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Chromosomal characterization of three species of the genus Mastomys in Senegal

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Abstract

Mastomys rats are present as three distinct karyomorphs in Senegal. Specific assignations were accorded to each form on the basis of chromosomal, reproductive and distribution characteristics. *Mastomys erythroleucus* (2n = 38, NFa = 52) is ecologically a generalist, *M. huberti* (2n = 32, NFa = 44) is restricted to humid biotopes and *M. cf natalensis* (2n = 32, NFa = 54) is strictly commensal and found in Southeastern Senegal.

Key words: Karyology – Systematics – *Mastomys* – Senegal

Introduction

The first diploid number known for the genus *Mastomys*, namely 2n = 36 for an individual from South Africa, was established by Matthey in 1954. Since then, two additional karyotypes were determined in Ivory Coast, 2n = 32 (Matthey 1955) and 2n = 38 (Matthey 1958). These results confirmed what Petter (1957) had established through morphological studies, i. e., the presence of two sympatric species in West Africa. Many individuals of *Mastomys* were karyotyped in the following years but are not taken into account here because the authors often failed to publish the fundamental number (NF), although polymorphism for the NF was described for the 2n = 32 chromosome form as early as 1966 by Matthey (1966a). Subsequently, more extensive studies were performed by Lyons et al. (1977, 1980), Green et al. (1978) and Gordon (1978) in Zimbabwe, Green et al. (1980) in South Africa and Robbins et al. (1983) in Sierra Leone. Finally, a synthesis on karyotype distribution in the genus in Africa was attempted by Hubert et al. (1983).

In Senegal, the existence of two different karyotypes was reported by Hubert et al. (1973), each corresponding to the species designated by Petter (1977) as *M. erythroleucus* for the 2n = 38 karyotype and *M. huberti* for the 2n = 32 karyotype. According to Hubert et al. (1973, 1983) and our own observations, *M. huberti*, (2n = 32) characterized by a black coat color, is restricted to humid zones. However, dark-colored rats were also trapped inside villages in the extreme south-east of the country. Additionally, important differences have been noted in the published fundamental numbers, particularly for the 2n = 32 karyotypes. These problems have led us to investigate the *Mastomys* genus in Senegal to clarify their chromosomal and specific status.

Material and methods

74 wild and laboratory bred rats were karyotyped. The localities are indicated in Fig. 1. Additionally, 11 hybrids from intergroup crosses were also analyzed.

Karyotypes were determined from bone marrow cells following the "air-drying" technique after yeast stimulation (Lee and Elder 1980). Slides were observed under a phase contrast Zeiss

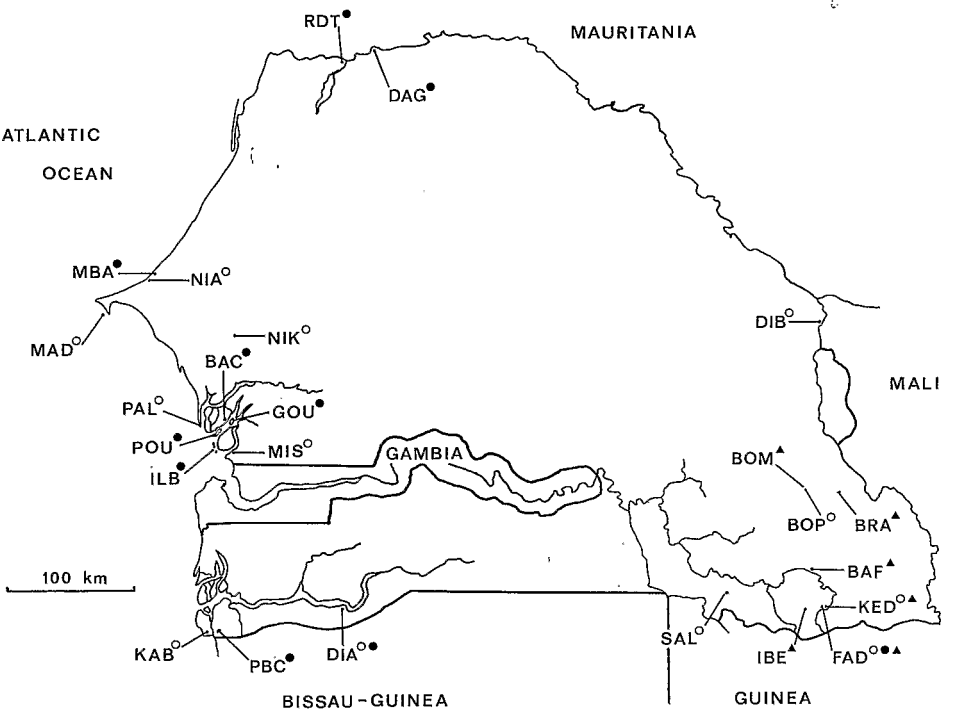

Fig. 1. Sample localities in Senegal; *M. erythroleucus* (empty circles), *M. huberti* (black dots), *M. cf. natalensis* (triangles). BAC = Bachalou, BAF = Bafoundou, BOM = Bombou-Mandingue, BOP = Bombou-Peuhl, BRA = Bransan, DAG = Dagana, DIA = Diattacounda, DIB = Diboli, FAD = Fadiga, GOU = Gouk Island, IBE = Ibel, ILB = Ile aux Boeufs, KAB = Kabrousse, KED = Kédougou, MAD = Madeleine Island, MBA = M'baouane, MIS = Missira, NIA = Niaga, NIK = Niakhar, PAL = Palmarin, PBC = Parc Basse-Casamance, Pou = Poutak Island, RDT = Richard-Toll, SAL = Salemata

microscope and photographed with a Zeiss C35M photographic equipment. At least five metaphases per individual were examined and three of these photographed. For individuals presenting anomalies in the diploid number, up to 50 metaphases were analyzed.

Chromosomes were grouped into three classes according to their form and size: M = metacentric: the two arms are approximatively of equivalent length; SM = submetacentric: the chromosome has a short and long arm; A = acrocentric: only one arm is observed, the centromere appears terminal. No attempt was made to measure more accurately the chromosomes since G-banding analyses allowing to identify homologous pairs are in preparation. It was possible, however, to assign the NFa polymorphism to specific chromosomes on the basis of G-banding (not presented here) in all cases except one (pair n° 17 of the 2n = 38 karyomorph), for which the chromosomal assignement based on morphology and size is tentative.

The fundamental number that is provided here is the autosomal fundamental number (NFa) and was determined by considering that both metacentrics and submetacentrics carry two arms whereas the acrocentrics have only one.

Results

All of the animals studied can be assigned to one of three karyomorphs characterized by a specific diploid number and/or fundamental number (Tables 1, 2 and 3). Only one exception was noted which was a wild caught rat showing a NFa intermediate between that of two of the three karyomorphs. Within each karyomorph, variability in the NFa was scored, that described for the group being the most commonly encountered.

2n = 38 and NFa = 52 karyotypes

33 individuals presented this diploid number (Fig. 2; Table 1). The most common karyotype consists of 4 pairs of submetacentric chromosomes, 4 pairs of metacentrics and 10 pairs of acrocentrics. The X chromosome is a large metacentric and the Y chromosome a submetacentric chromosome with two thirds of the size of the X.

Two types of variation were encountered, one involving the diploid number, the other the NFa. Four individuals from the same locality (Fadiga) showed a chromosomal mosaicism: only 8–10 % of the metaphases had 38 chromosomes, whereas 65–82 % had 39 chromosomes and 10–25 % had 40 chromosomes. The nature of these additional chromosomes and the origin of the mosaicisms are unknown. The polymorphism for the NFa was observed in 29 individuals and involved, in all cases but one, two different sets of chromosomes, a large one (pair n° 9) or a small one (pair n° 17) respectively. The NFa increased at the most to 55, due to replacement of acrocentrics by metacentric chromosomes (see Fig. 2). These chromosomal variants appeared in heterozygous or homozygous form. An additional variant was observed in one individual from Kabrousse that was heterozygous for chromosome 2 (Fig. 2).

Table 1. **Chromosomal distribution of the 2n = 38 karyomorph**
The asterisk represents individuals with chromosomal mosaicism

Locality	NFa	N	Polymorphism	
			Pair	State
Bombou-Peuhl (BOP)	55	1M	9	M/M
			17	M/A
Diattacounda (DIA)	52	1M	–	–
Diboli (DIB)	53	1F	9	M/A
	54	1F	9	M/M
	54	1F	9	M/A
			17	M/A
Fadiga (FAD)	52	1M, 2F	–	–
	53	1M, 1F	9	M/A
	54	2M	9	M/M
	*	3M, 1F	–	–
Kabrousse (KAB)	52	1M, 1F	–	–
	53	1M	9	M/A
Kedougou (KED)	52	1M	9	M/A
			2	M/A
	53	1F	9	M/A
	54	1M	9	M/M
Madeleine Island (MAD)	52	1F	–	–
	53	1M	9	M/A
	53	1M, 1F	17	M/A
Missira (MIS)	54	1M, 1F	9	M/A
			17	M/A
Niaga (NIA)	53	1M, 1F	9	M/A
Niakhar (NIK)	53	1F	9	M/A
Palmarin (PAL)	52	1F	–	–
Salemata (SAL)	53	1M	9	M/A

M = male, F = female, N = number of specimens analysed. The morphology of the chromosomes involved in the NFa polymorphism are indicated in the last column.

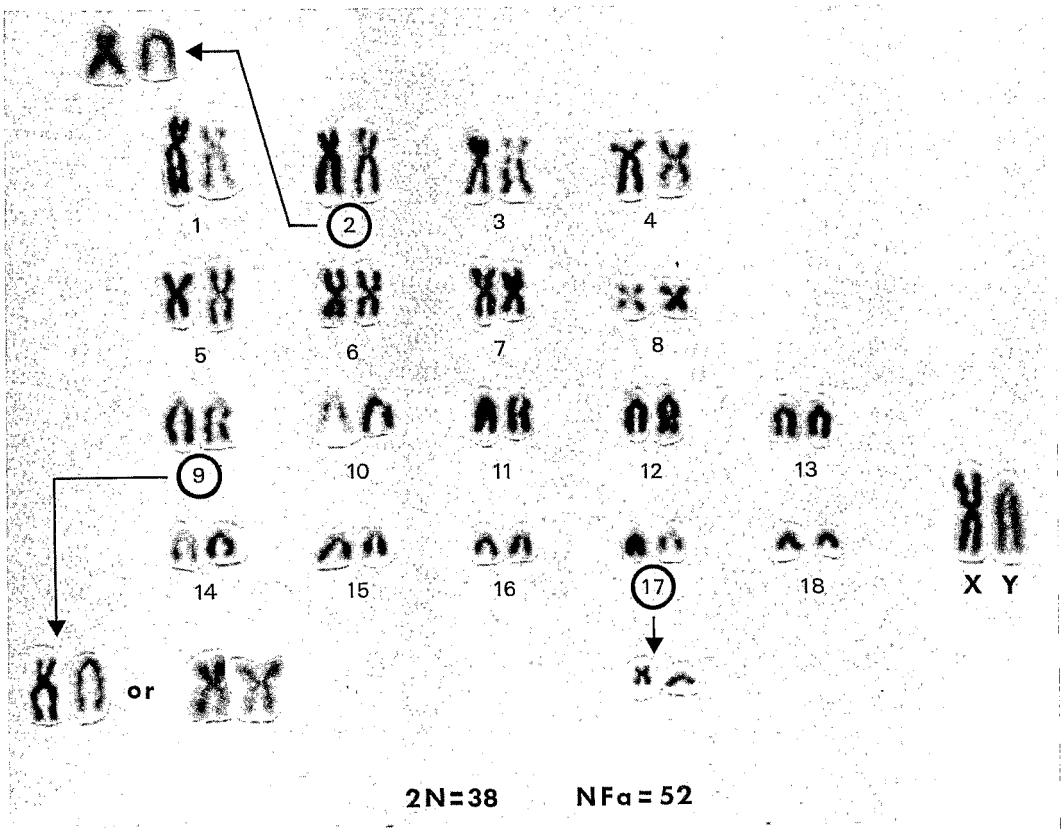

Fig. 2. Karyotype of the 2n = 38, NFa = 52 morph

2n = 32 and NFa = 44 karyotypes

Twenty six individuals belonged to this karyotype (Fig. 3; Table 2) which commonly consisted of 3 pairs of submetacentrics, 4 pairs of metacentrics and 8 pairs of acrocentrics; the X chromosome is a large metacentric and the Y an acrocentric, roughly half the size of

Table 2. **Chromosomal distribution for the 2n = 32/NFa = 44 karyomorph**

Locality	NFa	N
Bachalou (BAC)	44	1F
Dagana (DAG)	44	4M
Diattacounda (DIA)	44	2M
Fadiga (FAD)	45 a	1M
	45 b	1F
Gouk Island (GOU)	44	2F
Ile aux Boeufs (ILB)	44	1M, 1F
M'Baouane (MBA)	44	2M, 2F
Parc Basse Casamance (PBC)	44	1M
Poutak (POU)	44	2M
Richard-Toll (RDT)	44	3M, 3F

M = male, F = female, N = number of specimens analyzed. Chromosomally aberrant individuals are: a = heterozygous for chromosomes 1 and 11 (both are M/A); b = heterozygous for chromosome 11 (M/A).

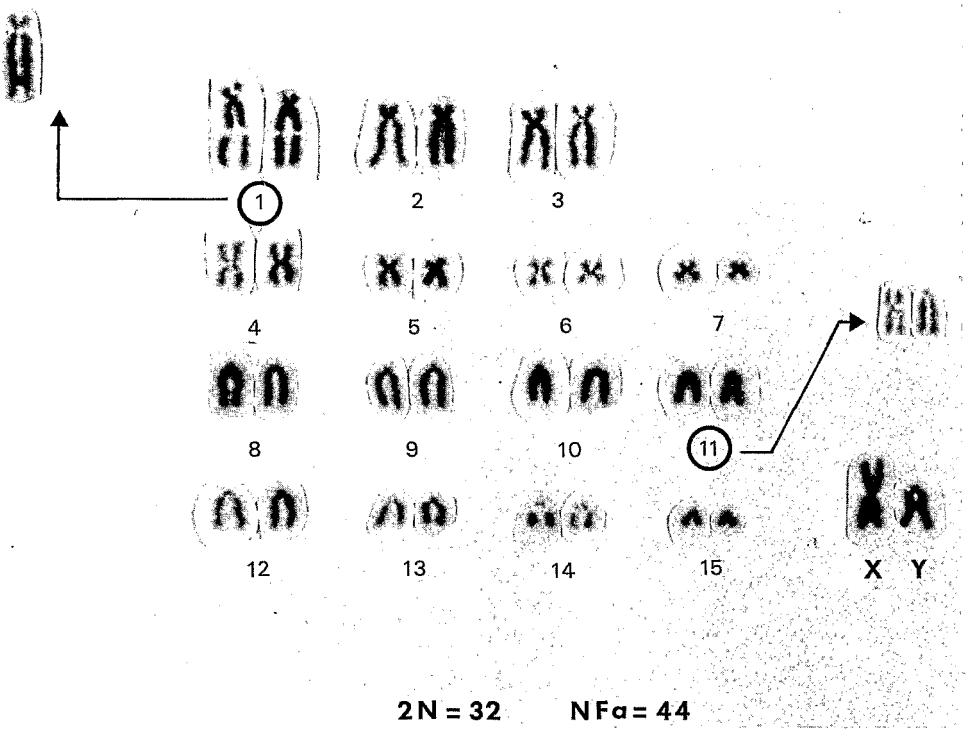

Fig. 3. Karyotype of the 2n = 32, NFa = 44 morph

the X. This is a very stable karyotype, the only variation observed concerned two rats from Fadiga, both of which were heterozygous for chromosome 11, and one of them also exhibited a chromosome 1 with a partial deletion of the short arm. These modifications involved only the NFa which varied from 44 to 45, the diploid number remained unchanged.

2n = 32 and NFa = 54 karyotypes

Fourteen rats were placed in this group (Fig. 4; Table 3). The most common karyotype is: 8 pairs of submetacentrics, 4 pairs of metacentrics and 3 pairs of acrocentrics; the X chromosome is a large metacentric and the Y chromosome an acrocentric almost as large as the X.

Table 3. **Chromosomal distribution for the 2n = 32/NFa = 54 karyomorph**

Locality	NFa	N	Chromosome 14
Bafoundou (BAF)	54	1M	SM/M
Bombou-Mand. (BOM)	53	1F	
Fadiga (FAD)	52	1F	–
	53	1M	A/M
	54	3M, 2F	M/M
		1F	SM/M
		1F	SM/SM
Ibel (IBE)	54	1M	M/M
Kedougou (KED)	54	1F	SM/M

M = male, F = female, N = number of specimens analysed. The morphology of chromosome 14 is indicated.

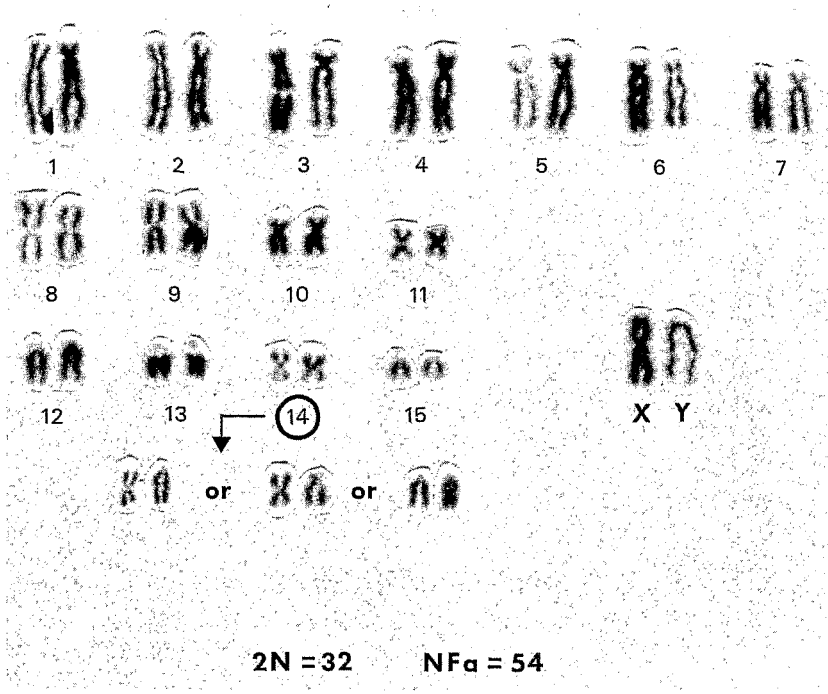

Fig. 4. Karyotype of the 2n = 32, NFa = 54 morph

Although the diploid number is identical with the preceeding group, the NFa is higher due to the presence of five submetacentrics. Variation in the NFa was commonly found, involving one pair of small chromosomes for which three forms were observed (Fig. 4): acrocentric, submetacentric (common form) and metacentric. The distinction between the submetacentric and metacentric forms may be artificial owing to a more or less expressed condensation of the chromosome, or may correspond to real differences, depending on the origin of the difference (more or less important additions of heterochromatin, for example).

Hybrids

Only one natural hybrid (female) was caught in the field and showed 2n = 32 chromosomes and NFa = 49. These numbers and the morphology of the chromosomes suggest that it most likely corresponds to a hybrid between the two 2n = 32 forms.

Table 4. **Reproductive parameters for crosses within and between karyomorphs**

Parental karyomorph	N of pairs	Reproductive rate %	Litter size	Survival at 30 days %
38–52	55	82	7.5	80
32–44	37	78	6.6	96
32–54	13	62	6.5	50
38–52 × 32–44	9	44*	3.9*	64*
38–54 × 32–54	15	13*	6.0	–
32–44 × 32–54	10	70	6.1	79

Asterisks represent cases where significant differences with the corresponding intramorph crosses were found.

Laboratory crosses between these three different chromosomal morphs were performed with varying degrees of success (Table 4); only two types of hybrids could be analyzed.

The first series of crosses involved the 2n = 38/NFa = 52 group with the 2n = 32/NFa = 44 karyotype, of which five individuals were analyzed. Four of these hybrids had a diploid number of 35, whereas the fifth showed metaphases with 34, 35 and 36 chromosomes respectively. The NFa, determined for only three of them, varied from 48, for a male and for a female, to 49 for the other male.

Six hybrids were studied in the second type of crosses involving the two 2n = 32 forms (NFa = 44 and NFa = 54). All share the same karyotype: 2n = 32 with a NFa of 50. It is worth noting that two of the autopsied rats presented atrophied femurs, a condition that had never been observed previously.

Discussion

Chromosomal characterization of the Mastomys rats from Senegal

Chromosomal systematics had allowed to identify three species of the genus *Mastomys* in Africa, each characterized by a different diploid number: 2n = 38, 36 and 32. In Senegal, three karyomorphs are described, one of them matches the previously recorded species with 38 chromosomes. However, the existence of two groups, both with 2n = 32 chromosomes but with different and non-overlapping NFa's raises the question of their relatedness to each other and to the third form. Since the chromosomal criterion is not sufficient to establish biological specificity, we will discuss the sympatric interactions as well as the hybridization capacities of these karyomorphs before attempting a taxonomic review.

Sympatry criterion

Extensive sampling throughout Senegal has allowed to determine the distribution of these three karyomorphs (DUPLANTIER and GRANJON 1988). The 2n = 38 group is the most widespread one and is sympatric with the 2n = 32/NFa = 44 group along the Western coast, the Senegal river and in the Casamance region and with the 2n = 32/NFa = 54 group in Southeastern Senegal. In both sympatric areas, instances of syntopy were observed, 1. in the Niayes area of Cap-Vert (West), and 2. in the villages of the Kedougou Department (Southeast). An exceptional case of temporary syntopy for the three morphs was recorded in the Fadiga locality (Southeast, DUPLANTIER 1988; DUPLANTIER and GRANJON 1988). Among all the rats analyzed from the syntopic areas, only one presented a hybrid karyotype in Fadiga. It most likely belonged to a first generation hybrid between the two 2n = 32 morphs.

Fertility

Laboratory crosses between the three morphs were performed and yielded hybrids but the reproductive success on the whole was considerably lower than that of intramorph crosses (DUPLANTIER 1988; see Table 2). Fertility levels as well as survival rates of progeny were lower for crosses between the 2n = 38 and either of the 2n = 32 groups. The crosses between the 2n = 32 morphs did not yield such a drastic reduction in reproductive value but the presence of femur malformations in two of the six autopsied hybrids suggests that developmental problems may exist.

Species attribution

The existence of three distinct chromosomal morphs both in sympatric and syntopic localities, as well as a lack of hybrids in the field, suggests that a species status may be given

to each of them. Even though they are fertile under laboratory conditions, hybridization in nature remains a rare event which indicates that prezygotic isolating mechanisms are present.

The following nomenclature is proposed, taking into account previous studies:

- the first species with a karyotype of 2n = 38/NFa = 52 is distinguished from the two others by its coat color: brown on the back and cream on the belly. This corresponds well to the species described as *M. erythroleucus* by PETTER (1957), the karyotype of which was published by MATTHEY (1958).
- the second species is represented by the 2n = 32/NFa = 44 morph. This NFa is known only from Senegal and corresponds to dark colored *Mastomys* rats restricted to humid biotopes as described by HUBERT et al. (1973), and named *M. huberti* by PETTER (1977). Its karyotype was published by HUBERT et al. (1983) and VIEGAS-PEQUIGNOT et al. (1983).
- the third chromosomal form 2n = 32/NFa = 54 was unknown in Senegal until now but is the most widespread in the genus. It was first described by MATTHEY (1955) in Ivory Coast, later in Congo, the Republic of Central Africa and Tchad (MATTHEY 1965, 1966a, 1966b). More recently, HALLET (1977, 1979) recorded it in South Africa and LYONS et al. (1977) in Zimbabwe. Finally, CAPANNA et al. (1982) found it also in Somalia.

GREEN et al. (1980) proposed a systematic revision of the genus *Mastomys* for Southern Africa based on the comparison of type localities and karyotype distributions. They conclude that the 2n = 36/NFa = 56 morph should be attributed to the *M. coucha* species whereas the 2n = 32/NFa = 54 corresponds to *M. natalensis*. This nomenclature is adopted here and the Senegalese *Mastomys* characterized by this karyotype will be named *M. cf natalensis*. The use of the restrictive term "cf" will be maintained until a direct comparison is made between Senegalese and South African rats since G-banding analyses with those published by CAPANNA et al. (1982) are very similar whereas those with LYONS et al. (1980) showed certain discrepancies.

Thus, the genus *Mastomys* is represented in Senegal by:

2n = 38/NFa = 52 – *M. erythroleucus*
2n = 32/NFa = 44 – *M. huberti*
2n = 32/NFa = 54 – *M. cf natalensis*

Polymorphism of the autosomal fundamental number

Within each species, the diploid number is constant (except the few instances in *M. erythroleucus* related to mosaicism), whereas variation in the NFa was regularly observed. This indicates that in all three species, these rearrangements are either additions or deletions of heterochromatic material or pericentric inversions.

In *M. cf natalensis*, the change in NFa is restricted to one pair of small chromosomes, and corresponds most likely to the known pericentric inversion polymorphism on pair n° 14 documented by several authors and reviewed by CAPANNA et al. (1982). These authors distinguished only two forms: acrocentric/submetacentric whereas a metacentric form seems to be also present in our samples. Further clarification will be needed before the type of rearrangement can be precisely determined.

M. huberti has a very stable karyotype since only two individuals were variant and restricted to the Fadiga locality. No comparative data are available since this species is known to occur only in Senegal.

In *M. erythroleucus*, on the other hand, polymorphism for two chromosomal variants (pairs n° 9 and 17) were recorded. Both are widespread, especially that for chromosome 9 for which no indication of a regional trend can be seen. HUBERT et al. (1983) noticed NFa's ranging from 50 to 52 in their samples from Senegal. This is lower than the NFa's in our observations, but within the range of what has been found for this species earlier

(50 to 56). Similar variations in NFa were recorded by MATTHEY (1966a) in Ivory Coast (NFa = 50 to 52). Finally, the exceptionally high NFa's recorded by KRAL (1970) in Zaire (NFa = 60) and by MATTHEY (in HUBERT et al. 1983) in Central Africa (NFa = 68 or 70) should be mentioned.

Particular attention should be paid to the chromosomal variability observed in the Fadiga samples. This observation and the fact that this locality yielded the only wild hybrid known to date suggest that a certain amount of introgression may be taking place locally there generating a chromosomal instability.

Conclusion

The three species of *Mastomys* in Senegal are chromosomally distinct and differ by their diploid and/or their autosomal fundamental number, which suggests that Robertsonian translocations, pericentric inversions and/or modifications of heterochromatin have occurred. Subsequent cytogenetic investigations using G- and C-banding and including the 2n = 36 species *M. coucha*, will allow to determine the mode of chromosomal evolution in the genus. Furthermore, chromosomal polymorphisms are present in the three species and need to be better characterized cytogenetically, particularly in syntopic localities and their relation to karyotypic change within the genus studied.

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Résumé

Caractérisation chromosomique chez trois espèces du genre Mastomys au Sénégal

Au Sénégal nous avons mis en évidence trois caryotypes différents dans le genre *Mastomys*. Au vu des résultats des croisements en captivité et des zones de syntopie observées dans la nature, on peut affirmer que chacun correspond à une espèce distincte. *Mastomys erythroleucus* (2n = 32, NFa = 52) est un généraliste sauvage et commensal, *M. huberti* (2n = 32, NFa = 44) est inféodé aux zones humides et *M. cf natalensis* (2n = 32, NFa = 54) est strictement commensal et limité au sud-est du Sénégal.

Zusammenfassung

Chromosomaler Aufbau von drei Arten der Gattung Mastomys im Senegal

Im Senegal wurden bei der Gattung *Mastomys* drei verschiedene Karyotypen gefunden. Die Ergebnisse aus Laborkreuzungen und Hinweise aus den in der Natur beobachteten sympatrischen Zonen zeigen, daß jeder Karyotyp einer eigenen Art entspricht. *Mastomys erythroleucus* (2n = 38, NFa = 52) ist ein freilebender, kommensaler Generalist, *M. huberti* (2n = 32, NFa = 44) ist nur an feuchten Plätzen zu finden. *M. cf. natalensis* (2n = 32, NFa = 54) kommt ausschließlich kommensal und nur im Südosten von Senegal vor.

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