An identification key for species within the genus *Praomys* (Rodentia: Muridae)

Emilie Lecompte

Christiane Denys

Laurent Granjon

Introduction

Within the Murinae (Rodentia, Muridae), African rats of the genus *Praomys* Thomas, 1915 are widely distributed in the intertropical zone, from West (Senegal to Angola) to East Africa (Uganda to Malawi). They live in closed (primary forest) to semi-opened (secondary forest, fringes, gallery forest and fallow) biotopes.

According to MUSSER and CARLETON (1993), the genus *Praomys* comprises nine species. However, the number of species and their geographical limits are not well understood due to the low level of morphological differentiation between species, making it difficult to find specific diagnostic characters. As a result, the systematics of this genus is yet to be resolved, particularly in the light of new species being described. For instance, VAN DER STRAETEN and KERBIS PETERHANS (1999) recently described a tenth species, *Praomys degraaffi*. Other studies based on morphometric, morphological and chromosomal data also strongly suggest the existence of another new species, which has yet to be described (MATTHEY, 1970; WELTZ and VAN DER STRAETEN, unpublished data).

Based on morphometric studies, VAN DER STRAETEN and DIETERLEN (1987) and VAN DER STRAETEN and DUDU (1990) proposed that the genus *Praomys* be divided into three species complexes. The relationships within and among these complexes remain unknown. It is only recently that a comprehensive study of intrageneric relationships based on a cladistic analysis of morphological characters and including most species within the genus has been undertaken (LECOMPTE *et al.*, in press). From the large set of characters used for cladistic analysis, it was possible to select a series of diagnostic characters to devise the identification key proposed here, together with a synopsis of nine out of the ten currently recognised species within the genus. This key mainly provides diagnostic skull characters for each species and, when possible presents several character combinations to define them. Notes on geographic distribution, based both on literature and museum specimens observations, and chromosomal data available to date are also presented.

Praomys diversity

The genus *Praomys* was defined by THOMAS in 1915 as a subgenus of *Epimys* Trouessart by its mammary formula: 1+2 = 6 or 2+2 = 8. ELLERMAN (1941) classified it as a subgenus of *Rattus* with most of the other Murinae. Then, DAVIS (1965) elevated it at the generic rank.

Data on *Praomys* are presented according to the three species complexes defined by VAN DER STRAETEN and DIETERLEN (1987) and VAN DER STRAETEN and DUDU (1990) as follows.

The tullbergi*-complex*

The *tullbergi*-complex includes *P. hartwigi* Eisentraut, 1968, *P. misonnei* Van der Straeten and Dieterlen, 1987, *P. morio* (Trouessart, 1881), *P. rostratus* (Miller, 1900), *P. tullbergi* (Thomas, 1894). This species complex is supported by some morphological characters such as palatal ridges (9 instead of 7 in the other species of the genus), a large foramen ovale, and supraorbital ridges that originate from the middle of the frontals.

Praomys hartwigi Eisentraut, 1968

Synonyms: *obscurus* Hutterer *et al.*, 1992. This taxon was described as a subspecies from Nigeria. However HUTTERER *et al.* (1992) think about it as a full species and Van der Straeten also considers it as a good species (oral communication). This species occurs in mountain forests of Cameroon (lake Oku) and Nigeria (Gotel Mts) (EISENTRAUT, 1970; HUTTERER *et al.*, 1992).

Praomys misonnei Van der Straeten & Dieterlen, 1987

This species is found in Central and East Africa (Zaire and Kenya) (VAN DER STRAETEN and DIETERLEN, 1987; VAN DER STRAETEN and DUDU, 1990, DUDU *et al.*, 1997). Some specimens from Kenya, attributed to this species, are characterised by a diploid number of 2N = 36 (QUMSIYEH *et al.*, 1990), but MUSSER and CARLETON (1993) suggested that these specimens need to be re-examined to confirm their identity. Van der Straeten looked at these specimens and considers them as *P. misonnei* (pers. comm.)

Praomys morio (Trouessart, 1881)

Synonyms: *maura* (Gray, 1862). TROUESSART in 1881 renamed this species *morio* because it was preoccupied by *Mus maura* Waterhouse, 1839.

This species is restricted to Mount Cameroon and Bioko (EISENTRAUT, 1970). The species has a diploid number of 2N = 34 (MATTHEY, 1965). PETTER (1965) discussed about specimens from Central African Republic, which finally appeared to be another species, here called *Praomys sp.* (see further).

Praomys rostratus (Miller, 1900)

This species has been recorded in West Africa from Liberia, Guinea to Ivory Coast (VAN DER STRAETEN and VERHEYEN, 1981; GAUTUN *et al.*, 1986) and is characterised by a diploid number of 2N = 34 (GAUTUN *et al.*, 1986). It was first considered as subspecies of *P. tullbergi* until VAN DER STRAETEN and VERHEYEN (1981) separated them on the basis on morphometric data. GAUTUN *et al.* (1986) also recorded different ecological requirements for *rostratus* and *tullbergi*.

Praomys tullbergi (Thomas, 1894)

Synonyms: *burtoni* (Thomas, 1892). THOMAS renamed in 1894 this species because it was preoccupied by *Mus burtoni* Ramsay, 1887.

This species is widely distributed in West and West and Central Africa. Like *P. rostratus*, it also has a diploid number of 2N = 34 (MATTHEY, 1958).

The yet to be described, *Praomys sp.* from central Africa, called *P. morio* in PETTER (1965), and *P. cf. lukolelae* in PETTER (1975) and CHEVRET *et al.* (1994), is included in the *tullbergi*-complex, on the basis of morphometric data (WELTZ and VAN DER STRAETEN, unpublished data). This species corresponds with specimens from Central Africa evoked by MUSSER and CARLETON (1993) as an undescribed species. It is characterised by a diploid number of 2N = 42 (MATTHEY, 1965, 1970).

The jacksoni-*complex*

The *jacksoni*-complex includes *P. jacksoni* (de Winton, 1897), *P. minor* Hatt, 1934, *P. mutoni* Van der Straeten and Dudu, 1990 and the recently described *P. degraaffi* Van der Straeten and Kerbis Peterhans, 1999. This species-complex is also supported by some morphological characters such as strong and straight supraorbital ridges, a small foramen ovale and a distinct t3 on M^1.

Praomys jacksoni (de Winton, 1897)

Synonyms: *peromyscus* (Heller, 1909) described as full species; *montis* (Thomas and Wrougthon, 1910), described as full species; *viator* (Thomas, 1911), described as subspecies; *sudanensis* Setzer, 1956 described as subspecies. Some of these taxa are considered as full species by VAN DER STRAETEN and DUDU (1990).

This species occurs widely in East, Central and West Africa. Its karyotype is characterised by a diploid number of 2N = 28 and an autosomal fundamental number of NFa = 30 (MATTHEY, 1959). This species represents the most widely distributed one of *Praomys*.

Praomys minor Hatt, 1934

This species is only known from three specimens from the type-locality in central Zaire, which were not available for examination in this study. However, previous morphometric analyses (VAN DER STRAETEN and DIETERLEN, 1987; VAN DER STRAETEN and DUDU, 1990) have shown this species to be closely related to *P. jacksoni.*

Praomys mutoni Van der Straeten & Dudu, 1990

It is only known from the type-locality in Northern Zaire (VAN DER STRAETEN and DUDU, 1990; DUDU *et al.*, 1997).

Praomys degraaffi Van der Straeten & Kerbis Peterhans, 1999

It is a mountain species from the Albertine Rift in Burundi, Rwanda and Uganda (VAN DER STRAETEN and KERBIS PETERHANS, 1999; MADDALENA *et al.*, 1989). Its karyotype is characterised by a diploid number of 2N = 26 and NFa = 24 (MADDALENA *et al.*, 1989).

The delectorum*-complex*

The *delectorum*-complex only includes *P. delectorum* (Thomas, 1910). This species is characterised by a distinct t3 on M^1, weak supraorbital ridges, and a large foramen ovale as in the *tullbergi* species complex.

Praomys delectorum (Thomas, 1910)

Synonyms: *taitae* (Heller, 1912), described as full species; *octomastis* Hatt, 1940, described as subspecies; *melanotus* Allen and Loveridge, 1933, described as subspecies.

This species is distributed on high plateaus and isolated mountains from Malawi, Tanzania to Kenya. *Praomys taitae*, considered as a synonym of *P. delectorum* was found to possess a diploid number of 2N = 48 (MATTHEY, 1965).

Identification key of the species of the genus *Praomys*

The number of specimens examined range from N = 15 to N = 100 per species. The widely distributed species were represented by large series of specimens encompassing the distributional range of the species while the endemic species such as *P. hartwigi* and *P. morio* were represented by the smallest samples. The selection of skull characters took into account the nature and extent of variability of the

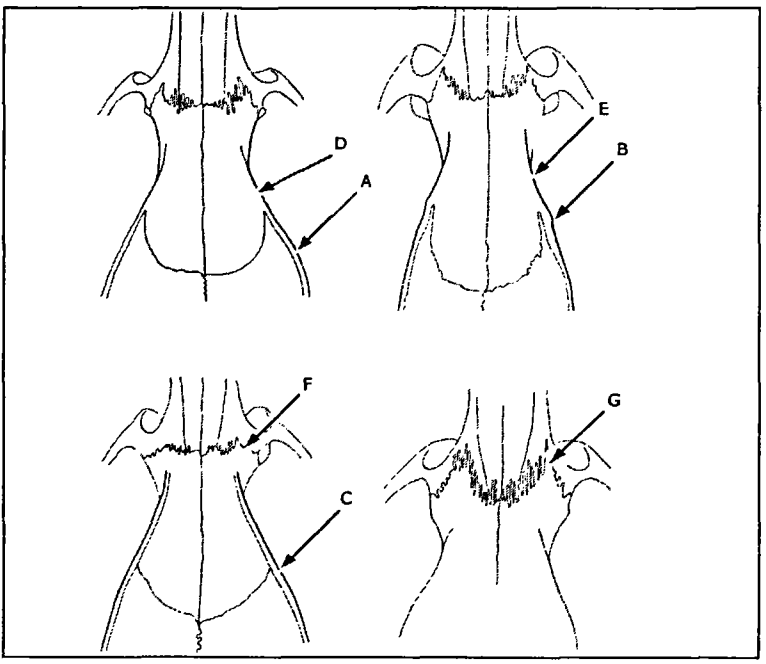

Figure 1
Dorsal views of the skull, showing the development of supraorbital ridges, interorbital constriction and the suture between nasals and frontals. The extent of development of the ridges, already used by PETTER (1965) can be absent or very weak (A), present, and originating from the middle of frontals (B), or very strong, prominent, straight, and originating in front of frontals (C). The interorbital constriction can be gradual and amphora-shaped (D) or more bold in the middle and as a broken line (E). The suture can be almost horizontal (F) or V-shaped (G).

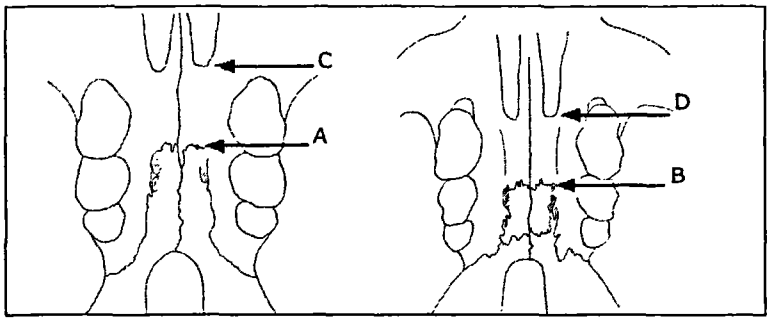

Figure 2
Ventral views of the skull, showing the limits of the palatine bone and the posterior limit of the anterior palatal foramina. The anterior limit of the palatine bone can extend to the level of the posterior part of M^1 (A), or between M^1 and M^2 (B). The posterior limit of the anterior palatal foramina can reach the front edge of the 1st root of M^1 (C) or reach the middle of the M^1, between its 1st and 2nd roots (D).

characters such the highly variable characters were not considered in devising the identification key.

The skull characters used in this identification key are illustrated in Figs. 1 and 2. The mammary formula was also included but may not be independently diagnostic, and is defined as the number of pectoral mammae plus the number of inguinal mammae on each side of the body. The mammary formula has previously been used to separate the genera *Myomys*, *Mastomys* and *Praomys* (THOMAS, 1915).

1. Supraorbital ridges absent or very weak (fig. 1 character A).... 2.
   Supraorbital ridges present, more or less pronounced..... 3.
2. Anterior limit of palatine bone extending to the level of the posterior part of M^1 (fig. 2 character A), nasal/frontal suture almost horizontal (fig. 1 character F), zygomatic bone of the same breadth as malar process, mammary formula: 1 + 2 = 6..... *P. morio.*
   Anterior limit of the palatine bone extending to between M^1 and M^2 (fig. 2 character B), nasal / frontal suture V-shaped (fig. 1 character G), zygomatic bone very thin (half of the breadth of malar process), mammary formula: 2 + 2 = 8..... *P. delectorum.*
3. Supraorbital ridges beginning in the middle of frontals (fig. 1 character B)..... .4.

Supraorbital ridges very strong, straight, beginning in front of frontals (fig. 1 character C)..... 7.

Posterior limit of anterior palatal foramina reaching anterior edge of first root of M^1 (fig. 2 character C)..... 5.

4. Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M^1 (fig. 2 character D)..... *P. hartwigi.*

5. Proportions of the teeth normal (ratio of molar row length / maximum length of skull > 15%)..... *P. tullbergi.*

   Microdonty (ratio of molar row length / maximum length of skull < 15%)..... 6.

6. Interorbital constriction gradual and amphora-shaped (fig. 1 character D)..... *P. misonnei.*

   Interorbital constriction more bold in the middle of frontal and as a broken line (fig. 1 character E)..... *P. rostratus.*

7. Posterior limit of anterior palatal foramina reaching anterior edge of first root of M^1 (fig. 2 character C)..... *P. mutoni.*

   Posterior limit of anterior palatal foramina reaching halfway between first and second roots of M^1 (fig. 2 character D)..... 8.

8. Four small accessory plantar pads, mammary formula: 1+2 = 6. ..... *P. jacksoni.*

   One or no small accessory pad, mammary formula: 2+2 = 8. ..... *P. degraaffi.*

The characters related to supraorbital ridges present some variation as a function of age, the ridges increasing with the age of the animals. It is thus important to be careful about the age of the specimens compared. For example, old *P. morio* can have ridges as young P. *tullbergi*, although they will generally not be so developed. The type of *P. morio*, a young adult, presents very weak ridges.

The characters related to posterior limit of anterior palatal foramina and anterior limit of the palatine bone used by ROSEVEAR (1969) also show some variation, but in a way which is compatible with their use as diagnostic characters.

To summarize, table 1 presents a list of the useful characters for each species.

	degraaffi	*delectorum*	*hartwigi*	*jacksoni*	*misonnei*	*morio*	*mutoni*	*rostratus*	*tullbergi*
Supraorbital ridges	prominent, beginning in front of frontals	very weak	beginning in the middle of frontals	prominent, beginning in front of frontals	beginning in the middle of frontals	very weak	prominent, beginning in front of frontals	beginning in the middle of frontals	beginning in the middle of frontals
anterior limit of palatine bone extending to	posterior part of M1	between M1 and M2	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1	posterior part of M1
Naso-frontal suture	almost horizontal	V-shaped	almost horizontal	almost horizontal	almost horizontal	almost horizontal	almost horizontal	almost horizontal	almost horizontal
Breadth of the zygomatic bone	as malar process	very thin	as malar process	as malar process	as malar process	as malar process	as malar process	as malar process	as malar process
Posterior limit of anterior palatal foramina	between first and second roots of M1	between first and second roots of M1	between first and second roots of M1	between first and second roots of M1	anterior edge of the first root of M1	between first and second roots of M1	anterior edge of the first root of M1	anterior edge of the first root of M1	anterior edge of the first root of M1
Ratio of molar row length / maximum length of skull	> 15%	> 15%	> 15%	> 15%	< 15%	> 15%	> 15%	< 15%	> 15%
Interorbital constriction	very bold in front of the frontals	bold, as a broken line	bold, as a broken line	very bold in front of the frontals	gradual, amphora-shaped	gradual, amphora-shaped	very bold in front of the frontals	bold, as a broken line	bold, as a broken line

Table 1
List of useful cranial characters for each species.

Discussion

The previous identification key for *Praomys* species by MISONNE (1974) only included the following five species: *P. tullbergi, P. morio, P. hartwigi, P. jacksoni* and *P. delectorum.* Due to the absence of appropriate diagnostic morphological characters, the identification of *P. tullbergi* was only based on its geographic distribution, but the species is now known to be sympatric with *P. rostratus* (GAUTUN *et al.*, 1986). Moreover, *P. morio sensu* MISONNE (1974), included a combination of specimens of *P. morio* from Cameroon and of the species referred here in as *Praomys sp.* from central Africa. By the fact, "*Praomys morio*" was considered to have a diploid number of 2N = 42, which in fact represents the diploid number of the species referred here in as *Praomys sp.*, whereas the "true" *P. morio* from Cameroon has a diploid number of 2N = 34 (MATTHEY, 1965). Next, the characters used by MISONNE (1974) to define "*P. morio*" are also present in species of the *tullbergi*-complex such as *P. rostratus* and *P. misonnei.* Furthermore, *P. jacksoni* and *P. delectorum* were both defined by straight supraorbital ridges, which are not prominent in the latter species. The two species can also be distinguished by their mammary formula, which only applies to females, and therefore cannot be used alone.

Consequently, a new identification key for *Praomys* species based on other morphological characters became necessary. For a more practical identification, additional characters involving external features need to be identified, particularly for those species lacking diagnostic characters. In addition, once enough evidence is available, it will be possible to provide species descriptions. For example, *Praomys* sp. has been known from the literature since 1965. It was initially referred to *P. morio* (MATTHEY, 1965; PETTER, 1965), and subsequently to *P. lukolelae* (PETTER, 1975). However, the species is currently considered to be distinct from both *P. morio* and *P. lukolelae* (= *Malacomys lukolelae* in MUSSER and CARLETON, 1993), and has yet to be described. An attempt has been made here to define species limits and their characteristics, but there is an urgent need to refine the key by using alternative techniques, such as cytogenetics and DNA sequencing.

Acknowledgements

For access to or loan of specimens, we thank P. Jenkins (British Museum of Natural History), R. Hutterer (Zoologisches Forstchungsinstitut und Museum Alexander Koenig), C. Chimimba (Transvaal Museum) and W. Van Neer (musée royal d'Afrique centrale de Tervuren). We thank Erik Van der Straeten for his useful personal communications. This is a publication from the "Systématique et évolution des vertébrés tétrapodes" team (MESR-EA. 2586).

References

ALLEN G.M. and LOVERIDGE A., 1933 — Reports on the scientific results of an expedition to the south-western highlands of Tanganyika territory. II. *Bulletin of the Museum of comparative Zoology, Harvard,* 75: 106-107.

CHEVRET P., GRANJON L., DUPLANTIER J.M., DENYS C. and CATZEFLIS F.M., 1994 — Molecular phylogeny of the *Praomys* complex (Rodentia: Murinae): a study based on DNA/DNA hybridization experiments. *Zoological Journal of the Linnean Society,* 112: 425-442.

DAVIS D.H.S., 1965 — Classification problems of African Muridae. *Zoologica africana,* 1 (1): 121-145.

DE WINTON W.E., 1897 — On a collection of small mammals from Uganda. *The Annals and Magazine of Natural History,* 6 (20): 318.

DUDU A., VERHAGEN R., GEVAERTS H. and VERHEYEN W., 1997 — Population structure and reproductive cycle of *Praomys jacksoni* (De Winton, 1897) and first data on the reproduction of *P. misonnei* Van der Straeten & Dieterlen, 1987 and *P. mutoni* Van der Straeten et Dudu, 1990 (Muridae) from Masako forest (Kisangani, Zaire). *Belgian Journal of Zoology,* 127 (suppl.): 67-70.

ELLERMAN J.R., 1941 — The families and genera of living rodents. Volume II: family Muridae. Bristish Museum (Natural History). 690 p.

EISENTRAUT M., 1968 — Beitrag zur Saügetierfauna von Kamerun. *Bonner Zoologische Beiträge,* 19: 1-14.

EISENTRAUT M., 1970 — Die Veirbreitung der Muriden-Gattung *Praomys* auf Fernando-Poo und in West-Kamerun. *Zeitschrift für Säugetierkunde,* 35: 1-15.

GAUTUN J.C., SANKHON I. and TRANIER M., 1986 — Nouvelle contribution à la connaissance des rongeurs du massif guinéen des monts Nimba (Afrique occidentale). Systématique et aperçu quantitatif. *Mammalia,* 50 (2): 205-217.

GRAY J.E., 1862 — List of Mammalia from the Cameroon mountains, collected by capt. Burton,

H.M. consul, Fernando Poo. *Proceedings of the Zoological Society of London*, 181.

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

HATT R.T., 1940 — Mammals collected by the Rockefeller-Murphy Expedition to Tanganyika and the eastern Belgian Congo. *American Museum Novitates*, 1070: 1-8.

HELLER E., 1909 — Two new rodents from British East Africa. *Smithsonian Miscellaneous Collections*, 52 (4): 471-473.

HELLER E., 1912 — New rodents from British East Africa. *Smithsonian Miscellaneous Collections*, 59 (16): 1-20.

HUTTERER R., DIETERLEN F. and NIKOLAUS G., 1992 — Small mammals from forest islands of eastern Nigeria and adjacent Cameroon, with systematical and biogeographical notes. *Bonner Zoologische Beiträge*, 43 (3): 393-414.

LECOMPTE E., GRANJON L. and DENYS C., in press — The phylogeny of the *Praomys* complex (Rodentia: Muridae) and its phylogeographic implications. *Journal of Zoological Systematics and Evolutionary Research.*

MADDALENA T., VAN DER STRAETEN E., NTAHUGA L. and SPARTI A., 1989 — Nouvelles données et caryotypes des rongeurs du Burundi. *Revue Suisse de Zoologie*, 96 (3) : 561-570.

MATTHEY R., 1958 — Les chromosomes et la position systématique de quelques Murinae africains (Mammalia-Rodentia). *Acta Tropica*, 15 (2) : 97-117.

MATTHEY R., 1959 — Formules chromosomiques de Muridae et de Spalacidae. La question du polymorphisme chromosomique chez les mammifères. *Revue Suisse de Zoologie*, 66 (5) : 173-209.

MATTHEY R., 1965 — Études de cytogénétique sur les Muridae africains appartenant aux genres *Arvicanthis*, *Praomys*, *Acomys* et *Mastomys* (Rodentia). *Mammalia*, 29 (2): 228-249.

MATTHEY R., 1970 — Caryotypes de Muridés et de Dendromuridés originaires de république Centrafricaine. *Mammalia*, 34 (3) : 459-466.

MILLER G.S., 1900 — A collection of small mammals from Mount Coffee Liberia. *Proceedings of Washington Academy of Sciences*, 2: 631-649.

MISONNE X., 1974 — Part 6, Rodentia. *In* MEESTER J. and SETZER H.W. (eds): *The mammals of Africa, an identification manual.* Smithsonian Institute Press, Washington, D.C.

MUSSER G.G. and CARLETON M.D., 1993 — Family Muridae. *In* WILSON D.E. and REEDER D.M. (éd.): *Mammal Species of the world: A Taxonomic and Geographical Reference.* Smithsonian Institution Press, Washington & London: 501-756.

PETTER F., 1965 — Les *Praomys* d'Afrique centrale. *Zeitschrift für Saügetierkunde*, 35 : 1-15.

PETTER F., 1975 — Les *Praomys* de la République centrafricaine (Rongeurs, Muridés). *Mammalia*, 39 : 51-56.

QUMSIYEH M.B., KING S.W., ARROYO-CABRALES J., AGGUNDEY I.R., SCHLITTER D.A., BAKER R.J. and MORROW K.J., 1990 — Chromosomal and protein in morphologically similar species of *Praomys sensu lato* (Rodentia, Muridae). *Journal of Heredity*, 81: 58-65.

ROSEVEAR D.R., 1969 — *The rodents of West Africa*. Trustees of the Bristish Museum (Natural History), 604 p.

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

THOMAS O., 1894 — Note on *Mus burtoni*, Thos. *The Annals and Magazine of Natural History*, 6 (13): 204.

THOMAS O., 1910 — New African mammals in the British Museum. *The Annals and Magazine of Natural History*, 8 (6): 426-432.

THOMAS O., 1911 — Mammals from Northern Nigeria. *The Annals and Magazine of Natural History*, 8 (7): 461.

THOMAS O., 1915 — List of mammals collected on the upper Congo by Christy for the Congo Museum, Tervueren. *The Annals and Magazine of Natural History*, 8 (16): 465-481.

THOMAS O. and WROUGHTON R.C., 1910 — *Transactions of Zoological Society of London*, 19: 503.

TROUESSART E.L., 1881 — Catalogue des mammifères vivants et fossiles. *Bulletin de la société d'études scientifiques d'Angers*, 10 : 121.

VAN DER STRAETEN E. and DIETERLEN F., 1987 — *Praomys misonnei*, a new species of Muridae from Eastern Zaïre (Mammalia). *Stuttgarter Beiträge zur Naturkunde*, serie A (Biologie), 402: 1-11.

VAN DER STRAETEN E. and DUDU A.M., 1990 – Systematics and distribution of *Praomys* from the Masako Forest Reserve (Zaïre), with the description of a new species. *In* PETERS G. and HUTTERER R. (eds): *Vertebrates in the Tropics*. Museum Alexander Koenig, Bonn: 73-83.

VAN DER STRAETEN E. and KERBIS PETERHANS J.C., 1999 — *Praomys degraaffi*, a new species of Muridae (Mammalia) from central Africa. *South African Journal of Zoology*, 34 (2): 80-90.

VAN DER STRAETEN E. and VERHEYEN W., 1981 — Étude biométrique du genre *Praomys* en Côte d'Ivoire. *Bonner Zoologische Beiträge*, 32: 249-264.