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Cytotaxonomy of rodent species from Ethiopia, Kenya, Tanzania and Zambia

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ABSTRACT. An extended survey of taxa belonging to two genera of Cricetomyinae (*Cricetomys* and *Saccostomus*), one Gerbillinae (*Gerbilliscus*), eight Murinae (*Acomys*, *Aethomys*, *Arvicanthis*, *Lemniscomys*, *Mus* (*Nannomys*), *Mastomys*, *Grammomys*, *Stenocephalemys*) and one Myoxidae (*Graphiurus*) was carried out as part of the EU programme "Staplerat" involving Ethiopia, Kenya, Tanzania and Zambia. Here we report the diploid and autosomal fundamental numbers of these rodent taxa. Seventeen of them were unknown, for four we report chromosomal variants and for another 16 new localities where they occur. We discuss their specific status taking into consideration our results together with data from literature and highlight the problems in taxonomy and systematics that are yet to be solved, due do their extended range and the occurrence of species complexes. We highlight cases for which there should be a re-evaluation of specific names that were not included in the last rodent checklist.

KEY WORDS : Cytogenetics, Rodents, taxonomy, East Africa.

INTRODUCTION

Current knowledge of African rodent taxonomy has been largely influenced by the history of colonization and by several expeditions organised independently by major museum Institutions carried out during the early part of the twentieth century. As a result, Natural History museums in Europe and in the United States posses the largest collections of African rodents, which include most species types so constituting a unique reference for correct taxonomic identification and classification purposes. It is worthy of note that, although essential from a scientific point of view, this resulted in a proliferation of names, as most descriptions were carried out with little or limited comparison to the large series, which is the only way to arrive at the correct identification of variation (e.g., the long list of taxa reported by ALLEN in 1939).

The second part of the twentieth century saw the development of new approaches, such as cytogenetics, genetics, molecular genetics and morphometrics which first separately and later combined into a multidisciplinary approach have been employed to study African rodent taxonomy, and often in collaboration with African Institutions. This approach was based on the biological species concept derived from the Modern Synthesis (DOBZHANSKY, 1937). However, most of this work was carried out on a local scale which has limited its full application. Much of the information on African Rodents is scattered over wide areas, and taxonomic revision for many of the genera is far from compete. This is also a consequence of the occurrence of sibling and cryptic species. Therefore, there is a need for continuing collaboration in order to allow investigations to cover larger areas.

The Staplerat project[1], founded by the European Union and involving Ethiopia, Kenya, Tanzania and Zambia as

* Walter Verheyen deceased late 2005 after acceptance of this paper. He was a great example for all other authors of this paper and for African rodent taxonomy in general.

[1] STAPLERAT, Protecting staple crops in eastern Africa: integrated approaches for ecologically based field rodent pest management. An international collaborative project, supported by the European Union's 5th Framework RTD Program.

African partners, constituted an excellent opportunity to investigate rodent taxonomy on a larger scale. The study concerned an area which extended from the Ethiopian plateau south to northern Zambia across the eastern side of the Great Rift Valley of Kenya and Tanzania. The programme involved the identification of integrated approaches for rodent pest control in agricultural areas. This naturally implied a need for a correct taxonomy of these captured species.

The areas studied formed two main biotic zones typical of the eastern part of Africa, i.e. the Somali-Maasai and the Zambezian (MENAUT, 1983; WHITE, 1986). These areas represent independent cradles of speciation and evolution for different rodent faunas, from the Late Miocene to the present day (DENYS, 1999). Our study reports the genera and species which, in addition to those in the dry and wet Miombo woodland savannas, provide evidence of this recent history.

The limit between the Somali-Maasai and the Zambezian biomes occurs in south western Tanzania and northwest Zambia (Fig. 1), and represents a crucial area where independently evolved rodent faunas converge. Furthermore, our sampling localities extend to the northwest of the Somali-Maasai, across the Pare and Uzambaras range dividing the Kenyan and Tanzanian savannas, up to the deciduous bushland and thicket which characterizes the bottom of the Rift which penetrates and bisects the Ethiopian plateaux.

During the three-year project there were several collections, both in fields and surrounding areas. Samples of each taxon found at each locality were studied using multidisciplinary approaches, including cytogenetics, molecular genetics and morphometrics. Here we present the cytotaxonomic results, providing the diploid (2n) and fundamental numbers (NFa) only. A description of each karyotype by means of differential staining will appear elsewhere for each genus as a separate paper.

Karyotype descriptions constitute the primary tool for rodent species identification, as it has been established and generally accepted that the reason behind the high diversity shown by this mammalian order is related to its high rate of chromosomal mutation (CORTI, 2002; KING, 1993). We present here the karyotypes for two genera of Cricetomyinae (*Cricetomys* and *Saccostomus*), one Gerbillinae (*Gerbilliscus*), eight Murinae [*Acomys, Aethomys, Arvicanthis, Lemniscomys, Mus (Nannomys), Mastomys, Grammomys, Stenocephalemys*] and one Myoxidae (*Graphiurus*).

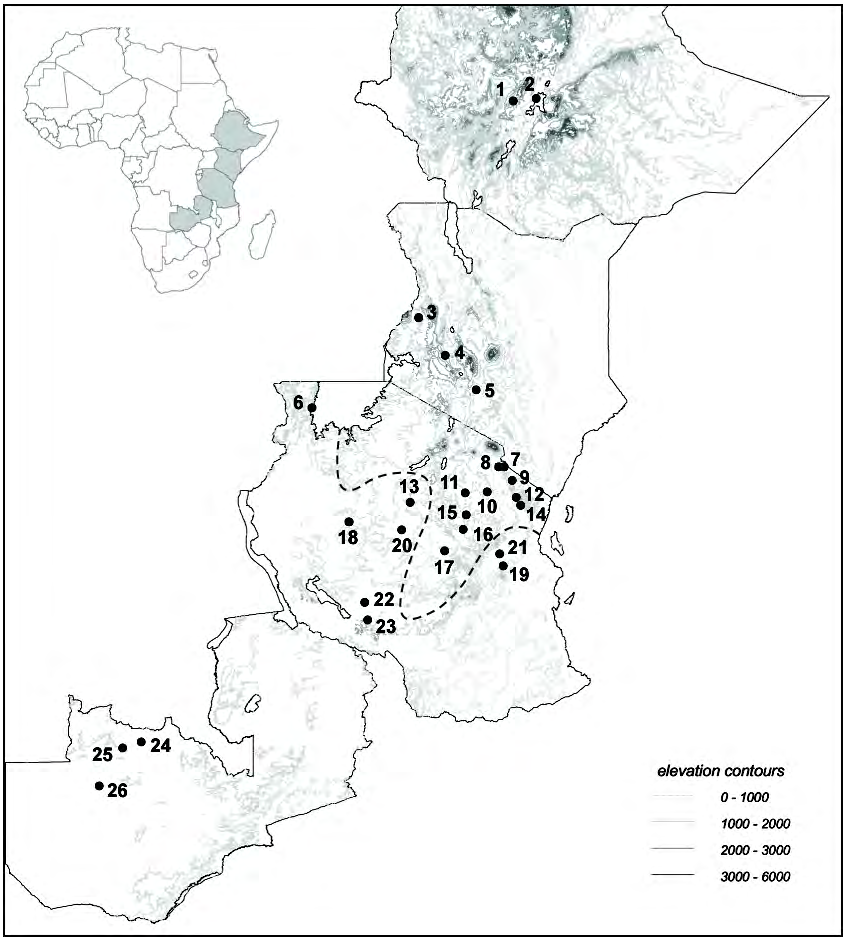

Fig. 1. – Map of Ethiopia, Kenya, Tanzania and Zambia (as indicated in the inset) with the collection localities (see Table 1 for the locality names and description). Elevation contour intervals are also shown. The dotted line represents the border between the Somali-Maasai (North) and the Zambezian (South) biotic zones.

MATERIAL AND METHODS

The following eight localities were sampled (STAPLERAT, 2003): Mugo and Zeway (Ethiopia); Rongai, Kitale and Nairobi (Kenya); Chunya (Tanzania); Meheba and Mutoma (Zambia) (Fig. 1; Table 1). These are prevalently arable fields (for the original habitat description, see Table 1). To achieve a more realistic representation of species range outside of the project areas, captures in surrounding localities were included, particularly in the geographic gaps between the field study areas (Fig. 1; Table 1).

Specimens were live-trapped using Sherman Folder traps and then transported alive to the following laboratories: Biology Department, Addis Ababa University (Ethiopia); Department of Zoology, Kenyatta University (Kenya); Pest Management Centre, Sokoine University of Agriculture, Morogoro (Tanzania); Mutanda Agricultural Research Station, Solwezi (Zambia).

Chromosome preparations were obtained from the bone marrow following the air-drying method of HSU & PATTON (1969). Cell suspensions in fixative were then transported to the Dipartimento di Biologia Animale e dell'Uomo, Università di Roma 'La Sapienza', where slides were prepared. Metaphases were stained by the Giemsa standard method (pH7). Pictures of metaphases were collected using the digital camera Photometrics Sensys 1600 and the Iplab software (Scanalytics, Inc, version 2.420).

Taxonomic definitions for Muroidea followed the most updated check-list by MUSSER & CARLETON (2005) and, for Myoxidae, HOLDEN (1993). Specimen identification was based on comparisons with type material and relevant series. We discuss the taxonomic problems encountered in species identification and description. For species whose taxon is in doubt, chromosomal comparisons and analysis of the sequences of mitochondrial genes were carried out in an integrated approach in order to make identification possible (such results will appear elsewhere). However, it was not possible to reach a definitive taxonomic definition for some. These are provisionally indicated in the following sections as "cf.", "cfr.", "sp.", or with an acronym.

A total number of 187 specimens representing 37 putative species were analysed. Specimens are preserved at the permanent collection of Musée Royal de l'Afrique Centrale, Tervuren (codes starting with a "T") and of the Museo di Anatomia Comparata dell'Università di Roma "La Sapienza" (codes with "ET", "ZM", "KE", "TZ").

TABLE 1

Collection localities, with the locality code for Fig. 1, latitude and longitude, and the current and original habitat (see, for habitat reference, White, 1983)

Country	Locality	Locality code	Latitude and Longitude	Habitat	Original habitat
Ethiopia	Mugo	1	07°50'N - 37°59'E	Enset fields	Highland with some alpine vegetation and moorland
	Zeway	2	07°55'N - 38°43'E	Maize fields	Savannah woodland with acacia trees
Kenya	Kitale	3	01°01'N - 35°00'E	Maize fields	Mosaic of lowland rainforest and secondary grassland
	Rongai	4	00°10'S - 35°51'E	Maize fields	Mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland
	Nairobi	5	01°16'S - 36°49'E	Grassland around buildings	" "
Tanzania	Kitundu Forest	6	01°53'S - 31°39'E	Rain forest	Rain forest
	Jipe	7	03°41'S - 37°42'E	Savannah bushes with scattered trees	Savannah bushes with scattered trees
	Lwami	8	03°41'S - 37°32'E	Bushland with scattered trees	Bushland with scattered trees
	Kisiwani	9	04°07'S - 37°57'E	Scattered bushes and grassland	Scattered bushes and grassland
	Ngasumet	10	04°29'S - 37°10'E	Grassland with scattered bushes	Grassland with scattered bushes
	Matongolo	11	04°31'S - 36°28'E	Bushland	Bushland
	Mkomazi	12	04°39'S - 38°05'E	Wooded grassland	Wooded grassland
	Singida	13	04°49'S - 34°44'E	Wooded grassland	Wooded grassland
	Mombo	14	04°54'S - 38°13'E	Grassland with scattered bushes	Grassland with scattered bushes
	Ndaleta	15	05°12'S - 36°30'E	Grassland	Grassland
	Zoissa	16	05°40'S - 36°25'E	Bushland	Bushland
	Mvumi Mission	17	06°20'S - 35°50'E	Wooded grassland	Wooded grassland
	Inala	18	05°25'S - 32°49'E	Grassland with scattered bushes	Grassland with scattered bushes
	Morogoro	19	06°49'S - 37°40'E	Cultivated areas, with fallow, scattered trees	Wooded grassland
	Itigi	20	05°41'S - 34°28'E	Bushland	Bushland
	Dakawa	21	06°26'S - 37°34'E	Miombo woodland	Miombo woodland
	Chunya B	22	07°58'S - 33°18'E	Cultivated fields, grassland with scattered trees	Wetter Zambezian Miombo woodland
	Chunya A	23	08°31'S - 33°24'E	Wetter Zambezian Miombo woodland	" "
Zambia	Mutanda Res. Station	24	12°22'S - 26°16'E	Maize fields	" "
	Meheba	25	12°33'S - 25°41'E	Maize fields	" "
	Mutoma	26	13°45'S - 24°57'E	Maize fields	" "

Karyotype descriptions

CRITETOMYNAE (Roberts, 1951).

The subfamily Cricetomyinae comprises three genera, *Beamys* (Thomas, 1909) [with two species *B. hindei* (Thomas, 1909) and *B. major* (Dollman, 1914)], *Cricetomys* (Waterhouse, 1840) (with four species), and *Saccostomus* (Peters, 1846), [with the two species *S. campestris* (Peters, 1846) and *S. mearnsi* (Heller, 1910)].

– *Cricetomys* (Waterhouse, 1840).

There are currently four recognised species of giant pouched rats (GENEST-VILLARD, 1967): *Cricetomys ansorgei* (Thomas, 1904), *C. emini* (Wroughton, 1910), *C. gambianus* (Waterhouse, 1840), and *Cricetomys kivuensis* (Lönnberg, 1917). Previously it was suggested that there existed six (ALLEN, 1939) or one (ELLERMAN et al., 1953) species, while GENEST-VILLARD (1967) described predominantly savannah-dwelling (*C. gambianus*) and lowland forest (*C. emini*) species. There are limited data regarding possible variation, so taxonomy must be considered as provisional for East Africa. Chromosomal descriptions are available for West African specimens only. MATTHEY (1954) described a karyotype for *C. gambianus* (unknown origin) with 2n=78. In Senegal, GRANJON et al. (1992) found a karyotype with 2n=80 and NFa=82, and in Benin, CODJA et al. (1994) described a karyotype with 2n=82 and NFa=88 for *C. gambianus*, and a karyotype of 2n=80 and NFa=88 for *C. emini*.

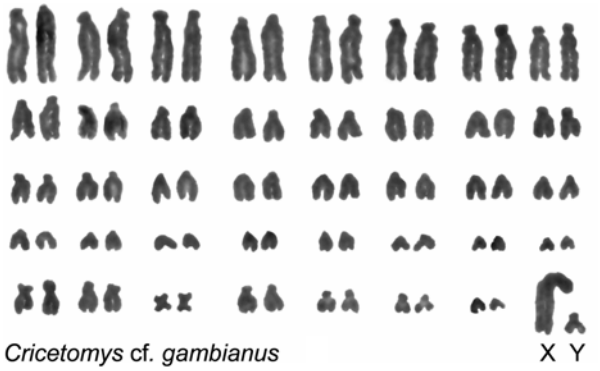

Fig. 2. – The karyotype of *Cricetomys* cf. *gambianus*, 2n=80 and NFa=84, X Y.

– *Cricetomys* cf. *gambianus* (Thomas, 1904).

One male from Morogoro (TZ), no voucher specimen. No morphological and DNA comparisons are possible for the moment. Therefore, we refer to this cytotype as "cf. *gambianus*". The diploid number is 2n=80 and the NFa=84. The autosomes are composed of seventy-four acrocentrics decreasing in size and by four medium and small metacentrics (Fig. 2). The X chromosome is one of the largest chromosomes of the whole karyotype and it is biarmed. The Y chromosome is a medium-size submetacentric. This karyotype differs from those in Senegal (GRANJON et al., 1992) and Benin (CODJA et al., 1994): not only are the diploid and NFa different, but also several pairs of acrocentrics are characterized by the occurrence of small arms, which do not occur in the other karyotypes. This karyotype is described here for the first time.

– *Saccostomus* (Peters, 1846).

Saccostomus is common and widespread in savannahs, scrubby areas, and cultivated fields from South Ethiopia and Somalia through East Africa down to the Cape Province. Despite this commonness, taxonomy has long been a source of debate (DELANY, 1975; ELLERMAN et al., 1953; MISONNE, 1974). In fact, the most recent rodent checklist (MUSSER & CARLETON, 2005) includes two species only, i.e. *S. campestris* (Peters, 1846) and *S. mearnsi* (Heller, 1910). However, a wide karyotypic polymorphism within the genus has been described, from the extreme south of the range (GORDON, 1986) to the north (CAPANNA et al., 1985; CORTI et al., 2004) through the central part of Africa (FADDA et al., 2001; HUBERT, 1978). Recently, a combined approach using both cytochrome *b* sequences groups and cytogenetics (CORTI et al., 2004) established that *mearnsi* and *campestris* represent two distinct natural groups and species complexes and was able to suggest a partial taxonomic resolution of the genus.

– *Saccostomus* cf. *elegans* (Thomas, 1897).

Three different karyotypes have been found. Two of them occur in two nearby localities (approximately 15 km apart) in south Tanzania, named Chunya A and B; a third is typical of northwest Zambia (Fig. 1, Tab. 1).

Tanzania, Chunya A (♀T50664). The diploid number is 2n=42 and the NFa is 46. The X chromosome is a medium-size submetacentric. The karyotype includes two pairs of large submetacentrics and two pairs of very small metacentrics, the remaining chromosomes being acrocentrics decreasing in size (see CORTI et al., 2004, for a Giemsa stained karyotype).

Tanzania, Chunya B 2 (♀TZ522, ♀TZ524, ♂TZ502, ♂TZ519, ♂TZ520). The diploid number is 2n=44 and NFa=46. The karyotype consists of three pairs of biarmed autosomes, one of which is a large subtelocentric and two are small metacentrics; the remaining autosomes are acrocentrics decreasing in size. The X and Y chromosomes are a large metacentric and a medium size submetacentric, respectively (see CORTI et al., 2004, for a Giemsa stained karyotype).

Zambia *Saccostomus* sp., Mutanda Research Station (♂ZM3, ♂ZM9, ♂ZM15, ♂ZM18). The diploid number is 2n=44 and the NFa is 48. The autosomal complement is identical to the one described for Chunya B, except for a pair of small metacentric chromosomes (No 20; in CORTI et al. 2004) that in Chunya B are acrocentrics. Furthermore, the X chromosome is a large submetacentric and Y is a medium size metacentric.

On the basis of the entire sequence of the cytochrome *b* mitochondrial gene, CORTI et al. (2004) have shown that these three karyotypic forms belong to the *campestris* species group and that they all form a monophyletic clade typical of the Zambezian domain, the northern limits of which occur in southern Tanzania. There is a low proportion of nucleotide substitutions between them, suggesting that the ongoing chromosomal differentiation has not led to full speciation. The southern Tanzanian specimens

(Chunya A and B) occur north (230 km) of Karonga, the locality on the northern shores of Lake Nyasa from which *S. elegans* (Thomas, 1897) was described. However, a craniological comparison of our specimens with the type of *S. elegans* (BMNH 97.18.1.207) and of two "co-types" of *S. campestris* (BMNH 7.1.1.181 and 58.6.18.19) revealed that the Chunya specimens could also be allocated to typical *campestris*, whereas the northern Zambian specimens closely resemble the *elegans* type skull. However, the skull differences between the two groups could also be due to age differences (indeed, the *elegans* type skull is of an old individual, and the "co-types" of *campestris* are young animals). It is obvious that this taxonomic problem will only be solved by undertaking an adequate study of 1) the sexual dimorphism and skull growth in a statistically relevant population of *Saccostomus* from the region concerned and of 2) the karyology and genetics of *Saccostomus* individuals from the Tette region in Mozambique (topotypical for *S. campestris*).

One must remember that a new undescribed species occurs in Tanzania north of the border with the Zambezian domain in the Maasai Steppe (FADDA et al., 2001). It has been shown (CORTI et al., 2004) that this new taxon belongs to the *Saccostomus* cf. *mearnsi* complex.

GERBILLINAE (Gray, 1825).

– *Gerbilliscus* (Thomas, 1897).

Gerbilliscus has been proposed recently as a distinct genus from *Tatera* (PAVLINOV, 1999; CHEVRET & DOBIGNY, 2005). It includes exclusively all the African species of the former *Tatera* (Lataste, 1882), an Asian monospecific with only *T. indica* (MUSSER & CARLETON, 2005). According to this checklist, the genus now includes 10 species. However, recent molecular data (COLANGELO et al., 2005; COLANGELO et al., submitted) suggest the occurrence of cryptic species which cannot be recognized through cytogenetics and/or morphometrics (i.e. *G. vicinus*). Moreover, there is molecular (CHEVRET & DOBIGNY, 2005; COLANGELO et al., sub.) and cytogenetic evidence indicating a close relationship between *Gerbilliscus* and *Gerbillurus*. An extensive systematic revision would probably indicate *Gerbillurus* as synonymous of *Gerbilliscus* (CHEVRET & DOBIGNY, 2005; COLANGELO et al., sub.).

There have been a high number of karyotypic studies performed on the genus, but they all originate from scattered areas, and no serious attempt has been made to summarize and include them in a general framework. Data available for the African species are as follows: *G. afra* (2n=44, NFa=66; MATTHEY, 1954; QUMSIYEH, 1986), a South African endemic. *G. brantsii* (2n=44, NFa=66; MATTHEY, 1954; QUMSIYEH, 1986), ranging from South Africa to Zambia. *G. leucogaster* (2n=40, NFa=66; GORDON & RAUTENBACH, 1980; QUMSIYEH, 1986), ranging from South Africa to Southwest Tanzania; MATTHEY (1954) identified a specimen from the Central African Republic as *G. schinzi* but this species is now considered synonymous of *G. leucogaster*. *G. nigricaudus* (2n=36, NFa=68, COLANGELO et al., 2005), occurring in Kenya and Tanzania. QUMSIYEH et al. (1987) reported a karyotype with 2n=40 from Kenya (one specimen) which was attributed to *G. nigricaudus*. However, there is evidence that this karyotype would be better attributed to another species (COLANGELO et al., 2005). *G. robustus* (2n=36, NFa=64; QUMSIYEH et al., 1987; FADDA et al., 2001), but this should be attributed to *G. vicinus* (DOBIGNY et al., 2002; GRANJON & DOBIGNY, 2003; see later), occurring from Chad to the Horn and East Africa; two specimens from Central African Republic with 2n=46 and NFa=64 were identified by MATTHEY & PETTER (1970) as *G. robustus*, but this was probably incorrect, as later they were ascribed by QUMSIYEH et al. (1987) to *G. phillipsi* (Somalia, Kenya, and Ethiopia); MATTHEY & PETTER (1970) described a karyotype with 2n=36 and NFa=62 from a Central African Republic specimen and attributed it to *G. kempi,* but this would be better referred to as *G. robustus*. *G. kempi* (2n=48, NFa=62-64; CODJA et al., 1994; COLANGELO et al., 2001); GAUTUN et al. (1986) referred to a specimen from Guinea with 2n=46 as *G. kempi*. Samples with 2n=48-50 and NFa=52-66, attributed to *G. nigrita* (now included in *G. kempi*), were reported from Chad, Zaire, Zambia and Angola. MATTHEY & PETTER (1970) attributed specimens from Burkina Faso and Ivory Coast to *G. hopkinsoni* (2n=48, NFa=62-64), now synonymous of *G. kempi*. *G. gambianus* (synonymous of *G. kempi*) (2n=52, HUBERT et al., 1973); MATTHEY (1969) described in a specimen from Senegal 2n=52 and NFa=64 and this was ascribed to *G. validus*, but probably it should be considered *G. gambianus* (MATTHEY & PETTER, 1970). DOBIGNY et al. (2002) reported the same karyotype from Nigeria. *G. guineae* (2n=50, NFa=64; MATTHEY & PETTER, 1970; BENAZZOU et al., 1984; GAUTUN et al., 1985). More recently, BULATOVA et al. (2002) reported a karyotype from Ethiopia with 2n=52 and NFa=62 that was attributed to *G. validus*.

Two different karyotypes were found in the present study. One shows 2n=36 and NFa=68, which is shared by three different species distinguishable on the basis of skull morphology and molecular analyses (COLANGELO et al., 2005), i.e. *G. nigricaudus*, *G. robustus* and *G. vicinus* (for a discussion of their systematic status see COLANGELO et al., 2005). The second karyotype shows 2n=40 and NFa=66 and characterizes *G. leucogaster*.

– *Gerbilliscus leucogaster* (Peters, 1852).

Dakawa (♂T50545, ♂T50546); Tanzania. The diploid number is 2n=40 and NFa=66. The karyotype is composed of fourteen pairs of biarmed chromosomes decreasing in size and five pairs of medium size acrocentrics. The X chromosome is a large metacentric, and the Y is a medium size submetacentric (see COLANGELO et al., 2005). Phylogenetic analyses based on the cytochrome *b* and 16S mitochondrial genes showed a marked divergence between these specimens and those attributed to the *robustus* species group (i.e. *G. robustus*, *G. nigricaudus and G. vicinus* (COLANGELO et al., 2005).

– *Gerbilliscus robustus* (Cretzscmar, 1826).

Zeway (♂ET107, ♂ET119, ♂ET127); Ethiopia. The diploid number is 2n=36 and NFa=68. All autosomes are biarmed decreasing in size. The X chromosome is a large metacentric, and the Y chromosome is a small acrocentric (see COLANGELO et al., 2005). This same chromosomal

formula has already been reported from several other localities from west Africa along the arid sub-Saharan belt to East Africa down to Tanzania across the arid savannahs (QUMSIYEH et al., 1987; FADDA et al., 2001), suggesting that this karyotype is highly represented in this biome.

– *Gerbilliscus nigricaudus* (Peters, 1878).

Mkomazi (♀T50216, ♀T50217), Lwami T50230, Jipe (♀T50453, ♀T50475, ♀T50476, T50456♂); Tanzania. The diploid number is 2n=36 and NFa=68. All autosomes are biarmed decreasing in size. The X chromosome is a large metacentric, and the Y chromosome is a small acrocentric (see COLANGELO et al., 2005). We found this species in a restricted area across the border of Tanzania and Kenya. MATTHEY (1969) and QUMSIYEH et al. (1987) reported for *G. nigricaudus* a diploid number of 40 with NFa respectively 66 and 68, but probably these specimens are referable to *G. leucogaster*.

– *Gerbilliscus vicinus* (Peters, 1878).

Itigi (♀T50339), Matongolo (♂T50062), Ndaleta (♂T50144, ♀T50153, ♀T50158), Inala (♂T50579), Ngasumet (♂T50190), Mombo (♀T50214, ♀T50215, ♀T50226, ♂T50227), Jipe (♀T50473); Tanzania. Nairobi (♀KE135); Kenya. The karyotype appears to be the same as *G. robustus* from Ethiopia, but these samples show a marked genetic divergence from the Ethiopian specimens suggesting that *G. vicinus* should be considered a separate species (COLANGELO et al., 2005). BATES (1988) reported a significant geographical variation in skull and body size in *G. robustus*, suggesting the possible occurrence of a distinct race in central Tanzania. He identified *G. swaythlingi* (Kershaw, 1921), type locality Morogoro, as the holotype for this race. However, an extensive morphometric and molecular genetic comparison would probably ascribe this race to *G. vicinus*.

MURINAE (Illiger, 1815).

– *Acomys* I. (Geoffroy, 1838).

These spiny mice are widespread throughout all of Africa, the near and Middle East, and some Mediterranean islands. The rodent checklist by MUSSER & CARLETON (2005) lists 19 species, but as for most of the other African rodent genera, their taxonomy and systematics are yet to be established. Cytogenetics, morphology and, recently, molecular genetics (BAROME et al., 1998; 2001) have been widely used to shed some light on the taxonomy and systematics of the genus.

Since the first descriptions of the karyotype of *Acomys* by MATTHEY (1956; 1963; 1965a, b; 1968), further data concerning chromosomal variation in the genus have been added by several authors. Originally there was considerable interest in the karyotype of *A. selousi*, long considered synonymous of *A. spinosissimus* (see MUSSER & CARLETON, 1993). The peculiar chromosomal sex determination found in the former, with a single and exceptionally large X chromosome in both males and females, was in striking contrast with the XX/XY typical of *A. spinosissimus* and the other species of the genus. Furthermore, MATTHEY (1965a, b, and unpublished) also showed an inter- and intra-individual variability in chromosome constitution in *A. selousi*. Later, DIPPENAAR & RAUTENBACH (1986) found the same 2n=60 and NFa=68, but with a submetacentric X in Transvaal (South Africa). All together, these data do not support the idea of maintaining the two taxa in synonymy, and they should be definitively considered as separate valid species.

The analysis of a partial fragment (715 bp) of the gene for cytochrome *b* in the Tanzanian samples, for which we report here the karyotypes (unpublished data), confirmed that *A. spinosissimus* and *A.* cf. *selousi*, although monophyletic, constitute two well separated species. This genetic and chromosomal distinction is also reported for the Tanzanian locality of Berega by BAROME et al. (2001). For these reasons, we decided to provisionally maintain the name *A.* cf. *selousi* for these specimens until the "*selousi*" – like group has received adequate investigation. The karyotypes known for other species are as follows: *A. cahirinus*, 2n=36 and NF=68 (VOLOBOUEV et al., 1996); *A. dimidiatus* (cf. *A. airensis*, Agades, Niger, 2n=42, NFa=66), 2n=38 and FN=70 (VOLOBOUEV et al., 1991); *A. ignitus*, 2n=50 and NF=66-68 (MATTHEY, 1956); *A. russatus*, 2n=66 and NF=66 (WAHRMAN & ZAHAVI, 1953).

Following the 1999 expedition in the Maasai Steppe, FADDA et al. (2001) reported three different karyotypes for this part of Tanzania, corresponding to *A. spinosissimus* (2n=60, NFa=70), *A. wilsoni* (2n=62, NFa=76) and *A. ignitus* (2n=36, NFa=68). Here we add further information from a higher number of localities and for a higher number of specimens for these species.

– *Acomys spinosissimus* (Peters, 1852).

Chunya (♀T50676, ♀T50673), Tabora-Inala (♀T50676), Zoissa (♀T50119, ♀T50088, ♂T50087, ♂T50202), Matongolo (♀T50003); Tanzania. The species occurs in a typical Zambezian domain (Southern Tanzania to Southern Transvaal). However, it extends north to the Maasai Steppe, which is a typical Somali-Maasai arid domain. The diploid number in the localities investigated is 2n=60 and the NFa=70. The karyotype is represented by 5 pairs of metacentrics and submetacentrics, 22 pairs of acrocentrics decreasing in size, and one pair of small metacentrics. The X chromosome is a large acrocentric and the Y-chromosome is a small subtelocentric. This karyotype is the same as the one described by FADDA et al. (2001) in the Maasai Steppe and by DIPPENAAR & RAUTENBACH (1986) in South Africa.

– *Acomys* cf. *selousi* (Roberts, 1951).

Dakawa (♀TZ521); Tanzania. The diploid number is 2n=59, NFa=68. The karyotype is constituted by five pairs of medium size biarmed chromosomes, 24 pairs of acrocentrics decreasing in size (Fig. 3). The single X chromosome is very large.

Fig. 3. – The karyotype of *Acomys* cf. *selousi*, 2n=59 and NFa=68. Note the single X chromosome of very large size.

– *Acomys wilsoni* (Thomas, 1892).

Jipe (♀T50467, ♂T50463, ♀T50466, ♂T50439, ♀T50440, ♀T50447, ♀T50446, ♀T50438, ♂T50437), Ngasumet (♂T50246, ♂T50247, ♀T50247); Tanzania. The range of the species includes Sudan, Ethiopia, Somalia, Kenya and Tanzania, but its limits are unknown. The first description of the karyotype of the species was first described by FADDA et al. (2001). The diploid number is 2n=62 and NFa=76. The autosomal set is composed of eight pairs of meta- and submetacentric chromosomes, three of which are the largest of the set and five of which range from medium to small, and of 22 pairs of acrocentrics decreasing in size. The X chromosome is acrocentric (the largest amongst the acrocentrics) and the Y chromosome is a small acrocentric.

– *Acomys ignitus* (Dollman, 1910).

Lwami (♂T50232, ♂T50527, ♀T50529, ♂T50528, ♂T50517, ♂T50499, ♂T50505), Ngasumet (♀T50185); Tanzania. The range includes Tanzania and Kenya, but its limits are unknown. Samples were collected at the extreme North of the Maasai Steppe, where a corridor with Southern Kenya is present through the Uzambaras and the Pare mountain range. The first description of the karyotype was given by FADDA et al. (2001) and shows 2n = 36 and NFa = 68. The karyotype resembles *A. cahirinus* and, in fact, the species was included by ELLERMAN (1941) in the *Cahirinus* group.

– *Aethomys* (Thomas, 1915).

The genus has traditionally been divided into two subgenera (DAVIS, 1975): *Micaelamys*, including *A. namaquensis* and *A. granti*, and *Aethomys*, for which nine species are currently recognised (MUSSER & CARLETON, 2005; VISSER & ROBINSON, 1986). Following the original hypothesis by DAVIS (1975), the two subgenera can be distinguished on the basis of tail length and colour of ventral parts.

Chromosomal studies (MATTHEY, 1954; VISSER & ROBINSON, 1986; BAKER et al., 1988) have shown that the karyotypes of the "*Micaelamys*" *A. namaquensis* (2n=24) (from Southeast Zambia to South Africa) and *A. granti* (2n=32) (Cape Province) are divergent from the other species studied, which are all characterized by higher diploid numbers (2n=44-50). Recent molecular analyses based on cytochrome *b* sequences (DUCROZ et al., 2001; RUSSO et al., 2001; CASTIGLIA et al., 2003a) confirmed the high genetic difference between the two subgenera and provided evidence for the paraphyly of the genus in a wider phylogenetic context involving several other African species of Murinae and Otomynae (DUCROZ et al., 2001; CASTIGLIA et al., 2003a). These data suggest the need for a definitive splitting of the genus.

There is also evidence indicating the occurrence of cryptic species. For example, it has been recognised that *A. chrysophilus,* widespread from Kenya to South Africa, must be separated into two species, corresponding to different cytotypes previously identified (GORDON & RAUTENBACH, 1980; GORDON & WATSON, 1986; VISSER & ROBINSON, 1986): the true *A. chrysophilus* (2n=50) and *A. ineptus* (2n=44). These two species occur sympatrically and differ in gross sperm and bacular morphology (VISSER & ROBINSON, 1986; BREED et al., 1988) as well as in their quantitative cranial traits (CHIMIMBA, 1998; CHIMIMBA et al., 1999).

– *Aethomys kaiseri* (Noack, 1887).

Meheba, Solwezi (♂ZM13, ♂ZM32); Zambia. The diploid number is 2n=50 and NFa=60. The karyotype is composed of forty-five pairs of acrocentric chromosomes decreasing in size and five pairs of small meta/submetacentrics. The sex chromosomes are very large and biarmed with the Y being slightly larger that the X chromosome. The length of each sex chromosome is approximately double the length of autosome pair 1. The karyotype is reported in CASTIGLIA et al. (2003a).

– *Arvicanthis* (Lesson**,** 1842).

Arvicanthis probably represents one of the African rodent genera that has received most attention over the last decade. As a result, the number of species recognised increased to seven after the latest rodent checklist (MUSSER & CARLETON, 2006). Previously, CORBET & HILL (1991) and MUSSER & CARLETON (1993) recognized five species only (although with some disagreement regarding their systematics and taxonomy). The numerous studies performed on a chromosomal (BASKEVICH & LAVRENCHENKO, 2000; CAPANNA & CIVITELLI, 1988; CAPANNA et al., 1996; CASTIGLIA et al., 2003b, 2006; CIVITELLI et al., 1995; FADDA et al., 2001; VOLOBOUEV et al., 1987; 1988; 2002a; GRANJON et al., 1992), allozymic (CAPULA et al., 1997), mtDNA sequencing (DUCROZ et al, 1997; CORTI et al., submitted), and morphometric (AFEWORK BEKELE et al., 1993; CORTI & FADDA, 1996; FADDA & CORTI, 1998; 2001) basis have shown that the genus is represented by a higher number of species.

Two major clades occur within *Arvicanthis*, roughly an eastern and a western one, although some of the western species extend into the East and vice versa (DUCROZ et al., 1997; CORTI et al., submitted). This result is based on molecular studies (and congruent with karyotypic analyses). Taxonomic confusion in the past, part of which remains unsolved, is probably due to the high level of convergence shown in morphology, which obscures species differences (FADDA & CORTI, 2001).

The karyotypes of the taxa recognized so far are as follows: *A.* cf. *somalicus*, 2n=62, NFa=62-63 (Ethiopia; Baskevich & Lavrenchenko, 2000). *A. abyssinicus*, 2n=62, NFa=62 (Ethiopia; Corti et al., 1996). *A. blicki*, 2n=48, NFa =64 (Ethiopia; Corti et al., 1995; 1996). *A. neumanni,* 2n=54, NFa=62 (Tanzania; Fadda et al., 2001; Castiglia et al., 2003b). *A. nairobae,* 2n=62 NFa=78 (Tanzania; Fadda et al., 2001; Castiglia et al., 2003b). *A. ansorgei*, 2n=62, NFa=74/76 (Senegal, Mali, Burkina-Faso; previously named ANI-3; Volobouev et al., 2002a). *A. rufinus* (Benin; previously named ANI-4; Civitelli et al., 1995; Volobouev et al., 2002a). "*A. niloticus"* complex, 2n=62, NFa=62/64, described from Egypt, Sudan, Ethiopia, northern Senegal and northern Burkina Faso, southern Mauritania, Mali, Niger, Chad; Volobouev et al., 1988; 2002a; Philippi, 1994; Ducroz et al., 1997; Civitelli et al., 1995).

There are further karyotypes described for which there is still no species assignment or evidence supporting the original allocation made by authors. This is the case for the karyotype with 2n=44 and FN=72 described in Somalia by Capanna & Civitelli (1988), which was attributed to *A. niloticus,* which evidently characterizes a different unidentified species. In their recent review, Castiglia et al. (2006) defined this taxon with the acronym ANI-8. Furthermore, the situation is particularly confusing in Ethiopia, where a karyotype with 2n=60 and NFa=76 has been described in Konso (Gamo-Gofa, South Ethiopia; Orlov et al., 1992) and another one with 2n=56 and NFa=78 in Gambella (Bulatova et al., 2002).

The karyotypic results following the field studies of the Staplerat project are presented here for *A. nairobae* and for a number of taxa for which there is yet to be any definitive taxonomic solution. The latter highlight a complex pattern of sibling species and speciating taxa. This is particularly true for the *A. niloticus* complex that will be discussed first. Two other unknown karyotypes are indicated as ANI-5 and ANI-6.

– *Arvicanthis niloticus* (Desmarest, 1822 complex).

The two taxa *A. niloticus* and *A. dembeensis* (Rüppel, 1842) have been considered either as synonymous (see Musser & Carleton, 1993) or as separate species (see Yalden et al., 1976). *A. niloticus* (type localities: Upper Egypt, Fayum and Giza areas, part of the Nile delta), surprisingly, has received limited attention in all studies. Fadda & Corti (1998) examined, through three dimensional geometric morphometrics, the geographic variation in *A. niloticus* along the Nile Valley from Cairo down to the extreme south of Sudan, also including *A. testicularis* (Dollman, 1911) (synonymous of *A. niloticus*; Musser & Carleton, 2005). They evidenced in *A. niloticus* a north-south clinal variation in morphometric traits which somehow contrasts in direction that characterizing *A. testicularis*. This was considered by the Authors as sufficient to keep them as separate taxa, but the problem should be better addressed through a cytogenetic and molecular approach. Moreover, also the karyotype and the DNA analyses on *A. niloticus* were from samples of breeding colonies outside the topotypical area. *A. dembeensis* has been described as endemic to Ethiopia, and is considered a relatively 'lowland' taxon, occurring from sea level to 2000 mt a.s.l. (Yalden et al., 1976). However, there are problems regarding the taxonomic status of the samples so far analysed in different studies. The first one concerns the type specimen. To date, the most complete study was carried out through multivariate morphometrics (Afework Bekele et al., 1993) on eight localities (four of them from the bottom of the Rift along the Ethiopian lakes), which confirmed a clear morphological distinction from the other major taxon occurring in the country, i.e. *A. abyssinicus*. One of the populations examined was from Lake Tana, on the western side of the Rift Valley, i.e. the topotypical area from which Rüppel described the type specimen in 1842 (Deraske, 12° 25' N - 37° 20' E). This population clustered with the others that occurred on the eastern side of the Rift at altitudes below 2000 mt a.s.l. This morphological relatedness was considered sufficient to include them all under *A. dembeensis*. On this morphological basis, Corti et al. (1995) attributed the karyotype of specimens from Koka to *A. dembeensis*, and so far this has been considered the typical karyotype of this species. However, the species was included by Musser & Carleton (2005) in *A. niloticus*. The comparison of the cytochrome *b* sequences of samples of *A. dembeensis* and *A. niloticus* from Egypt (although from a breeding colony, but with very low genetic differences from Ethiopian samples) (Ducroz et al., 1998; Corti et al., submitted) and the fact that the two share the same karyotype (Corti et al., 1996) do not support a specific distinction so that its synonymy with *A. niloticus* should be definitively accepted. On the other hand, due to the variability characterizing this complex, Corti et al. (submitted) still suggest this taxon should be referred to as *A.* cf. *niloticus* 1.

Zeway (♂ET110, ♂ET114, ♂ET125, ♂ET126, ♂ET127); Ethiopia. Kitale (♂KE119); Kenya. The diploid number is 2n=62 and the NFa is 62. The autosomal set is characterized by 58 acrocentrics decreasing in size and a pair of small metacentrics. The X chromosome is a large submetacentric (the largest chromosome in the set) and the Y chromosome is a metacentric of medium size. Although these Ethiopian and Kenyan specimens seem to all have the same karyotype, they show a genetic differentiation in progress (Corti et al., submitted). Therefore, these authors referred to the specimen from Kenya as *A.* cf. *niloticus* 5 and to those from Ethiopia as *A.* cf. *niloticus 2.* Furthermore, this karyotype is identical to the one described for *A.* cf. *niloticus* 1 (Koka, Ethiopia) by Corti et al. (1996) and for *A. somalicus* (Awash National Park, Ethiopia) by Baskevich & Lavrenchenko (2000).

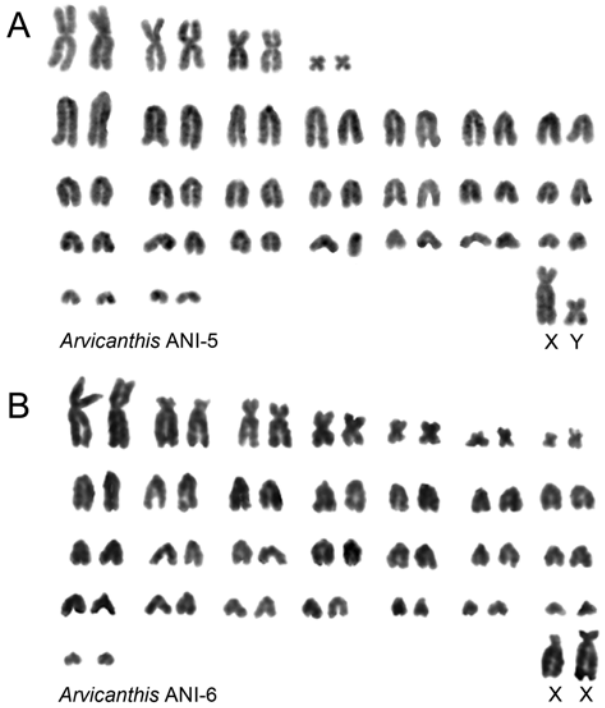

Fig. 4. – A) The karyotype of *Arvicanthis* ANI-5, 2n=56, NFa=62, X Y. B) The karyotype of *Arvicanthis* ANI-6, 2n=60, NFa=72, X X.

Arvicanthis sp ANI-5. Rongai (♂KE100, ♂KE103, ♂KE133, ♀KE127, ♀KE147); Kenya. The diploid number is 2n=56 and the NFa is 62. The autosomes are composed by three pairs of large metacentrics, one pair of small metacentrics, and 23 pairs of acrocentrics decreasing in size (Fig. 4A). The X chromosome is a large submetacentric and the Y chromosome is a medium size metacentric. This karyotype is described here for the first time. A banding study to assess the karyotype relationships with the other *Arvicanthis* in east Africa will appear elsewhere (Castiglia et al., 2005). A phylogenetic tree based on the entire sequence of the cytochrome *b* gene (Corti et al., submitted) suggests that this species is a member of the A. *niloticus sensu lato* group.

Arvicanthis sp ANI-6. Zeway (♀ET129); Ethiopia. The diploid number is 60 and the NFa is 72. The karyotype is composed by four pairs of large metacentric chromosomes, three pairs of small-sized metacentrics, and 22 pairs of acrocentrics decreasing in size (Fig. 4B). The X chromosome is a large submetacentric (Fig. 4B). This karyotype is described here for the first time. A banding study to assess the karyotype relationships with the other *Arvicanthis* in east Africa will appear in print elsewhere (Castiglia et al., 2005). Orlov et al. (1992) found a karyotype in Konso (Gamo-Gofa region, South of Zeway, along the Rift Valley) which is very similar to this one, with the exception of two additional pairs of small metacentrics. It is still questionable whether all these South Ethiopian cytotypes represent a chromosomally polytypic species. A phylogenetic tree based on the entire sequence of the cytochrome *b* gene (Corti et al., submitted) has shown that the Zeway karyotype constitutes the sister group of *A. ansorgei* and belongs to the West African clade of *Arvicanthis*, which extends along the south Ethiopian Rift Valley at lower altitudes. Furthermore, karyotypic variants have been found in the Konso (2n = 60 and NFa = 76) and in the Gambella (2n = 56 and NFa = 78) regions by Baskevich & Lavrenchenko (2000), all resembling morphologically *A. niloticus*. It should be noted that these areas are more than 5° latitude south of the type locality, so that it is questionable whether these results highlight a chromosomally polytypic or different species. Baskevich & Lavrenchenko (2000) provisionally named the specimens from Konso and Gambella *Arvicanthis sp.*1 and *Arvicanthis sp.* 2, respectively. Fadda & Corti (2001) morphometrically examined the specimens from Konso, Gambella, and Omo (plus a Somalian population) and found that they share unique morphometric characteristics, so that they were provisionally named *A. sp.* 3.

– *Arvicanthis nairobae* (Allen, 1909).

Nairobi, type locality (♂KE145); Kenya. The karyotype is characterized by 2n=62 and NFa=78. The autosomal set is composed of 9 pairs of biarmed autosomes and 21 pairs of acrocentric chromosomes decreasing in size. The biarmed chromosomes are represented by two large submetacentrics, four pairs of medium size submetacentrics and three pairs of small metacentrics. The X and Y chromosomes are subtelocentric, of large and small size respectively. This karyotype is identical to the one described in Tanzania (Fadda et al., 2001; Castiglia et al., 2003b).

– *Lemniscomys* (Trouessart, 1881)

The striped grass mice genus *Lemniscomys* is widely distributed throughout the African sub-Saharan savannahs and in Northwest Africa. The taxonomy and systematics of the genus is complex as it includes twelve recognised species (Musser & Carleton, 2005) which are probably at different levels of morphological differentiation (Ellerman, 1941; Van der Straeten & Verheyen, 1980) and are included in different groups. These are the "*barbarus*" group (striped species), including *L. barbarus*, and *L. hoogstrali*; the *striatus* group (spotted species), including *L. bellieri*, *L. macculus*, *L. mittendorfi* and *L. striatus*; the *rosalia* group (plain coloured species), which includes *L. griselda*, *L. rosalia*, *L. linulus*, and *L. roseveari.* Van der Straeten & Verheyen (1980) found morphometric differences within the "s*triatus*" group, with *L. striatus* being similar to *L. linulus* (*Rosalia* group) and well differentiated with respect to *L. bellieri* and *L. macculus*, which instead clusters with *L. barbarus*. On the basis of multivariate morphometrics of skull linear measurements, Carleton & Van der Straeten (1997) recently split *L. barbarus* into two species, i.e. *L. barbarus* restricted to scrub vegetation along a narrow coastal strip in Morocco, Algeria and Tunisia, and *L. zebra* with a sub-Saharan distribution. Relationships between species still remain unresolved, except for the close relationship between *L. bellieri* and *L. macculus* (Ducroz et al., 2001).

There is a conspicuous number of karyotypic data showing the occurrence of several different diploid and fundamental numbers. Considerable chromosomal variation has been shown in West and Central Africa for *L.*

striatus by Van der Straeten & Verheyen (1985; Burkina Faso; 2n=44, NFa= 58), Gautun et al. (1985; Burkina Faso; 2n=43), Matthey (1959; Congo; 2n=48, NFa= ~56), Capanna et al. (1997; Benin; 2n=44; NFa=72-74), Castiglia et al. (2002b; 2n=44, NFa=68), Ducroz (1998) and Van der Straeten & Verheyen (1978) (Ivory Coast; 2n=44, NFa=58). The large differences in NFa in these specimens may be due, in part, to different interpretations of small heterochromatic chromosomal arms. *L. bellieri* seems to be characterized by a constant 2n=56 and NFa=60 karyotype in Burkina Faso and Ivory Coast (Van der Straeten & Verheyen, 1978; Ducroz, 1998; Tranier & Gautun, 1979). *L. barbarus* also seems to have the same constant karyotype across Morocco (Stitou et al., 1997; 2n=54, NFa=58), Ivory Coast (Matthey, 1954; 2n=54) and the Algerian Coast (Filippucci et al., 1986; 2n=54, NFa =58). *L. macculus* has been studied in Central African Republic (Ducroz, 1998; 2n=56, NFa=62) and *L. mittendorfi* in Cameroon (Fülling, 1992; 2n=56). Recent findings in Tanzania (Castiglia et al, 2002b; Fadda et al., 2001) have shown a karyotype with 2n=54, NFa=68 for *L. zebra*, and 2n=54, NFa=62 for *L. rosalia*. The latter presents striking differences with the 2n=48, NFa =62 form described by Ducroz et al. (1999) for *L. rosalia* in Kwazulu Natal. The two differ due to several rearrangements and, on this basis, Castiglia et al. (2002b) argued that the two taxa should be considered as separate species. The type locality of *L. rosalia* is Monda, Nguru Mtns., Tanzania and, therefore, the name should be kept for the Tanzanian specimens, and it was suggested that *L. calidior* (Thomas and Wroughton, 1908) should be used as the oldest available name for the South African taxon.

Furthermore, Castiglia et al. (2002b) maintained that species relationships based on karyotypes contrast with the views that consider the plain coloured species as primitive and the multi-striped ones as derived. *L. bellieri*, *L. macculus* and *L. zebra* have an ancestral karyotype and are characterised by a multi-striped or spotted pelage, while *L. rosalia* has a derived karyotype and is a plain coloured species. This hypothesis is also in agreement with the morphometric relationships outlined by Van der Straeten & Verheyen (1980), who found a strict morphological similarity between *L. barbarus* and *L. bellieri* /*L. macculus*.

Here we present the karyotype of *L.* cf. *striatus massaicus* from Kenya and additional material for *L. rosalia* and *L.* cf. *zebra* from Tanzania (these two occur sympatrically in several of the localities studied).

– *Lemniscomys rosalia* (Thomas, 1904).

Zoissa (♂50083), Jipe (♂T50458, ♂T50460, ♂T50461, ♂T50462, ♂T50479, ♀T50442, ♀T50459, ♀T50477, ♀T50478), Kisiwani (♀T50428, T50427, ♂T50391, T50429), Mbugani-Chunya (T0672), Morogoro (T50201, ♂T50208, ♂T50547, ♀T50490, ♀T50491, ♀T50548), Ngasumet (♂T50172, ♂T50186), Dakawa (T50551, T50552); Tanzania. The species is characterised by 2n=54 and NFa=62. The autosomes comprise three pairs of large subtelocentrics, two pairs of small metacentrics and twenty-one pairs of acrocentrics decreasing in size. The X chromosome is a submetacentric and the Y is a medium size submetacentric, with a polymorphism occurring in the former (Castiglia et al., 2002b). This karyotype has already been reported and described by Fadda et al. (2001) for other localities from the Maasai steppe.

– *Lemniscomys* cf. *zebra* (Heuglin, 1864).

Matongolo (♂T50030), Mvumi Mission (♀T50333), Ngasumet (♀50179, ♀T50178, ♂T50174), Kisiwani (♀T50429), Mbugani-Chunya (♀T50699), Itigi (♀T50348), Lwami (♂T50492, ♂T50518, ♂T50524, ♂T50525, ♀T50502, ♀T50523, ♀T50526, ♀T50507, ♀T50501) Ndaleta (♀T50152); Tanzania. The 2n is 54, and the NFa is 58. Autosomes are represented by one pair of large submetacentrics (the largest of the autosomal set), by two pairs of very small metacentrics and by acrocentrics decreasing in size. The X chromosome occurs in two forms, both submetacentric, differing in the length of the short arm. Castiglia et al. (2002b) studied the occurrence of the two forms and found similar frequencies. The Y chromosome is a medium size metacentric. This karyotype has already been reported and described by Fadda et al. (2001) for other localities from the Maasai steppe.

– *Lemniscomys* cf. *striatus massaicus* (Pagenstecher, 1885).

Rongai (♂KE105, ♀KE116), Nairobi (♂KE110, ♂KE112, ♀KE125, ♀KE137, ♀KE146); Kenya. These specimens are characterised by 2n=48 and NFa=54. The karyotype is composed of four pairs of meta-submetacentrics, the remaining autosomes being acrocentrics decreasing in size (Fig. 5). The chromosome X is a large submetacentric, the Y is a small metacentric. This karyotype is presented here for the first time. The chromosomal differences between these specimens and *L. striatus* from West Africa are significant. A description of chromosomal differences based on differential staining will be described elsewhere.

Fig. 5. – The karyotype of *Lemniscomys* cf. *striatus massaicus*, 2n=48, NFa=54, X Y.

– *Mus* (L., 1758), subgenus *Nannomys (*Peters, 1876).

The African species of the subgenus *Nannomys*, known also as *Leggada*, constitute one of the major taxonomic puzzles and an emblematic group due to their fast rate of speciation often associated with chromosomal rearrangements. They form a monophyletic group, the ancestor of

which migrated from Asia through Iraq, Iran, and Saudi Arabia into Ethiopia (JOTTERAND, 1972). CORBET (1990) has highlighted that although there can be no doubt regarding the dichotomy between *Nannomys* and *Mus sensu strictu*, the recognition of the former as a separate genus is still far from being solved. MUSSER & CARLETON (2005) listed 19 species in the subgenus, but this number is likely to increase due to the occurrence of cryptic and chromosomal species (VEYRUNES et al., 2004). Furthermore, VEYRUNES et al. (2005) recognised seven clades on the basis of cytochrome *b* sequences, probably corresponding to more species since some of these may correspond to species complexes.

Previous cytogenetic studies divided the species into two large cytotaxonomic groups, differing in the morphology of the sex chromosomes (JOTTERAND, 1972). The sex chromosomes of the first group are primitively acrocentric. In the second group, both primitive X and Y chromosomes have been translocated onto a pair of autosomes. Subsequent analyses showed that three different pairs of autosomes were involved in the Robertsonian translocation event (JOTTERAND-BELLOMO, 1986; 1988). A definite taxonomic revision will require multidisciplinary studies integrating molecular, cytogenetics, morphological and morphometrics analyses. In addition, the distributional extent of chromosomal polymorphism and of the different cytotypes through differential staining and *in situ* hybridisation still needs to be elucidated to provide a clear assessment of patterns of chromosomal evolution in this group.

Nannomys sp. Rongai – A (*minutoides* complex), Nairobi (♂KE106, ♂KE111, ♂KE144); Kenya. Species identification was possible by analysing the skull and cytochrome *b* phylogeny (unpublished data). The karyotype of this species is 2n=22, FN=36. The autosomes are constituted by six pairs of metacentrics and four pairs of acrocentrics; the X chromosome is a large metacentric and the Y a large submetacentric (Fig. 6A). This karyotype is presented here for the first time. The morphology of the sex chromosomes strongly suggests the fusion of the original sex chromosomes with a pair of autosomes, thus indicating the strict similarity of this karyotype to of *N. minutoides* from Zambia. Therefore, further banding analyses are needed to define relationships between these species within a wider taxonomic framework.

Nannomys sp. (*minutoides* complex), Mutanda Research Station, Mutoma, Solwezi (♂ZM8, ♀ZM16, ♀ZM24); Zambia. The chromosomal complement was 2n=25 in a male and a female, while another female had 2n=24. However, the NF is 36 in all specimens. The karyotype is composed of five large metacentric chromosomes, and six pairs of acrocentrics decreasing in size. The heterochromosomes are fused with an autosome. In both females studied, one of the X chromosomes showed a partial deletion, thus resembling the Y in size. This karyotype differs significantly from the one reported by JOTTERAND (1972) from Kafue (Zambia, Lusaka region), characterized by a 2n=34 with all-acrocentric autosomes. The reduction in diploid number (2n=24-25), together with the maintenance of the FN and the occurrence of large biarmed chromosomes is due to the presence of Rb fusions (for identification, see CASTIGLIA et al., 2002a). The high chromosomal diversification of the Zambian samples together with the occurrence of "all-acrocentrics" and Rb populations in other areas confirm the extensive chromosomal variability of this taxon (MATTHEY, 1964). As the type locality for the species is Cape Town (South Africa), the attribution of these specimens (including those reported by JOTTERAND, 1972) to this species is therefore questionable.

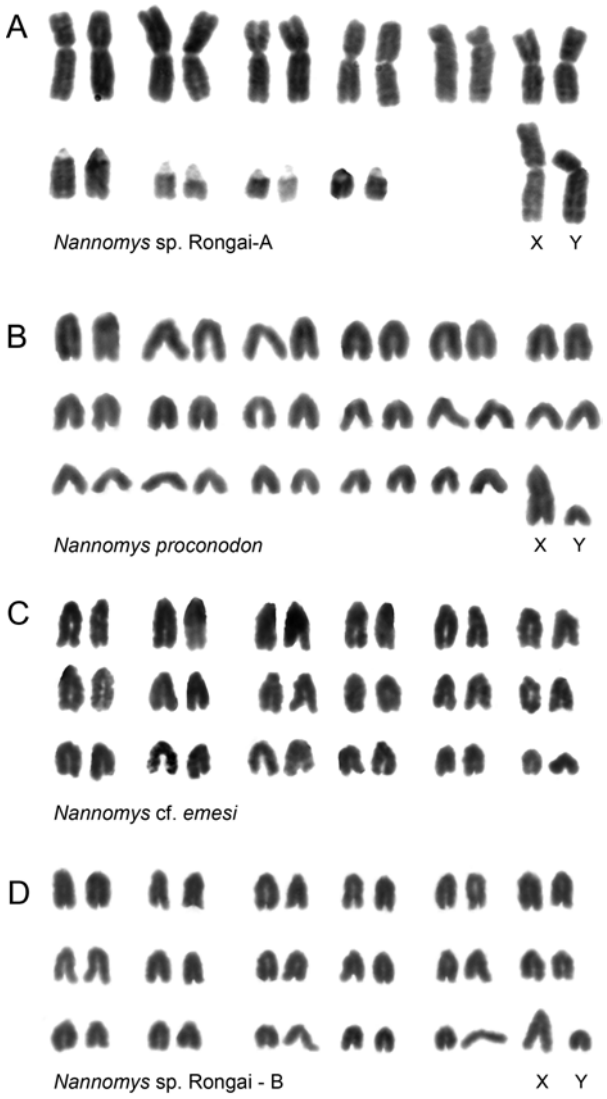

Fig. 6. – A) The karyotype of *Nannomys sp.* Rongai – A (*minutoides complex*), 2n=22, FN=36, X Y. B) The karyotype of *Nannomys proconodon*, 2n=36 and NFa=34, X Y. C) The karyotype of *Nannomys* cf. *emesi*, 2n=36, FN=36. D) The karyotype of *Nannomys* sp. Rongai – B, 2n=36, NFa=34, X Y.

– *Nannomys proconodon* (Rhoads, 1896).

Zeway (♂ET105, ♂ET113); Ethiopia. The karyotype is characterized by 2n=36 and NFa=34. All chromosomes are acrocentrics decreasing in size. The X chromosome is a large acrocentric with Y being small (Fig. 6B). This species was identified in Ethiopia by YALDEN et al. (1976) on the basis of skull measurements. It was considered a synonym of *M. setulosus* by MUSSER & CARLETON (1993) and confirmed hesitantly by YALDEN et al. (1996). The

type locality is Sheikh Hussein, Ethiopia (East of the Rift Valley, at the same latitude of Zeway), and the species seems to occur in the same habitats as *N. tenellus*, i.e. from lowland forests to arid savannas.

Nannomys cf. *emesi.* Kitale (♀KE117); Kenya. The chromosomal complement is 2n=36, FN=36. All chromosomes are acrocentrics decreasing in size (Fig. 6C). The sex chromosomes have been not yet identified. This karyotype is presented here for the first time, and is very similar in morphology *N. proconodon*. The identification of the species was based on skull measurements. *N. emesi* was considered synonymous of *M. mahomet* by MUSSER & CARLETON (2005), who underlined that the series of *emesi* could not be distinguished from the large samples of *mahomet* collected by Osgood in Ethiopia.

Nannomys sp. Rongai – B. (♀KE107, ♂KE136, ♀KE140); Kenya. This species carries the same "all acrocentric" karyotype (2n=36, NFa=34; Fig. 6D) as *N. cf. emesi,* but there are important differences in the external body morphology, the specimens from Kitale being much smaller than those from Rongai. No species assignment for the moment has been attempted for these specimens. This karyotype is presented here for the first time. The X and the Y chromosomes are large and medium size acrocentrics, respectively.

– *Mastomys* (Thomas, 1915).

The species of this genus are widespread in the African continent where they represent an important component of the rodent fauna and constitute a serious problem for agriculture and human plague (SINGLETON et al., 1999). However, their taxonomy has been subject to discussion for a long time. Several papers (GREEN et al., 1980; HUBERT et al., 1983; CHEVRET et al., 1994; BRITTON-DRAVIDIAN et al., 1995; GRANJON et al., 1996; GRANJON et al., 1997; LECOMPTE et al., 2002; VOLOBOUEV et al., 2002b; COLANGELO et al., in prep.), employing cytogenetic, morphological and molecular approaches, have assessed the monophyly of the genus and clarified the phylogenetic relationships within the genus and what was considered the *Praomys sensu lato* group. However, the most recent morphological and cytogenetic studies have indicated the possible occurrence of sibling species and/or new cryptic species (LAVRENCHENKO et al., 1998; VOLOBOUEV et al., 2001; 2002b).

The four species *M. natalensis*, *M. huberti*, *M. coucha*, *M. erythroleucus* are phylogenetically closely related, while the taxonomical and systematic position of the other taxa included in the genus is still uncertain (GRANJON et al., 1997; LECOMPTE et al., 2002).

The available karyotypic data are as follows. The diploid number of *M. natalensis* is 32 and the NFa varies from 52 to 54 across the distribution range; this is the most representative species, and occurs in sub-Saharan Africa. *M. huberti* has the same diploid number as *M. natalensis* (2n=32) but the NFa ranges from 44 to 46 (DUPLANTIER et al., 1990; GRANJON et al., 1997); the range is restricted to Mauritania, Mali, Burkina Faso and Senegal (GRANJON et al., 1997). *M. coucha* has been described from southern Africa (RSA and Zimbabwe) and presents 2n=36 and NFa=52-54 (LYONS et al., 1980; LEE & MARTIN, 1980; GREEN et al., 1980); however, HALLET (1979) reported additional NFa variability (54 – 56). *M. erythroleucus* ranges from Senegal to Ethiopia and Uganda and shows 2n=38; the NFa varies from 40 to 60. However, the comparison of the G-banded karyotypes and cytochrome *b* based phylogeny suggests that the specimens showing NFa=40 represent a separate species (VOLOBOUEV et al., 2002b), while the taxonomic status of the other cytotypes (NFa=50, NFa=52-53 and NFa=60) remains uncertain (VOLOBOUEV et al., 2001; 2002b). *M. shortridgei* occurs in the extreme northwest of Botswana and in northeast Namibia. GORDON (1985) reported in Namibia a karyotype with 2n=36 and NFa=50.

QUMSIYEH et al. (1990) reported a karyotype with 2n=32 and NF=50-54 from Kenya which they considered to be different from *M. natalensis* and that attributed to *M. hildebrandtii*. This karyotype was considered by QUMSIYEH et al. (1990) to be similar to the one described by CAPANNA et al. (1982) in Somalia as *M. huberti*, although there was no comparison with type material. QUMSIYEH et al. (1990) argued that *M. hildebrandtii* (type locality Ndi, Tahita Hills, in Kenya) is an older name for *M. huberti* (type locality Zungeru, N. Nigeria). However, the karyology for the West African specimens assigned to *huberti* (2n=32, FN=44) is different from that of the Kenyan specimens that QUMSIYEH et al. (1990) considered to be *hildebrandtii* (2n=32, FN=50-54). Therefore, GRANJON et al. (1997) claimed that these taxa are not synonyms and *M. huberti* is a different species, even though specimens from the type region have not yet been investigated karyologically and the type locality lies outside the distribution range of what is currently called *M. huberti* (GRANJON et al., 1997). For the time being there is no indication that *hildebrandtii* (with a type locality in southern Kenya) is different from *M. natalensis.* Therefore, while waiting for a definitive comparison with the karyotypes from type localities, *M. hildebrandtii* should be considered only as a younger synonym of *M. natalensis.*

Finally, LAVRENCHENKO et al. (1998) described a new species from the Awash Valley (Ethiopia) and named it *M. awashensis*; its diploid number is 32 and the NFa is 54, but it differs form *M. natalensis* in chromosome morphology and C-banding pattern.

Three different chromosomal formulas have been found in our samples. The more common karyotype shows 2n=32 and NFa=52-54 and here has been attributed to *M. natalensis*. However, one specimen collected in Ethiopia (Zeway) shares the same 2n=32 and NFa=54 karyotype, but was found not to be closely related phylogenetically to *M. natalensis* on the basis of the analysis of cytochrome *b* sequences (COLANGELO et al., in prep). Therefore, in absence of further comparisons, it is here provisionally referred to *M. awashensis* described in Ethiopia by LAVRENCHENKO et al. (1998).

– *Mastomys natalensis* (Smith, 1834).

Nairobi (♂KE142), Kitale (♀KE123); Kenya. Matongolo (♂T50012), Morogoro (♀T50198, ♀T50199, ♂T50200), Singida (♀T50197); Tanzania. Mutoma, Meheba (♀ZM2, ♀ZM5, ♂ZM34, ♀ZM36, ♀ZM38); Zambia. All the karyotypes show 2n=32 and both NFa=52 and 54 were found. The most common karyotype is composed of 12 pairs of biarmed chromosomes of

decreasing size and three pairs of acrocentrics. The X chromosome is a large submetacentric, and the Y chromosome is a large acrocentric. This karyotype is comparable to those described for *M. natalensis* from other localities (Matthey, 1955, 1966a, b; Capanna et al., 1982; Hubert et al., 1983; Orlov et al., 1989; Duplantier et al., 1990; Baskevich & Orlov, 1993; Leirs, 1994; Britton-Davidian et al., 1995; Codja et al., 1996; Fadda et al., 2001).

Fig. 7. – The karyotype of *Mastomys erythroleucus*, Zeway, Ethiopia 2n=38, NFa=53-54, X Y. Note the heteromorphic condition of one of the smallest metacentrics.

– *Mastomys* cfr. *awashensis* (Lavrenchenko et al., 1998).

Zeway (ET102♂); Ethiopia. The karyotype presents the same chromosomal formula as *M. natalensis* (2n=32 and NFa=54) and is composed of thee pairs of acrocentrics and twelve pairs of biarmed chromosomes, six of which are metacentrics and six subtelocentrics. The X and the Y chromosomes are submetacentrics, the former being medium-large and the latter medium-small. A preliminary G-banding analysis (the complete comparison will appear elsewhere) has shown differences probably due to deletions and/or additions in the autosomal complement. According to the cytochrome *b* sequences (Colangelo et al., in prep), this specimen is not related to the *M. natalensis* clade. Therefore, there is strong evidence suggesting that this taxon represents a separate species from *M. natalensis.* Further analysis will probably confirm the attribution of this taxon to *M. awashensis*.

– *Mastomys erythroleucus* (Temminck, 1953).

Rongai (♂KE101, ♂KE115, ♀KE132); Kenya. Zeway (♀ET128, ♂ET122, ♂ET128); Ethiopia. The Kenyan karyotype consists of 12 pairs of biarmed and six pairs of acrocentric chromosomes. The X chromosome is a medium size submetacentric and the Y is a small submetacentric. The Ethiopian karyotype is represented by 17-18 biarmed and 19-20 acrocentric chromosomes. The X is a large submetacentric and the Y is a small subtelocentric (Fig. 7). All the samples show the typical *M. erythroleucus* diploid number (2n=38). However, the Ethiopian and Kenyan specimens differ in NFa which is 52-53 in the former and 60 in the latter. A wide variability in NFa has been reported from other East and West African localities, with numbers ranging from 40 up to 60 (Matthey, 1965b; 1966a; 1967; Kral, 1971; Tranier, 1974; Hubert et al., 1983; Viegas-Péquignot et al., 1987; Orlov et al., 1989; Britton-Davidian et al., 1995; Codja et al., 1996; Bulatova et al., 2002; Volobouev et al., 2001; 2002a). According to the analysis of cytochrome b (Colangelo et al., in prep.) the genetic divergence between these two cytotypes it is very low in spite of the remarkable NFa variation.

– *Stenocephalemys* (Frick, 1914).

The genus now includes the three Ethiopian endemic species *S. albocaudata, S. albipes* and *S. griseicauda* (Musser & Carleton, 2005). It has been recognised recently, on the basis of cytogenetic, molecular and morphometric data (Chevret et al., 1994; Corti et al., 1995, 1999; Fadda et al., 2001; Lavrenchenko et al., 1999; Lecompte et al., 2002) that they constitute a monophyletic assemblage phylogenetically related to species of *Praomys, Mastomys, Myomyscus, Heimyscus,* and *Hylomyscus* (Lecompte et al., 2002). These studies have also shown that *S. albipes* should not be referred to *Myomys albipes* or *Praomys* (Misonne, 1969; Qumsiyeh et al., 1990; Yalden et al., 1976).

This genus has long been considered taxonomically confused, as it was included in a group of genera together with *Praomys*, *Mastomys*, *Hylomyscus*, *Colomys* and *Stenocephalemys* which are closely related (Chevret et al., 1994). There are available cytogenetic data for *S. albipes,* 2n=46 and NFa=50-53 (various localities in Ethiopia), S. *albocaudata* (2n=54, NFa=60) and *S. griseicauda* (2n=54, NFa=54) (Corti et al., 1999).

– *Stenocephalemys albipes* (Rüppell, 1842).

Mugo (♂ET108, ♂ET109, ♂ET111, ♀ET121, ♀ET123); Ethiopia. The species is widespread all over Ethiopia in forest blocks at altitudes ranging from 800 m up to 3300 mt a.s.l. (Yalden et al., 1976; Afework Bekele & Corti, 1997). The diploid number is 46 and the NFa is 50-53 (Fig. 8). The X is a large submetacentric and the Y (not shown) a medium size metacentric. All karyotypes are composed of 4 pairs of large biarmed chromosomes, 17 pairs of acrocentric chromosomes decreasing in size (on some of them very small arms are visible), and of one pair of small biarmed chromosomes. The chromosome pair numbers 1 and 3 are polymorphic (the latter not shown), i.e. they are found either as acrocentrics or submetacentrics due to a pericentric inversion. Corti et al. (1999) described the karyotype of this species from other localities in Ethiopia, and found the same diploid number and the same variation in NFa (50-53), due to the occurrence of a polymorphism. It is interesting to note that the polymorphism found in Zeway involves the same autosomes as those described by Corti et al. (1999) except for one specimen (ET123) that showed a polymorphism involving the largest chromosome pair (n° 1) of the entire autosomal set (Fig. 8).

Fig. 8. – The karyotype of *Stenocephalemys albipes*. 2n=46, NFa=50-53, X X. Note the heteromorphic condition of the largest autosome.

– *Grammomys* (Thomas, 1915).

The genus includes 12 species (MUSSER & CARLETON, 2005). The species cytogenetically studied so far show a wide variation in B chromosomes. CIVITELLI et al. (1989) described specimens of *G. gazellae* (synonym of *G. macmillani)* from Central Africa 2n=56-71, with 2-17 B chromosomes. The occurrence of B-chromosomes as well as Robertsonian fusions has been documented by ROCHE et al. (1984) in five specimens (a mother and four pups) of *G. dolichurus* from Somalia (2n=54-61, NFa=70-75).

MATTHEY (1971) described the karyotype of *G. surdaster* from Katanga (2n=52; NFa=62). FADDA et al. (2001) found a karyotype in the Maasai steppe with 2n=27 and NFa=39 that could not be allocated to any species. They maintained that, after craniological and craniometrical comparison with extensive Tanzanian material including most of the relevant type-specimens, the taxonomic situation of the *Grammomys-Thamnomys* complex of this part of Africa is yet to be established. More recently, on the basis of 16S rRNA gene analyses of extensive samples, VERHEYEN et al. (2003) reported the occurrence, in this part of Africa, of at least three species complexes, i.e. *G. macmillani, G. dolichurus* and *G. surdaster.* Taxonomic attribution made here is based on morphological comparison with larger series and mtDNA analysis (VERHEYEN et al., 2003), but apart from including the cytotype in a species group, no definitive allocation or new classification was possible.

– *Grammomys* sp. *surdaster* (Thomas and Wroughton, 1908) complex.

Mutanda Research Station (♂ZM25, ♀ZM14); Zambia. The diploid number is 2n=51 in the male and 2n=50 in the female and the NFa is 61 (Fig. 9A). The difference between the male and female depends on a structural Robertsonian fusion in the former concerning the largest metacentric (not shown in the figure). The autosomes are represented by one pair of large metacentric chromosomes, a heteromorphic pair formed by a small metacentric and a small acrocentric, five pairs of small metacentrics, and 17 pairs of acrocentrics decreasing in size (Fig. 9A). There are two different X configurations: a submetacentric (in the male) and a subtelocentric occurring together with the submetacentric (in the female). The Y chromosome is a small subtelocentric (not shown). This karyotype is presented here for the first time, but it resembles the one described from Katanga by MATTHEY (1971).

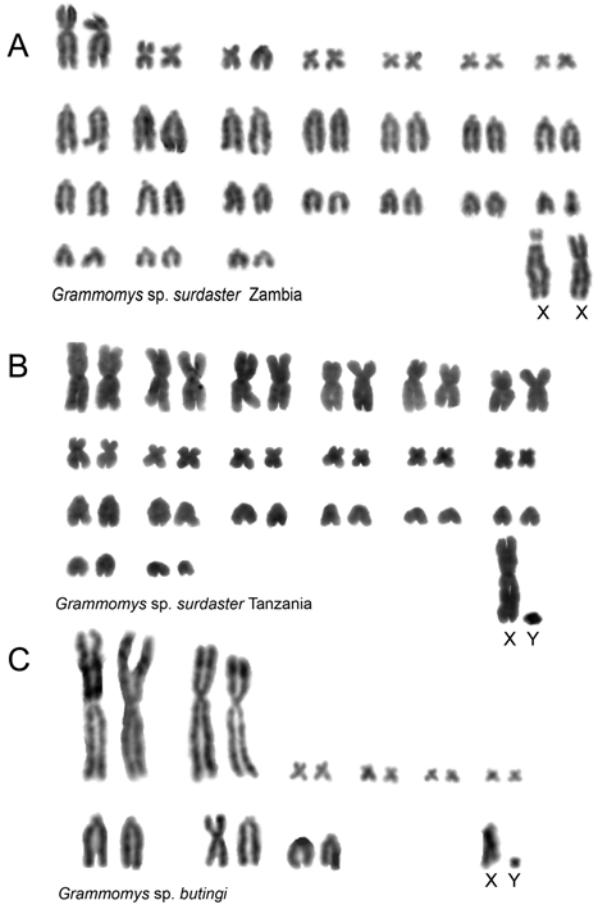

Fig. 9. – A) The karyotype of *Grammomys* sp. *Surdaster* (Zambia), 2n=50-51, NFa=61, X X. Note the heteromorphic condition of one of the smallest metacentrics an of the X. B) The karyotype of *Grammomys* sp. *surdaster* (Tanzania), 2n=42, NFa=64, X Y. C) The karyotype of *Grammomys* sp. *butingi*, 2n=20, NFa=31, X Y. Note the heteromorphic condition of one of the medium size chromosomes.

Grammomys sp. *surdaster* complex Kitundu Forest, Uluguru Mt. range (♂T50235, ♀T50237); Tanzania. The karyotype is 2n=42, and the NFa is 64 (Fig. 9B). The karyotype comprises 12 pairs of biarmed chromosomes decreasing in size, from large to small, and 8 pairs of acrocentrics of medium to small size. The X is a large metacentric and the Y is the smallest acrocentric. This karyotype is presented here for the first time.

– *Grammomys* sp. *butingi* (Thomas, 1911 complex).

Jipe (♂T50485); Tanzania. The karyotype is characterized by 2n=20 and NFa=31. The autosomal set is represented by two pairs of very large metacentrics, two pairs of medium size subtelocentrics, a pair of medium size heteromorphic chromosomes (a metacentric and a subtelocentric) and four pairs of small metacentrics (Fig. 9C). The X chromosome is a medium size subtelocentric and the Y a small metacentric. This karyotype is presented here for the first time.

MYOXIDAE (Gray, 1821).

– *Graphiurus* (Smuts, 1832).

The systematic relationships and the taxonomy within the genus are at present not fully resolved (BENTZ & MONTGELARD, 1999; GENEST-VILLARD, 1978; SCHLITTER et al., 1985; HOLDEN, 1993; 1996). Revisions made over the last twenty years, all of which are exclusively based on size and morphology, have reached different conclusions: the number of species described varies from five (MEESTER & SETZER,1971) and six (GENEST-VILLARD, 1978), to fourteen (HOLDEN, 1993). More recently, MONGELARD et al. (2003) examined six taxa of *Graphiurus* through nuclear and mitochondrial genes, amongst which *G. microtis* from Tanzania. They showed that the low resolution found for the genus most probably accounts for their rapid diversification.

In general, the karyotypes of *Graphiurus* are characterized by the prevalence of biarmed autosomes (ZIMA et al., 1994), but diploid numbers are known for only a few species: *G. cf. parvus*, 2n=70 (DOBIGNY et al., 2002); *G. murinus*, 2n=70 (TRANIER & GAUTUN, 1979); *G. hueti*, 2n=40 (TRANIER & DOSSO, 1979). One should recall, however, that chromosomal variation is common in Myoxidae, as shown in the European *Eliomys* (FILIPPUCCI et al., 1988; 1990) and it would not be surprising to find an even larger one in *Graphiurus*.

Five individuals from three different localities were analyzed and their karyotypes are presented here. Because their taxonomy is still under discussion (the most recent checklist by HOLDEN, 1993, highlighted that taxonomic assignment must be considered provisional), we provide no definite specific allocation for our specimens. For the moment, we refer to them as belonging to *Graphiurus* cf. *murinus*, *Graphiurus* sp. 1 and *Graphiurus* sp. 2.

Graphiurus cf. *murinus*. Zeway (♀ET100, ♀ET 104, ♂ET106); Ethiopia. The karyotype is characterized by 2n=60 and NFa=76. The autosomal set is composed of a large pair of metacentrics, one medium size pair of metacentrics, four pairs of subtelocentrics of medium size, three pairs of medium to small metacentrics and 20 pairs of acrocentrics decreasing in size (Fig. 10A). The X chromosome is a large acrocentric and the Y a very small one. This karyotype is presented here for the first time. YALDEN et al. (1976) attributed to this species the "relative small number of records" for Ethiopia. The type locality of the species is the Cape of Good Hope, South Africa, but it is questionable whether this wide distribution reflects the occurrence of a single species.

Graphiurus sp. 1. Meheba (♂ZM6); Zambia. The diploid number is 2n=54 and NFa=78. The karyotype is composed of nine pairs of metacentric chromosomes decreasing in size (from the largest of the entire set to nearly the smallest), four pairs of subtelocentrics, and 13 pairs of acrocentrics decreasing in size (from the second in size of the entire set to the smallest one) (Fig. 10B). The X chromosome is a medium size metacentric, and the Y is the smallest element of the set. This karyotype is presented here for the first time.

Graphiurus sp. 2. Chunya (♂TZ506); Tanzania. Unfortunately the quality of the preparations is only sufficient for a general description of the karyotype. The 2n is 50 and the NFa is 66. The karyotype is composed of nine pairs of metacentrics decreasing in size and 15 pairs of acrocentrics decreasing in size (Fig. 10C). Both the X and the Y are acrocentrics but the former is the largest one of the complement and the latter is very small. This karyotype is presented here for the first time.

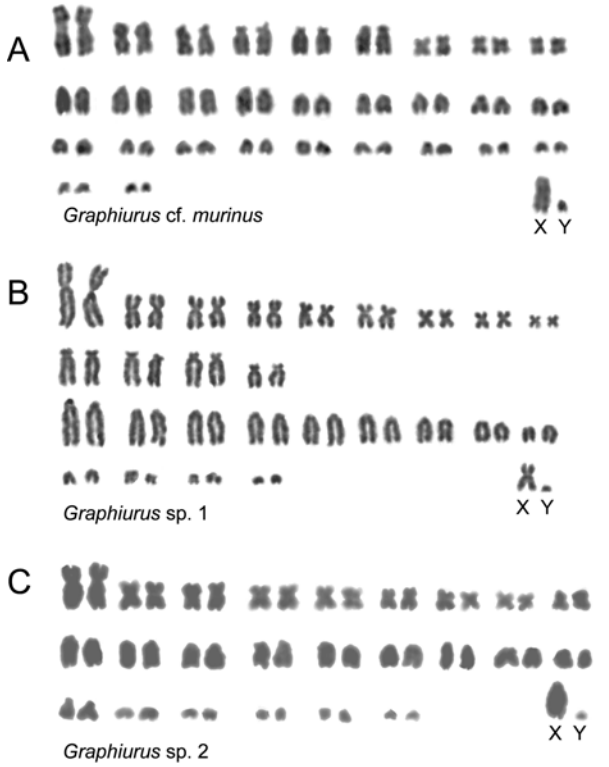

Fig. 10. – A) The karyotype of *Graphiurus* cf. *murinus*, 2n=60, NFa=76, X Y. B) The karyotype of *Graphiurus* sp. 1 (Zambia), 2n= 54, NFa=78, X Y. C) The karyotype of *Graphiurus* sp. 2 (Tanzania), 2n=50, NFa=66, X Y.

DISCUSSION

The number of karyotypes discussed here totals 37. Seventeen are described here for the first time. For four species or species complexes, we report chromosomal variants and for sixteen karyotypes additional localities of occurrence. Some of the karyotypes characterize taxa that have been either fully accepted by the most recent checklists or need taxonomic re-evaluation or a new description. The latter are *Cricetomys* cf. *gambianus, Saccostomus* cf. *elegans*, *Gerbilliscus nigricaudus, G.* cfr. *muansae, Arvicanthis* (ANI-5 and ANI-6), *A. nairobae*, *Acomys selousi*, *Lemniscomys zebra, L.* cf. *striatus massaicus, Nannomys proconodon, Nannomys* cf. *emesi, Nannomys* sp., *Grammomys surdaster*, *Grammomys* sp.1 and sp. 2, *Graphiurus* cf. *murinus, Graphiurus* sp. 1 and sp. 2. In all other cases, as the karyotypes have been or will be described elsewhere, we have reported the occurrence of chromosomal variants, new sampling sites or have provided a more precise taxonomic attribution. Fur-

thermore, we have highlighted problems in taxonomy, due to the occurrence of sibling and cryptic species or species complexes, for which further detailed analyses are needed.

There is a general pattern emerging from this report that confirms all recent suggestions regarding African rodent taxonomy and systematics researchers, i.e. biodiversity is much higher than has been previously estimated, at least that revealed by cytogenetics, so that the list of 386 species (MUSSER & CARLETON, 1993) will increase rapidly. This is true for the all genera investigated, with the exception of *Aethomys*, for which there was no apparent problem of taxonomic attribution at species level, but for which karyotypes are known from a limited number of localities (one only for *A. kaiseri*) and variants cannot be excluded a-priori.

However, it is difficult to state whether the chromosomal variants detected warrant a different species attribution in all cases. For many this is undoubtedly true. *Acomys* cf. *selousi*, *Arvicanthis* ANI-5, *Arvicanthis* ANI-6, *Nannomys tenellus*, *N. proconodon*, *N.* cf. *emesi, Nannomys* sp. (Rongai), *Grammomys* sp.1 and sp. 2 represent cases that would strongly suggest a specific attribution. For others, it would be premature to do so until more extensive analyses have been performed, possibly including estimates of gene flow between cytotypes. For example, the different karyotypes of *Cricetomys* cf. *gambianus* found in West (GRANJON et al., 1992; CODJA et al., 1994) and East Africa could correspond to different biological species or represent extremes of some form of chromosomal variation. Nonetheless, these data and parallel analyses suggest that at least seven specific names that were not included in MUSSER & CARLETON's (1993) checklist need to be restored and accepted at the full species rank. These are *Saccostomus* cf. *elegans*, *Gerbilliscus* cfr. *muansae*, *Acomys* cf. *selousi*, *Lemniscomys* cf. *zebra*, *Nannomys proconodon*, *N.* cf. *emesi* and *Grammomys surdaster.*

Within species chromosomal variation is a common phenomenon in rodents (recent literature is rich in references; see, for example, those cited here for *Arvicanthis*) and the cases we report here of the *Stenocephalemys albipes* and *Saccostomus* cf. *elegans* are evident examples. These could represent instances of raciation but, for the moment, this is impossible to establish. On the contrary, the cytotypes of the *Arvicanthis niloticus* complex (Zeway, Kitale, ANI-5) clearly suggest a process of divergence in action that might have reached full speciation as suggested by the analysis of the cytochrome b mitochondrial gene (CORTI et al., submitted). However, we are cautious when considering most of the taxa studied here, as we believe that extensive comparisons with type material using a multidisciplinary approach is needed before reaching a definite taxonomic conclusion.

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