Praomys degraaffi, a new species of Muridae (Mammalia) from central Africa

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A new *Praomys* species from Burundi, Rwanda and Uganda, *Praomys degraaffi* n. sp., is described in the *P. jacksoni* species-complex. It occurs at high elevations in montane forests of the Albertine Rift. The new species is compared with *P. jacksoni* from the same region and with the other species in the *P. jacksoni* species-complex.

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Introduction

During field surveys in Kibira National Park (Burundi) in 1990 and 1991, two sympatric morphotypes of *Praomys* were recognized. Although both forms belong to the *P. jacksoni* species-complex (*sensu* Van der Straeten & Dudu 1990), they differ in number of mammae. Subsequent surveys in the Albertine Rift Mountains and examination of museum collections further defined the distribution of one of the morphotypes, which we describe as a new species, *Praomys degraaffi*. It is distinguishable by external, cranial and karyological characters. The distribution of the new species includes montane forests, from Bururi Forest in southern Burundi to Bwindi-Impenetrable National Park in southwestern Uganda. As such, this species can be added to the Albertine Rift zone of endemism.

Material and methods

For this study we examined 638 *Praomys* specimens from the following museums and private collections: American Museum of Natural History, New York (AMNH); Carnegie Museum of Natural History, Pittsburgh (CM); Field Museum of Natural History, Chicago (FMNH); Institut de Zoologie et d'Ecologie Animale, Lausanne (IZEA); Koninklijk Museum voor Midden Afrika, Tervuren (KMMA); National Museum of Natural History, Washington DC (USNM); The Natural History Museum, London (NHM); Staatliches Museum für Naturkunde, Stuttgart (SMNS); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK); A. Dudu (DUD) from the République Démocratique du Congo, and D.C.D. Happold (HAP) from Nigeria. The following specimens were used:

Praomys degraaffi

See list under holotypes and paratypes.

Praomys jacksoni

Burundi: Gatare Stream, Giserama Colline (FMNH 149246, 149248, 149260, 149262, 149267, 149279); Gitenge River Swamp (FMNH 148842-43); Kwogofe Colline (FMNH 149333); Nyagatarugwa Valley (FMNH 148791); Nyamugari Colline (FMNH 138013).

Kenya: Kakamega Forest Station (CM 98425, 98428, 98522-23)

Rwanda: Gahinga (KMMA M.98038.2152); Gasiza (KMMA M.98038.2148-2151, M.98038.2153-2154); Kayove (KMMA M.98038.2069-2075, M.98038.2155-2160); Kinigi Bureau: (KMMA M.98038.2044-2047, M.98038.2064-2068); Muhabura (KMMA M.98038.2142-2147); Ntango (KMMA M.98038. 2037-2040, M.98038.2048-2063); Routabansougera: (KMMA M.98038.2007-2034, M.98038.2076-2144); Uwinka: (KMMA M.98038.2035-2036, M.98038.2041-2043).

Uganda: Buhoma (FMNH 160822); Entebbe (NHM 99.8.4.68 holotype); region Entebbe (NHM 64.602-604, 64.606-612, 64.614, 64.616-620, 64.622-623, 64.625, 64.627-628).

Praomys cf. jacksoni

Kenya: Ikuywa River Bridge (CM 98524).

Praomys minor

République Démocratique du Congo: Lukolela (AMNH 86814, 86816 holotype, 86822, 96824; KMMA 13037).

Praomys montis

Uganda: Mubuku Valley (NHM 6.7.1.96, 6.7.1.97 holotype, 6.7.1.98, 6.7.1.100-103, 6.7.1.105-107).

Praomys mutoni

République Démocratique du Congo: Batiabongena (DUDU 893, 1138, 1161, 1308, 1177; KMMA 92.151.M1 holotype, 92.151.M2-M22; ZFMK 92.328-29).

Praomys peromyscus

Kenya: Ngarri Narak (USNM 162365, 162368, 162376-77, 162381-83); Njoro O Nyiro (USNM 161905 holotype).

Praomys sudanensis

Sudan: Gilo (SMNS 27177, 27181-82, 27184, 27189-191, 27193, 27196, 27199-200, 27225, 27877, 27879-880, 27892-94, 27898, 27903-904, 27910-11, 27932); Iwatoku (SMNS 30419, 30422-23); Kagelu (SMNS 27987); Katire (SMNS 27905); Korobe Forest (SMNS 27980-81, 27983, 27985); Lotti Forest (FMNH 67268 holotype); Nagichot (SMNS 27169-72, 27195, 30415-16); Talanga Forest (SMNS 27937, 27941, 28276-77, 30411-12); Yei (near) (SMNS 27203, 27205, 27207, 27209-14, 27216-20, 27222, 27946, 27948, 27950, 27957, 27960, 27962, 27965, 27968, 27973-74, 27977).

Praomys viator

Nigeria: Abuja (HAP 1175, 1185); Panyam (NHM 11.3.24.18 holotype).

Statistical methods, definitions and descriptions of measurements (see Table 1) follow Van der Straeten & Van der Straeten-Harrie (1977) and Van der Straeten & Dieterlen (1987). For the canonical analysis (Seal 1964) we used the method, terminology and programs adapted by Hebrant (1974). This analysis maximizes the between groups variation in relation to the within groups variation. The original variables are transformed to a new set of canonical variables. Thereto eigenvalues and eigenvectors are calculated. This permits representation of the specimens and of the group centroids. For a specimen each original variable (measurement) is multiplied by its corresponding coefficient of the eigenvector (see Table 3 or 4) and the resultant values are added up. This is done for all specimens in each of the canonical variates. Now, using the obtained values, each specimen can be plotted in a diagram of canonical variates represented as an abscissa or an ordinate. Neighbouring groups are biometrically more related than distant ones (Van der Straeten & Dieterlen 1987). Nomenclature of cranial foramina and cranial bones follows Carleton & Musser (1989) while the terminology and arrangement of plantar pads is adopted from Kimura, Schaumann & Plato (1994). External body measurements were recorded from specimen labels. Measurements of foot length and breadth of fluid-preserved Rwandan specimens were recorded by EVDS, while those from Burundi and Uganda were recorded by JCKP. Foot length included the claw while foot breadth was measured at the base of the first toe. Specimens were divided into arbitrary age groups using the degree of wear on the first and second upper molar (Verheyen & Bracke 1966). These age groups were tested to evaluate their statistical integrity. To identify the specimens used in the multivariate analyses, we used only external characters: structure of the small accessory pads of the hindfoot (for the alcohol-preserved specimens), the mammary formula (for adult females), foot breadth and colour. Using this combination of characters it was possible to identify all the adult specimens.

***Praomys degraaffi* n.sp.**

Holotype

Adult female (age class 4), alcohol specimen and skull, FMNH 137573 [original number 1089], Nyamugari (abris) (Burundi), 2200 m, collected by J.C. Kerbis Peterhans, on 30 March 1990. For measurements see Table 1.

Paratypes

Listed as follows: specific locality, total number, sex and specimen number associated with museum acronym.

Burundi (238): Busekera (7), male FMNH 138051-52, 138060, female FMNH 138059, 138073-74, 138076; Gitenge River Swamp (11), male FMNH 148841, 148844, 148846-47, female FMNH 148833-34, 148836, 148838-40, 148845; Gitenge Valley (1), male 148832; Kivuso, Abris (1), male FMNH 148830; Kwogofe Colline (9), male FMNH 148827, 148820, 148823-25, female FMNH 148814, 148826, 148818, 148822; Mabay (1), male IZEA 2708; Mumushwizi Valley (38), male FMNH 156028, 156031, 156033, 156041, 156043-48, 156050, 156052-54, 156060, 156063, 156066-68, female FMNH 156029-30, 156033, 156036, 156039-40, 156042, 156049, 156051, 156055, 156057-59, 156061-62, 156064-65, 156069-70; Myrianthus Campground (6), male FMNH 148875-78, 148880, female FMNH 148879, Nyabikona River (3), male FMNH 148756, female FMNH 148750, 148768; Nyamugari Abris (116), male FMNH 137552, 137556-59, 137561-62, 137569, 137571, 137701, 137829, 137900, 137910, 137914-15, 137917, 137922-23, 137925, 137927, 137934, 137939, 137941, 137943-44, 137946, 137953, 137957, 137960, 137962-66, 137968-69, 137971-72, 137974-78, 137980-84, 137986-88, 137990, 137993-94, 137999-8000, 138003, 138005-06, 138008, 138010-12, 138020-21, 138027, 138030, 138032, 138036, 148852, 148856-57, 148863, 148866, 148868, 148872-73, female FMNH 137551, 137553, 137555, 137560, 137563-64, 137566, 137572, 137898-99, 137932, 137950, 137951-52, 137961, 137967, 137970, 137973, 137979, 137985, 137992, 137995-96, 138001, 138009, 138015-16, 138019, 138023, 138025, 138029, 138033, 148851, 148853, 148858, 148860, 148869, 148871, 148874; Nyamugari, N of Abris (14), male FMNH 138040, 138046-47, 138050, female FMNH 137574-75, 138037, 138039, 138041-43, 138045, 138048-49; Ruhinga Hill (29), male FMNH 156072, 156077, 156082-84, 156086, 156092, 156097-98, 156102-03, 156105-06, female FMNH 156073-76, 156079-81, 156085, 156090-91, 156093-96, 156099, 156104; Teza Park Headquarters (2), male FMNH 148884-85.

Rwanda (22): Gahinga (1), male KMMA M.98038.2182; Kayove (3), male KMMA M.98038.2169, female KMMA M.98038.2170, M.98038.2183; Muhabura (11), male KMMA M.98038.2171-2172, M.98038.2176, M.98038.2178-2180, female KMMA M.98038.2173-2175, M.98038.2177, M.98038.2181; Uwinka (6), male KMMA M.98038.2163-2167, female KMMA M.98038.2162; Visoke Camp (1), female KMMA M.98038.2168.

Uganda (56): Bwindi-Impenetrable National Park (8), male NHM 63.725-63.728, female NHM 63.732, 63.734, 63.738-739; Echuya Forest (18), male NHM 63.742, FMNH 161127-28, 161132, 161134-39, female NHM 63.743-744, FMNH

Table 1 Measurements (taken in mm by EVDS) and weight in gram of holotype (FMNH 137573) and adult specimens of *Praomys degraaffi* n.sp. from central Africa (Uganda, Rwanda, Burundi). Numbers represent sample size, mean, range and standard deviation, respectively

symbol	Variable	holotype	age class 2-3	age class 4-7
W	weight	45,5	11; 31,3 (26,0 - 37,0) 3,6	39; 40,4 (28,0 - 64,0) 6,2
HB	head and body length	118,0	11; 102,3 (90,0 -111,0) 7,9	38; 110,8 (92,0 -124,0) 7,6
HL	length of tail	144,0	12; 126,6 (111,0 -136,0) 7,4	40; 136,3 (115,0 -151,0) 9,2
HL+N	length of hind foot + nail	25,50	18; 25,6 (23,0 - 27,0) 1,1	48; 26,4 (24,0 - 29,0) 1,2
EL	length of ear	18,00	16; 18,9 (17,0 - 22,0) 1,6	41; 19,6 (17,0 - 22,0) 1,3
HL/HB	ratio: length hind foot/ breadth hind foot	6,37	4; 6,62 (6,45 - 6,81) 0,20	16; 6,28 (5,91 - 6,63) 0,25
GRLE	greatest length of skull	31,05	20; 30,02 (28,50- 32,40) 1,02	48; 31,28 (29,10- 32,90) 0,84
PRCO	prosthion-condylion (condylobasal length)	28,65	20; 27,19 (26,05- 28,95) 0,81	48; 28,50 (26,65- 30,30) 0,86
HEBA	henselion-basion (basilar length)	24,60	20; 23,33 (22,25- 25,00) 0,74	48; 24,56 (23,00- 26,15) 0,73
HEPA	henselion-palation (palatilar length)	13,80	20; 13,07 (12,05- 14,10) 0,52	49; 13,74 (12,70- 14,65) 0,44
PAF	length of palatal foramina	7,15	20; 6,70 (6,15 - 7,30) 0,30	49; 7,02 (6,10 - 7,75) 0,30
DIA1	length of diastema	8,25	20; 7,94 (7,40 - 8,55) 0,28	49; 8,38 (7,65 - 9,15) 0,33
DIA2	distance between the anterior border of the alveolus of M^1 and the edge of upper incisor	8,90	20; 8,52 (7,95 - 9,15) 0,27	48; 9,07 (8,30- 10,00) 0,35
INT	interorbital breadth	4,75	19; 4,87 (4,65 - 5,10) 0,16	49; 4,98 (4,55 - 5,35) 0,18
ZYG	zygomatic breadth on the zygomatic process of the squamosal	14,75	20; 14,23 (13,50- 15,30) 0,51	48; 14,71 (13,20- 15,65) 0,46
PAL	palate breadth between M^1's	3,15	19; 2,89 (2,70 - 3,15) 0,13	49; 2,98 (2,65 - 3,35) 0,17
UPTE	length of upper cheekteeth	5,10	20; 5,03 (4,55 - 5,40) 0,25	49; 5,19 (4,90 - 5,55) 0,15
UPDE	breadth of upper dental arch (breadth across M^1's)	5,95	20; 5,78 (5,40 - 6,10) 0,16	49; 6,01 (5,65 - 6,40) 0,18
M^1	breadth of first upper molar (crown breadth)	1,45	20; 1,48 (1,40 - 1,55) 0,05	49; 1,48 (1,35 - 1,60) 0,05
ZYPL	breadth of zygomatic plate	3,50	20; 3,30 (3,00 - 3,75) 0,19	49; 3,49 (3,05 - 3,90) 0,17
BNAS	greatest breadth of nasals	3,15	20; 3,06 (2,85 - 3,40) 0,15	49; 3,22 (2,95 - 3,70) 0,15
LNAS	greatest length of nasals	11,90	20; 11,55 (10,75- 12,65) 0,55	49; 12,20 (10,60- 13,10) 0,47
LOTE	length of lower cheekteeth	4,80	20; 4,73 (4,45 - 5,10) 0,18	49; 4,78 (4,50 - 5,25) 0,15
CHOA	breadth of choanae (mesopterygoid fossa)	1,90	20; 1,58 (1,35 - 1,95) 0,15	48; 1,64 (1,20 - 2,00) 0,17
BUL	length of auditory bulla	4,95	20; 4,73 (4,40 - 5,05) 0,17	49; 4,83 (4,55 - 5,05) 0,11
BRCA	braincase breadth	12,50	20; 12,36 (11,20- 13,45) 0,55	48; 12,58 (11,75- 13,60) 0,39
DIN	depth of incisors	1,45	20; 1,42 (1,25 - 1,42) 0,07	49; 1,53 (1,40 - 1,70) 0,08
ROH	rostrum height at anterior border of M^1	6,75	20; 6,52 (6,25 - 7,10) 0,23	49; 6,90 (6,25 - 7,45) 0,27
ROB	rostrum breadth at anterior border of zygomatic plate	5,30	20; 4,94 (4,50 - 5,45) 0,22	49; 5,32 (4,80 - 5,90) 0,23
PCPA	distance between the extreme points of coronoid process and angular process	9,00	18; 8,64 (7,80 - 9,55) 0,51	42; 9,14 (8,15 - 9,95) 0,42

161126, 161129-31, 161133, 161140; Gahinga, slope of (Kabiranyuma pipeline) (14), male FMNH 157785-86, 157788-90, 157792-93, 157795-97, female FMNH 157784, 157787, 157791, 157794; Mgahinga and Sabinyo (pas between) (2), female FMNH 26126-27; Ruhija (15), male FMNH 157971-73, 157979, 157983, 160863-64, 160866, 160869 female FMNH 157964, 157977-78, 157982, 160865, 160867.

Diagnosis

Differs from other members of the *Praomys jacksoni* species-complex by its darker colour, different mammary formula (2-2=8), different configuration of accessory pads on the hind-foot and a unique karyotype (2n=26, NF=28, AA=24; Maddalena, Van der Straeten, Ntahuga & Sparti 1989). Restricted to moist montane forest of the Albertine Rift.

Etymology

This species is named *Praomys degraaffi* in honour of the late Gerrie de Graaff, our friend and colleague, and this is to express our appreciation for his life and work.

Description

The skull of *P. degraaffi* has all the characters typical of the *P. jacksoni* species-complex. The supraorbital temporal ridges are raised and the outer cusp of the first transverse lamina (t3) of the upper M^1 is well developed (Van der Straeten &

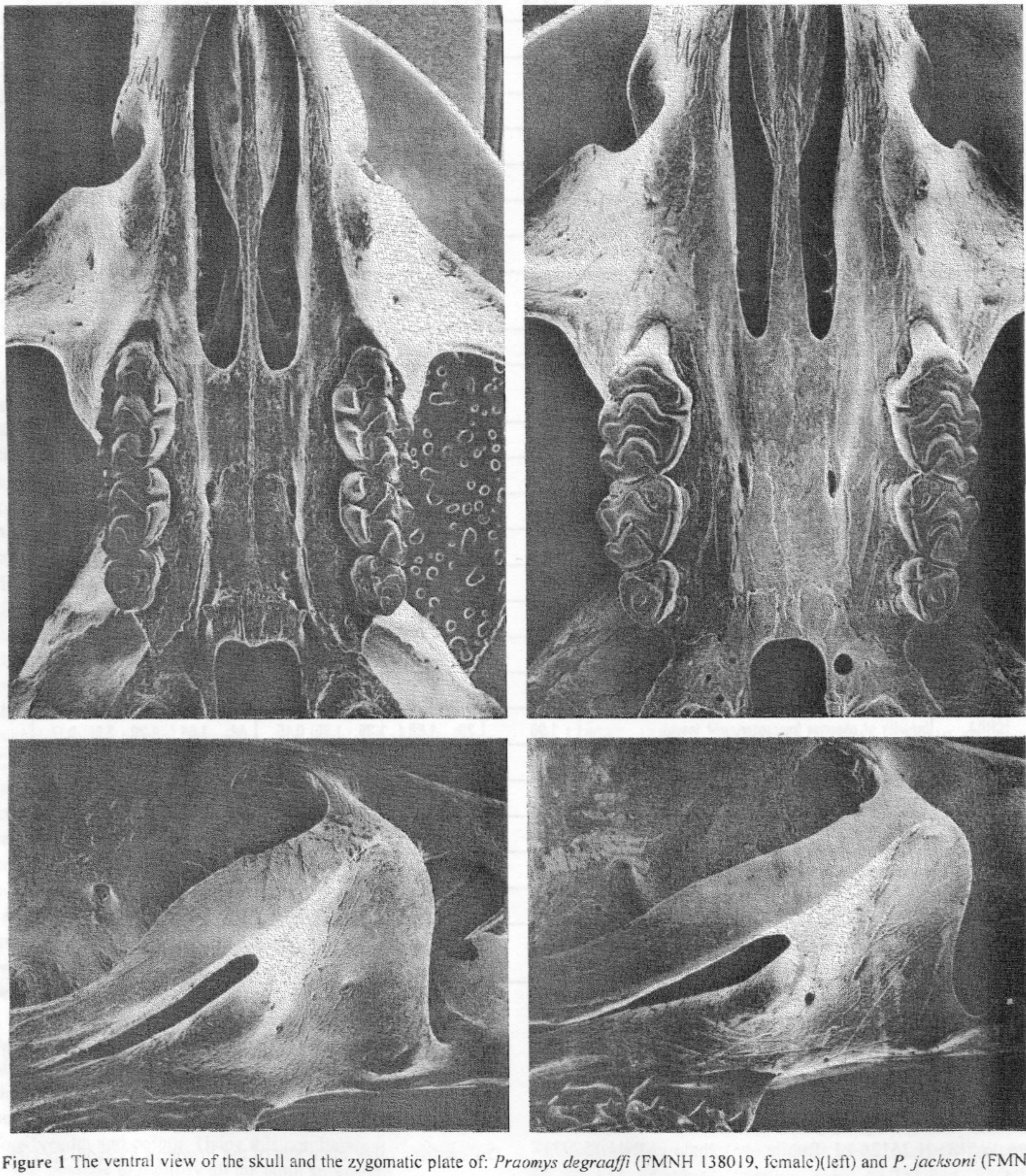

Figure 1 The ventral view of the skull and the zygomatic plate of: *Praomys degraaffi* (FMNH 138019, female)(left) and *P. jacksoni* (FMNH 160882, male) (right).

Dieterlen 1987). On the second upper molar t3 is small. The incisive foramina are usually rounded and broad and reach well between the first upper molars (Figure 1). The palatine bone reaches forward into M^1. For measurements of type and paratypes see Table 1. (For measurements of other species in the *jacksoni* species-complex see Van der Straeten & Dieterlen [1987] [*Praomys jacksoni*] and Van der Straeten & Dudu [1990] [*Praomys mutoni*]).

The overall pelage is dark, typically a dark grey or sooty black. There are two pairs of pectoral and two pairs of inguinal mammae, 2–2=8. The hindfoot has six large plantar pads with either one or no small accessory pad (Figure 2). Seven palatal ridges are present: 2+5.

An unnamed species of *Praomys* mentioned in Maddalena *et al.* (1989) is referable to *P. degraaffi*. This study recorded the karyotype as: 2n=26, NF=28 and AA=24. The karyotypic difference with *P. jacksoni* is in the absence of one pair of acrocentric chromosomes.

Comparisons

Praomys degraaffi is significantly larger (t-test, 1% significance level) than *P. jacksoni* (same age and region) in two measurements: the breadth of the mesopterygoid fossa (CHOA) and the breadth of the zygomatic plate (ZYPL).

Qualitative characters (Figure 1) of the skull are quite subtle and more variable than external characters. Rarely all characters are found on the same specimen. Compared with *P. jacksoni* from the same region, the posterior palatine foramina is often between the first lamina of M^2 (in *P. jacksoni* between M^1 and M^2) while the suture between the palatine bones and the maxillae extends more posteriorly. The ends of the incisive foramina in *P. degraaffi* are often more rounded and usually reach beyond the front edge of the first root of M^1. As exemplified by the immature holotype of *P. jacksoni* which has rounded incisive foramina, these two latter characters are difficult to interpret.

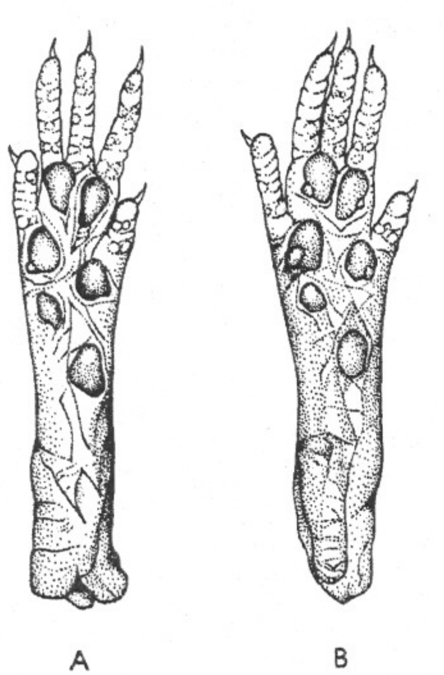

Figure 2 The right foot of: (A) *Praomys degraaffi* (KMMA M.98038.2174, female) and (B) *P. jacksoni* (KMMA M.98038.2017, female).

Several researchers have observed colour morphs within *Praomys* from Albertine Rift mountaintops. Although *Praomys* can be quite variable, in this case the differences are consistent with species differences. For example, Delany (1975) states: 'A collection from Impenetrable Forest contained a large percentage of adult animals with a sooty black fur' and 'many of the largest animals have an almost completely black upper pelage'. Maddalena *et al.* (1989), described the skin of a specimen with a 2N=26 karyotype as 'ce *Praomys* ne se distingue pas de la forme *jacksoni* typique sinon par la couleur plus sombre de son pelage'. In Burundi, JCKP distinguished sympatric *Praomys* with the notations 'grey/brown' *versus* 'grey/grey'. When EVDS captured the first specimen of the new species he noted: 'back very dark, almost black; belly greyish'. In *Praomys*, a certain degree of rufous colouring always develops with increasing age and brightly hued specimens are in all cases fully mature. This is not the case in the new species where the adult specimens are very dark.

With four inguinal mammae, *P. degraaffi* is the only member of the *P. jacksoni* species-complex with eight mammae. All other species have a single pair of inguinal mammae, yielding a total of six mammae.

The hindfoot of *P. degraaffi* is similar to *P. jacksoni* in that they both possess the standard murine component of six large pads: proximal component of the thenar pad, proximal component of the first interdigital pad, the second, third and fourth interdigitial pads, and the proximal component of the hypothenar pad. The new species differs from *P. jacksoni* in the reduced number of accessory pads. *Praomys jacksoni* generally maintains a full complement of four additional small pads, termed distal component of interdigitial pad I, distal component of interdigital pad IV (by analogy), distal component of the hypothenar pad and the distal component of the thenar pad (Figure 2). In a sample of 65 sympatric specimens of *P. jacksoni* from Burundi, all four additional small pads occurred 83% of the time with three additional small pads occurring in nine specimens (14%). In contrast, *P. degraaffi* generally has either one small accessory pad (predominantly the distal component of the hypothenar pad, 53%, n=64) or no small accessory pads (31%). In the remaining 16%, the distal component of the hypothenar pad and the distal component of the thenar pad co-occur.

While both species possess a hindfoot of approximately the same length, the new species has a significantly (t-test; 5% significance level) narrower hindfoot (measurements in mm: sample size, observed range and mean). Foot breadth for the age classes 4–7: *P. jacksoni* n=59 (3,8-5,2) 4,6 and *P. degraaffi* n=62 (3,1–4,9) 4,0 (measured by JCKP) (Figure 3). The proportion of the hindfoot length/hindfoot breadth is highly significantly higher (1% significance level) in the new species: *P. jacksoni* n=91 (4,71–6,36) 5,66 and *P. degraaffi* n=20 (5,91–6,81) 6,35 (measured by EVDS comprising all age classes).

The ear is significantly longer in *P. degraaffi* (ear length measured by JCKP). Age classes 4–7: *P. jacksoni* n=59 (15,5-20,0) 17,3 and *P. degraaffi* n=62 (16.5–21,0) 18,9. This is also clear from a plot of the ear length *versus* the foot breadth (Figure 4).

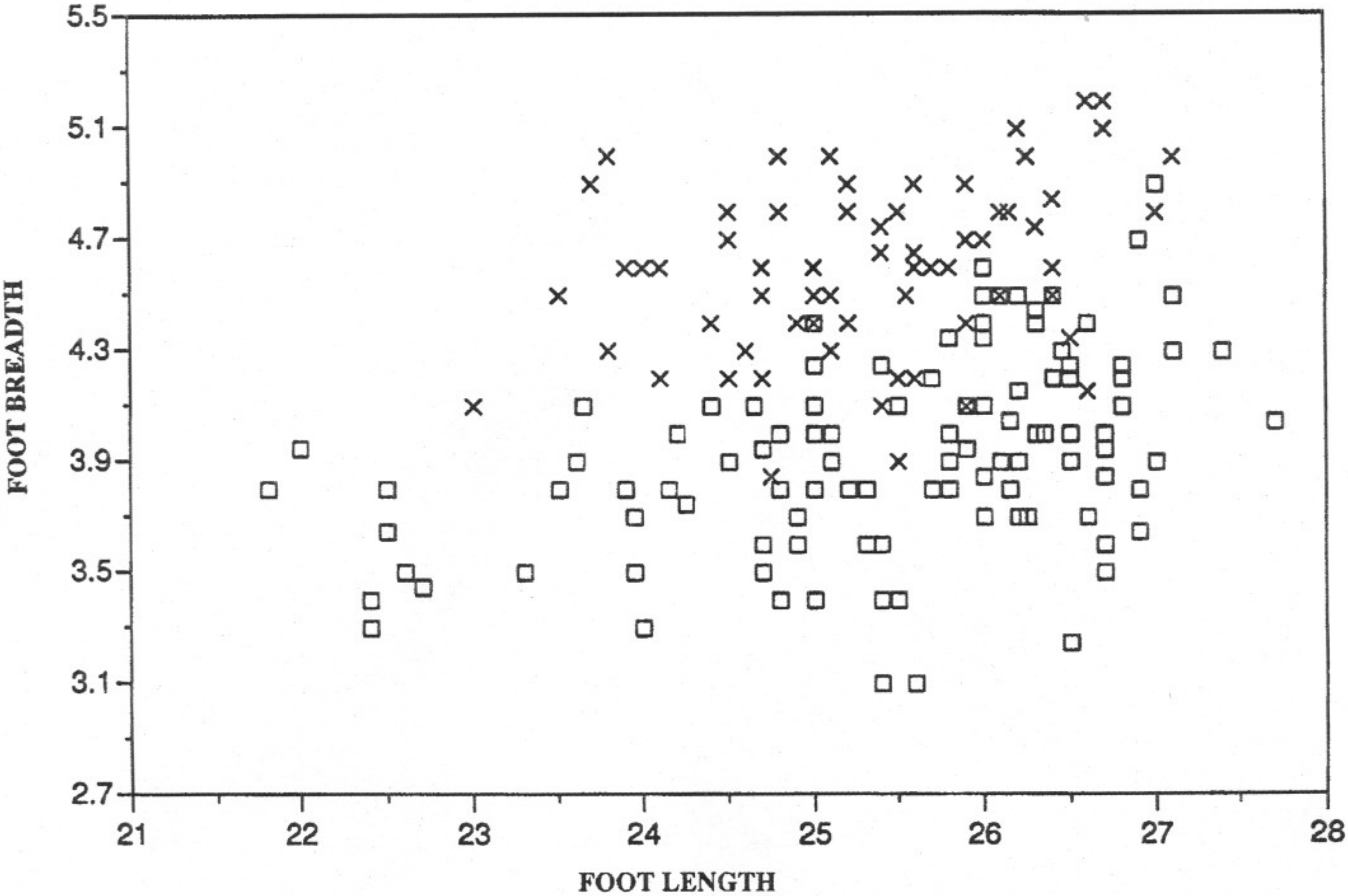

Figure 3 Foot length plotted against foot breadth (measurements taken in mm by JCKP) for sympatric samples of *Praomys degraaffi* (□) and *P. jacksoni* (X).

Distribution

Praomys degraaffi is a high-elevation species confined to the Albertine Rift mountains in Burundi, Rwanda and Uganda (Figure 5).

Ectoparasites

Both taxa of sympatric Burundian *Praomys* have the following ectoparasites in common: *Microtrombicula* sp. (Trombiculidae), *Trichoecius angolensis* (Myocoptidae), *Listrophoroides* (*Afrolistrophorus*) near *scambophallus* (an undescribed species) and *Radfordia praomys* (Myobiidae). Only *Praomys degraaffi* contains the nest mite *Glycyphagus* (an undescribed species; Glycyphagidae). Sympatric *Praomys jacksoni* exclusively host the following: *Hoplopleura inexpectans* (Hoplopleuridae), *Schoengastia* sp., *Neotrombicula* sp., *Gahrliepia* probably *hypoderma*, *Demodex* (an undescribed species; Demodicidae) and *Listrophoroides* (*Afrolistrophorus*) near *mastomys* (Atopomelidae).

Biotope

In Uwinka (Nyungwe Forest, Rwanda) and in Mabay (Kibira National Park, Burundi) *P. degraaffi* was captured in moist montane forest. Many specimens including the holotype, were collected in degraded forest in the vicinity of Nyamugari (abris; Kibira National Park) at an elevation exceeding 2400m.

Although *P. degraaffi* have been captured together with *P. jacksoni* in the same traplines they are often separated by elevation. In the Echuya Forest (2380 m), the Ugandan slope of Gahinga (2680 m) and at higher elevations in the Bururi Forest (>1850 m), *P. degraaffi* was caught to the exclusion of *P. jacksoni*. With the exception of the highest collecting localities in Bwindi-Impenetrable National Park (the vicinity of Ruhija, ca. 2350 m where the two species co-occur), all BINP area specimens represent *P. jacksoni* (n=98). Collecting localities include Omubiyanja Swamp (1850 m), Nteko (1600 m), Ngoto Swamp (1500 m), Byumba (1540 m) and Buhoma (1500 m). Likewise, at several Rwandan localities, only *P. jacksoni* was captured: Gasiza (2360 m), Kinigi (bureau, 2250 m), Ntango (1900 m) and Routabansougera (1750 m). The absence of *P. degraaffi* at Gasiza and Kinigi could be due to heavy cultivation and the degraded habitat, while the low elevation may explain the absence of *P. degraaffi* from the latter two forested sites.

In the vicinity of Ruhija, *P. jacksoni* was caught in higher frequencies in seasonally inundated *Brillantasia* forest, in the valley bottoms adjacent to slow-flowing streams. *Praomys degraaffi* was more common on the drier slopes above, closer to the inhabited compound. Both species were regular but infrequent members of the small mammal community. As the data from Echuya suggests (see below), this may reflect an elevational rather than a habitat preference.

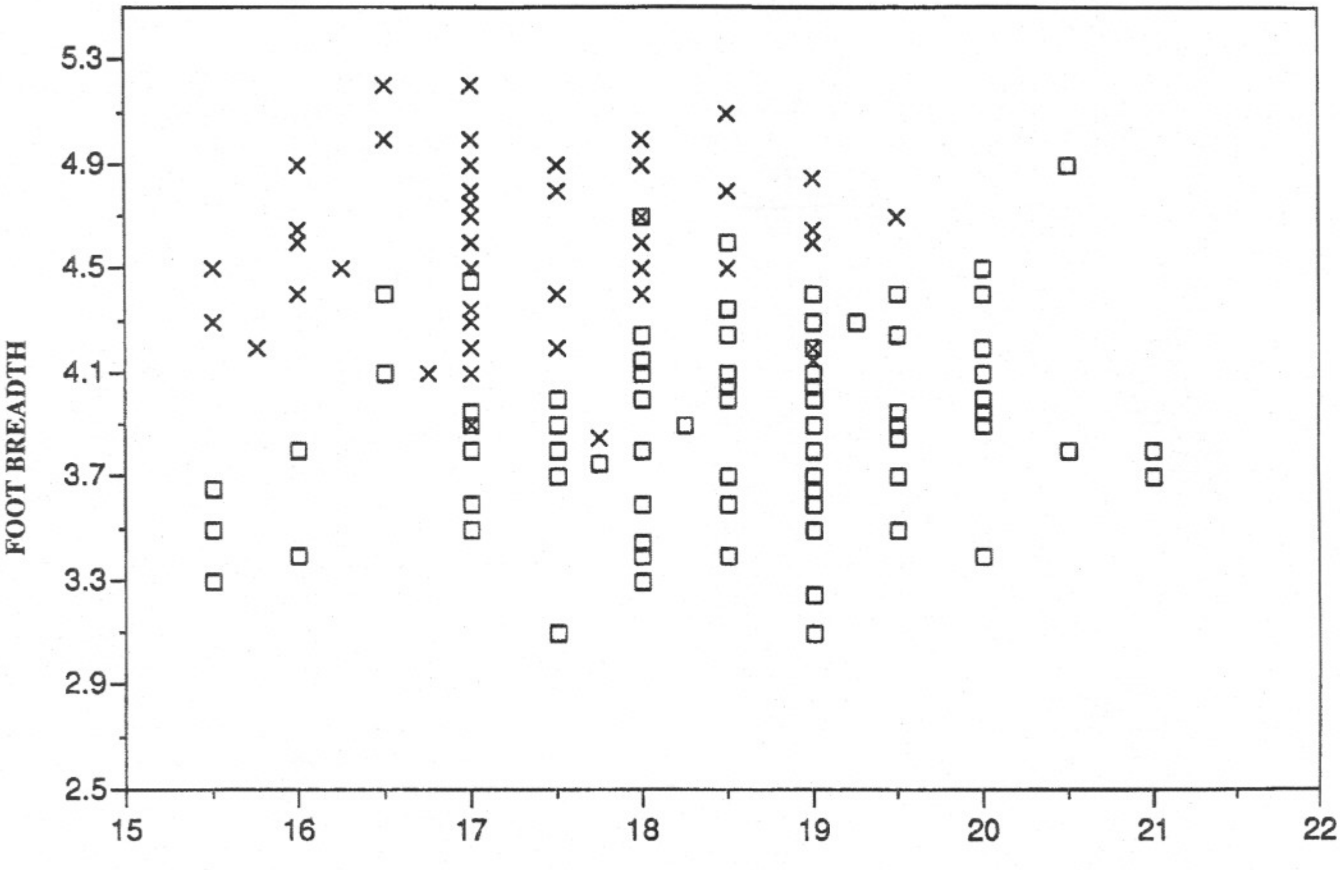

Figure 4 Ear length plotted against foot breadth (measurements taken in mm by JCKP) for sympatric samples of *Praomys degraaffi* (□) and *P. jacksoni* (X).

In the high elevation (mostly bamboo) Echuya Forest *P. degraaffi* was the only *Praomys* species captured (n=15, specimens in the FMNH). The species was relatively common, occurring at a frequency of ca. 16% of the snap-trapped small mammals in the Echuya Forest area. It was rare outside the forest, particularly in Echuya Swamp and its open, peripheral habitats. Preferred habitats included thick stands of bamboo, secondary herbaceous growth, fast-flowing stream edge, along dark trails with dense shrubs in wet forest and, on one occasion, in *Rubus* between Echuya Swamp and the bamboo forest.

On the Ugandan slope of the Virungas, *P. degraaffi* was again the only *Praomys* captured (FMNH specimens). It was not captured above treeline at 3000 m and made up only 6–7% of the snap-trapped small mammal fauna at ca. 2680 m. It consistently but infrequently occurred in monodominant stands of *Hagenia* and in patches of *Myrianthus* sp. It was particularly uncommon on the open, formerly cultivated terraced slopes where *Hagenia* saplings were less than 1 meter in height. Two older museum specimens at FMNH were captured in the saddle between Mgahinga and Sabinyo in bamboo. It was likewise caught in the saddle between Muhabura and Gahinga amidst bamboo and trees with dense undergrowth. At Visoke (Rwanda), *P. degraaffi* was captured in small cultivated plots, in bamboo and on the forest edge, while on the eastern flank of Muhabura it was caught at the edge of the park and in rather dry dense bush and sometimes up to 1 meter high in trees.

The frequency of *P. degraaffi* in the southern end of its range (southern Burundi) greatly exceeded its frequency in the north (SW Uganda). In Bururi Forest (Ruhinga Hill), *P. degraaffi* was not captured in the ericaceous zone (which descends to 2170 m) but was especially common in secondary forest. Above 2000 m, it made up 40% of the snap-trapped small mammal fauna (n=72). In the Mumushwizi Valley (1880 m), *P. degraaffi* comprised 54% of the snap-trapped small mammal fauna where it was especially common in primary forest and in an *Entandophragma* dominated open valley.

In southern Burundi, *P. degraaffi* descends to lower elevations (1880 m) than it does in more equatorial (northerly) latitudes (Table 2). The displacement of *P. jacksoni* by *P. degraaffi* at lower elevations in higher latitudes is assumed to be associated with reduced temperatures and associated floristic gradients.

Canonical analysis

Several canonical analyses were conducted. Here we treat only two of them. The other analyses performed were pairwise comparisons of the different species, analyses on sympatric material and analyses with other combinations of measurements. All results were broadly similar.

The first canonical analysis focused on specimens of *P. jacksoni* and *P. degraaffi* from Rwanda, Burundi and Uganda. We

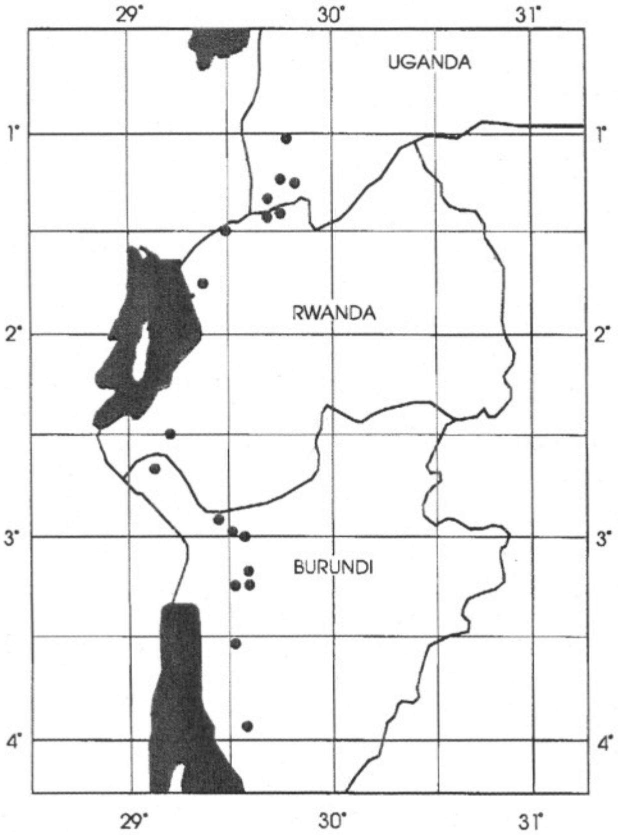

Figure 5 The distribution of *Praomys degraaffi* in central Africa.

used 19 measurements (see Table 3) and 149 specimens divided as follows into four groups: 1/ *Praomys jacksoni* age class 2–3: 32, 2/ *Praomys jacksoni* age class 4–7: 60, 3/*Praomys degraaffi* age class 2–5: 37, 4/ *Praomys degraaffi* age class 6-7: 20.

As the result we mention the eigenvectors for the 19 measurements in the two first canonical variates (Table 3). In Figure 6 we give the graphical presentation of the first and second canonical variate. For each group the centroid and the most extreme values are indicated by a polygonal delimitation. The different age classes are represented individually on the graph although some of them were treated as one group in the analysis. The first canonical variate contains 82,06% of the total variance and shows a good separation between the two species while the second canonical variate (16,48% variance) separates the different age classes. The available types of species in the *Praomys jacksoni* species-complex were added to the scattergram *a posteriori*. Until recently seven species of the *jacksoni* species-complex have been described: *jacksoni*, *minor*, *montis*, *mutoni*, *peromyscus*, *sudanensis* and *viator*. The type of *P. jacksoni* could not be used as it is a juvenile, the skull is damaged and no paratypes were designated. As the skull of the *P. minor* type is damaged, a paratype (KMMA 13037) was used. None of the types lies within the *P. degraaffi* cluster.

The second canonical analysis focused on the differences among species in the *jacksoni* species-complex, and included all types and available paratypes. For *P. jacksoni* we used a set of topotypes (collected in and around Entebbe). The same set of specimens were used in a previous publication (Van der Straeten & Dudu 1990). To optimize the number of specimens only 15 measurements were used (see Table 4). This resulted into 207 adult specimens devided into the following 6 groups: 1/ *Praomys degraaffi*: 66, 2/ *Praomys mutoni*: 29, 3/ *Praomys sudanensis*: 73, 4/ *Praomys jacksoni*: 21, 5/*Praomys montis*: 10, 6/ *Praomys peromyscus*: 8.

As the result we mention the eigenvectors for the 15 measurements in the three first canonical variates (Table 4). Two samples were too small to be used in the canonical analysis:

Table 2 Frequency (%) of *Praomys degraaffi* in *Praomys* populations at various elevations and latitudes in central Africa. Superscript indicates sample size. Frequencies greater than 40% appear in bold

	South Latitude							
	0,8°-1,2°	1,2°-1,6°	1,6°-2,0°	2,0°-2,4°	2,4°-2,8°	2,8°-3,2°	3,2°-3,6°	3,6°-4,0°
Elevation (meters)								
2700	–	–	–	–	–	–	–	–
2600	–	**100^{10}**	–	–	–	–	–	–
2500	–	**65^{17}**	–	–	–	**80^{5}**	**80^{5}**	–
2400	**74^{19}**	**100^{8}**	–	**55^{11}**	–	**100^{10}**	**100^{35}**	–
2300	**71^{7}**	0^{6}	–	–	–	–	**84^{75}**	–
2200	29^{7}	–	–	–	–	**43^{21}**	**44^{72}**	–
2100	0^{2}	–	–	–	–	1^{68}	33^{30}	**83^{36}**
2000	–	19^{16}	–	–	–	3^{38}	17^{12}	–
1900	–	–	–	–	0^{20}	2^{47}	0^{7}	–
1800	0^{10}	–	–	–	–	–	–	**90^{42}**
1700	–	–	–	0^{94}	–	0^{14}	–	0^{15}
1600	0^{28}	–	–	–	–	–	–	–
1500	0^{36}	–	–	–	–	–	–	–
1400	–	–	–	–	–	–	–	–

Table 3 Eigenvectors of 19 variables for the two first canonical variates

Variable symbol	1	2
HL + N	0,0219	−0,0991
GRLE	−0,1231	0,2033
HEBA	0,0581	0,4974
HEPA	0,0444	0,0128
PAF	0,0543	0,1884
DIA1	−0,2606	0,3885
DIA2	−0,0334	0,3280
INT	0,2111	0,2011
ZYG	−0,1511	0,0989
UPTE	0,2689	0,1657
UPDE	−0,1632	0,1905
M^1	−0,2550	−0,2125
ZYPL	0,6359	−0,1017
BNAS	0,0287	0,1064
LNAS	0,2290	0,3954
CHOA	−0,4388	−0,1015
BUL	−0,0248	0,0675
BRCA	−0,1465	−0,1986
PCPA	−0,0578	0,1257

P. minor (n=5) and *P. viator* (n=3). These were added a posteriori to Figure 7 using the eigenvectors.

The first three canonical variate axes contain 39,1%, 33,7% and 5,9% of the total variation respectively. The graphical presentation of the first and second canonical variate is presented in Figure 7. The first canonical variate clearly separates *P. mutoni* from all the other species. With some overlap the second canonical variate separates the remaining species as follows, but with some overlap: 1/ *degraaffi*, 2/ *jacksoni-montis-peromyscus* and 3/ *sudanensis*. The overlap between the two latter groups being considerable. *Praomys degraaffi* is clearly separated from the others.

Along the third canonical variate (not illustrated) *P. minor*, *P. montis* and *P. peromyscus* are separated from the other species, with a little overlap between *P. montis* and *P. peromyscus*. In all canonical variates there is an almost complete overlap between *P. jacksoni* and *P. sudanensis*.

From these analyses it is clear that on biometrical characters *P. degraaffi* cannot be identified as one of the described species of the *P. jacksoni* species-complex.

Discussion

Qumsiyeh, King, Arroyo-Cabrales, Aggundey, Schlitter, Baker & Morrow (1990) compared different species of *Praomys* and *Mastomys* using chromosomal and electrophoretic data, and presented a phytogenetic hypothesis. Five of their *Praomys* specimens were included in our morphological and biometrical comparisons (Kenya specimens in list of material). These five specimens have all characters typical for the *P. jacksoni* species-complex. They were plotted *a posteriori* on the graphical presentation of both canonical analysis and all fall within the *P. jacksoni* cluster. This means that the

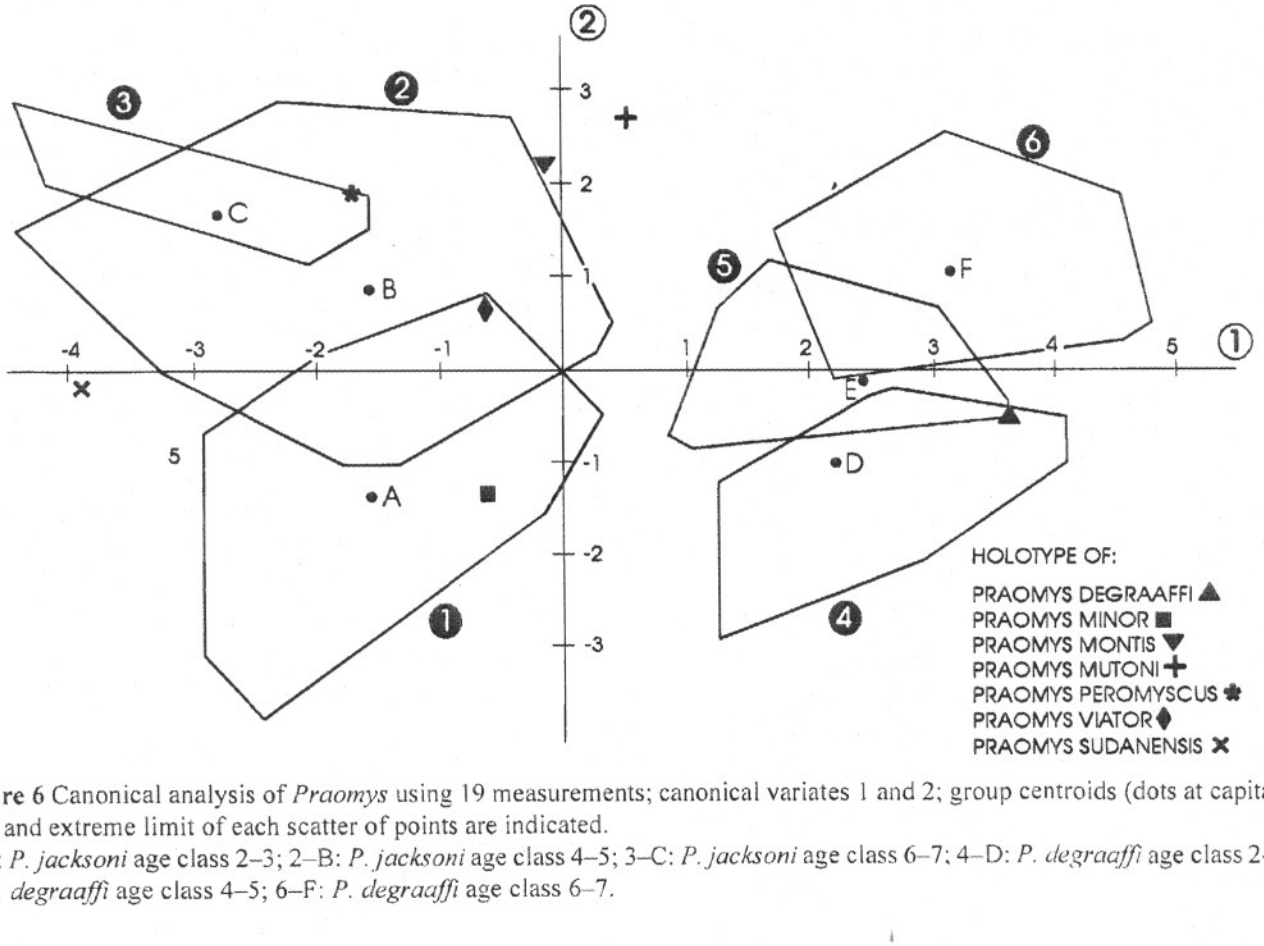

Figure 6 Canonical analysis of *Praomys* using 19 measurements; canonical variates 1 and 2; group centroids (dots at capital letters) and extreme limit of each scatter of points are indicated.
1–A: *P. jacksoni* age class 2–3; 2–B: *P. jacksoni* age class 4–5; 3–C: *P. jacksoni* age class 6–7; 4–D: *P. degraaffi* age class 2-3; 5–E: *P. degraaffi* age class 4–5; 6–F: *P. degraaffi* age class 6–7.

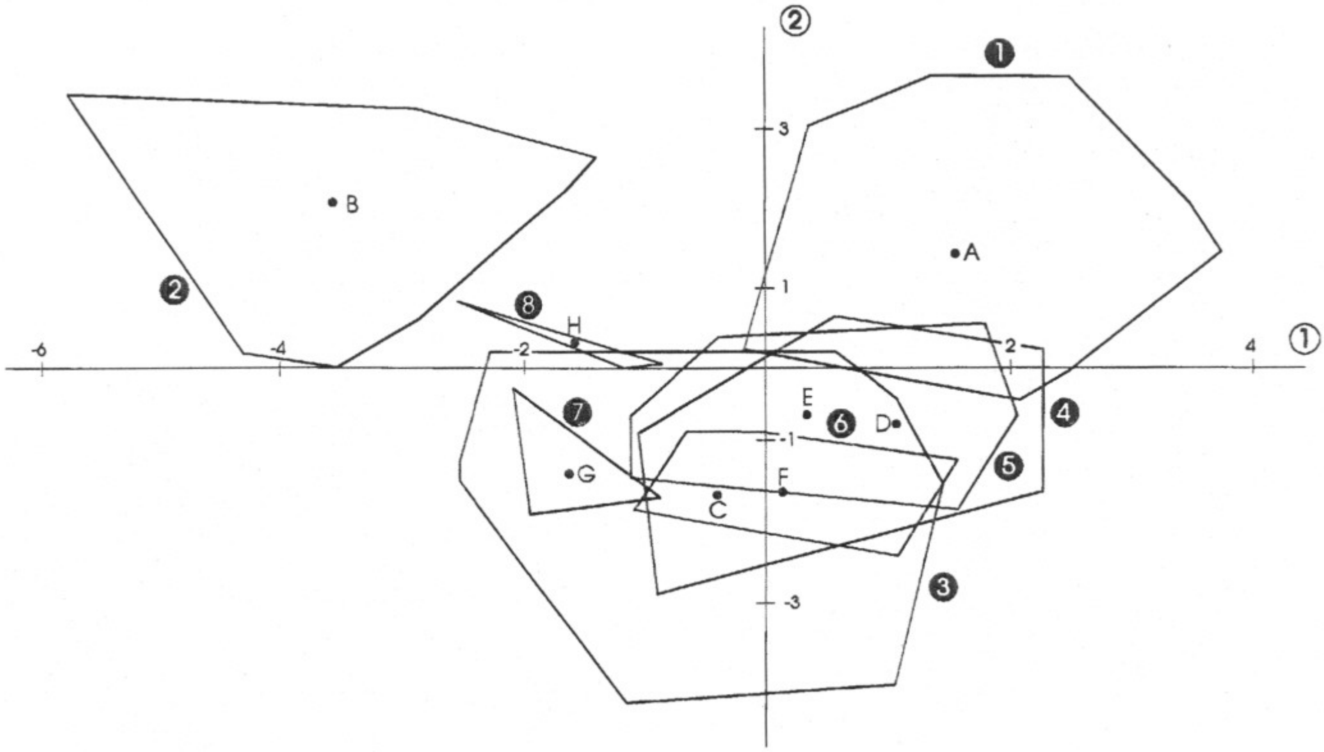

Figure 7 Canonical analysis of *Praomys* using 15 measurements; canonical variates 1 and 2; group centroids (dots at capital letters) and extreme limit of each scatter of points are indicated.
1–A: *Praomys degraaffi*; 2–B: *Praomys mutoni*; 3–C: *Praomys sudanensis*; 4–D: *Praomys jacksoni*; 5–E: *Praomys montis*; 6–F: *Praomys peromyscus*; 7–G: *Praomys minor*; 8–H: *Praomys viator*.

specimen CM 98524 (special number TK 33554) with the different chromosome pattern (2n=35, AA=32) is not a *Praomys* cf. *tullbergi* as mentioned by Qumsiyeh *et al.* (1990) but an undescribed species in the *jacksoni* species-complex. Using the new determination, the dendrograms provided by Qumsiyeh *et al.* (1990) show an important difference between the *jacksoni* and *tullbergi* species-complexes.

Praomys jacksoni always will remain a systematic problem (Van der Straeten & Dudu 1990) as the type is a juvenile specimen characterized by a very small first upper molar (1,35 mm) and short upper and lower cheekteeth (4,65 mm and 4,50 mm). This is the reason why we use a set of topotypical *P. jacksoni* for comparison. To resolve this problem, we propose considering in the future as *P. jacksoni* the form of eastern Africa with karyotype 2n=28, NF=30, AA=26.

Table 4 Eigenvectors of 15 variables for the three first canonical variates

Variable symbol	1	2	3
HEPA	–0,2078	0,1778	0,0365
PAF	0,4543	–0,3193	0,3030
DIA1	–0,1453	0,0259	0,1445
DIA2	0,0534	0,1270	0,0598
INT	–0,0359	0,5542	–0,0554
PAL	–0,2665	0,0316	0,1247
UPTE	0,0192	–0,0795	0,5040
M^1	–0,3753	–0,1336	0,3251
ZYPL	0,5214	0,4461	0,0822
BNAS	–0,1570	–0,0279	–0,0681
LNAS	0,0486	0,0368	0,1169
LOTE	–0,0885	–0,0413	0,5456
CHOA	0,0803	0,4719	0,2631
BUL	0,4222	–0,3006	–0,1109
ROH	–0,1468	–0,0363	–0,3144

The description of *P. degraaffi* brings the number of species within the *jacksoni* species-complex to eight: *degraaffi*, *jacksoni*, *minor*, *montis*, *mutoni*, *peromyscus*, *sudanensis* and *viator*, with at least one undescribed species. Van der Straeten & Dudu (1990) recognised four species-complexes within the genus *Praomys*: 1/ the *jacksoni* species-complex, 2/ the *tullbergi* species-complex (with four species: *misonnei*, *morio*, *rostratus* and *tullbergi*), 3/ the *delectorum* species-complex (containing four species *delectorum*, *melanotus*, *octomastis* and *taitae*) and 4/ the *lukolelae* species-complex enclosing *lukolelae* and probably *verschureni* (described as *Malacomys*). So each of these species-complexes consists of several well-defined and closely related species. Differences between these species-complexes are also well marked. We believe that elevation of these species-complexes to the status of genera should be considered. For example, the morphological differences between the *P. tullbergi* species-complex and the *P. jacksoni* species-complex are equal to those between *Lemniscomys* and *Rhabdomys*.

Gazetteer

Abuja (N)	09 10'N	07 11'E	
Batiabongena (C)	00 36'N	25 13'E	
Buhoma (U)	00 59'S	29 37'E	1500
Byumba (U)	00 56'S	29 42'E	1540
Busekera (B)	03 15'S	29 32'E	1970–2160
Echuya Forest, NHM (U)	01 14'S	29 46'E	
Echuya Forest, FMNH (U)	01 15'S	29 49'E	2380

Entebbe (U)	00 05'N	32 29'E	1134
Gahinga (R)	01 24'S	29 40'E	2700
Gahinga, slope of			
(Kabiranyuma pipeline)(U)	01 22'S	29 39'E	2680
Gasiza (R)	01 25'S	29 40'E	2360
Gatare Stream (B)	02 51'S	29 24'E	1950
Gilo (S)	04 02'N	32 50'E	
Gitenge River Swamp (B)	02 57'S	29 30'E	2180
Gitenge Valley (B)	03 00'S	29 32'E	2200
Ikuywa River Bridge			
(6,5 km south, 19 km east			
Kakamega) (K)	00 13'N	34 55'E	
Iwatoku (S)	03 45'N	30 38'E	
Kagelu (S)	04 03'N	30 36'E	
Kakamega Forest Station			
(3,5 km south, 12 km east			
Kakamega) (K)	00 14'N	34 52'E	
Katire (S)	04 02'N	32 47'E	
Kayove (R)	01 48'S	29 21'E	2000
Kinigi Bureau (R)	01 26'S	29 36'E	2250
Kivuso Abris (B)	03 00'S	29 33'E	2430
Korobe Forest (S)	03 58'N	30 52'E	
Kwogofe Colline (B)	02 51'S	29 26'E	2200–2250
Lotti Forest (S)	04 02'N	32 33'E	
Lukolela (C)	01 10'S	17 11'E	
Mabay (B)	02 40'S	29 17'E	2300
Mgahinga & Sabinyo, pass			
between (U)	01 22'S	29 37'E	2440
Mubuku Valley (U)	00 22'N	30 02'E	1980-3050
Muhabura (R)	01 22'S	29 42'E	2500
Mumushwizi Valley (B)	03 56'S	29 35'E	1880
Myrianthus Campground (B)	03 12'S	29 33'E	2200
Nagichot (S)	04 20'N	33 32'E	
Ngarri Narak (K)	00 29'S	35 50'E	
to	01 65'S	35 50'E	
Ngoto Swamp (U)	00 54'S	29 44'E	1500
Njoro O Nyiro (K) ca	00 50'S	35 05'E	
Ntango (R)	02 36'S	29 13'E	1900
Nteko Parish (U)	01 02'S	29 37'E	1600
Nyabikona River (B)	03 11'S	29 33'E	1950–2120
Nyagatarugwa Valley (B)	03 58'S	29 36'E	1785–1800
Nyamugari, Abris (B)	03 12'S	29 33'E	2150–2415
Nyamugari, N of Abris (B)	03 11'S	29 33'E	2480–2520
Panyam (N)	09 27'N	09 09'E	
Omubiyanja Swamp (U)	00 59'S	29 38'E	1850
Routabansougera (R)	02 26'S	29 11'E	1750
Ruhinga Hill (B)	03 56'S	29 36'E	2170
Ruhija (U)	01 02'S	29 45'E	2350
Talanga Forest (S)	04 00'N	32 44'E	
Teza Park Headquarters (B)	03 14'S	29 35'E	2200
Uwinka (R)	02 29'S	29 12'E	2450
Visoke Camp (R)	01 27'S	29 30'E	2700
Yei (S)	04 07'N	30 40'E	

B = Burundi; C = Democratic Republic of Congo; K = Kenya; N = Nigeria; R = Rwanda; S = Sudan; U = Uganda.
Elevation in meters

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