia	Kabompo-Lunga Confluence	72	12°30'S, 24°53'E	4	0	3
<i>D. incomtus</i>	Zambia	Luansongwe River	72	12°30'S, 24°53'E	1	0	0
<i>D. incomtus</i>	Zambia	Nsangi-Kabompo Confluence	72	12°30'S, 24°53'E	2	4	0
<i>D. incomtus</i>	Zambia	Kasempa Boma	72	13°25'S, 25°50'E	1	0	0
<i>D. incomtus</i>	Zambia	Temwa	72	13°25'S, 25°50'E	1	0	0
<i>D. incomtus</i>	Zambia	Ndola	73	12°50'S, 28°40'E	11	8	3
<i>D. incomtus</i>	Zambia	Laha Lusiwash	74	13°00'S, 30°47'E	1	0	0
<i>D. incomtus</i>	Zambia	Chibale	74	13°36'S, 30°08'E	2	2	1
<i>D. incomtus</i>	Zambia	Kasinga	75	13°33'S, 23°08'E	11	9	8
<i>D. incomtus</i>	Zambia	Fort Jameson	76	13°39'S, 32°40'E	7	5	5
<i>D. incomtus</i>	Zambia	Kabombo-Zambesi Confluence	77	14°17'S, 23°12'E	1	1	0
<i>D. incomtus</i>	Zambia	Manyinga River	77	14°17'S, 23°12'E	2	0	0
<i>D. incomtus</i>	Zambia	Mankoya	77	14°48'S, 24°48'E	1	0	0
<i>D. incomtus</i>	Zambia	Limalunga	78	15°16'S, 23°08'E	51	39	30
<i>D. incomtus</i>	Zambia	Senanga	78	16°07'S, 23°15'E	1	0	0
<i>D. incomtus</i>	Zambia	Chilanga	79	15°35'S, 28°18'E	2	2	2
<i>D. incomtus</i>	Zambia	Kafue River	79	15°52'S, 27°45'E	4	5	5
<i>D. incomtus</i>	Zambia	Choma	79	16°37'S, 26°58'E	2	2	2
<i>D. incomtus</i>	Zambia	Abercorn Natl. Park	-	8°50'S, 31°20'E	1	0	0
<i>D. incomtus</i>	Zambia	Hot Springs	-	19°32'S, 34°14'E	2	0	0
<i>D. incomtus</i>	Malawi	Kasungu	80	13°01'S, 33°30'E	3	2	2
<i>D. incomtus</i>	Malawi	Zomba Plateau	81	15°20'S, 35°16'E	3	4	3
<i>D. incomtus</i>	Malawi	Mulanje Plateau	82	16°03'S, 35°31'E	7	5	6
<i>D. incomtus</i>	Malawi	Chowo Forest	-	10°35'S, 33°42'E	2	0	0
<i>D. incomtus</i>	Mozambique	Furancungo	83	14°26'S, 33°23'E	2	2	2
<i>D. incomtus</i>	Mozambique	Vila Vasco De Gama	83	14°54'S, 32°15'E	2	2	2
<i>D. incomtus</i>	Mozambique	Vila Coutinho	84	14°44'S, 34°22'E	4	5	5
<i>D. incomtus</i>	Mozambique	Zambue	85	15°10'S, 30°50'E	3	3	3
<i>D. incomtus</i>	Mozambique	Beira	86	19°51'S, 34°54'E	5	5	5
<i>D. incomtus</i>	Namibia	Gangongo	87	17°54'S, 21°12'E	2	2	2
<i>D. incomtus</i>	Namibia	Sinjemba	87	17°56'S, 21°18'E	4	3	3
<i>D. incomtus</i>	Namibia	Okavango-Omatako	88	17°56'S, 20°29'E	27	13	12
<i>D. incomtus</i>	Namibia	Kabuta Village	88	17°48'S, 25°05'E	1	0	0
<i>D. incomtus</i>	Namibia	Linyati River	88	18°06'S, 24°02'E	0	1	1
<i>D. incomtus</i>	Namibia	Diwai	89	18°07'S, 21°37'E	1	0	0

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<i>D. incomtus</i>	Namibia	Mohango Drift	89	18°10'S, 21°16'E	3	3	1	
<i>D. incomtus</i>	Namibia	Popa Falls	89	18°06'S, 21°37'E	0	1	0	
<i>D. incomtus</i>	Namibia	Yanyongo	-	ca. 18°06'S, 21°37'E	1	0	0	
<i>D. incomtus</i>	Botswana	Kasane	90	17°49'S, 25°09'E	12	13	8	
<i>D. incomtus</i>	Botswana	Moremi	91	17°58'S, 24°08'E	7	6	6	
<i>D. incomtus</i>	Botswana	Xhangha Island	-	19°16'S, 22°42'E	2	1	1	
<i>D. incomtus</i>	Zimbabwe	Nyamnyetsi	92	16°50'S, 30°52'E	3	3	2	
<i>D. incomtus</i>	Zimbabwe	Chinyika River	92	17°48'S, 31°24'E	1	0	0	
<i>D. incomtus</i>	Zimbabwe	Harare	93	17°50'S, 31°04'E	12	6	6	
<i>D. incomtus</i>	Zimbabwe	Chibeto	93	17°00'S, 31°00'E	0	2	2	
<i>D. incomtus</i>	Zimbabwe	Troutbeck Lake	94	18°16'S, 32°45'E	1	0	0	
<i>D. incomtus</i>	Zimbabwe	Umtali	94	18°58'S, 32°40'E	4	2	3	
<i>D. incomtus</i>	Zimbabwe	Banti Reserve	94	19°10'S, 32°25'E	1	1	1	
<i>D. incomtus</i>	Zimbabwe	Mt. Selinda	95	20°27'S, 32°40'E	7	7	6	
<i>D. incomtus</i>	Zimbabwe	Mazoe	95	17°30'S, 30°58'E	1	0	0	<i>D. i. fuscus</i>
<i>D. incomtus</i>	Zimbabwe	Musirizwi River	95	20°30'S, 32°34'E	2	3	2	
<i>D. incomtus</i>	Zimbabwe	Matopos	96	20°28'S, 28°30'E	4	2	2	
<i>D. incomtus</i>	Zimbabwe	Munenga Reserve	-	??	2	0	0	
<i>D. incomtus</i>	Zimbabwe	Inyantue Park	-	18°32'S, 26°41'E	1	0	0	
<i>D. incomtus</i>	Zimbabwe	Zimbabwe Ruins	-	20°17'S, 30°45'E	1	1	1	
<i>D. incomtus</i>	South Africa	Punda Milia	97	22°41'S, 30°57'E	5	8	8	
<i>D. incomtus</i>	South Africa	Soutpansberg	98	23°00'S, 29°40'E	9	4	4	
<i>D. incomtus</i>	South Africa	Tzaneen	99	23°48'S, 30°10'E	6	5	5	
<i>D. incomtus</i>	South Africa	Potgietersrus	100	23°50'S, 28°23'E	4	3	3	
<i>D. incomtus</i>	South Africa	Klipfontein	101	24°08'S, 28°18'E	46 ₅	11	11	11
<i>D. incomtus</i>	South Africa	Nylsvlei	101	24°29'S, 28°42'E	2	2	2	
<i>D. incomtus</i>	South Africa	Pretoria	-	25°45'S, 28°11'E	1	1	1	
<i>D. incomtus</i>	South Africa	Vaalwater	102	24°13'S, 27°52'E	3	3	3	
<i>D. incomtus</i>	South Africa	Barberton	103	25°49'S, 31°01'E	1	0	0	
<i>D. incomtus</i>	South Africa	Gladdespruit	103	26°01'S, 30°48'E	2	1	1	
<i>D. incomtus</i>	South Africa	Arnhemburg	103	26°03'S, 30°50'E	2	1	1	
<i>D. incomtus</i>	South Africa	de Hoop Reserve	103	24°57'S, 29°57'E	1	1	1	
<i>D. incomtus</i>	South Africa	Lydenburg	103	25°06'S, 30°27'E	1	0	0	
<i>D. incomtus</i>	South Africa	Hectorspruit	103	25°26'S, 31°41'E	1	1	0	
<i>D. incomtus</i>	South Africa	Joshua Moolman Res.	104	26°41'S, 30°36'E	2	0	0	
<i>D. incomtus</i>	South Africa	Itala Reserve	104	27°34'S, 30°13'E	3	1	2	
<i>D. incomtus</i>	South Africa	Vryheid	105	27°45'S, 30°48'E	5	5	3	
<i>D. incomtus</i>	South Africa	Dukuduku	106	28°23'S, 32°20'E	1	1	1	
<i>D. incomtus</i>	South Africa	Futululu	106	28°25'S, 32°16'E	1	1	1	
<i>D. incomtus</i>	South Africa	Hazelmere Reserve	106	29°35'S, 31°02'E	1	0	1	
<i>D. incomtus</i>	South Africa	Richards Bay	106	28°45'S, 32°05'E	38 ₅	1	1	1
<i>D. incomtus</i>	South Africa	Eshowe	106	28°54'S, 31°28'E	1	1	1	
<i>D. incomtus</i>	South Africa	Durban	106	29°51'S, 31°01'E	1	1	0	<i>D. incomtus</i>
<i>D. incomtus</i>	South Africa	Mfongosi	107	28°43'S, 30°48'E	9	8	6	
<i>D. incomtus</i>	South Africa	Karkloof	108	29°19'S, 30°12'E	1	1	1	
<i>D. incomtus</i>	South Africa	Kamberg	108	29°24'S, 29°40'E	38 ₆	1	1	1
<i>D. incomtus</i>	South Africa	Albert Falls	108	29°28'S, 30°23'E	1	1	1	
<i>D. incomtus</i>	South Africa	Kilgobbin	108	29°28'S, 30°07'E	1	0	0	
<i>D. incomtus</i>	South Africa	Coleford Reserve	108	29°57'S, 29°27'E	1	1	0	
<i>D. incomtus</i>	South Africa	Port St Johns	-	31°36'S, 29°30'E	2	2	2	
<i>D. incomtus</i>	South Africa	Wolseley	109	33°28'S, 19°12'E	3	2	2	<i>D. i. capensis</i>
<i>D. incomtus</i>	South Africa	Humansdorp	110	33°57'S, 23°44'E	2	1	2	
<i>D. incomtus</i>	South Africa	Knysna	110	33°57'S, 23°10'E	2	2	2	

¹Volobouev *et al.* 2000, ²Granjon *et al.* 1992, ³Tranier and Gautun 1979, ⁴Gautun *et al.* 1985, ⁵Gordon 1991, ⁶Mullin 1999.

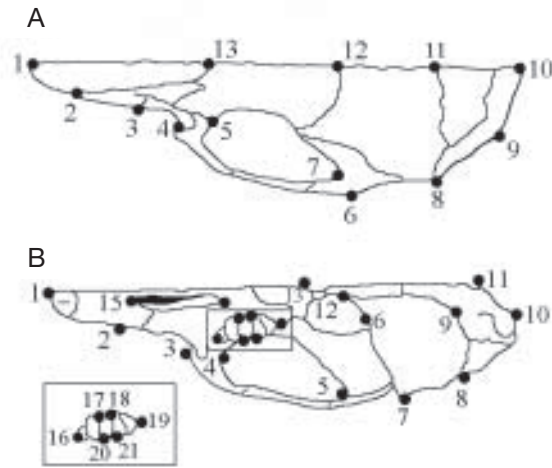


FIG. 1. – Landmarks, defined in Table 2, for the dorsal and ventral views of the *Dasymys* skull.

the ventral sides of the skull. Each file was saved in JPEG format. The landmarks collected are described in Table 2 and shown in Fig. 1. In total, 698 dorsal and 595 ventral views were collected from specimens representing the localities described in Table 1. Landmarks (Fig. 1) were placed on image using tpsDig (Rohlf 2000a). TpsSmall (Rohlf 2000b) confirmed that the correlation between tangent and shape space was high enough to carry out subsequent analyses. The data were then scaled, aligned and transformed using the Procrustes procedure in tpsRelw (Rohlf 2001). The centroid size for each specimen was extracted and subjected to a one-way ANOVA to test for differences between the centroid size for each group. GRF-nd (Slice 1999) was used to extract the eigenvectors and the landmark residuals and to examine the data for outliers. The program TPS-Relw (Rohlf 2001) was used to compute a partial weights matrix (W) based on the consensus configuration for the data, as well as to complete a relative warps analysis, which included the affine components, U_1 and U_2 . NTSYS-pc (Rohlf 1996) was used to undertake a CVA and a PCA based on among-OTU correlations and CA based on Mahalanobis distances analyses on the dorsal and ventral weight matrices. TpsRegr (Rohlf 2000c) was used to regress the first and second canonical variates onto both the dorsal and ventral weight

TABLE 2. – Descriptions of landmarks recorded on the dorsal skull (represented in Fig. 1); **LM**, landmark; **Type 1**, discrete juxtaposition of tissues; **Type 2**, maximum curvatures and bony process tips; **Type 3**, extremal points.

View	LM	Description (LM type)
Dorsal	1	Anterior tip of nasals (2)
	2	Anterior point at suture between nasals and premaxilla (1)
	3	Narrowest point of rostrum (3)
	4	Anterior point of upper maxillary process (2)
	5	Anterior point of interior orbit (2)
	6	Widest point of zygomatic arch (3)
	7	Posterior point of interior orbit (2)
	8	Exterior tip of external auditory meatus (2)
	9	Edge of supraoccipital ridge (2)
	10	Posterior point of supraoccipital (2)
	11	Junction between interparietal, parietal and midline (1)
	12	Junction between parietal, frontal and midline (1)
	13	Junction between frontal, nasals and midline (1)
Ventral	1	Anterior tip of nasals (2)
	2	Widest point of rostrum (3)
	3	Anterior point of upper maxillary process (2)
	4	Anterior point of internal orbit (2)
	5	Posterior point of internal orbit (2)
	6	Maximum anterior curvature of tympanic bulla (2)
	7	Exterior tip of external auditory meatus (2)
	8	Maximum external curvature of posterior tympanic bulla (2)
	9	Maximum interior curvature of posterior tympanic bulla (2)
	10	Posterior tip of foramen magnum (2)
	11	Anterior tip of foramen magnum (2)
	12	Posterior tip of sphenopalatine vacuities (2)
	13	Junction of presphenoid, palatine and midline (1)
14	Posterior tip of palatine foramen (2)	
15	Anterior tip of palatine foramen (2)	
16	Anterior edge of M1 (2)	
17	Interior junction between M1 and M2 (2)	
18	Interior junction between M2 and M3 (2)	
19	Posterior edge of M3 (2)	
20	Exterior junction between M1 and M2 (2)	
21	Exterior junction between M2 and M3 (2)	

matrices (in order to examine the thin-plate splines associated with each axis) and to regress the centroid size on to both the dorsal and ventral data.

An unexpected level of heterogeneity seen between populations from the Democratic Republic of Congo (DRC, formerly Zaïre; see results section)

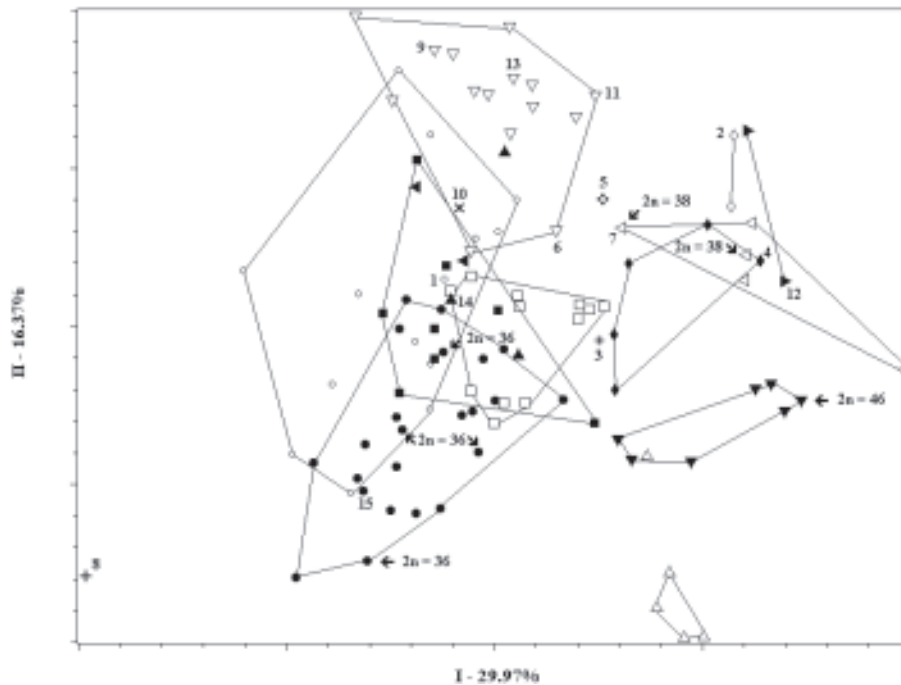


FIG. 2. – Plot of the first two canonical variates using the traditional morphometric data. ●, West African *D. rufulus*; ◊, *D. foxi*, π, Ethiopia and Sudan; ♦, *D. i. griseifrons*; ◊, Cameroon, Central African Republic, Congo, Democratic Republic of Congo; ▷, *D. i. longipilosus*; σ, East Africa; ∠, *D. montanus*; ■, Malawi, Mozambique and Tanzania; τ, *D. incomtus* from Angola; υ, *D. nudipes*; ρ, Botswana and Namibia; ≤, Zambia; ◆, Zimbabwe; θ, Limpopo and Mpumalanga Provinces, South Africa; σ, KwaZulu-Natal Province, South Africa; +, *D. i. capensis*. OTUs (defined in Table 6.1) containing karyotyped individuals are demarcated by the diploid number. Eleven type specimens are identified: 1-*D. i. capensis*, 2-*D. foxi*, 3-*D. i. fuscus*, 4-*D. i. griseifrons*, 5-*D. incomtus*, 6-*D. i. longipilosus*, 7-*D. montanus*, 8-*D. i. nigridius*, 9-*D. nudipes*, 10-*D. i. palustris*, 11-*D. rufulus*.

led us to test Wright's (1943) isolation by distance theory on populations from this country. A matrix of Mahalanobis distances between populations was computed from ventral landmark data using the program TPS-Small (Rohlf 2000b) and was compared to a matrix of geographic distances using NTSYS-pc (Rohlf 1996).

RESULTS

MACRO-SCALE PATTERNS

The data suggest that size rather than shape was more important in identifying species or species groups on a large geographic level (Figs 2-4), as indicated by the strong patterns seen with traditional morphometric data. The first two axes of the

CVA based on traditional measurements explained 46.34% of the variation compared to 27.62% and 27.22% in the dorsal and ventral data, respectively. In addition, the Wilks λ value was higher for the traditional dataset (Wilks $\lambda = 0.001$, $p < 0.001$, $F_{169,5764} = 41.83$, $p < 0.01$) than it was for the both of the geometric morphometric datasets: dorsal (Wilks $\lambda = 0.00000008$, $p < 0.001$, $F_{484,8298} = 6.67$, $p < 0.01$) and ventral (Wilks $\lambda = 0.0003$, $p < 0.001$, $F_{1444,11502} = 11.56$, $p < 0.01$). The importance of size in this study was confirmed when the centroid sizes for both the dorsal and ventral views were regressed onto the landmark data. Between the two shape datasets, the ventral view showed stronger patterns than the dorsal view and generally confirmed the results seen using the traditional dataset.

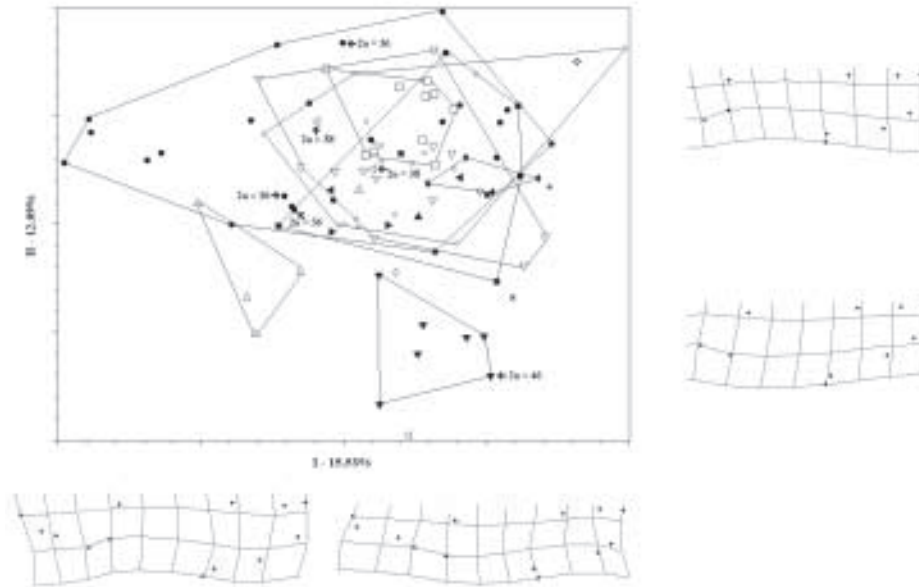


FIG. 3. – Plot of the first two variates of a multi-group canonical variates analysis of the dorsal skull partial warp matrix. The thin-plate splines (at a magnification factor of 10) depict dorsal skull deformations along the first and second variates. ●, West African *D. rufulus*; ♪, *D. foxi*, π, Ethiopia and Sudan; ✦, *D. i. griseifrons*; ◻, Cameroon, Central African Republic, Congo, Democratic Republic of Congo; ▷, *D. i. longipilosus*; σ, East Africa; ∠, *D. montanus*; ■, Malawi, Mozambique and Tanzania; τ, *D. incomtus* from Angola; υ, *D. nudipes*; ρ, Okavango Delta; ≤, Zambia; ◆, Zimbabwe; θ, Limpopo and Mpumalanga Provinces, South Africa; ♂, KwaZulu-Natal Province, South Africa; +, *D. i. capensis*. OTUs (defined in Table 6.1) containing karyotyped individuals are demarcated by the diploid number.

Traditional measurements suggested the presence of 9 distinct phenotypes in the CVA biplot (Fig. 2): *D. foxi*, *D. nudipes*, *D. i. longipilosus*, *D. i. capensis*, *D. i. griseifrons*, *D. i. incomtus* from the KwaZulu-Natal Province, *D. i. incomtus* from the Limpopo and Mpumalanga Provinces, material from Zimbabwe and material from the Okavango Delta. Only one of the Okavango Delta OTUs, Kasane-90, grouped with the Limpopo Province (South Africa) specimens, while the other four OTUs from this region were distinct on the second axis. *Dasymys i. longipilosus* from Mt Cameroon was distinct on the first axis and was clearly different from other material. The two Angolan OTUs representing *D. incomtus* grouped with east and central African OTUs. *Dasymys foxi* from Jos Plateau in Nigeria was on the periphery but outside the minimum

convex polygon enclosing other west African material, and was seen to be more similar to material from Zambia and Zimbabwe than to other west African individuals. Similarly, *D. i. griseifrons* from Lake Tana, Ethiopia was similar to other east African OTUs, but it appeared to be morphologically separate as it was outside the east Africa group. Two of the Zimbabwean OTUs (95-Mt Selinda, 96-Matopos) fell within the KwaZulu-Natal Province (South Africa) group. The remainder of the OTUs (92-Nyamnetsi, 93-Harare, 94-Umtali) appeared to be morphologically similar to *D. i. incomtus* from the Limpopo Province as well as to Zambian material and one Mozambican OTU (85-Zambue). Finally, material from eastern, central and western Africa fell into one of three groups. East African OTUs separated from the

west African material on the second axis, the former comprising OTUs from Kenya, Ethiopia, Burundi, Rwanda, Uganda and the eastern part of the DRC (representing *D. incommutis*). The group containing west (*D. rufulus*) and central African (*D. incommutis*) material appeared to adhere loosely to a geographic pattern, although there was no clear separation between groups. This second group comprised material from Cameroon, Congo, the DRC, west Africa (from Senegal to eastern Nigeria), Tanzania, Malawi, Mozambique and Zambia with the exception of one of the Mozambique OTUs (84-Vila Coutinho), which was more similar to the east African material. Material from central Africa (Cameroon, Congo and the DRC) and Zambia both overlapped with west African OTUs but did not overlap with each other.

With respect to the dorsal skull shape, most of the OTUs overlapped extensively showing that they had very similar skull shapes (Fig. 3). Nineteen of the 26 affine and non-affine components were statistically significant ($p < 0.01$), with 91.60% unexplained. Specimens from the Limpopo and Mpumalanga Provinces, the Okavango Delta, *D. i. capensis*, *D. montanus*, *D. foxi* and *D. i. griseifrons* were distinct. The first axis, explaining 15.98% of the variation, suggested a possible divergence within west African *D. rufulus*, material from Ivory Coast, Guinea and Liberia forming one subgroup and material from Nigeria, Togo and Benin forming another. The east African material was embedded within this west African group, as was material from Angola, central Africa, Zambia, Malawi, Mozambique, Tanzania, Zimbabwe and the KwaZulu-Natal Province of South Africa. With the exception of one OTU (105-Vryheid), specimens from the KwaZulu-Natal and Limpopo/Mpumalanga Provinces (all representing *D. i. incommutis*) were separate from each other on the second axis. The Zimbabwe OTUs formed a separate group from both of the South African *D. i. incommutis* populations (KwaZulu-Natal and Limpopo/Mpumalanga Provinces) and the Zambian group. Given the level of overlap seen in the CVA scatterplot, it was difficult to determine which specimens the thin-plate splines (depicted along the first and second axes) represented.

The ventral view of the skull (Figure 4) was more important in distinguishing groups than the dorsal view, and appeared to provide in some instances similar, or clearer, results to the traditional data. Twenty-eight of the 36 affine and non-affine components were statistically significant ($p < 0.01$), with 93.46% unexplained. Both *D. i. capensis* and west African material were distinct on the first axis, while there were no clear groups on the second axis. A clear separation between these three groups was seen using traditional measurements and dorsal skull coordinates. *Dasymys i. griseifrons* and *D. foxi* did not adhere to geographic patterns by grouping with either east or west African material respectively, and instead were more similar to OTUs representing the KwaZulu-Natal Province and Zambia. The second Ethiopian OTU (30-Jimma) was embedded within the East African group. Although the Mozambique OTU (84-Vila Coutinho) that was more similar to East African material in Figure 2 fell within the *D. rufulus* group in Figure 4, two different OTUs from Mozambique (83-Furnacungo, 86-Beira) were found within the East African group.

East, central and west African material (including OTUs from Zambia, Malawi and Mozambique) formed more separate groups than seen previously. The DRC OTUs were again divided between east and west African material (as was seen using traditional measurements). A separation was also seen within *D. i. incommutis* between OTUs from the KwaZulu-Natal and the Limpopo/Mpumalanga Provinces. Material from Zimbabwe was similar to materials from both the Limpopo/Mpumalanga and KwaZulu-Natal Provinces. Zimbabwean OTUs were also similar to individuals from Zambia, Malawi (Zomba and Mulanje Plateau) and Mozambique (Zambue).

The thin-plate splines along the canonical variate axes for the ventral data (Figure 4) showed that the west African material had a shorter distance between the anterior tip of the skull and the anterior tip of the palatal foramen, a longer palatal foramen, wider nasals, longer sphenopalatine, larger foramen magnum width, wider tooththrow, larger M_1 and a wider tympanic bulla, as seen on the first axis. On the second axis, East African

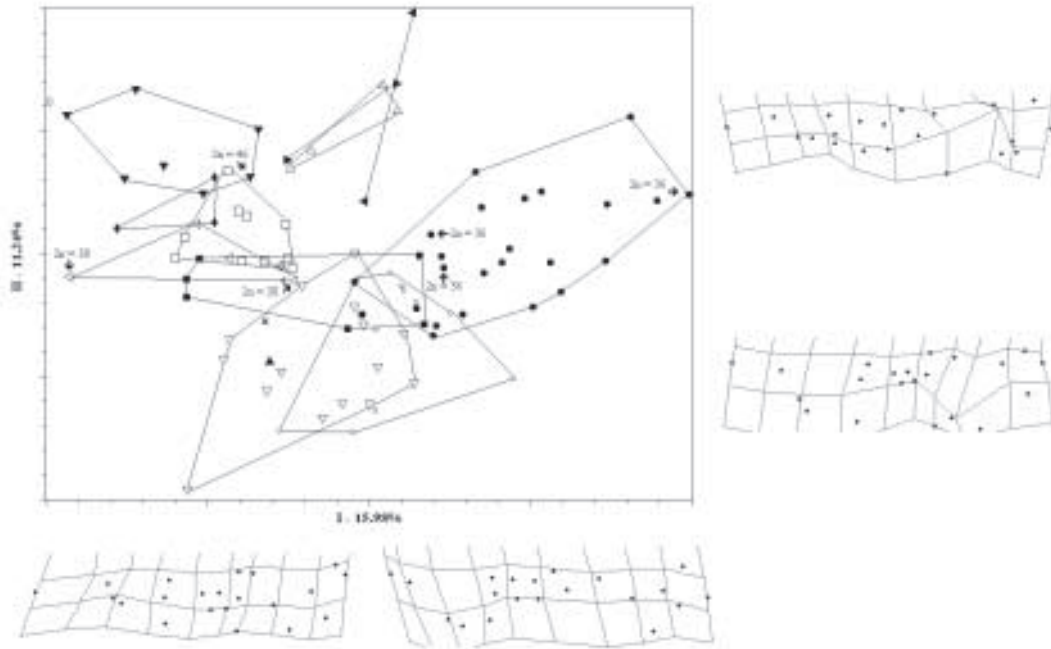


FIG. 4. – Plot of the first two variates of a multi-group canonical variates analysis of the ventral skull partial warp matrix. The thin-plate splines (at a magnification factor of 10) depict ventral skull deformations along the first and second variates. ●, West African *D. rufulus*; ♪, *D. foxi*, π, Ethiopia and Sudan; ♠, *D. i. griseifrons*; ◊, Cameroon, Central African Republic, Congo, Democratic Republic of Congo; ▷, *D. i. longipilosus*; σ, East Africa; ∠, *D. montanus*; ■, Malawi, Mozambique and Tanzania; τ, *D. incomtus* from Angola; υ, *D. nudipes*; ρ, Okavango Delta; ≤, Zambia; ◆, Zimbabwe; θ, Limpopo and Mpumalanga Provinces, South Africa; ⌘, KwaZulu-Natal Province, South Africa; +, *D. i. capensis*. OTUs (defined in Table 6.1) containing karyotyped individuals are demarcated by the diploid number.

material was characterised by a narrow toothrow, larger M_1 , more elongated bullae, a wider rostrum and shorter sphenoplatine. Material from Angola, the Okavango Delta and the Limpopo Province, South Africa had a wider toothrow (in particular M_2), smaller bullae and a narrower skull.

MICRO-SCALE PATTERNS

The variation seen between the DRC populations was not the result of isolation by distance as shown by the Mantel's t-test ($t = 3.18$, $p = 0.99$). Selected data subsets were used to resolve taxonomic questions between OTUs, which were analyzed in different combinations (Figs. 5, 6). In particular, we analyzed subsets from east, central and west Africa in an attempt to determine group boundaries and to clarify the ambiguous results for material from Angola (*D. incomtus*), Malawi, Mozambique, Cameroon, Congo and the Democratic Republic

of Congo (Figs. 5A, C, D, 6B, C, D). Although there appeared to be a geographic structure in the dataset, and each of the CVA plots had significant ($p < 0.01$) Wilks values, there were no clear boundaries between OTUs. However, the data did confirm the morphological distinctness of the following: *D. i. capensis* (Figs. 5A: cluster B3, 5B: cluster B2 and 6A); *D. nudipes* (Figs. 5B: cluster C, 5C: cluster B and 6d); *D. montanus* (Fig. 5D); *D. incomtus* from Angola (Figs. 5B: cluster A; 6D), Okavango Delta (Fig. 5B: cluster B1), *D. i. incomtus* from Limpopo and Mpumalanga Provinces (Figs 5A: cluster B1 and B2, and 6A) and *D. i. incomtus* from the KwaZulu-Natal Province (Figs 5A: cluster B2b and 6A).

Fig. 5A shows a clear separation between OTUs representing Malawi, Mozambique, Tanzania and Zambia (Cluster A) and Zimbabwe and South Africa (Cluster B). Within Cluster B, OTUs

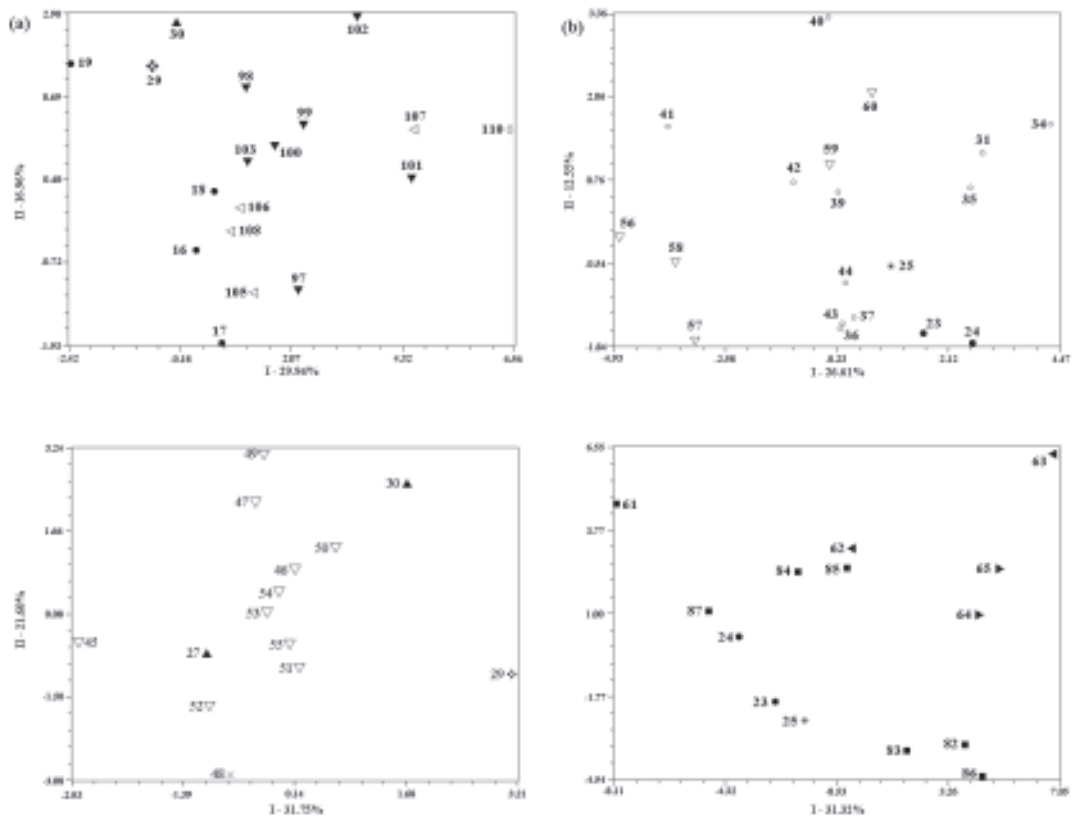


FIG. 6. – CVA plot based on (a) Ventral weight matrix of specimens from Burkina Faso, Ghana, Ethiopia and South Africa; (b) Ventral weight matrix of specimens from Cameroon, Burundi, Nigeria, Rwanda and Democratic Republic of Congo; (c) Traditional measurements of specimens from Ethiopia, Sudan, Kenya, Burundi, Rwanda, Tanzania and Uganda; (d) Traditional measurements of specimens from Angola, Malawi, Mozambique, Nigeria and Tanzania. ●, West African *D. rufulus*; ◊, *D. foxi*; π, Ethiopia and Sudan; ♦, *D. i. griseifrons*; ◊, Cameroon, Central African Republic, Congo, Democratic Republic of Congo; σ, East Africa; ◊, *D. montanus*; ■, Malawi, Mozambique and Tanzania; τ, *D. inornatus* from Angola; v, *D. nudipes*; θ, Limpopo and Mpumalanga Provinces, South Africa; ω, KwaZulu-Natal Province, South Africa; +, *D. i. capensis*. OTUs are defined in Table 1.

and 86-Beira) as separate from Cluster B containing the majority of the East African OTUs. *Dasymys montanus* (C) did not group with other East African material, emphasizing its distinct cranial features, especially since it did not even cluster with other material from the Ruwenzori Mountains (Minunga, OTU 45) which is found at a lower altitude than *D. i. montanus*. Cluster D represents the two Malawian OTUs (from the Zomba and Mulanje Plateaux, OTUs 81 and 82), which consistently grouped with Zambian material in previous figures. On the CVA plots, material from Ethiopia, Ghana and Burkina Faso separated on the first

axis, as did *D. i. capensis* (Wilks $\lambda = 0.000$, $p < 0.01$; Fig. 6A). The two Ethiopian OTUs (29 and 30) appeared to be more similar to western African than to southern African material. South African OTUs overlapped on the first axis, but separated on the second axis with the exception of OTU 107 from Mfongosi (KwaZulu-Natal Province, South Africa), which appeared to be more similar to Limpopo Province material. Fig. 6B indicated that *D. foxi* was similar to material from the other two Nigerian OTUs representing *D. rufulus* (Wilks $\lambda = 0.000$, $p < 0.01$). A separation was seen again within the DRC on the first axis

(explaining 26.61% of the variation) with western and northern OTUs more similar to west African material and eastern OTUs more similar to east Africa material. This pattern was not due to isolation by distance as indicated by the non-significance of the matrix correlation between geographical and morphometric distances for the DRC localities. Figure 6c (Wilks $\lambda = 0.007$, $p < 0.01$) showed a plot of material from Ethiopia, Sudan, Kenya, Uganda, Rwanda and Burundi. Both Ethiopian OTUs (29-Lake Tana and 30-Jimma) were distinct from other East African material on the first axis while *D. montanus* was distinct on the second axis. In Figure 6d (Wilks $\lambda = 0.000$, $p < 0.01$), the relationship between OTUs from Angola, Malawi, Mozambique, Tanzania and Nigeria was examined (Wilks $\lambda = 0.000$, $p < 0.01$). The Tanzania OTU (61) was distinct on the first axis. Two OTUs from Malawi (81-Zomba Plateau and 82-Mulanje Plateau) and one from Mozambique (85-Zambue) were distinct on the second axis. Chitau (OTU 63, representing *D. incomtus* from Angola) was distinct on both the first and second axis, while the second Angolan *D. incomtus* OTU (62-Duque de Braganca) was similar to material from Mozambique (OTUs 83, 84 and 87). *Dasymys foxi* and *D. rufulus* were similar to each other and morphologically in-between Malawi and Mozambique specimens on the second axis.

ANALYSES BASED ON THE 11 DISTINCT GROUPS

A one-way ANOVA was done on traditional measurements and centroid sizes to examine the relationship between the 11 distinct morphological groups discerned above (Figs 2-6). This included *D. i. capensis*, *D. foxi*, *D. rufulus*, *D. i. longipilosus* (not included in the geometric morphometric analysis), *D. nudipes*, *D. montanus*, material from East Africa, *D. i. incomtus* from the KwaZulu-Natal Province, *D. i. incomtus* from the Limpopo and Mpumalanga Provinces, *D. i. griseifrons* and material from the Okavango Delta. For this analysis, *D. rufulus* only included specimens from west Africa since we were not able to discern its distributional limits. Neither specimens from Zimbabwe nor Botswana (Kasane) were included in *D. i. incomtus* from the Limpopo and Mpumalanga

Provinces as their exact taxonomic position was also not clear. The east Africa group included material from eastern DRC (Kwiro, Muganzo, Lubero and Buhengeri), Kenya, Uganda, Burundi and Rwanda and was included principally to examine the relationship between east Africa and both *D. rufulus* and *D. i. griseifrons* from Ethiopia. Results from the one-way ANOVA (Table 3) showed that significant differences ($p < 0.05$) existed among species in terms of both cranial and external measurements. Ten of the 22 characters had overlapping non-significant subsets. The remaining 12 characters had non-overlapping subsets indicating that they represent good separating characteristics between species: TL, HF, TOT, HB/TL, GSL, ZYN, FRO, FMW, UMW, ZPW, GML, MTR, dorsal centroid size (CS) and ventral CS. Table 3 showed *D. montanus* to have a significantly shorter tail, smaller total body length, smaller head-body/tail ratio, smaller GSL and a small overall size as indicated by the centroid size (for both the dorsal and ventral skull). *Dasymys i. longipilosus* had a shorter hind foot length, smaller GSL, narrower ZYN, shorter FRO, smaller GML and smaller MTR than the other specimens examined. *Dasymys nudipes* had a significantly longer tail, longer hind foot, larger head-body/tail ratio, larger GSL, longer FRO, larger FMW, larger MTR and larger ventral skull size (CS); material from the Okavango Delta had a longer tail length and *D. i. capensis* had a longer MTR. *Dasymys nudipes* was the only species to have an average tail length that was longer than the average body length as well as a HB/TL ratio above 100%.

The F -values ranged from 9.81 –66.84. UTR (F -value = 66.84), UMW (46.95) and GML (41.76) had the highest F -values, indicating that they showed the greatest level of interspecies variation. NAS (9.81) and HF (10.28) had the lowest F -values. Generally, *D. i. longipilosus*, *D. montanus* and *D. rufulus* had the smallest sizes (both measurements and centroid size) while *D. nudipes*, *D. i. griseifrons*, *D. i. capensis*, *D. i. incomtus* from the KwaZulu-Natal Province and material from the Okavango Delta. *Dasymys foxi*, individuals from East Africa and *D. i. incomtus*

TABLE 3. – Results of a Student-Newman Keuls multiple range test on 11 morphological species. Non-significant subsets (NSS; $p > 0.05$) are indicated by vertical lines to the right of each array of means. Characters are defined in the Materials and Methods section; **S.D.**, Standard Deviation; **X (n)**, Arithmetic Mean (sample size); **CS**, centroid size; **L/MP**, Limpopo and Mpumalanga Provinces; **KZN**, KwaZulu-Natal Province.

Character	Species	SD	X (n)	NSS	Character	Species	SD	X (n)	NSS		
HB F-value = 13.20	<i>D. montanus</i>	8.33	141.83 (6)	TL F-value = 28.36	<i>D. montanus</i>	6.80	103.50 (6)	TL F-value = 28.36	<i>D. montanus</i>	6.80	103.50 (6)
	<i>D. rufulus</i>	16.28	146.76 (643)		<i>D. incomtus</i> L/MP	13.25	127.80 (49)		<i>D. incomtus</i> L/MP	13.25	127.80 (49)
	<i>D. incomtus</i> L/MP	17.11	148.59 (49)		<i>D. i. longipilosus</i>	0	130.00 (3)		<i>D. i. longipilosus</i>	0	130.00 (3)
	East Africa	16.05	150.04 (255)		<i>D. i. capensis</i>	11.50	132.00 (8)		<i>D. i. capensis</i>	11.50	132.00 (8)
	<i>D. foxi</i>	17.44	151.77 (66)		East Africa	14.58	133.60 (252)		East Africa	14.58	133.60 (252)
	<i>D. i. capensis</i>	18.34	152.88 (8)		<i>D. foxi</i>	11.16	133.80 (66)		<i>D. foxi</i>	11.16	133.80 (66)
	<i>D. incomtus</i> KZN	19.84	156.87 (47)		<i>D. i. griseifrons</i>	14.11	135.00 (10)		<i>D. i. griseifrons</i>	14.11	135.00 (10)
	<i>D. i. longipilosus</i>	2.83	158.00 (3)		<i>D. rufulus</i>	14.60	137.20 (641)		<i>D. rufulus</i>	14.60	137.20 (641)
	Okavango Delta	14.97	163.49 (110)		<i>D. incomtus</i> KZN	13.86	139.20 (45)		<i>D. incomtus</i> KZN	13.86	139.20 (45)
	<i>D. i. griseifrons</i>	11.67	165.70 (10)		Okavango Delta	15.89	153.40 (109)		Okavango Delta	15.89	153.40 (109)
	<i>D. nudipes</i>	12.68	167.33 (9)		<i>D. nudipes</i>	9.73	175.10 (10)		<i>D. nudipes</i>	9.73	175.10 (10)
HF F-value = 10.28	<i>D. i. longipilosus</i>	4.24	22.00 (3)	E F-value = 22.13	<i>D. montanus</i>	1.03	18.33 (6)	E F-value = 22.13	<i>D. montanus</i>	1.03	18.33 (6)
	<i>D. montanus</i>	1.67	28.00 (6)		<i>D. rufulus</i>	2.21	18.65 (445)		<i>D. rufulus</i>	2.21	18.65 (445)
	East Africa	2.81	30.51 (244)		Okavango Delta	1.59	19.16 (110)		Okavango Delta	1.59	19.16 (110)
	<i>D. incomtus</i> KZN	3.30	31.94 (43)		<i>D. i. capensis</i>	0.79	19.57 (7)		<i>D. i. capensis</i>	0.79	19.57 (7)
	<i>D. incomtus</i> L/MP	4.92	32.01 (49)		East Africa	2.52	20.47 (198)		East Africa	2.52	20.47 (198)
	<i>D. rufulus</i>	7.42	32.99 (649)		<i>D. incomtus</i> L/MP	1.97	20.51 (48)		<i>D. incomtus</i> L/MP	1.97	20.51 (48)
	<i>D. foxi</i>	1.68	33.02 (66)		<i>D. incomtus</i> KZN	2.55	20.68 (30)		<i>D. incomtus</i> KZN	2.55	20.68 (30)
	<i>D. i. griseifrons</i>	1.78	34.40 (10)		<i>D. foxi</i>	1.14	20.70 (67)		<i>D. foxi</i>	1.14	20.70 (67)
	<i>D. i. capensis</i>	0.92	34.63 (8)		<i>D. i. longipilosus</i>	7.78	22.50 (3)		<i>D. i. longipilosus</i>	7.78	22.50 (3)
	Okavango Delta	2.34	35.64 (110)		<i>D. nudipes</i>	2.91	24.00 (10)		<i>D. nudipes</i>	2.91	24.00 (10)
	<i>D. nudipes</i>	1.75	41.80 (10)		<i>D. i. griseifrons</i>	-	-		<i>D. i. griseifrons</i>	-	-
TOT F-value = 17.95	<i>D. montanus</i>	13.22	247.00 (6)	Mass F-value = 33.32	<i>D. montanus</i>	18.38	82.00 (3)	Mass F-value = 33.32	<i>D. montanus</i>	18.38	82.00 (3)
	<i>D. incomtus</i> L/MP	27.92	276.43 (49)		<i>D. rufulus</i>	21.25	82.29 (466)		<i>D. rufulus</i>	21.25	82.29 (466)
	East Africa	27.82	282.31 (254)		<i>D. incomtus</i> L/MP	26.72	90.16 (27)		<i>D. incomtus</i> L/MP	26.72	90.16 (27)
	<i>D. rufulus</i>	29.66	283.10 (642)		East Africa	30.30	106.55 (64)		East Africa	30.30	106.55 (64)
	<i>D. incomtus</i> KZN	44.00	284.22 (45)		<i>D. i. capensis</i>	18.25	111.25 (4)		<i>D. i. capensis</i>	18.25	111.25 (4)
	<i>D. i. capensis</i>	21.42	284.88 (8)		<i>D. foxi</i>	25.20	116.59 (56)		<i>D. foxi</i>	25.20	116.59 (56)
	<i>D. i. longipilosus</i>	2.83	288.00 (3)		<i>D. shortridgei</i>	20.42	119.30 (5)		<i>D. shortridgei</i>	20.42	119.30 (5)
	<i>D. foxi</i>	27.09	288.35 (66)		<i>D. incomtus</i> KZN	33.47	130.53 (22)		<i>D. incomtus</i> KZN	33.47	130.53 (22)
	<i>D. i. griseifrons</i>	24.94	300.70 (10)		<i>D. i. longipilosus</i>	-	-		<i>D. i. longipilosus</i>	-	-
	Okavango Delta	29.24	317.00 (109)		<i>D. nudipes</i>	-	-		<i>D. nudipes</i>	-	-
	<i>D. nudipes</i>	20.29	340.44 (9)		<i>D. i. griseifrons</i>	-	-		<i>D. i. griseifrons</i>	-	-
HB/TL F-value = 15.91	<i>D. montanus</i>	0.06	73.13% (6)	GSL F-value = 25.50	<i>D. i. longipilosus</i>	0.36	30.63 (3)	GSL F-value = 25.50	<i>D. i. longipilosus</i>	0.36	30.63 (3)
	<i>D. i. griseifrons</i>	0.04	81.36% (10)		<i>D. montanus</i>	1.54	32.54 (3)		<i>D. montanus</i>	1.54	32.54 (3)
	<i>D. i. longipilosus</i>	0.01	82.29% (3)		<i>D. rufulus</i>	1.51	34.73 (200)		<i>D. rufulus</i>	1.51	34.73 (200)
	<i>D. incomtus</i> L/MP	0.08	86.47% (49)		East Africa	1.58	35.86 (112)		East Africa	1.58	35.86 (112)
	<i>D. i. capensis</i>	0.12	87.44% (8)		<i>D. incomtus</i> L/MP	1.77	36.05 (50)		<i>D. incomtus</i> L/MP	1.77	36.05 (50)
	<i>D. foxi</i>	0.08	88.40% (65)		<i>D. foxi</i>	1.65	36.06 (13)		<i>D. foxi</i>	1.65	36.06 (13)
	East Africa	0.08	89.68% (249)		<i>D. i. griseifrons</i>	1.83	36.46 (5)		<i>D. i. griseifrons</i>	1.83	36.46 (5)
	<i>D. incomtus</i> KZN	0.08	89.91% (45)		<i>D. incomtus</i> KZN	2.75	37.04 (36)		<i>D. incomtus</i> KZN	2.75	37.04 (36)
	<i>D. rufulus</i>	0.09	93.90% (637)		Okavango Delta	1.49	37.25 (56)		Okavango Delta	1.49	37.25 (56)
	Okavango Delta	0.08	94.35% (109)		<i>D. i. capensis</i>	1.86	38.03 (7)		<i>D. i. capensis</i>	1.86	38.03 (7)
	<i>D. nudipes</i>	0.04	103.68% (9)		<i>D. nudipes</i>	1.14	39.80 (10)		<i>D. nudipes</i>	1.14	39.80 (10)
UTR F-value = 66.84	<i>D. i. longipilosus</i>	0.07	6.48 (3)	NAS F-value = 9.81	<i>D. montanus</i>	3.65	3.65 (3)	NAS F-value = 9.81	<i>D. montanus</i>	3.65	3.65 (3)
	<i>D. montanus</i>	0.08	6.67 (3)		<i>D. foxi</i>	3.79	3.79 (14)		<i>D. foxi</i>	3.79	3.79 (14)
	<i>D. rufulus</i>	0.24	6.69 (203)		<i>D. rufulus</i>	3.87	3.87 (200)		<i>D. rufulus</i>	3.87	3.87 (200)
	East Africa	0.31	6.96 (111)		East Africa	3.90	3.90 (101)		East Africa	3.90	3.90 (101)
	<i>D. i. griseifrons</i>	0.18	7.00 (5)		<i>D. incomtus</i> L/MP	3.94	3.94 (52)		<i>D. incomtus</i> L/MP	3.94	3.94 (52)
	<i>D. foxi</i>	0.22	7.11 (14)		<i>D. i. griseifrons</i>	4.09	4.09 (5)		<i>D. i. griseifrons</i>	4.09	4.09 (5)
	<i>D. incomtus</i> KZN	0.52	7.36 (38)		<i>D. incomtus</i> KZN	4.12	4.12 (39)		<i>D. incomtus</i> KZN	4.12	4.12 (39)
	<i>D. i. capensis</i>	0.23	7.40 (7)		Okavango Delta	4.13	4.13 (55)		Okavango Delta	4.13	4.13 (55)
	<i>D. incomtus</i> L/MP	0.25	7.43 (48)		<i>D. i. longipilosus</i>	4.17	4.17 (3)		<i>D. i. longipilosus</i>	4.17	4.17 (3)
	Okavango Delta	0.20	7.47 (58)		<i>D. nudipes</i>	4.31	4.31 (10)		<i>D. nudipes</i>	4.31	4.31 (10)

	<i>D. nudipes</i>	0.20	7.74 (10)		<i>D. i. capensis</i>	4.41	4.41 (7)
ZYN	<i>D. i. longipilosus</i>	0.07	16.92 (3)	BBC	<i>D. rufulus</i>	0.48	13.20 (193)
F-value = 37.30	<i>D. rufulus</i>	0.80	17.79 (195)	F-value = 37.09	<i>D. montanus</i>	0.32	13.50 (3)
	East Africa	0.79	18.63 (113)		<i>D. i. longipilosus</i>	0.19	13.68 (3)
	<i>D. montanus</i>	0.81	18.67 (3)		East Africa	0.52	13.80 (100)
	<i>D. foxi</i>	0.66	18.83 (14)		<i>D. foxi</i>	0.35	13.83 (13)
	Okavango Delta	0.55	18.91 (51)		Okavango Delta	0.42	14.00 (55)
	<i>D. i. griseifrons</i>	0.76	19.20 (5)		<i>D. incomtus</i> L/MP	0.51	14.04 (50)
	<i>D. incomtus</i> L/MP	0.84	19.31 (49)		<i>D. incomtus</i> KZN	0.50	14.17 (5)
	<i>D. incomtus</i> KZN	1.30	19.52 (36)		<i>D. i. griseifrons</i>	0.75	14.21 (38)
	<i>D. nudipes</i>	0.51	20.24 (10)		<i>D. nudipes</i>	0.32	14.73 (10)
	<i>D. i. capensis</i>	1.02	20.88 (6)		<i>D. i. capensis</i>	0.54	15.04 (7)
FRO	<i>D. i. longipilosus</i>	0.81	11.39 (3)	IOB	<i>D. i. longipilosus</i>	0.01	4.03 (3)
F-value = 27.50	<i>D. montanus</i>	0.52	12.77 (3)	F-value = 19.41	Okavango Delta	0.18	4.20 (56)
	<i>D. rufulus</i>	0.57	13.20 (198)		<i>D. montanus</i>	0.21	4.20 (3)
	East Africa	0.55	13.49 (101)		<i>D. rufulus</i>	0.24	4.46 (204)
	<i>D. incomtus</i> L/MP	0.69	13.64 (50)		East Africa	0.28	4.53 (116)
	<i>D. incomtus</i> KZN	0.93	13.71 (40)		<i>D. foxi</i>	0.20	4.55 (14)
	<i>D. i. griseifrons</i>	0.57	13.85 (5)		<i>D. incomtus</i> L/MP	0.20	4.66 (52)
	<i>D. foxi</i>	0.81	13.86 (14)		<i>D. incomtus</i> KZN	0.21	4.68 (39)
	Okavango Delta	0.55	14.39 (54)		<i>D. nudipes</i>	0.15	4.69 (10)
	<i>D. i. capensis</i>	0.90	14.52 (7)		<i>D. i. capensis</i>	0.27	4.79 (7)
	<i>D. nudipes</i>	0.63	15.12 (10)		<i>D. i. griseifrons</i>	0.39	4.94 (5)
	<i>D. i. longipilosus</i>	0.05	5.45 (3)	Character	<i>D. montanus</i>	0.18	0.86 (3) FMW
FMW	<i>D. rufulus</i>	0.22	5.68 (192)	UMW	<i>D. i. longipilosus</i>	0.04	0.93 (3)
F-value = 13.64	<i>D. montanus</i>	0.04	5.68 (3)	F-value = 46.95	East Africa	0.16	0.97 (101)
	<i>D. incomtus</i> KZN	0.31	5.73 (37)		<i>D. rufulus</i>	0.15	1.13 (203)
	Okavango Delta	0.29	5.75 (52)		<i>D. foxi</i>	0.15	1.20 (14)
	<i>D. incomtus</i> L/MP	0.35	5.80 (50)		<i>D. incomtus</i> KZN	0.16	1.24 (40)
	East Africa	0.22	5.80 (99)		<i>D. i. capensis</i>	0.22	1.29 (7)
	<i>D. foxi</i>	0.18	5.85 (13)		<i>D. nudipes</i>	0.16	1.30 (10)
	<i>D. i. capensis</i>	0.32	5.97 (7)		<i>D. i. griseifrons</i>	0.13	1.32 (5)
	<i>D. i. griseifrons</i>	0.07	6.15 (5)		<i>D. incomtus</i> L/MP	0.23	1.39 (52)
	<i>D. nudipes</i>	0.15	6.54 (9)		Okavango Delta	0.17	1.47 (58)
ZPW	<i>D. i. longipilosus</i>	0.04	3.57 (3)	GML	<i>D. i. longipilosus</i>	0.01	20.69 (3)
F-value = 37.79	<i>D. montanus</i>	0.47	3.61 (3)	F-value = 41.76	<i>D. montanus</i>	0.96	23.93 (3)
	<i>D. rufulus</i>	0.31	3.93 (204)		<i>D. rufulus</i>	1.11	24.19 (190)
	East Africa	0.30	3.96 (101)		<i>D. foxi</i>	1.23	25.47 (14)
	<i>D. i. griseifrons</i>	0.33	4.19 (5)		East Africa	1.21	25.49 (98)
	<i>D. foxi</i>	0.29	4.22 (14)		<i>D. incomtus</i> L/MP	1.41	26.24 (50)
	<i>D. incomtus</i> L/MP	0.33	4.35 (52)		<i>D. i. griseifrons</i>	1.12	26.27 (5)
	<i>D. incomtus</i> KZN	0.37	4.53 (40)		Okavango Delta	1.16	26.65 (57)
	<i>D. nudipes</i>	0.21	4.55 (10)		<i>D. incomtus</i> KZN	2.14	27.04 (36)
	Okavango Delta	0.24	4.56 (58)		<i>D. i. capensis</i>	1.48	27.67 (7)
	<i>D. i. capensis</i>	0.36	4.70 (7)		<i>D. nudipes</i>	1.10	28.74 (9)
MTR	<i>D. i. longipilosus</i>	0.31	6.26 (3)	GHS	<i>D. montanus</i>	0.21	11.11 (3)
F-value = 34.36	<i>D. rufulus</i>	0.24	7.17 (201)	F-value = 35.65	<i>D. rufulus</i>	0.43	11.12 (190)
	<i>D. montanus</i>	0.16	7.22 (3)		<i>D. i. longipilosus</i>	0.01	11.35 (3)
	Okavango Delta	0.29	7.35 (58)		<i>D. incomtus</i> L/MP	0.45	11.39 (50)
	East Africa	0.30	7.38 (116)		Okavango Delta	0.36	11.51 (56)
	<i>D. foxi</i>	0.37	7.48 (14)		<i>D. foxi</i>	0.37	11.74 (13)
	<i>D. incomtus</i> L/MP	0.31	7.49 (53)		<i>D. incomtus</i> KZN	0.58	11.80 (35)
	<i>D. i. griseifrons</i>	0.16	7.50 (5)		East Africa	0.44	12.01 (93)
	<i>D. incomtus</i> KZN	0.60	7.60 (38)		<i>D. i. griseifrons</i>	0.47	12.02 (5)

	<i>D. i. capensis</i>	0.28	7.94 (7)		<i>D. nudipes</i>	0.35	12.28 (8)
	<i>D. nudipes</i>	0.24	8.62 (10)		<i>D. i. capensis</i>	0.31	12.36 (7)
Dorsal CS	<i>D. montanus</i>	35.39	607.65 (3)	Ventral CS	<i>D. montanus</i>	23.43	618.64 (3)
F-value = 23.00	<i>D. rufulus</i>	29.21	644.07 (172)	F-value = 26.26	<i>D. rufulus</i>	29.24	651.67 (146)
	East Africa	31.38	664.94 (94)		East Africa	30.23	678.17 (96)
	<i>D. i. griseifrons</i>	33.14	670.21 (4)		<i>D. i. griseifrons</i>	37.31	682.75 (4)
	<i>D. incomtus</i> L/MP	32.60	673.97 (43)		<i>D. incomtus</i> L/MP	37.66	686.91 (39)
	<i>D. foxi</i>	36.27	679.17 (13)		<i>D. foxi</i>	33.7	695.61 (11)
	Okavango Delta	33.68	690.91 (30)		Okavango Delta	32.67	702.98 (21)
	<i>D. nudipes</i>	45.22	706.51 (20)		<i>D. incomtus</i> KZN	34.14	719.37 (22)
	<i>D. incomtus</i> KZN	31.18	710.63 (24)		<i>D. i. capensis</i>	38.07	720.52 (6)
	<i>D. i. capensis</i>	30.52	715.85 (5)		<i>D. nudipes</i>	26.77	755.99 (9)

from the Limpopo and Mpumalanga Provinces were generally characterised as having an intermediate size. *Dasymys foxi* was larger than *D. rufulus* in all of the characters except four: HB/TL, NAS, GML and GHS. Within the subspecies *D. incomtus*, specimens from the KwaZulu-Natal were larger than *D. i. incomtus* from the Limpopo and Mpumalanga Provinces in all of the characters excepting HF, UTR, FMW and UMW.

Fig. 7 provides a CA phenogram based on the 11 distinct groups. The correlation coefficient was 0.951 indicating a very good fit of the data. Cluster 1 comprised 7 of the 11 distinct morphological forms, with the exception of the montane forms, *D. i. longipilosus* and *D. montanus*, and the two largest forms, *D. nudipes* and Okavango Delta *Dasymys*. Within Cluster 1, *D. i. capensis* and KwaZulu-Natal *D. i. incomtus*, South Africa formed a distinct grouping (Subcluster A) from Subcluster B, which had three distinct groups: 1-*D. foxi* and *D. i. incomtus* from the Limpopo and Mpumalanga Provinces; 2-material from East Africa and *D. rufulus*; and 3-*D. i. griseifrons*. Cluster 2 comprised Cluster 1 as well as the Okavango Delta *Dasymys*, *D. montanus* and *D. nudipes*, while Cluster 3 separated *D. i. longipilosus* from the other *Dasymys* specimens.

DISCUSSION

Our dataset was somewhat cumbersome to analyze given the large geographic area considered as well as the lack of clear-cut boundaries between groups.

Although the morphological evidence presented here is helpful in providing insight into the inter-specific relationships within *Dasymys*, it is apparent that genetic data are needed to resolve certain aspects of its phylogeny. Additional material, particularly from the DRC, Sudan, Malawi, Mozambique and Tanzania is also required in future studies as these areas appear to be key in discerning distributional limits of species or species complexes in *Dasymys* as well as in clarifying the taxonomic position of the genus within these areas. Five species of *Dasymys* are currently recognised: *D. foxi*, *D. montanus*, *D. nudipes*, *D. rufulus* and *D. incomtus* (Musser & Carleton 1993). The results from this study confirm the existence of all of these species but do not agree with the current distribution limits for *D. rufulus* and *D. incomtus*. The data also suggest that six additional morphological species may exist. Two of them would not correspond to previously described forms and four would result from the elevation of already recognised subspecies, bringing the proposed total number of *Dasymys* species to 11.

Karyotypic evidence supports a polytypic *Dasymys* genus, with chromosomal differences indicating separate species (Maddalena *et al.* 1989; Granjon *et al.* 1992; Volobouev *et al.* 2000). The morphometric and geometric results presented here confirm the chromosomal separation noted below in that west African material has a similar skull structure to the two karyotypic races of *D. i. incomtus* in South Africa and that material from Ethiopia, west Africa and east Africa all have different

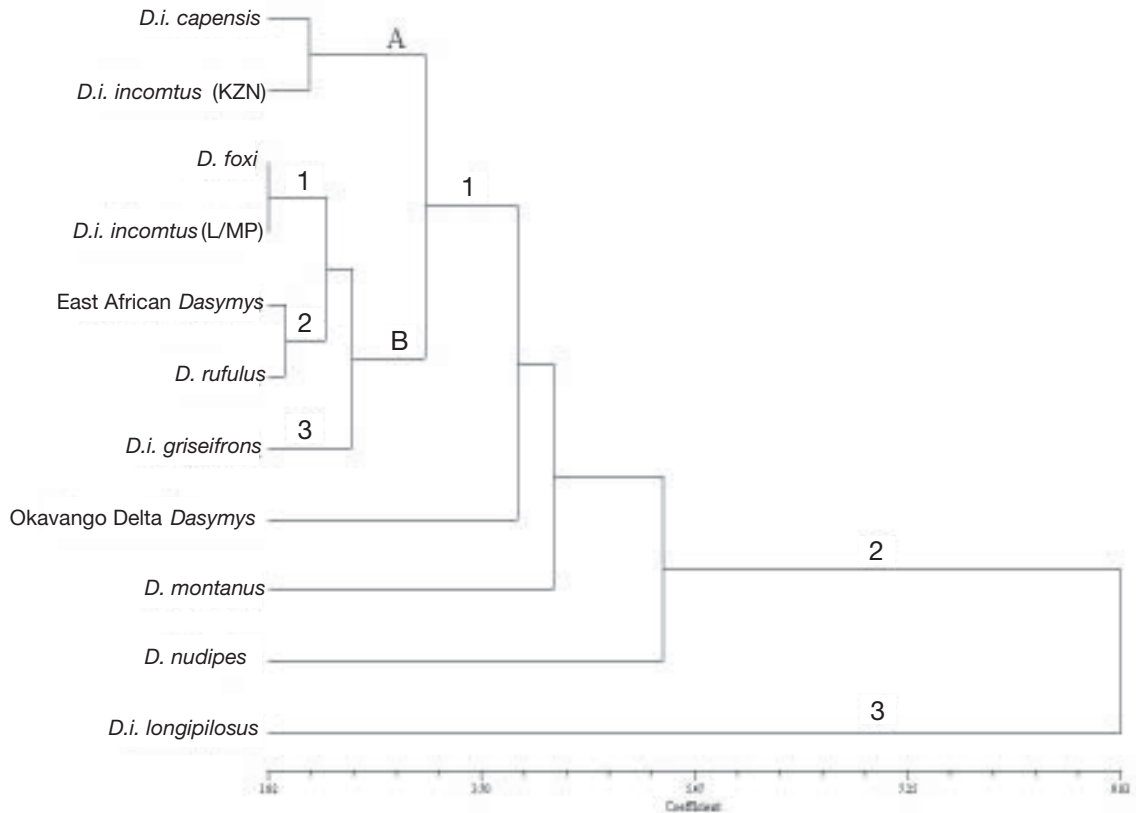


FIG. 7. – CA phenogram of 11 morphologically defined *Dasymys* groups. Cophenetic correlation coefficient, 0.951. KZN, KwaZulu-Natal Province; L/MP, Limpopo and Mpumalanga Provinces.

karyotypes and distinct skull sizes and shapes from each other. West African material is karyotypically stable with $2n = 36$, $FN = 48$ (Matthey 1958; Tranier & Gautun 1979; Granjon *et al.* 1992; Gautun *et al.* 1985; Volobouev *et al.* 2000), although specimens from Niayes, Senegal have a different FN (44) and those from Kangaba, Mali have 0–3 B chromosomes (Volobouev *et al.* 2000). Ethiopian specimens are characterised by different diploid numbers (Harenne forest, $2n = 40$; Baleta forest, $2n = 38$), but have the same FN as the west African forms (Volobouev *et al.* 2000). Maddalena *et al.* (1989) found $2n = 40$, $FN = 50$ in East Africa specimens from Burundi, representing the sole documented karyotype from east central Africa. The other known karyotyped specimens come from South Africa, where two

karyotypes exist, one from the Limpopo Province (Klipfontein; $2n = 46$) and the other from the KwaZulu-Natal Province (Richards Bay and Kamberg; $2n = 38$; Gordon 1991; Mullin 1999). *Dasymys foxi* is restricted to Jos Plateau in Nigeria, an area historically associated with several different endemic rodent species (Swanepoel & Schlitter 1978; Happold 1985, 1987; Hutterer *et al.* 1992). In the original description of *D. foxi*, Miller (1900) hypothesised that this species was more similar to East African material than to *D. rufulus* from west Africa. Later, Carleton & Martinez (1991) also suggested that *D. foxi* has a skull similar to that of *D. incommutus*. The results from our study agree more with Carleton & Martinez (1991) than Miller (1900) as it seemed that *D. foxi* had a closer affinity with material

from South Africa than East Africa. Both Osgood (1936) and Rosevear (1969) considered *D. foxi* and *D. rufulus* to be subspecies of *D. incommutatus*, which is not correct, and recommended that neither *D. foxi* nor *D. rufulus* should attain species status as both forms appeared similar to each other with respect to pelage colour, body size and cranial shape and size. Carleton & Martinez (1991) confirmed that external measurements of both species overlap and that both have similar pelage colours, but felt that the wider skull, larger molars and general larger size of *D. foxi* and the slightly redder colour of *D. rufulus* adequately separated the two groups at a species level.

In this study, the taxonomic position of *D. foxi* was slightly confusing as it was typically found on the periphery of, but always separate from, *D. rufulus* in the macro scale analyses, but appeared to have a similar skull size and shape to *D. rufulus* in the micro scale analyses. Put another way, the macro scale analysis suggested that *D. foxi* represented a good morphological species while the micro scale analysis indicated that it represented a valid subspecies of *D. rufulus* rather than a separate species. However, the remainder of the analyses indicated that *D. foxi* was a valid species that separates from *D. rufulus*. The phenogram based on the 11 morphological groups clearly showed *D. foxi* as separate from *D. rufulus* and the results from the ANOVA showed that the overall larger *D. foxi* was significantly larger than *D. rufulus* with respect to upper toothrow length (UTR) and greatest skull height (GHS). Therefore, we suggest that *D. foxi* should be retained as a species.

Eisentraut (1963) originally examined *D. montanus*, which is restricted to high altitudes in the Ruwenzori Mountains of Uganda, and suggested that this subspecies be awarded species status (i.e. *D. montanus*) due to longer and darker pelage as well as a shorter tail than *D. incommutatus*. *Dasymys montanus* was considered a valid species by Musser & Carleton (1993), despite it never having been statistically examined prior to this study. *Dasymys montanus* certainly has both darker and longer pelage than other *Dasymys* and this study showed it to have a small size (in both external and cranial measurements) and the shortest tail

length as well as the smallest head-body/tail ratio, making all of these features good distinguishing characteristics. Montane forms generally have a smaller size and darker pelage (Kingdon 1974; Misonne 1974), in accordance with Bergmann's (1847) and Gloger's (Rapoport 1969) Rule. Other endemic rodent species, considered relict populations, seem to be common not only from Mount Ruwenzori but also from other Mountains in east Africa (e.g. Mt Elgon, Mt Kenya; Maddalena *et al.* 1989; Van der Straeten & Peterhans 1999; Clausnitzer & Kityo 2001; Taylor & Kumirai 2001). We recommend that *D. montanus* be considered a distinct species based on its skull size and shape especially when its restricted habitat is considered.

We attempted to examine correlations between environmental factors and both skull size and shape of all of the morphologically defined *Dasymys* species by analyzing rainfall and temperature data primarily to ascertain the effects of the environment on the high-altitude forms, *D. montanus* and *D. i. longipilosus*. We obtained weather data from the National Oceanic and Atmospheric (NOAA) database (www.ncdc.noaa.gov/ol/climate/research/ghcn/ghcn) and to ensure the relevance of the weather data, we chose the closest weather station (within 1 degree of latitude, 1 degree of longitude and 500 m of altitude) to each locality. A problem arose, however, in trying to obtain weather data for the localities representing these two montane forms as there were no weather stations within an acceptable distance to the localities (mainly in terms of altitude), making the analysis of environmental correlates impossible. Therefore, it does not seem possible to ascertain whether *D. montanus* or *D. i. longipilosus* constitute altitudinal races or represent valid species.

Dasymys nudipes has long been considered a valid species that is separate from *D. incommutatus* based on its large size and the fact that it has five plantar pads, unlike the other *Dasymys* specimens which have six (Cabrera & Ruxton 1926; Crawford-Cabral 1983; Crawford-Cabral & Pacheco 1989). Both the morphological data and the ANOVA results presented in this study confirmed the distinctness of *D. nudipes* and that this species generally had

the largest size of all of the *Dasymys* specimens examined here. Another distinguishing character of *D. nudipes* is that its tail length is longer on average than its body length, a unique trait that makes *D. nudipes* distinguishable from all other species (Table 3). *Dasymys nudipes* occurs in an Angolan escarpment zone that is associated with several other endemic rodent species (Hall 1960; Crawford-Cabral 1983; Taylor & Kumirai 2001). The biological importance of this area is thought to be due to palaeoclimatic changes, mainly the expansion of the Kalahari Desert into northern Angola and Congo disrupting what was considered to be a continuous forest from Angola to Cameroon. Several workers have suggested that Okavango Delta specimens might represent a subspecies of *D. nudipes* due to its large size (Shortridge 1934; Roberts 1951; Crawford-Cabral & Pacheco 1989; Musser & Carleton 1993). Although the ventral skull shape is similar to *D. nudipes*, the traditional measurements, dorsal shape of the skull as well as the ANOVA results suggest that this material may delineate a good morphological species that is distinct from *D. incommutus* (both from South Africa and Angola) and *D. nudipes*. Only one of the Botswana OTUs (Moremi) is part of the Okavango Delta group. Individuals from the second Botswana OTU (Kasane) consistently grouped away from the other Okavango Delta material and instead had a similar skull shape and size to South African *D. incommutus sensu lato* and should be included within an *incommutus* group. We suggest that Okavango Delta *Dasymys* be named *D. shortridgei*, after G.C. Shortridge who provided the majority of the collection from this region, pending genetic confirmation of species status (see Appendix 1).

Dasymys rufulus is distinct from South African *D. incommutus* as well as from *D. i. griseifrons* and *D. nudipes*, but does not appear to be restricted to west Africa as suggested by Carleton & Martinez (1991), who previously hypothesised that the range of *D. rufulus* at least extended into Cameroon. Specimens from north Africa (Sudan and Chad), central Africa (Cameroon, Congo, western DRC and northern Angola), and central east Africa (Zambia, Tanzania, Malawi and

Mozambique) are all currently recognised as *D. incommutus* (Musser & Carleton 1993) yet appear to have similar skull sizes and shapes to *D. rufulus* based primarily on traditional measurements and dorsal skull shape data. The apparent large range of *D. rufulus*, spanning from Senegal to Tanzania (excluding East Africa) is in part confirmed by Ducroz *et al.* (2001) who found a low percentage of genetic divergence (7.2%) between *D. rufulus* from Lake Retba, Senegal and *D. incommutus* from Berega, Tanzania using cytochrome b data.

Ventral skull data showed possible boundaries between (a) west African and Zambian and (b) central African and Zambian material, which led us to hypothesise that central African and Zambian material may represent distinct groups (either species or subspecies) within a *rufulus* species complex. Known historical faunal links between Nigeria, Gabon, Cameroon, the DRC and Angola support such a large area for a species complex (Hall 1960; Swanepoel & Schlitter 1978; Van der Straeten & Verheyen 1982; Robbins & Van der Straeten 1989; Louette 1990; Dieterlen & Van der Straeten 1992; Happold 1996). Also, the three regions that the *rufulus* complex covers (west, central and central east Africa) have been associated with other species complexes, variable karyotypes, newly identified species and a high occurrence of endemics in rodents (Hamilton 1982; Van der Straeten & Dudu 1990; Hutterer *et al.* 1992; Van der Straeten & Dieterlen 1992; Stuart *et al.* 1993; Verheyen *et al.* 1996; Burgess *et al.* 1998; Grubb 1999; Grubb *et al.* 1999; Schlitter *et al.* 1999; Dobigny & Volobouev 2000; Barome *et al.* 2001; Burda 2001; Kawalika *et al.* 2001; Lecompte *et al.* 2001; Taylor & Kumirai 2001). Fauna from the Guineo-Congolian forest block has also been linked to eastern Tanzania (Poynton 1990; Kingdon & Howell 1993; Howell 1993) in addition to material from west Africa. Musser & Carleton (1993) indicated that *D. rufulus* needed to be compared to material from central Africa and in particular to individuals representing *D. i. bentleyae* (occurring in southwestern DRC and northern Angola). In our study, material from the DRC was split into two morphologically

defined groups with material from the west, southwest and northeast more similar to *D. rufulus* and material from the east more similar to east African *Dasymys*. The morphometric separation seen within the DRC was not dependent on geographical distances between the populations (i.e. isolation by distance), but rather the distinctions in skull size and shape more likely reflect previous environmental and/or biogeographical restrictions (Davis 1962; Happold 1996; Verheyen *et al.* 1996). Musser & Carleton (1993) considered *D. i. bentleyae* (from southwest DRC) as a synonym within *D. incomtus* despite workers suggesting that *D. i. bentleyae* represented a valid species (Cabrera & Ruxton 1926; Allen 1939; Schouteden 1948; Sanborn 1952; Crawford-Cabral & Pacheco 1989). Our study partially confirms the assessment made by Musser & Carleton (1993) in that it showed that *D. i. bentleyae* should retain its current status, but we suggest that *D. i. bentleyae* represents a synonym within *D. rufulus* rather than *D. incomtus*. The taxonomic position of material from central east Africa (Zambia, Malawi, Mozambique and Tanzania) was not entirely clear in this study. One certainty was that the data showed that *Dasymys* from this region were not similar to the nominate *D. incomtus* from the KwaZulu-Natal Province of South Africa, indicating that these specimens are incorrectly named as *D. incomtus*. It was apparent that some central east African *Dasymys* (particularly specimens from Mozambique) shared cranial similarities with *Dasymys* from East Africa. Although, faunal links have been well established between east and central east Africa (e.g. Carcasson 1964; Happold & Happold 1989; Poynton 1990; Stuart *et al.* 1993; Burgess *et al.* 1998), it appears that east and central east African *Dasymys* examined in this study have been isolated from each other for a significant period of time. Carcasson (1964), Happold & Happold (1989), and Stuart *et al.* (1993) further hypothesised that central Africa provided a faunal link between west and central east Africa. This appears to have more importance for *Dasymys* as central east African specimens seem to have a skull size and shape more similar to west African *D. rufulus* than to *Dasymys* from east Africa.

The fifth species listed by Musser & Carleton (1993), *D. incomtus*, occupies a much smaller range than suggested. *Dasymys incomtus* is currently listed as occurring in Chad, southern Sudan, Ethiopia, Cameroon, Central African Republic, the DRC, Uganda, Kenya, Rwanda, Burundi, Tanzania, Angola, Zambia, Malawi, Mozambique, Zimbabwe and South Africa (Meester *et al.* 1986; Carleton & Musser 1993). Instead, the data provided here indicated that *D. incomtus* would be confined to Zimbabwe and South Africa although the relationship between Zimbabwe specimens and South African *D. i. incomtus* was not clear. Dorsal skull data suggested they represent three distinct groups, the ventral skull shape showed Zimbabwe specimens to be in-between the KwaZulu-Natal and the Limpopo and Mpumalanga Province specimens and similar to material from Zambia, Malawi (Zomba and Mulanje) and Mozambique (Zambue), while traditional data showed a connection between south-western Zimbabwe (representing *D. i. fuscus*) and KwaZulu-Natal Province of South Africa. Despite the ambiguity of these data, the Limpopo and Mpumalanga Province OTUs were distinct from all other material and never grouped with KwaZulu-Natal Province material (although both groups represent *D. i. incomtus sensu lato*). We feel this is significant in that it emphasises the karyotypic and electrophoretic differences within *D. i. incomtus* shown by Gordon (1991) and Mullin *et al.* (2002). Three subspecies are recognised in South Africa and Zimbabwe (excluding *D. i. capensis* which will be discussed separately below): *D. i. incomtus*, *D. i. fuscus* and *D. i. nudipes* (southwestern Zambia and northwestern Zimbabwe; Fitzsimons 1920; Smithers & Wilson 1979; Meester *et al.* 1986; Crawford-Cabral & Pacheco 1989; Skinner & Smithers 1990). Crawford-Cabral & Pacheco (1989) examined cranial differences between *D. i. incomtus* (from the Limpopo and Mpumalanga Provinces) and *D. i. fuscus* and suggested they represented allospecies; we found similar results. *Dasymys i. incomtus* has also been listed as possibly occurring in Mozambique and Malawi (Smithers & Tello 1976; Meester *et al.* 1986; Skinner & Smithers 1990), which contrasts

with our findings: Mozambican and Malawian specimens appeared to be most similar to Zambian material, which appears to be part of a *D. rufulus* complex. It has been previously suggested that two *D. incomtus* subspecies found in southern Africa (*D. i. incomtus*, *D. i. nudipes*) were distinguished by pelage colour alone (Rautenbach 1982). The only difference between *D. i. fuscus* from Zimbabwe and *D. i. incomtus* from KwaZulu-Natal appears to be the darker dorsal pelage with less yellow grizzling in *D. i. fuscus* (Fitzsimons 1920). Ellerman *et al.* (1941) were the first to include Limpopo and Mpumalanga Province specimens in *D. i. incomtus* with previously described specimens from the KwaZulu-Natal Province. Rautenbach (1982) concurred with this but stated that this arrangement was temporary and needed to be confirmed with morphological studies, something that was not examined until recently (Mullin *et al.* 2002). Roberts (1951) named *D. i. incomtus* from Hectorspruit (Mpumalanga Province) as a type of *D. i. incomtus*, which is confusing since the type for this subspecies is already described from Durban (KwaZulu-Natal Province, South Africa). The Hectorspruit type was never identified (no accession number), described or accepted as valid, and Roberts (1951) was not even able to present skull measurements for this specimen in his table of individual measurements. Accordingly, we identify a new type specimen for this material (see Appendix 1) and suggest that this material be named *D. robertsii*. *Dasymys i. capensis*, *D. i. longipilosus* and *D. i. griseifrons* appear to represent good morphological species and are hereafter referred to as *D. capensis*, *D. longipilosus* and *D. griseifrons*). All three have restricted ranges and occur in areas characterised by high numbers of endemic rodent species (Davis 1962; Eisentraut 1968; Eisentraut 1970; Avery 1977; Lamotte & Petter 1981; Petter 1982, 1986; Hutterer & Yalden 1990; Dieterlen & Van der Straeten 1992; Hutterer *et al.* 1992; Gelderblom & Bronner 1995; Capanna *et al.* 1996; Yalden *et al.* 1996; Schlitter *et al.* 1999; Fadda & Corti 2000; Lavrenchenko *et al.* 2000; Bannikova *et al.* 2001; Lecompte *et al.* 2001). *Dasymys capensis* ranges from the extreme southwest

to the Tsitsikamma coastal area approximately 400km to the east and is found only in the Western Cape Province of South Africa. Roberts (1951) reported *D. capensis* as larger than *D. i. incomtus*, and with notably darker pelage colour, which we confirm in this study. *Dasymys longipilosus*, occurring at high altitudes on Mt Cameroon, has small cranial features, dark pelage and a short tail, which, as stated previously, appears to be characteristic of montane rodents (Kingdon 1974; Misonne 1974). *Dasymys griseifrons* occurs at Lake Tana in Ethiopia and the results from this study suggest it is a distinct species based on its large cranial and external features. Although there does appear to be a link between Ethiopian and East African (e.g. Kenya and Uganda) material, particularly in the case of the second Ethiopian OTU examined in this study (Jimma), it seems more likely that Ethiopian *Dasymys* are isolated, especially since arid northern Kenya can be considered a barrier to mesic species. Already, two distinct karyotypic races of *Dasymys* are found in Ethiopia, neither of which was represented in this study (Volobouev *et al.* 2000).

The final material to be discussed is the East African group, which encompasses eastern DRC, Uganda, Kenya, Burundi and Rwanda. Although this group contains several type specimens: *D. i. belukus* (Heller 1911), *D. i. medius* (Thomas 1906), *D. i. nigridius* (Hollister 1916), *D. i. orthos* (Heller 1924) and *D. i. savannus* (Delany 1975), it appears to represent a homogenous sample (i.e. this material is not part of a species complex). Morphological evidence presented here suggests that these individuals delineated a separate species and as *D. i. medius* is the oldest synonym for the taxon in this region, we suggest it that it is elevated to a species level (*D. medius*). *Dasymys medius* was previously considered a separate species (Thomas 1906) that was later considered a subspecies of *D. bentleyae* (Hollister 1916; Hatt 1934; Allen & Loveridge 1942), a species listed as occurring in central Africa until it was recognised as a synonym within *D. incomtus* (Musser & Carleton 1993). Neither of these taxonomic positions is correct as *D. medius* does not appear to be similar to either *D. bentleyae* or *D. incomtus*.

CONCLUSION

Although taxonomic positions within *Dasymys* are not fully resolved, our study is important for deciphering the morphological relationship within this genus. The examination of the entire genus at one time is crucial to understand the taxonomic affinities of species and subspecies. As *Dasymys* individuals are rare in nature, which unfortunately makes genetic studies difficult, morphological studies highlight the important areas for future genetic studies of this genus. Preliminary analyses have suggested that morphometrics alone will probably not be able to resolve any remaining taxonomic questions concerning the *D. incomtus* or *D. medius* group delineated in this study, but might be able to tease apart groups within *D. rufulus*. We suggest that these 11 morphological species remain provisional until genetic confirmation is obtained. The data presented in this study will provide a solid framework for further taxonomic, molecular and/or genetic based studies on *Dasymys*. In the meantime, we have provided an outline of synonymy in Appendix 1 based on the results of this study.

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REFERENCES

- ALLEN G. M. 1939. — A checklist of African mammals. *Bull. Mus. Comp. Zool. Harv. College* 83: 1-763.
- ALLEN G. M. & LOVERIDGE A. 1942. — Scientific results of a fourth expedition to forested areas in East and Central Africa. *Bull. Mus. Comp. Zool., Harv.* 89: 147-214.
- APIIAH S. O. & ATTUQUAYETIO D. K. 2000. — Preliminary observations of the economic importance of rodents in the establishment of oil palm (*Elaeis guineensis*) plantations in the eastern region of Ghana. *J. Ghana Sci. Assoc.* 2: 164-169.
- EVERY D. M. 1977. — Past and present distribution of some rodent and insectivore species in the southern Cape Province, South Africa: new information. *Ann. S. Afr. Mus.* 74: 201-209.
- EVERY D. M. 1991. — Late Quaternary incidence of some micromammalian species in Natal. *Durban Museum Novitates* 16: 1-11.
- EVERY D. M. 1998. — An assessment of the Lower Pleistocene micromammalian fauna from Swartkrans Members 1-3, Gauteng, South Africa. *Geobios* 31: 393-414.
- BANNIKOVA A. A., LAVRENCHENKO L. A., LOMOV A. A. & MEDNIKOV B. M. 2001. — Molecular diversity of some *Crocidura* species (Insectivora, Soricidae) from Ethiopia, in DENYS C. *et al.* (eds), *African Small Mammals*. IRD Editions, Paris: 55-64.
- BAROME P. O., VOLOBOUEV V., MONNEROT M., MFUNE J. K., CHITAU KALI W., GAUTUN J. C. & DENYS C. 2001. — Phylogeny of *Acomys spinosissimus* (Rodentia, Muridae) from north Malawi and Tanzania: evidence from morphological and molecular evidence. *Biological Journal of the Linnean Society* 73: 321-340.
- BELLIER L. 1965. — Evolution du peuplement des rongeurs dans les plantations de palmier à huile. *Oleagineux* 20: 573-576.
- BERGMANN C. 1847. — Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe. *Gött. Stud.* 3: 595-708.
- BURDA H. 2001. — Determinants of the distribution and radiation of African mole-rats (Bathyergidae, Rodentia). Ecology or geography?, in DENYS C. *et al.* (eds), *African Small Mammals*. IRD Editions, Paris: 264-277.
- BURGESS N. D., FIELDSA J. & BOTTERWEG R. 1998. — Faunal importance of the Eastern Arc Mountains of Kenya and Tanzania. *J. E. Afr. Nat. Hist.* 87: 37-58.
- CABRERA A. & RUXTON A. E. 1926. — On mammals from Luluabourg, Southern Congo. *Ann. Mag. Nat. Hist.* 9: 591-601.
- CAPANNA E., BEKELE A., CAPULA M., CASTIGLIA R., CIVITELLI M. V., CODJIA J. T., CORTI M. & FADDA C. 1996. — A multidisciplinary approach to the systematics of the genus *Arvicanthis* Lesson, 1842 (Rodentia, Murinae). *Mammalia* 60: 677-696.
- CARCASSON R. H. 1964. — A preliminary survey of the zoogeography of African butterflies. *East African Wildlife Journal* 1964: 122-157.
- CARLETON M. D. & MARTINEZ C. 1991. — Morphometric differentiation among west African populations of the rodent genus *Dasymys* (Muroidea: Murinae), and its taxonomic implications. *Proc. Biol. Soc. Wash.* 104: 419-435.

- CLAUSNITZER V. & KITYO R. 2001. — Altitudinal distribution of rodents (Muridae and Gliridae) on Mt Elgon, Uganda. *Tropical Zoology* 14: 95-118.
- CRAWFORD-CABRAL J. 1983. — Patterns of allopatric speciation in some Angolan muridae. *Ann. Mus. Roy. d'Afr. Centr.* 237: 153-157.
- CRAWFORD-CABRAL J. 1986. — A discussion of the taxa to be used in a zoogeographical analysis as illustrated in Angolan muroidea. *Cimbebasia* Ser. A 8: 161-166.
- CRAWFORD-CABRAL J. 1998. — *The Angolan rodents of the superfamily Muroidea. An account of their distribution.* Instituto de Investigação Científica Tropical.
- CRAWFORD-CABRAL J. & PACHECO A. 1989. — A craniometrical study on some water rats of the genus *Dasymys* (Mammalia, Rodentia, Muridae). *Garcia de Oria, Ser. Zool.* 15: 11-24.
- DAVIS D. H. S. 1962. — Distribution patterns of southern African Muridae, with notes on some of their fossil antecedents. *Ann. Cape Prov. Mus.* 2: 56-76.
- DE GRAAFF G. 1961. — On the fossil mammalian microfauna collected at Kromdraai by Draper in 1895. *South African Journal of Science* 57: 259-260.
- DE GRAAFF G. 1981. — *The Rodents of South Africa.* Butterworth and Company, Durban.
- DELANY M. J. 1975. — *Rodents of Uganda.* Trustees of the British Museum (Natural History), London.
- DELANY M. J. & HAPPOLD D. C. D. 1979. — *Ecology of African Mammals.* Longman Group, Limited, London.
- DENYS C. 1999. — Of mice and men, in BROMAGE, G. T. & SCHRENK F. (eds), *African biogeography, climate change, and human evolution.* Oxford University Press, Oxford: 226-252.
- DIETERLEN F. & VAN DER STRAETEN E. 1992. — Species of the genus *Otomys* from Cameroon and Nigeria and their relationship to East African forms. *Bonner Zoologische Beiträge* 43: 383-392.
- DOBIGNY G. & VOLOBOUEV V. 2000. — Comparative cytogenetics and phylogeography of the west African species of *Taterillus* (Rodentia, Gerbillinae). Small Mammal Conference, Abstracts, Paris.
- 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: 173-206.
- DUPLANTIER J.M. & BÂ K. 2001. — Swimming ability in six West-African rodent species under laboratory conditions?, in DENYS C. et al. (eds), *African Small Mammals.* IRD Editions, Paris: 331-342.
- DUPLANTIER J. M., GRANJON L. & BÂ K. 1997. — Répartition biogéographique des petits rongeurs au Sénégal. *J. Afr. Zool.* 111: 17-26.
- EISENTRAUT M. 1963. — *Die Wirbeltiere des Kamerungebirges.* Verlag Paul Parey, Hamburg; Berlin.
- EISENTRAUT M. 1968. — Beitrag zur Säugetierfauna von Kamerun. *Bonner Zoologische Beiträge* 19: 1-14.
- EISENTRAUT M. 1970. — Die Verbreitung der Muriden-Gattung *Praomys* auf Fernando-Poo und in West-Kamerun. *Zeitschrift für Säugetierkunde* 35: 1-15.
- ELLERMAN J. R., HAYMAN R. W. & HOLT G. W. 1941. — *The families and genera of living rodents.* Volume II: Family Muridae, T. o. t. B. Museum, British Museum (Natural History), London.
- FADDA C. & CORTI M. 2000. — Three dimensional geometric morphometric study of the Ethiopian *Myomys* — *Stenocephalemys* complex (Murinae, Rodentia). *Hystrix* 11: 131-143.
- FITZSIMMONS F. W. 1920. — *Natural History of South Africa.* Longmans, Green and Co., Ltd., London.
- FRIEDMANN Y., DALY B., KEITH M., PEDDEMORS V., CHIMIMBA C. & BYERS O. 2002. — *Conservation Assessment and Management Plan for the Mammals of South Africa: Draft Report.* CBSG South Africa/Endangered Wildlife Trust, Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, MN, USA.
- GAUTUN J.-C., TRANIER M. & SICARD B. 1985. — Liste préliminaire des rongeurs du Burkina Faso (ex Haute-Volta). *Mammalia* 49: 537-542.
- GELDERBLUM C. M. & BRONNER G. N. 1995. — Patterns of distribution and protection status of the endemic mammals in South Africa. *South African Journal of Zoology* 30: 127-135.
- GLASS B. P. 1965. — The mammals of eastern Ethiopia. *Zoologica Africana* 1: 177-179.
- GORDON D. H. 1991. — Chromosomal variation in the water rat *Dasymys incomtus*. *Journal of Mammalogy* 72: 411-414.
- GRANJON L., DUPLANTIER J., CATALAN J. & BRITTON-DAVIDIAN J. 1992. — Karyotypic data on rodents from Senegal. *Israelian Journal of Zoology* 38: 263-276.
- GRUBB P. 1999. — Evolutionary processes implicit in distribution patterns of modern African mammals, in BROMAGE G. T. & SCHRENK F., *African biogeography, climate change, and human evolution.* Oxford University Press, Oxford: 150-164.
- GRUBB P., SANDROCK O., KULLMER O., KAISER T. M. & SCHRENK F. 1999. — Relationships between eastern and southern African mammal faunas in BROMAGE G. T. & SCHRENK F., *African biogeography, climate change, and human evolution.* Oxford University Press, Oxford: 253-267.
- HALL B. P. 1960. — The faunistic importance of the scarp of Angola. *Ibis* 102: 420-442.
- HAMILTON A. C. 1982. *Environmental history of East Africa.* Academic Press, London.
- HANNEY P. 1965. — The Muridae of Malawi (Africa: Nyasaland). *J. Zool.* 146: 577-633.

- HAPPOLD D. C. D. 1985. — Geographical ecology of Nigerian mammals. *Ann. Mus. Roy. de l'Afr. Centr., Sci. Zool.* 246: 5-49.
- HAPPOLD D. C. D. 1987. — *The mammals of Nigeria*. Clarendon Press, Oxford.
- HAPPOLD D. C. D. 1996. — Mammals of the Guinea-Congo rain forest. *Proc. Roy. Soc. Edin.* 104B: 243-284.
- HAPPOLD D. C. D. & HAPPOLD M. 1989. — Biogeography of montane small mammals in Malawi, Central Africa. *Journal of Biogeography* 16: 353-367.
- HATT R. T. 1934. — Fourteen hitherto unrecognized African rodents. *American Museum Novitates* 708: 1-15.
- HELLER E. 1924. — Five new rodents from British East Africa. *Smith. Misc. Coll.* 54: 1-4.
- HELLER E. 1911. — New species of rodents and carnivores from Equatorial Africa. *Smith. Misc. Coll.* 56: 13-15.
- HILTON-TAYLOR C. 2000. — *IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland and Cambridge, UK.
- HOLLISTER N. 1916. — Three new murine rodents from Africa. *Smith. Misc. Coll.* 66: 1-3.
- HOWELL K. M. 1993. — Herpetofauna of the eastern African forests, in LOVETT J. C. & WASSER S. K. (eds), *Biogeography and ecology of the rain forests*. Cambridge University Press, Cambridge: 173-201.
- HUTTERER R., DIETERLEN F. & NIKOLAUS G. 1992. — Small mammals from forest islands of eastern Nigeria and adjacent Cameroon, with systematical and biogeographical notes. *Bonn. Zool. Beitr.* 43: 393-414.
- HUTTERER R. & YALDEN D.W. 1990. — Two new species of shrews from a relic forest in the Bale Mountains, Ethiopia, in PETERS G. & HUTTERER R. (eds), *Vertebrates in the Tropics*. Alexander Koenig Museum, Bonn: 63-72.
- KAWALIKA M., BURDA H. & BRÜGGERT D. 2001. — Was Zambia a cradle of the genus *Cryptomys* (Bathyergidae, Rodentia)? A further new ancestral (?) species of *Cryptomys* from Zambia, in DENYS C. et al. (eds), *African Small Mammals*. IRD Editions, Paris: 253-261.
- KINGDON J. 1971. — *East African Mammals. An Atlas of Evolution in Africa*. Academic Press, London.
- KINGDON J. 1974. — *East African Mammals*. Volume IIB: *Hares and Rodents*. University of Chicago, Chicago.
- KINGDON J. 1997. — *The Kingdon Field Guide to African Mammals*. Harcourt Brace and Company Publishers, San Diego.
- KINGDON J. & HOWELL K. M. 1993. — Mammals in the forests of eastern Africa, in LOVETT J. C. & WASSER S. K. (eds), *Biogeography and ecology of the rain forests*. Cambridge University Press, Cambridge: 229-241.
- LAMOTTE M. & PETER F. 1981. — Une taupe dorée nouvelle du Cameroun (Mt Oku, 6°15'N, 10°26'E): *Chrysochloris stuhlmanni baksaci* ssp. nov. *Mammalia* 45: 43-48.
- LAVOCAT R. 1956. — La faune des rongeurs des grottes à australopithèques. *Palaeontologia Africana* 4: 69-75.
- LAVRENCHENKO L. A., MILISHNIKOV A. N. & WARSHAVSKY A. A. 2000. — Allozymic phylogeny: evidence for coherent adaptive patterns of speciation in Ethiopian endemic rodents from an isolated montane massif. *Bonn. Zool. Monogr.* 46: 245-253.
- LECOMPTE E., DENYS C. & GRANJON L. 2001. — An identification key for species within the genus *Praomys* (Rodentia: Muridae), in DENYS C. et al. (eds), *African Small Mammals*. IRD Editions, Paris: 127-139.
- LOUETTE M. 1990. — Distribution patterns in African lowland forest birds, in PETERS G. & HUTTERER R. (eds), *Vertebrates in the Tropics*. Alexander Koenig Museum, Bonn: 237-247.
- 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 Trop.* 15: 7-117.
- MEESTER J., RAUTENBACH I. L., DIPPENAAR N. J. & BAKER C. M. 1986. — *Classification of Southern African mammals*. Transvaal Museum, Pretoria.
- MEESTER J. A. J. 1976. — *South African Red Data Book — Small Mammals*. South African National Scientific Programmes, Pretoria (Report; 11).
- MILLER G. S. 1900. — A collection of small mammals from Mount Coffee, Liberia. *Proc. Wash. Acad. Sci.* II: 631-649.
- MISONNE X. 1969. — African and Indo-Australian Muridae: evolutionary trends. *Mus. Roy. Afr. Centr. Ter. Belg. Zool.* 172: 1-219.
- MISONNE X. 1974. — Order Rodentia, in MEESTER J. & SETZER S. W. (eds), *The Mammals of Africa: an identification manual*. Smithsonian Institution Press, Washington D.C.: 1-39.
- MISONNE X. & Verschuren J. 1976. — Les rongeurs du Nimba Libérien. *Acta Zool. Path. Antverp.* 66: 199-220.
- MUGO D. N., LOMBARD A. T., BRONNER G. T., GELDERBLUM C. M. & BENN G. A. 1995. — Distribution and protection of endemic or threatened rodents, lagomorphs and macroscelidids in South Africa. *S. Afr. J. Zool.* 30: 115-126.
- MULLIN S. K. 1999. — Genetic and morphometric variations among populations of the water rat *Dasymys incomtus* Sundevall, 1847. Unpublished MSc dissertation, Zoology Department, University of the Witwatersrand, Johannesburg.
- MULLIN S. K., PILLAY N. & TAYLOR P. J. 2001. — Non-geographic morphometric variation in the water rat *Dasymys incomtus* (Rodentia: Muridae) in southern Africa. *Durban Museum Novitates* 26: 38-44.
- MULLIN S. K., N. PILLAY N., TAYLOR P. J. & CAMPBELL G. K. 2002. — Genetic and morphometric variation in populations of South African *Dasymys incomtus incomtus*. *Mammalia* 66.

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- MUSSER G.D. & CARLETON M.D. 1993. — Family Muridae, in WILSON D. E. & REEDER D. M. (eds), *Mammal species of the world: A taxonomic and geographic reference*. Smithsonian Institution Press, Washington D.C.: 501-755.
- OSGOOD W.H. 1936. — New and imperfectly known small mammals from Africa. *Zool. Ser. Field Mus. Nat. Hist.* 20: 217-256.
- PETTER F. 1982. — Les parentés des *Otomys* du Mont Oku (Cameroun) et des autres formes rapportées à *O. irroratus* (Brants, 1827) (Rodentia, Muridae). *Bonn. Zool. Beitr.* 33: 215-222.
- PETTER F. 1986. — Un rongeur nouveau du Mont Oku (Cameroun) *Lamottemys okuensis* gen. nov. sp. nov.; (Rodentia, Muridae). *Cimbebasia* 8: 97-105.
- PILLAY N. 2003. — Reproductive biology of a rare African rodent, the water rat, *Dasymys incomtus*. *Journal of Mammalogy* 84 (2): 505-512.
- POYNTON J. C. 1990. — Composition and subtraction patterns of the East African lowland Amphibian fauna, in PETERS G. & HUTTERER R. (eds), *Vertebrates in the Tropics*. Alexander Koenig Museum, Bonn.
- RAPOPORT E. H. 1969. — Gloger's rule and pigmentation of Collembola. *Evolution* 23: 622-626.
- RAUTENBACH I. L. 1982. — *Mammals of the Transvaal*. Ecoplan Monograph, Pretoria.
- ROBBINS C. B. & VAN DER STRAETEN E. 1989. — Comments on the systematics of *Mastomys* Thomas 1915 with a description of a new West African species (Mammalia: Rodentia: Muridae). *Sencken. Biol.* 69: 1-14.
- ROBERTS A. 1951. — *The Mammals of South Africa*. Pretoria: The Trustees of "The mammals of South Africa" Book Fund.
- ROHLF F. J. 1996. — NTSYS-pc, Ver. 2.01b. [Computer software and manual]. Setaouket, New York: Exeter Software.
- ROHLF F. J. 2000a. — tpsDig, Ver. 1.31. [Computer software and manual]. Stony Brook, New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- ROHLF F. J. 2000c. — tpsRegr, Ver. 1.25. [Computer software and manual]. Stony Brook, New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- ROHLF F. J. 2000b. — tpsSmall, Ver. 1.17. [Computer software and manual]. Stony Brook, New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- ROHLF F. J. 2001. — tpsRelw, Ver. 1.24. [Computer software and manual]. Stony Brook, New York: Department of Ecology and Evolution, State University of New York at Stony Brook.
- ROSEVEAR D. R. 1969. — *Rodents of West Africa*. Trustees of the British Museum (Natural History), London.
- SANBORN C. C. 1952. — Rodents (Muridae) from Lunda District, Northeastern Angola. *Publ. cult. Comp. Diam. Ang.* 14: 107-119.
- SCHLITTER D. A., HUTTERER R., MADDALENA T. & ROBBINS L.W. 1999. — New karyotype of shrews (Mammalia: Soricidae) from Cameroon and Somalia. *Ann. Carn. Mus.* 68: 1-14.
- SCHOUTEDEN H. 1948. — Faune de Congo Belge et du Ruanda-Urundi. I. — Mammifères. *Ann. Mus. Congo Belg. Terr.* Ser. 8 Sci. Zool. 1: 283.
- SCHWETZ J. 1956. — Role of wild rats and domestic rats (*Rattus rattus*) in schistosomiasis of man. *Trans. Roy. Soc. Trop. Med. Hyg.* 50: 275-282.
- SHEPPE W. & OSBORNE T. 1971. — Patterns of use of a flood plain by Zambian mammals. *Ecol. Monogr.* 41: 179-205.
- SHORTRIDGE G. C. 1934. — *Mammals of South West Africa*. Volume I. William Heinemann Limited, London.
- SKINNER J. D. & SMITHERS R. H. N. 1990. — *The Mammals of the Southern African Subregion*. University of Pretoria, Pretoria.
- SLICE D. E. 1999. — GRF-ND: *Generalized rotational fitting of n-dimensional data*. [Computer software and manual]. Stony Brook, Department of Ecology and Evolution, State University of New York.
- SMITHERS R. H. N. 1986. — *Land Mammals of Southern Africa*. Macmillan South Africa (Publishers) (Pty) Ltd., Johannesburg.
- SMITHERS R. H. N. 1971. — *The mammals of Botswana*. Mardon Printers, Ltd., Salisbury, Rhodesia.
- SMITHERS R. H. N. & TELLO J. L. P. L. 1976. — *Check List and Atlas of the Mammals of Mozambique*. Trustees of the Natural Museums and Monuments of Rhodesia, Salisbury, Rhodesia.
- SMITHERS R. H. N. & WILSON V. J. 1979. — *Checklist and atlas of the Mammals of Zimbabwe Rhodesia*. The Trustees of the National Museums of Rhodesia, Salisbury (Harare).
- SODEINDE O. A. 1995. — The ecology, reproductive, biology and economic importance of rodents in an arable agroecosystem in southwest Nigeria. Unpublished PhD thesis, University of Ibadan.
- STATSOFT INC., 2001. — *Statistica for windows* (Computer program manual), Ver. 6. [Computer software and manual]. Tulsa, Oklahoma.
- STUART S. N., JENSEN F. P., BROGGER-JENSEN S. & MILLER R. I. 1993. — The zoogeography of the montane forest avifauna of eastern Tanzania, in LOVETT J. C. & WASSER S. K. (eds), *Biogeography and ecology of the rain forests of eastern Africa*. Cambridge University Press, Cambridge: 203-228.
- SWANEPOEL P. & SCHLITTER D. A. 1978. — Taxonomic review of the fat mice (genus *Steatomys*) of West Africa (Mammalia: Rodentia). *Bull. Carn. Mus. Nat. Hist.* 6: 53-76.
- TAYLOR P. J. 1998. — *The smaller mammals of KwaZulu-Natal*. University of Natal Press, Durban.
- TAYLOR P. J. & KUMIRAI A. 2001. — Craniometric relationships between the Southern African Vlei rat, *Otomys irroratus* (Rodentia, Muridae, Otomyinae) and allied species from North of the Zambezi River, in DENYS C. *et al.* (eds), *African Small Mammals*. IRD Editions, Paris: 161-181.

- TAYLOR P. J. & MEESTER J. 1993. — Morphometric variation in the yellow mongoose, *Cynictis penicillata* (Cuvier, 1829) (Carnivora: Viverridae), in southern Africa. *Durban Museum Novitates* 18: 37-71.
- THOMAS O. 1906. — Descriptions of new mammals from Mount Ruwenzori. *Ann. Mag. Nat. Hist., Ser. 7*, 13: 143.
- TRANIER M. & GAUTUN J.-C. 1979. — Recherches caryotypiques sur les Rongeurs de Côte d'Ivoire : résultats préliminaires pour les milieux ouverts. Le cas d'*Oenomys hypoxanthus ornatus*. *Mammalia* 43: 252-254.
- VAN DER STRAETEN E. 1975. — *Lemniscomys bellieri*, a new species of Muridae from the Ivory Coast. *Rev. Zool. Afr.* 89: 906-908.
- VAN DER STRAETEN E. & DIETERLEN F. 1992. — Craniometric comparison of four populations of *Praomys jacksoni* captured at different heights in Eastern Zaire (Kivu). *Mammalia* 56: 125-131.
- VAN DER STRAETEN E. & DUDU A. M. 1990. — Systematics and distribution of *Praomys* from the Masako Forest Reserve (Zaire), with the description of a new species, in PETERS G. & HUTTERER R. (eds), *Vertebrates in the Tropics*. Alexander Koenig Museum, Bonn.
- VAN DER STRAETEN E. & PETERHANS J. C. K. 1999. — *Praomys degraaffi*, a new species of Muridae (Mammalia) from central Africa. *S. Afr. J. Zool.* 34: 80-90.
- VAN DER STRAETEN E. & VERHEYEN W. N. 1978. — Karyological and morphological comparisons of *Lemniscomys striatus* (Linnaeus, 1758) and *Lemniscomys bellieri* Van der Straeten, 1975, from Ivory Coast (Mammalia: Muridae). *Bull. Carn. Mus. Nat. Hist.* 6: 41-47.
- VAN DER STRAETEN E. & VERHEYEN W. N. 1982. — Différences biométriques entre *Hybomys univittatus* (Peters) et *Hybomys trivirgatus* (Temminck) de l'Afrique de l'ouest. *Bonn. Zool. Beitr.* 33: 205-213.
- VERHEYEN W.N., COLYN M. & HULSEMANS J. 1996. — Re-evaluation of the *Lophuromys nudicaudus* HELLER, 1911 species-complex with a description of a new species from Zaire (Muridae — Rodentia). *Bull. Konink. Belg. Instit. Natuur.* 66: 241-273.
- 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). *Chrom. Res.* 8: 689-697.
- YALDEN D. W., LARGEN M. J., KOCK D. & HILLMAN J. C. 1996. — Catalogue of the mammals of Ethiopia and Eritrea. 7. Revised checklist, zoogeography and conservation. *Trop. Zool.* 9: 73-164.

APPENDIX 1

Outline of synonymy for the *Dasymys* genus. Comparisons between species were based primarily on significant results ($p < 0.05$) from the one-way ANOVA. A map representing this outline is provided in Fig. 8.

Dasymys capensis Roberts, 1936
Annals of the Transvaal Museum 18: 254.

TYPE LOCALITY. — La Plisante, Wolseley, Western Cape Province, South Africa (TM).

SPECIMENS EXAMINED. — South Africa (Wolseley, Knysna, Humansdorp).

DIAGNOSIS. — *Dasymys capensis* is characterised by a wide nasal, zygomatic arch and braincase breadth. Its skull structure is most similar to that of *D. foxi*, *D. incomtus* from the KwaZulu-Natal Province and *D. griseifrons*. The ANOVA indicated that the skull of *D. capensis* has the most significant differences with those of *D. montanus*, *D. longipilosus* and *D. rufulus*.

REMARKS. — This subspecies should be elevated to species status based on distinct morphological characteristics in addition to a restricted and isolated distribution range. Distinguishing characteristics include a significantly wider zygomatic arch width, braincase breadth and maxillary tooththrow than the other specimens.

Dasymys foxi Thomas, 1912
Annals and Magazine of Natural History series 8, 9: 685.
TYPE LOCALITY. — Jos Plateau, Panyam, 4000 ft, Nigeria (USNM).

SPECIMENS EXAMINED. — Nigeria (Panyam, Ugar Jabar).

DIAGNOSIS. — The one-way ANOVA does not show *D. foxi* to have any significant distinguishing characteristics among the 11 species examined. *Dasymys foxi* has an overall intermediate size when compared to the other species and is generally larger than *D. rufulus*. Significant differences between *D. foxi* and *D. rufulus* were limited to longer upper tooththrow and larger skull height in *D. foxi*. Otherwise, univariate methods showed that *D. foxi* and *D. rufulus* have similar skull sizes. Its skull is most similar to material from Eastern (*D. griseifrons*, *D. medius*) and southern Africa (*D. incomtus* and *D. robertsii*) and the most distinct from *D. nudipes*, *D. montanus* and *D. longipilosus*, with few measurements in common.

REMARKS. — *Dasymys foxi* is provisionally being recognised here as a separate species, but genetic data are needed to resolve whether it might be a subspecies of *D. rufulus* based on some of the multivariate results presented in this study.

Dasymys griseifrons Osgood, 1936
Field Museum Publications of Zoology 10: 255.

TYPE LOCALITY. — South-west side of Lake Tana, near Dungulbar, Gojjam, Ethiopia (FMNH). SPECIMENS EXAMINED. — Ethiopia (Lake Tana, Jigga).

DIAGNOSIS. — Although *D. griseifrons* has a large body and skull size, it is generally not as large as those of *D. nudipes*, *D. capensis* or *D. shortridgei*. It is distinguished in that it has the widest interorbital constriction and an overall large size in terms of both external and cranial measurements. This species has a similar skull to *D. foxi*, *D. robertsii*, *D. shortridgei*, *D. incomtus* and *D. medius* in terms of its larger cranial features. *Dasymys griseifrons* was significantly distinct from *D. montanus*, *D. nudipes* and *D. longipilosus*.

REMARKS. — *D. griseifrons* has a similar skull (in terms of both size and shape) to *D. medius*, its geographically closest neighboring species, but morphological data suggest it is distinct. The skull of the second Ethiopian OTU (Jimma) was more similar to East African material (*D. medius*) than was the case for *D. griseifrons*. Despite this similarity, we believe that all of the Ethiopian material belongs within a separate group (and not *D. medius*), although it is unclear what the exact relationship is between individuals from Jimma and Lake Tana. For this reason, Jimma is represented by a question mark in the map provided in Figure 8. We feel that all Ethiopian material should be examined further using genetic techniques, as biogeography would suggest the separation between Ethiopian material and *D. medius*. Furthermore, Volobouev *et al.* (2000) documented two different karyotypic races of *Dasymys* occurring in Ethiopia, neither of which were represented in this study.

Dasymys incomtus (Sundevall, 1847)
Öfversigt af Kungliga Svenska Vetenskapsakademiens Förhandlingar 1846, 2: 120 [1847].

TYPE LOCALITY. — Durban, KwaZulu-Natal, South Africa.

SYNONYMS. — *Dasymys incomtus incomtus* (*Mus incomtus*) Sundevall, 1847. South Africa, "Caffraria prope Portum Natal" (Durban, Natal). *Dasymys incomtus fuscus* De Winton 1869: Proceedings of the Zoological Society, London, (1869): 804. Mazoe, Mashonaland, northeastern Zimbabwe.

SPECIMENS EXAMINED. — The KwaZulu-Natal Province of South Africa (Vryheid, Dukuduku, Futululu, Hazelmere Nature Reserve, Richards Bay, Eshowe, Durban, Mfongosi, Karkloof, Kamberg, Albert Falls, Kilgobbin, Coleford Nature Reserve, Port St Johns) and southeastern Zimbabwe (Matopos, Mt Selinda, Mazoe and Musirizwi River).

DIAGNOSIS. — *Dasymys incomtus* has an intermediate skull size and significantly larger upper tooththrow length when compared to the other species examined. Although it has a general larger size than *D. robertsii* (from the Limpopo/Mpumalanga Provinces of South Africa), none of the characters showed significant differences. The ANOVA results showed that the skull is most similar to those of *D. foxi*, *D. robertsii* and

D. griseifrons and most distinct from those of *D. nudipes*, *D. montanus* and *D. longipilosus*.

REMARKS. — Although univariate results (ANOVA) do not show a difference between *D. incommutus* from the KwaZulu-Natal Province and specimens from the Limpopo and Mpumalanga Provinces (referred to here as *D. robertsii*), multivariate results and genetic data (Mullin *et al.* 2002) unequivocally show *D. incommutus* and *D. robertsii* as separate.

Dasymys longipilosus Eisentraut, 1963.

Die Wirbeltiere des Kammerungebirges: 132.

TYPE LOCALITY. — Musaka Hut, southern slope of Mount Cameroon, 2200 m, Cameroon (SMNS).

SPECIMENS EXAMINED. — Cameroon (Mount Cameroon).

DIAGNOSIS. — This species has dark pelage and a short tail, although not as dark or short as seen in *D. montanus*. Distinguishing features include a small hind foot and a small total body length in addition to a small condylobasal length, upper tooththrow length, internal diameter of the zygomatic arch, greatest mandible length and mandibular tooththrow length. This species has a skull similar to *D. medius* and *D. foxi* and its small size makes it particularly distinct from *D. nudipes*, *D. capensis*, *D. griseifrons* and *D. shorridgei*.

REMARKS. — *Dasymys longipilosus* was represented by a small sample size in this study. More individuals should be examined before it is erected as a separate species. *Dasymys longipilosus* is restricted to high altitudes (> 2000m) and is only known from Mount Cameroon.

Dasymys medius Thomas, 1906.

Annals and Magazines of Natural History series 7 18: 143.

TYPE LOCALITY. — Toro, Mubuku Valley, E. Ruwenzori, Uganda (NHM).

SPECIMENS EXAMINED. — Burundi, eastern Democratic Republic of Congo (Buhengeri, Kahungu, Kalehe, Medje, Lubero, Lushala, Medje, Muganzo, Rutshuru), Kenya, Rwanda and Uganda (all localities except the single locality representing *D. montanus*).

SYNONYMS. — *Dasymys incommutus helukus* Heller, 1910: *Smithsonian Miscellaneous Collections* 54: 2. Sirgoit, Guas Ngishu Plateau, Kenya. *Dasymys incommutus nigridius* Hollister, 1916: *Smithsonian Miscellaneous Collections* 10: 2. Naivasha, Kenya. *Dasymys incommutus orthos* Heller, 1911: *Smithsonian Miscellaneous Collections* 56: 13. Butiaba, Albert Nyanza, Uganda. *Dasymys incommutus savannus* Heller, 1911: *Smithsonian Miscellaneous Collections* 17: 14. Fort Hall, Kenya. *Dasymys incommutus shawi* Kershaw, 1924: *Annual Magazine of Natural History* 9: 25. Mount Baginzi, Bahr-el-Ghazal, Sudan.

DIAGNOSIS. — *Dasymys medius* is distinct in terms of its small upper tooththrow length and small upper zygomatic arch width. The skull of *D. medius* was most similar to those of *D. foxi* and *D. rufulus*. *Dasymys medius* was most distinct from *D. nudipes* and *D. capensis*.

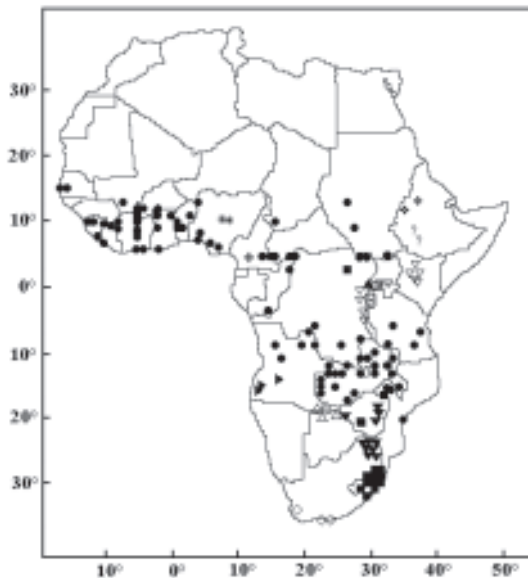


FIG. 8. — Map of localities used in this study (provided in Table 1). ●, *rufulus* complex (including *D. rufulus* from West Africa and material from CAR, Cameroon, northern Angola, Zambia, Tanzania, Malawi and Mozambique); ○, *D. foxi*; ◆, *D. cf. griseifrons*; ◻, unknown; ▷, *D. cf. longipilosus*; ◁, *D. cf. medius*; π, *D. montanus*; υ, *D. nudipes*; ρ, *D. cf. shorridgei*; ■, *D. incommutus*; ⋈, *D. cf. robertsii*; +, *D. cf. capensis*.

REMARKS. — *Dasymys medius* does not appear to be part of a species complex. It is somewhat surprising that this material was not more similar to material from Tanzania or Malawi, but perhaps a future study including material from these two countries (and particularly from northern Tanzania) would show otherwise.

Dasymys montanus Thomas, 1906

Annals and Magazines of Natural History, series 7 18: 143.

TYPE LOCALITY. — Toro, Mubuku Valley, eastern Ruwenzori Mountains, 12,500 ft, Uganda (NHM).

SPECIMENS EXAMINED. — Uganda (Ruwenzori Mountains at high altitudes only).

DIAGNOSIS. — *Dasymys montanus* has a small size overall (both in terms of cranial and external measurements). Distinct characteristics include dark pelage and a short tail (head-body/tail ratio) in addition to small cranial features (greatest skull length, upper zygomatic arch width, zygomatic plate width, greatest mandible length and greatest height of the skull). The skull of *D. montanus* is most similar to that of *D. medius* and although its skull does not appear to be similar to many of the other species, it is most distinct from those of *D. nudipes*, *D. capensis* and *D. griseifrons*.

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REMARKS. — Cranial measurements for type are not available. The type skull, deposited in the Museum of Natural History, London, is not intact. An allotype must be designated. Although it has a similar skull to *D. medius* (perhaps due to the small sample size for this species in this study), we feel that its dark pelage, short tail, small cranial and external measurements and its restriction to high altitudes confirms its species status. *Dasymys montanus* has been recorded from 3000 m while *D. medius* is found closer to 1000 m.

Dasymys nudipes (Peters, 1970)

Jornal de ciencias mathematicas, physicas e naturaes, series 1 3: 126.

TYPE LOCALITY. — Huila, Angola.

SPECIMENS EXAMINED. — Angola (Dondi, Huila, Humpata).

DIAGNOSIS. — *Dasymys nudipes* generally has a larger size (both external and cranial) than all of the specimens examined. Distinguishing features include a significantly longer tail, hind foot, total body length and head-body/tail ratio in addition to the following cranial characters: condylobasal length, upper toothrow, hard palate width, zygomatic arch width, braincase breadth, internal diameter of the zygomatic arch, foramen magnum width, mandible length, maxillary toothrow and incisor to condyle length. Also, *D. nudipes* appears to be the only *Dasymys* species with a longer tail than body length. Its skull is most similar to *D. capensis* and is significantly distinct from the other nine species examined.

REMARKS. — Restricted to the southwestern plateaus of Angola.

Dasymys robertsii n. sp.

HOLOTYPE. — TM40249; skin and skull; adult male; collected by Bronner *et al.* on August 24, 1988.

TYPE LOCALITY. — Klipfontein, 30 km NE Vaalwater, Waterberg; 1091 m, South Africa.

SPECIMENS EXAMINED. — The Limpopo and Mpumalanga Provinces of South Africa (Punda Milia, Soutpansberg, Tzaneen, Potgietersrus, Klipfontein, Nylsvlei, Pretoria, Vaalwater, Barberton, Gladdespruit, Arnheimburg, de Hoop Private Nature Reserve, Lydenburg, Hectorpsruit), eastern Botswana (Kasane) and western/northwestern Zimbabwe (Nyamnyetsi, Chinyika River, Harare, Chibeto, Umtali and Troutbeck Lake).

ETYMOLOGY. — The name “robertsii” honours A. Roberts who was the first to suggest that Limpopo and Mpumalanga *D. incommutis* were separate from KwaZulu-Natal Province *D. incommutis*; however, Roberts (1951) did not provide an accession number or a description of the “type” for Limpopo and Mpumalanga specimens he mentioned.

DIAGNOSIS. — *Dasymys robertsii* n. sp. is generally smaller in size than *D. incommutis* from the KwaZulu-Natal Province. Its skull is most similar to material representing *D. foxi*, *D. incommutis* from the KwaZulu-Natal Province and *D. griseifrons*. *Dasymys robertsii* n.

sp. is most distinct from *D. rufulus*, *D. nudipes* and *D. longipilosus*. Standard measurements of the skull: GSL = 36.81, UTR = 7.64, PWM = 3.22, NAS = 4.17, ZYN = 13.04, BBC = 14.17, FRO = 14.27, IOB = 4.61, FMW = 5.72, UMW = 1.31, ZPW = 4.43, GML = 27.49, MTR = 7.30, GHS = 11.60, HB = 157 mm, TL = 135 mm, HF = 35.0 mm, E = 21.0 mm, TOT = 292, M = 102 g, HB/TL ratio = 85.99%.

REMARKS. — Tissue samples for the type specimen are in storage at the TM museum. *Dasymys robertsii* n. sp. is not similar to *D. incommutis* from the KwaZulu-Natal Province, confirming genetic studies (Gordon 1991; Mullin *et al.* 2002).

Dasymys rufulus Miller, 1900

Proceedings of the Washington Academy of Sciences 2: 639.

TYPE LOCALITY. — Mount Coffee, Liberia (MCZ).

SYNONYMS. — *Dasymys incommutis allenii* Lawrence & Loveridge, 1953: *Bulletin of the Museum of Comparative Zoology at Harvard College* 100 (1): 53. Iloilo, Mount Rungwe, southwestern Tanzania; *Dasymys bentleyae* Thomas, 1892, Ngombe, Zaire. *Mus (Dasymys) incommutis bentleyae* Thomas, 1892: *Annals and Magazines of Natural History* 10 (6): 179. *Dasymys incommutis edsoni* Hatt, 1934: *American Museum Novitates* 708: 6. Lukolela, Middle Congo (Democratic Republic of Congo).

SPECIMENS EXAMINED. — Senegal, Guinea, Sierra Leone, Liberia, southern Mali, Burkina Faso, Ivory Coast, Ghana, Togo, Benin, Nigeria, Southern Chad, southern Sudan, Cameroon, Central African Republic, Congo, western and northern Democratic republic of Congo (Bagbele, Bukarabwa, Faradje, Kinshasha, Likouala, Lubumbashi, Lukolela, Luluabourg, Nambira, Nambirima, Ngombe), Tanzania, northern Angola (Chitau, Dundo, Duque de Braganca, Mombolo), Zambia, Malawi and Mozambique.

DIAGNOSIS. — *Dasymys rufulus* has a significantly smaller zygomatic plate width, mandible length, incisor to condyle length and skull height than the other 10 groups examined. It is most similar to *D. medius* and *D. foxi* in terms of its overall skull size. The skull of *D. rufulus* is most distinct from *D. nudipes*, *D. capensis*, *D. longipilosus* and *D. shortridgei*.

REMARKS. — *Dasymys rufulus* appears to be part of a species complex that includes material from central (Cameroon, CAR, DRC, northern Angola, Zambia) and east Africa (Tanzania, Malawi and Mozambique).

Dasymys shortridgei n. sp.

HOLOTYPE. — AM5899; skin and skull; adult male; collected by G.C. Shortridge on June 28, 1929.

TYPE LOCALITY. — Okavango-Omatoko, Grootfontein; 1080m, Namibia.

SPECIMENS EXAMINED. — Botswana (Boro Island, Moremi) and Namibia (Diwai, Gangongo, Mohango Drift, Okavango-Omatoko Junction, Sinjamba).

ETYMOLOGY. — The name *shortridgei* honours G.C. Shortridge as he collected the majority of the *Dasymys* specimens from the Okavango Delta.

DIAGNOSIS. — *Dasymys shortridgei* n. sp. is characterised as having a long tail and large head-body/tail ratio in addition to a large upper toothrow length and internal diameter of the zygomatic arch. This species is most similar to *D. foxi*, *D. griseifrons* and *D. robertsii* n. sp. *Dasymys shortridgei* is most distinct from *D. nudipes*, *D. montanus* and *D. longipilosus*. Standard measurements of the skull: GSL = 38.63, UTR = 7.11,

PWM = 3.33, NAS = 4.26, ZYN = 18.36, BBC = 14.13, FRO = 14.64, IOB = 4.39, FMW = 5.74, UMW = 1.59, ZPW = 4.33, GML = 27.40, MTR = 7.24, GHS = 11.70, HB = 171mm, TL = 150mm, HF = 37.0mm, E = 19.0mm, TOT = 321, M = N/A, HB/TL ratio = 87.72%.

REMARKS. — *Dasymys shortridgei* n. sp. is not similar to *D. nudipes* and should not be considered its subspecies.

PROOF