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**A cytotaxonomic survey of Rodents from Niger :
implications for systematics, biodiversity and biogeography**

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Summary

We here present an inventory of rodents from Niger, mainly based on cytotaxonomic data because of the presence of many groups providing sibling species. A total of 39 species are listed, one of which is a new chromosomal form (*Taterillus* sp.). Moreover, three other cytotypes already described but still not specifically attributed were found (*Mastomys* sp., *Acomys* sp. and *Tatera* sp.). New karyotypic data are presented for *Gerbillus nancillus*, *Graphiurus* cf. *parvus*, *Massouteria mzabi*, and *Xerus erythropus*. Once again, the efficiency of cytotaxonomy for small mammals inventories is enhanced.

Specific distribution maps of poorly known species are thus completed. No clear gradients could be observed between what is currently defined as the West and the East African faunas. The distributions are mainly structured in a latitudinal manner. The Air massif appears as a continuous prolongation of the Sahelian area, rather than as a Sahelian refuge in the Sahara. Five biogeographical groups of species were distinguished : 1) a Sudanian group in the area receiving less than 700 mm rainfall, 2) a group of very widespread species largely overlapping the Sudanian (more than 700 mm rainfall) and the Sahelian areas, and sometimes including some Saharan localities, 3) a typical Saharan group, 4) some species infested to the mountainous Saharan area, and 5) few strictly commensal species. A global southward extension of several taxa confirms the desertification of the Sahel, as a result of both natural global warming and human activities.

Résumé :

Nous avons réalisé un inventaire des rongeurs du Niger qui s'appuie essentiellement sur des données cytotaxonomiques non ambiguës à cause de la présence de nombreux complexes d'espèces jumelles. Trente neuf espèces ont pu être recensées, l'une d'entre-elles correspondant à une nouvelle forme chromosomique de *Taterillus*. De plus, 3 cytotypes toujours sans attribution spécifique ont été retrouvés (*Mastomys* sp., *Tatera* sp. et *Acomys* sp.) et des données caryotypiques nouvelles sont présentées pour *Gerbillus nancillus*, *Graphiurus* cf. *parvus*, *Massouteria mzabi* et *Xerus erythropus*. Les cartes de répartition de nombreuses espèces peu connues sont complétées. Aucun gradient observé entre les faunes d'Afrique occidentale et celles d'Afrique Orientales, les espèces se répartissant essentiellement en fonction de la latitude. Le massif de l'Air apparaît plutôt comme un prolongement de la zone sahélienne que comme un refuge sahélien dans le Sahara. Parmi les espèces de rongeurs inventoriées, cinq grands groupes biogéographiques peuvent être distingués : 1) des espèces inféodées à la zone soudanienne recevant moins de 700 mm, 2) un groupe d'espèces très largement réparties de la zone soudanienne (plus de 700 mm) au nord de la zone sahélienne, et incluant parfois des localités sahariennes, 3) des espèces typiquement sahariennes, 4) des espèces inféodées aux massifs sahariens montagneux, et 5) quelques espèces strictement commensales. Par ailleurs, la progression de plusieurs taxons vers le sud confirme la désertification du Sahel qui résulte à la fois d'une aridification naturelle et des activités humaines.

INTRODUCTION

Rodents represent the largest (but also probably one of the most neglected) component of mammalian biodiversity (43.7%, cf. Wilson & Reeder, 1993). This is no exception in Sahara and Sahel (Le Berre 1990), where they also cause great damages to cultures and stored foods, and can be hosts for many parasites causing cattle and human diseases (Gratz 1997; reviews in Buckle and Smith 1994; Delattre *et al.* 1998). Although rodents are more and more considered as an important parameter in agricultural development and pest control, management of rodents requires knowledge of species-specific dynamics (e.g. Leirs 1995) which relies on precise systematic data. In Niger, rodents are important pest for crops and probably reservoirs of many animal and human pathogens. Yet, only very scarce (e.g. Tranier 1974, 1975b; Poché 1976; Tranier and Julien-Laferrière 1990; Poilecot 1996) or old (e.g. Thomas 1925) data dealing with rodents from this area are available. This huge African country (1.267.000 square kilometers) spreads on the one hand from the Sahara desert to the Sudanian area, and on the other hand between what is currently recognized as West and Central Africa. Such a geographical position makes this country a suitable area for such a biodiversity and biogeographical survey.

We here propose an inventory of rodent species from Niger. For such a purpose, our data largely rely on non ambiguous cytotoxic analysis, meaning determinations at the specific level were assumed by the study of karyotypes. Indeed, this technique constitutes a powerful tool discriminating for an inventory of small mammals in general, and rodents in particular (Petter 1971; Robinson 2001), as many cases of morphologically sibling but karyotypically well differentiated species have now been evidenced, especially among African genera (e.g., *Arvicanthis*: Volobouev *et al.* 1988a; Ducroz *et al.* 1997; *Mastomys*: Meester 1988; Granjon *et al.* 1997a; Volobouev *et al.* 2001; *Tatera*: Matthey 1969; *Taterillus*: Matthey 1969; Matthey and Petter 1970; Sicard *et al.* 1988; *Gerbillus*: Granjon *et al.* 1999; *Otomys*: Taylor 2000).

MATERIAL AND METHODS

The study area

Five main zones (Fig. 1) were defined in Niger, on the basis of phytogeographical and hygrometric data, thus corresponding to major ecological areas (White 1986; Saâdou 1991; Poilecot 1999). The Sudanian zone is characterised by average rainfall exceeding 600 mm per year. The Sahel was separated into Southern and Northern parts, defined by 400 – 600 mm and 200 – 400 mm average rainfall per year, respectively. The Saharan area receives less than 200 mm per year, but two parts are distinguished, namely the complete desert and the mountainous desert. A total of 55 localities and 94 sites (Annexe) were sampled, covering these 5 zones. The number of trap-nights for each site ranged from 50 to 200, and each site was studied for 1 to 4 nights (and dozens of nights for Kollo ; Nomao unpubl.). As some species of rodents may be rare at a given period of time (due to estivation, migration, particularly low seasonal densities, ...), the period at which the field work was performed in the different localities is indicated (Annexe). Animals were caught with wire-mesh traps, pitfalls or by hand, in various habitats, including natural ones, fields, cultivated gardens, and human houses and stores (Annexe).

Cytogenetic techniques

For a rapid aid in the determination of the specimens examined (especially in problematic genera), karyotypes were prepared using bone marrow techniques. Forty five minutes before being sacrificed, animals were injected with 0.01 ml per gram of a Velbe solution (10 mg vinblastine sulfate in 40 ml NaCl 8.5 ‰). Bone marrow cells were burst in a hypotonic solution (KCl 0.075 M) for 20 minutes at 37°C, and then fixed in a 3:1 methanol / acetic acid solution at 4°C for at least 20 minutes. At least 10 metaphases per specimen were then observed with a standard stain using Giemsa R (4% in a phosphate buffer pH=6.8). Some specimens were sent to the Laboratoire Mammifères et Oiseaux of the Muséum National d'Histoire Naturelle, Paris, where the karyotypes were obtained from cryopreserved cell lines. Skull, skin and organs in alcohol of all the specimens studied are deposited in the Laboratoire Mammifères et Oiseaux.

RESULTS AND COMMENTS

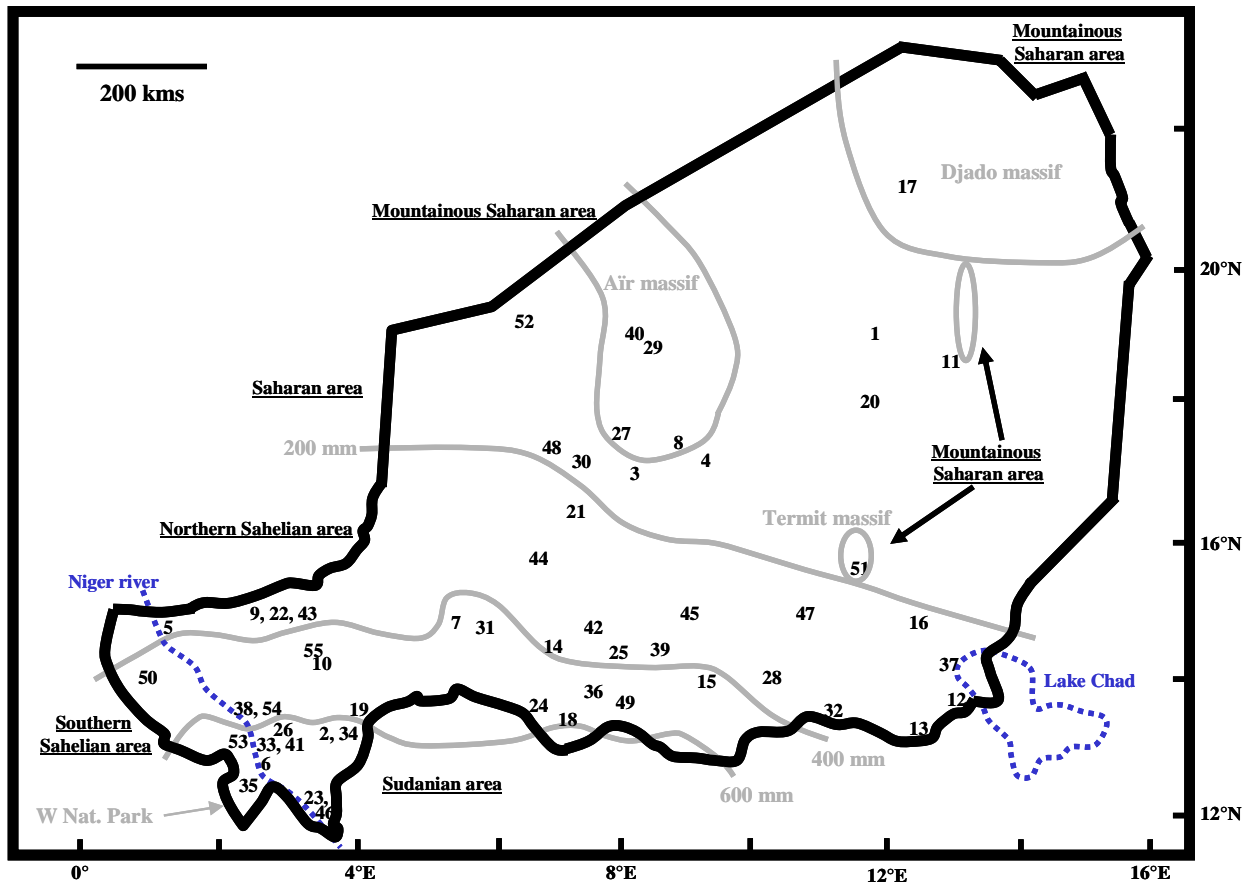
The results presented here rely on the study of 328 specimens, 320 of which were karyotyped. External measurements of all the specimens, chromosomal results, and a review of those available in the literature for Niger are compiled in Table 1.

Table 1 : External measurements and chromosomal data of rodents from Niger. 2N, NFa : diploid and autosomal fundamental numbers, HB : head and body, T : tail, tuft included, E : ear, HF : hindfoot, claw included. Chromosomal data are compiled from this study and previous works. External measurements are based only on karyotyped (except when precised) specimen studied in this work (n, sample size in brackets).

Species	2N	NFa	X	Y1	Y2	HB (mm)	T (mm)	E (mm)	HF (mm)
Acomys airensis (n=9)	41-43, 46	66	A	A		98.7 (89-107) (n=8)	95.5 (80-104) (n=6)	16.5 (15-17.5) (n=8)	17.6 (17-19) (n=8)
<i>Acomys</i> sp. (n=2)	66	66	A	A		?	?	?	?
<i>Arvicanthis niloticus</i> (n=12)	62	62	sM	sM		155.3 (128-183)	125.2 (92-141) (n=9)	17.5 (16-19)	34.1 (29.5-37)
<i>Arvicanthis ansorgei</i> (n=4)	62	74 ?, 76	sM	sM		159.5 (151-168)	132-140 (n=2)	20.5 (19-22)	35.8 (35-37)
<i>Lemniscomys zebra</i> (n=2)	54	58	M	M		105-112	124-116	15-15	25-24
<i>Mastomys natalensis</i> (n=7)	32	54	sM	A		129.3 (93-152)	115.9 (98-140) (n=6)	18.8 (17-20) (n=6)	25.9 (25-27)
<i>Mastomys erythroleucus</i> (n=21)	38	50-53	sM	A		121.4 (92.5-153)	107.1 (95-130) (n=16)	18.9 (18-20)	24 (22-26)
<i>Mastomys</i> sp. (n=6)	38	40	sM	sM		118.5 (86-168)	96.3 (76-123)	18.5 (15.5-20)	24.8 (23-26) (n=5)
<i>Mus musculus</i> (n=2)	40	38	A			82-70	?-82	14-14	18-16
<i>Mus Nannomys haussa</i> (n=8)	31-34	36	A	A		50.6 (47-58)	37.8 (34-43)	8.8 (8-9)	12.6 (12-13)
<i>Myomys daltoni</i> (n=5 *)	?	?	?	?		93.3 (67-107)	101 (86-120)	15.4 (13-17)	23.6 (22-25)
<i>Rattus rattus</i> (n=3)	38	58	A	A		138.7 (125-157)	173 (150-196)	21.5 (19-23)	34.8 (32.5-38)
<i>Desmodilliscus braueri</i> (n=6)	76, 77 ?	104 ?	?	?		68.3 (63-71) (n=5)	40 (34-43) (n=5)	9.4 (9-10) (n=5)	15.8 (15-17) (n=5)
<i>Gerbillus campestris</i> (n=3)	56	68	sM	sM		84-103 (n=2)	123-138 (n=2)	15-16 (n=2)	23-25 (n=2)
<i>Gerbillus gerbillus</i> (n=5)	42/43	72, 74	sM	M	sM	90.9 (89-93)	126.1 (117-132)	12.6 (11-14)	30.9 (29-32.5)
<i>Gerbillus henleyi</i> (n=4)	52	59, 62	M	A		66.3 (64-69)	91.3 (85-100)	9.9 (9.5-10)	19.3 (18-20)
<i>Gerbillus pyramidum</i> (n=18)	38	72	sM	sM		108.7 (98-125)	152.4 (123-167) (n=14)	14.4 (13-16)	32.4 (29-36)
<i>Gerbillus nancillus</i> (n=11)	56	54	sM	sM		60.2 (55-66.5) (n=8)	83.1 (80-89) (n=8)	10.6 (10-11.5) (n=8)	17.3 (16.5-18.5) (n=8)
<i>Gerbillus nanus</i> (n=17)	52	58, 59	sM	A		79.3 (64-89.5)	106.2 (83-121) (n=13)	12 (10-14)	22.7 (21-26)
<i>Gerbillus nigeriae</i> (n=112)	60-74	116-144	A	sM		95.2 (69-111) (n=109)	119.7 (90-145) (n=88)	14.4 (12-16) (n=109)	25.5 (23-28) (n=109)
<i>Gerbillus tarabuli</i> (n=19)	40	74	sM	sM		94.7 (76-109)	132.3 (110-147) (n=17)	13.5 (11.5-14.5)	28.6 (26-31)
Meriones cf. crassus (n=5 **)	59 ?, 60	?, 72	M	sM		117.1 (100.5-150)	113.7 (93-124)	14.3 (13.5-16)	32 (30-34.5)
Tatera gambiana (n=1)	52	64	sM			134	?	17.5	42
<i>Tatera</i> sp. (n=2)	36	68	M			152-155	197.6 (n=1)	22.5-21	40.5-40
<i>Taterillus petteri</i> (n=4)	18/19	25-29	sM	sM	M	107-113 (n=2)	125 (n=1)	19-21 (n=2)	29-30 (n=2)
<i>Taterillus gracilis</i> (n=17)	36-39	42, 44	sM	sM	M	119.3 (103-129)	165.1 (147.5-186) (n=10)	20.2 (19-22)	31.6 (28-34)
<i>Taterillus pygargus</i> (n=8)	22/23	40	sM	sM	M	115.4 (102-125)	157 (148-164) (n=3)	19.6 (18-21)	32.4 (30-37)
<i>Taterillus</i> sp. (n=6)	24/25	44	sM	sM	M	116 (108-124)	144-162 (n=2)	20 (19-21)	33.4 (32.5-34)
<i>Cricetomys gambianus</i> (n=2 ***)	79?, 80?	82 ?	A	sM		177-192.5	170-182	27-29	46-52
<i>Jaculus jaculus</i> (n=2)	48	86 ?	sM ?	sM ?		94-115	177-208	17-23	61-62
<i>Graphiurus</i> cf. <i>parvus</i> (n=1)	70	?	?	?		80	41+18	14	17
<i>Massouteria mzabi</i> (n=3 ****)	36	68	sM	A		161 (152-168)	61 (53-73)	17 (16-18)	36.2 (35-38)
<i>Xerus erythropus</i> (n=1)	38	>68	sM	sM		275	261	16	70

* no specimen karyotyped
 ** only three of them were karyotyped
 *** two young animals
 **** only two of them were karyotyped

Figure 1 : Major biogeographic areas (cf. text) and localities of capture. The numbers refer to the annexe.



MURIDAE

Murinae

Arvicanthis niloticus (Desmarest, 1822)

This Sudanian to Sahelian species is well differentiated from its sibling species (*A. ansorgei*) by a $2N=62$ / $NFa=62$ to 64 karyotype, known from Mauritania, Senegal, Burkina-Faso, Mali, Niger (Niamey and Kollo), Chad, Uganda, Kenya, Ethiopia and Egypt (review in Ducroz 1998). We karyotyped twelve specimens from several sites of the northern Sudanian and the Sahelian zones till the southern edge of the Aïr massif (3a, 12b, 13b, 26, 28, 33a, 37a, 38a, 45b, 54b), in which grass rats were observed, too. The karyotypes are invariant and in agreement with those previously published (see Viegas-Péquignot *et al.* 1983 ; review in Volobouev *et al.*, 2002) with $2N=62$, $NFa=62$, the X and Y chromosomes being both submetacentric (data not shown). It is a very frequent species in most wild bushy areas, gardens, villages and towns.

Arvicanthis ansorgei Thomas, 1910

The specimens of *Arvicanthis* ($n=4$) trapped in the Sudanian area (46b) also have $2N=62$ chromosomes. But their autosomal fundamental number reaches 76 (and maybe 74 in one specimen). The X and Y chromosomes are both submetacentric (data not shown). In the absence of banding data, this chromosomal morphology may correspond either to ANI-3 or ANI-4 *sensu* Volobouev *et al.* (1988a) and Ducroz (1998), respectively (review in Volobouev *et al.*, 2002). But results of molecular phylogenetics using cytochrome b sequences (Ducroz pers. comm.) show that these specimens can unambiguously be referred to ANI-3, i.e. *A. ansorgei* (Ducroz 1998).

Mastomys natalensis (Smith, 1834)

In West Africa, the karyotype of *M. natalensis* was described from Senegal where it allows to distinguish it from *M. erythroleucus* and *M. huberti* (Duplantier, Britton-Davidian and Granjon 1990). We found this species in western Niger (6a, 10a, 38a, 46a, 46b, 53, 54b) but it is probably present in a much larger zone, as this species was found also in Chad, around Lake Chad (Granjon and Dobigny submitted), thus suggesting its occurrence throughout the Sudanian and the Sahelian zones, to as far as eastern and southern Africa (review in Granjon *et al.* 1997a). Our cytogenetic results are in agreement with those previously observed in Senegal, Benin, Chad, Niger, Ethiopia, Kenya, Tanzania, and Southern Africa (review in Granjon *et al.* 1997a; Lavrentchenko *et al.* 1998), i.e., $2N=32$ and $NFa=54$ with a submetacentric X and an acrocentric Y chromosomes ($n=7$; data not shown).

Mastomys erythroleucus (Temminck, 1853)

Mastomys erythroleucus was trapped in very distant sites (5a, 6c, 13b, 13c, 18b, 32b, 33a, 35c), from West to East, in both Sudanian and Sahelian areas, thus suggesting a large geographic distribution in Niger. The X and Y chromosomes are submetacentric and acrocentric, respectively, in agreement with previous data (see Britton-Davidian *et al.* 1995). Its diploid number remains 38, but its autosomal fundamental number ranges from 50 to 53 ($n=21$; data not shown). This range is in agreement with the variations previously described from Morocco, Senegal, Ivory Coast, Mali, Burkina-Faso, Benin, Chad, Cameroon, Zaïre, Sudan and Ethiopia (review in Volobouev *et al.* 2001; Granjon pers. comm.).

Mastomys sp.

A few large-sized specimens with silky and thick fur were trapped in the Ighazer plains, West of the Aïr massif (30b). They are characterised by a diploid number of 38, and an autosomal fundamental number of 40 ($n=6$). The X and Y chromosomes are submetacentric and metacentric, respectively. All the autosomes are acrocentric, except two small metacentric pairs (Fig. 2). This karyomorph, the taxonomic status of which needs to be determined, has also been found in the Sudanian area in Chad (Volobouev *et al.* 2001; Dobigny, unpubl.), and Sudan (Viegas-Péquignot *et al.* 1987), suggesting a quite large distribution area and various habitats.

Myomys daltoni (Thomas, 1892)

Five specimens of *Myomys* with pure white belly were trapped in the northern Sudanian area on both sides of the Niger river (33a; Dareyna, $13^{\circ}34'N$ $2^{\circ}00'E$). No chromosomal analysis could be performed, but the distribution data available for this genus (cf. Musser and Carleton 1993) and the morphological traits of our specimens (Rosevear 1969) strongly suggest that these animals should be referred to *M. daltoni*. This species has also been mentioned near the W National Park by Poché (1976). As a consequence, this species may inhabit quite a large area from the Sudanian to the Northern Sahelian zone.

Figure 2 : Karyotype of a male *Mastomys* sp. (2N=38 / NFa=40).

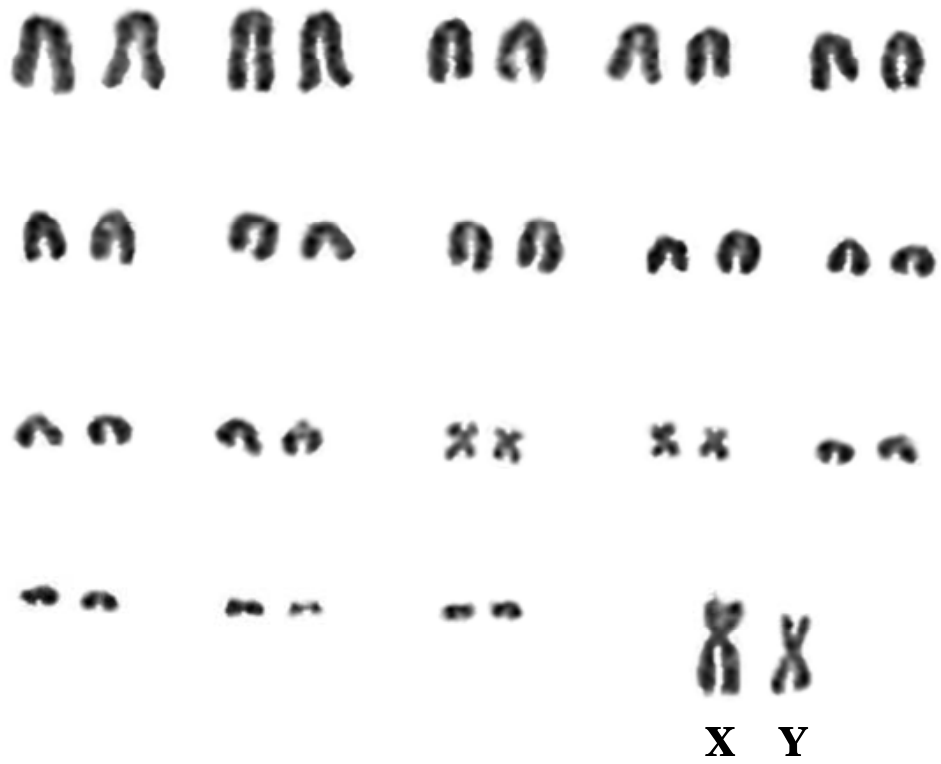
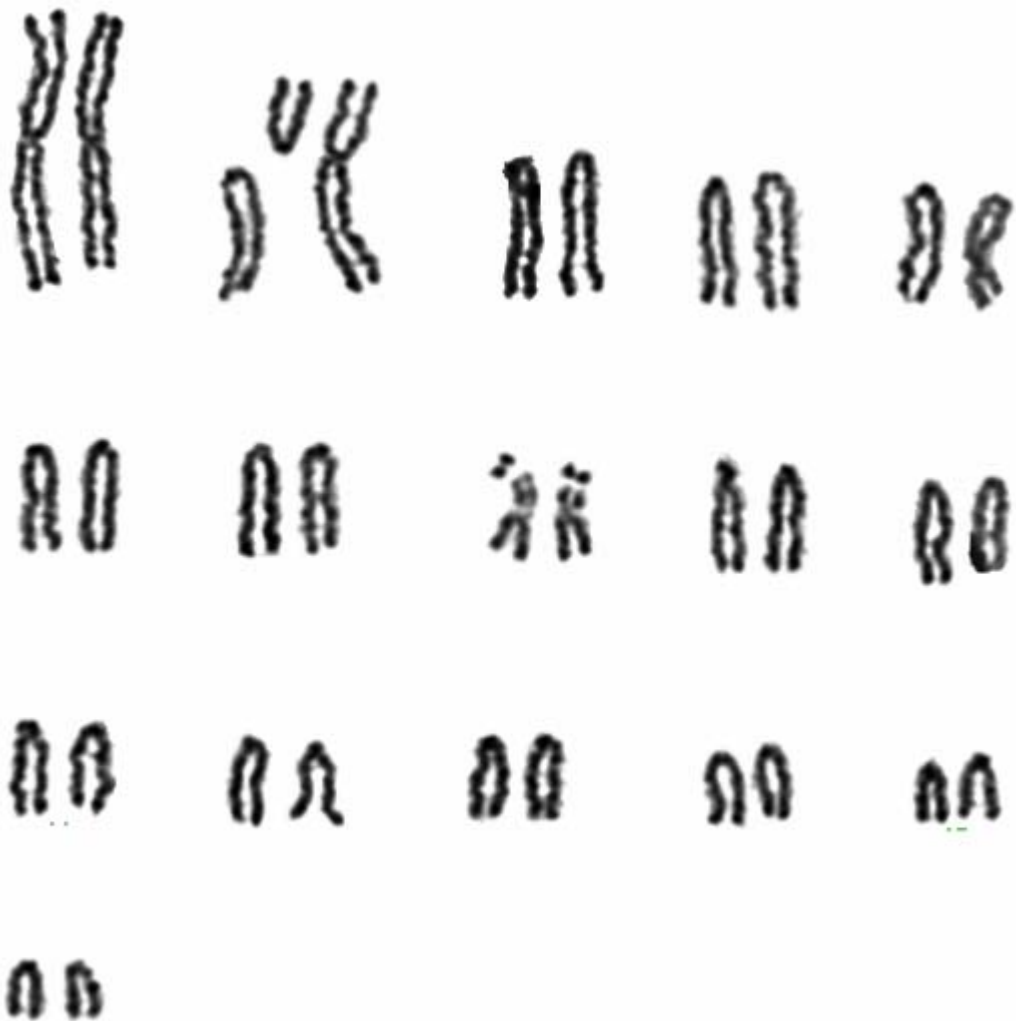


Figure 3 : Karyotype of *Mus Nannomys haussa* (2N=33 / NFa=36). Note the well-marked satellites on the 8th pair.



Lemniscomys zebra (Thomas, 1905)

Two females *Lemniscomys* from the W National Park (35a) were characterized by $2N=54$ and $NFa=58$. The morphology of the chromosomes is in agreement with the results obtained for specimens of *L. barbarus* from Algeria by Filippucci, Civitelli and Capanna (1986). We here follow Carleton and Van der Straeten (1997) who distinguished the maghrebi and subsaharan forms of *Lemniscomys*, though both with $2N=54$ and $NFa=58$, and assigned them respectively to *L. barbarus* and *L. zebra*. This species may be confined only to Sudanian areas.

Mus Nannomys haussa Thomas and Hinton, 1920

This very small species (Table 1) was trapped only in 3 localities around Niamey (6b, 26, 33a), but it may be present over quite a larger area probably overlapping at least the southern Sahelian and northern Sudanian zones. The 8 specimens we could karyotype and unambiguously analyse possessed between $2N=31$ and 34 chromosomes, with a constant $NF=38$ (Fig. 3). In the absence of replication patterns, the X and Y chromosomes could not be identified with certainty, but they may be both acrocentric, as previously suggested (Jotterand 1972). The range in diploid numbers is larger than the one described in the literature ($2N=32$ to 34; Matthey 1967; Jotterand 1972) based on specimens from Niger (Niamey) and North of Ivory Coast, and may be due to additional polymorphism for a Robertsonian translocation, as already suggested by the authors cited above.

Mus musculus Linnaeus, 1758

Only a few domestic mice were trapped in the city of Niamey (38a). It may be strictly commensal, as already observed in Senegal (Duplantier, Granjon and Bâ 1997). The karyotype of the 2 females studied showed $2N=40$, $NFa=38$ and an acrocentric X chromosome (data not shown), and is referable to the all-acrocentric European race (review in Sage, Atchley and Capanna 1993).

Rattus rattus (Linnaeus, 1758)

A few specimens of *Rattus rattus* were caught in Niamey and near Gaya (6b, 38a, 46a), and three of them could be karyotyped. No difference with the most common karyotype of West European and African black rats could be found ($2N=38$; $NFa=58$; X and Y acrocentric; data not shown) (Capanna and Civitelli 1971a, 1971b). This species may be strictly commensal, as already suggested for specimens from Senegal (Duplantier *et al.* 1997).

Gerbillinae

Desmodilliscus braueri Wettstein, 1916

This small species known throughout Western and Central Sahelian area (review in Hutterer and Dieterlen 1986) was logically found in several Sahelian and one Saharan sites dispersed throughout the country (localities 14, 30a, 36, 55c, cf. Annexe and Fig. 1). A Sudanian mention from the W National Park was made by Poché (1976), and specimens were captured in Babaganta and Gaya (6c, 23). The karyotype of *D. braueri* is only known from Senegal ($2N=78$, $NFa=104$; Granjon *et al.* 1992). In spite of the low quality of chromosomal preparations, our results show $2N=76$ chromosomes ($n=6$; NFa not precisely defined, but probably 104). These variations in diploid number would deserve further analyses including banding studies.

Gerbillus campestris (Loche, 1867)

This dark and naked-soled gerbil has been found in rocky areas of Aïr (8, 27a) where it has already been reported (Dekeyser 1950) and karyotyped (Dobigny *et al.* 2001b). Karyotypes ($n=3$) are in agreement with those found in the Maghreb (Matthey 1953; Wassif, Ramsis and Lufty 1969; Jordan, Davis and Baccar 1974; Lay, Agerson and Nadler 1975) and Northern Mali (Dobigny *et al.* 2001b). They are characterised by $2N=56$ chromosomes and $NFa=68$. The X and Y chromosomes are a large and a medium-sized submetacentric element, respectively.

Gerbillus gerbillus (Olivier, 1801)

Hairy-soled specimens of *G. gerbillus* have been found in the Tenere desert, and the sandy areas of Djado and Aïr (1, 4, 17, 27b), thus providing the first non ambiguous mention of this species in Niger (see Giazzi 1996 for other data). South of the Maghreb, *G. gerbillus* has only been karyotyped from Mauritania (Granjon *et al.* 1997b). The karyotypes of the specimens from Niger ($n=5$; $2N=42/43$; $NFa=72$ and 74; X large submetacentric; Y1 and Y2 meta- and submetacentric, respectively) are within the range described from Algeria (Matthey 1954), Tunisia (Jordan *et al.* 1974), Morocco (Lay *et al.* 1975), Israel and Egypt (see review in Wahrman, Richler and Ritte 1988). The XY₁Y₂ formula is the result of a double autosome-gonosome translocation studied in detail by Wahrman *et al.* (1988).

Gerbillus henleyi (de Winton, 1903)

This small naked-sole species is a good example of the limits of standard cytotaxonomy. Indeed, only banding analysis can discriminate *G. henleyi* (2N=52; NFA=58 to 62) from *G. nanus* (2N=52; NFA=58 to 60) (see Volobouev *et al.* 1995). In this particular case, we used external and cranial traits to assign these specimens to *G. henleyi* (HF<20 mm including claw; total cranial length < 25 mm; upper M1 width around 1 mm; molar row length around 3 mm; bullae not exceeding the occipital posteriorly; morphology of the upper M1) (Petter 1961; Harrison 1981; Maddalena *et al.* 1988). Based on these considerations, *G. henleyi* was found in typically Sahelian areas (21, 45a, 50b), which is not surprising as it seems to be a typical but poorly known peri-desertic species in Africa and the Middle East (cf. Musser and Carleton 1993). Its karyotype, in agreement with previously published data (Maddalena *et al.* 1988; Granjon *et al.* 1992; Volobouev *et al.* 1995), is characterised by 2N=52 and NFA= 59 to 62 (n=4). The X and Y chromosomes are metacentric and acrocentric, respectively.

Gerbillus nancillus Thomas and Hinton, 1923

A very small species of *Gerbillus* with naked sole was found in sandy northern Sudanian and typical Sahelian areas (33a, 43, 55c) and. Its karyotype (n=11) is composed of 56 acrocentric or subtelocentric chromosomes (NFA=54) (Fig. 4). The sex chromosomes could not be identified unambiguously. We here follow Tranier and Julien-Laferrière (1990) who referred these small gerbils to *G. nancillus* on the basis of the morphological traits of one specimen from Toukounous (55c). First described from Darfur, Sudan (Thomas and Hinton, 1923), this very poorly known species has now been identified in Chad, Niger (Tranier and Julien-Laferrière 1990; this study) and Mali (Granjon pers. comm.).

Gerbillus nanus Blanford, 1875

As mentioned above, *G. nanus* cannot be unambiguously discriminated by its standard karyotype from *G. henleyi*. However, several external and cranial traits (see *G. henleyi*) provide a good diagnosis of these two small naked-sole gerbils (Petter 1961; Harrison 1981; Maddalena *et al.* 1988). As *G. nanus* is known from Asia Minor, the Middle East, Maghreb and Western Africa (Musser and Carleton 1993; Granjon *et al.* 1997b; Dobigny *et al.* 2001b), it was not surprising to find it in Niger. It was trapped in Sahelian localities near Lake Chad, and Saharan sites, including Air, Termit, and an oasis of the Tenere desert (3a, 11, 12c, 13a, 29, 37b, 37c, 40a, 40c). The Lake Chad is the southernmost one known for this species, and may represent its southern limit of distribution. Our standard chromosomal data, i.e. 2N=52, NFA=58 and 59, X submetacentric, Y acrocentric (n=17) are in agreement with previous works (Wassif *et al.* 1969; Jordan *et al.* 1974; Lay and Nadler 1975, Lay *et al.* 1975; Qumsiyeh 1986; Wahrman *et al.* 1988; Volobouev *et al.* 1995; Granjon *et al.* 1997b; Dobigny *et al.* 2001b).

Gerbillus nigeriae Thomas and Hinton, 1920

This medium-sized species is very widespread in Niger and can be found in almost all sandy sites of the Sudanian and Sahelian areas. Chromosomal data are available for Burkina-Faso (Gautun, Tranier and Sicard 1985; Volobouev *et al.* 1988b), Mali (G. Dobigny, L. Granjon, V. Volobouev unpubl.) and Mauritania (Granjon *et al.* 1997b; Volobouev unpubl.). It has also been already karyotyped in Niger, from Niamey, Keita and Tillabery (Tranier 1975a; Volobouev *et al.* 1988b; Volobouev unpubl.). We were able to obtain the karyotypes for 112 specimens from 34 sites throughout Niger (2, 3, 5b, 6c, 7, 10b, 12c, 12d, 13a, 14, 15, 18a, 19, 23, 24, 25, 28, 33a, 33c, 36, 39b, 41, 42, 44a, 44b, 45a, 46c, 49, 50a, 50b, 50c, 55a, 55b, 55c). Diploid numbers range from 2N=60, the lowest one ever observed for this species, to 74. The presence of heterochromatic arms on all non-translocated autosomes (Volobouev *et al.* 1988b) leads to an autosomal fundamental number ranging from 116 to 144. The X chromosome is a large acrocentric, the Y being submetacentric (data not shown), in agreement with previous data (Tranier 1975a; Viegas-Péquignot *et al.* 1982). As already observed between distant localities (Volobouev *et al.* 1988b), karyotypes greatly differ from one site to another, but also within the same site. These variations seem to be non randomly distributed and would deserve a detailed analysis.

Gerbillus pyramidum Geoffroy, 1825

This large hairy soled gerbil is known from Egypt, Sudan, Mauritania, and Northern Mali (review in Granjon *et al.* 1999; Dobigny *et al.* 2001b). It has recently been found in the Sahelian area near the Lake Chad (Granjon and Dobigny, in prep.). In Niger, we found *G. pyramidum* in sandy zones of the Air and Termit massifs, and several localities of the Saharan area, till an oasis of Tenere desert (20a, 27b, 29, 30c, 40a, 48a, 48b, 51a, 51b). Our chromosomal data (n=18) are in agreement with those previously published (review in Granjon *et al.* 1999), i.e. 2N=38 chromosomes, all of which are metacentric (NFA=72), except the sex chromosomes which are submetacentric (data not shown).

Figure 4 : Karyotype of *Gerbillus nancillus* (2N=56 / NFa=54).



Gerbillus tarabuli Thomas, 1902

This hairy-soled species is comparable in size to *G. pyramidum* (Table 1) with which it is easily confounded (review in Granjon *et al.* 1999). Its well differentiated karyotype has already been described from Southern Mauritania, Senegal, Northern Mali, Morocco, Algeria, Tunisia and Libya (review in Granjon *et al.* 1999; Dobigny *et al.* 2001b) and seems to be very stable. In agreement with previous data, the karyotypes obtained from 19 animals present 2N=40 chromosomes, all autosomal pairs being meta- or submetacentric, except the smallest pair which is acrocentric (NFa=74) (data not shown). It was trapped in complete sandy areas in Aïr, in a Saharan oasis near the Algerian border, and in several localities of Northern Sahel, from the Tillabery district to Lake Chad (16a, 16b, 30c, 37b, 37c, 47, 48a, 52, 55b). *G. tarabuli* definitely seems to be a common peri-Saharan and Saharan species.

Meriones crassus Sundevall, 1842

Five specimens of *Meriones* were caught in the Ighazer plains, South-West of Aïr (30a, 30b), which represent one of the southernmost localities for this genus. Thomas (1925) proposed to refer the jirds of Niger to *M. crassus* based on morphological traits. The chromosomal preparations (n=3; data not shown), in spite of low quality, support this view, as the karyotype was characterized non ambiguously in one case by 2N=60 and NFa=72, which has been attributed to *M. crassus* (Matthey, 1957; Benazzou *et al.* 1982; Wahrman *et al.* 1988).

Tatera gambiana Thomas, 1910

One single specimen was trapped inside a hut in Kojimairi, in an oasis depression (32a). Its karyotype (2N=52; NFa=64; large submetacentric X chromosome; data not shown) perfectly matches the one referred to *T. valida* (Matthey 1969) and then later to *T. gambiana* (Matthey and Petter 1970). This geographic distribution is quite interesting as it appears very far from the only locality where cytotaxonomic data are available, i.e. Dakar, Senegal (Matthey 1969).

Tatera sp.

Two females from N'Guigmi and Bosso, near Lake Chad, and trapped inside a garden and next to the dry bed of the Komadougou river respectively (12d, 37a), had 2N=36 all metacentric chromosomes (NFa=68). In the absence of banding data, the X chromosome could not be defined (Fig. 5). This chromosomal morphology has already been described from Kenya (*Tatera* sp., Qumsiyeh, Hamilton and Schlitter 1987).

Taterillus gracilis (Thomas, 1892)

We trapped *T. gracilis* in south-western Niger (6d, 23, 33a, 35b, 38b, 54a). The karyotypes (n=17) are in agreement with previous data (Matthey and Jotterand 1972) with diploid numbers ranging from 2N=36 to 39, and autosomal fundamental numbers from 42 (n=9) to 44 (n=8). The 36/37 (n=2) and 38/39 (n=12) karyotypes are distinguished by a Robertsonian translocation (banding data; Dobigny unpubl.). The conspecificity of these two cytotypes is assumed by the occurrence in the wild of three specimens heterozygous for this translocation. Such Robertsonian polymorphism has already been observed in Burkina-Faso (Matthey and Jotterand 1972) and South West Nigeria (Tranier unpubl.).

Taterillus pygargus (Cuvier, 1838)

Non ambiguous chromosomal data for *T. pygargus* are only available from Senegal. This species was mentioned from Mali (Meinig 2000) but without cytotaxonomic confirmation. As its occurrence in Mali could not be confirmed in spite of extensive sampling (Granjon and Sicard pers. comm.), its presence in both Sahelian and Sudanian zones of Niger (23, 39a, 44a, 44b, 45a, 46c) is quite surprising. Its karyotype is characterised by 2N=22/23 chromosomes, and NFa=40. The X chromosome is a large submetacentric. The Y1 and Y2 chromosomes, resulting from an X-autosome translocation (review in Volobouev and Granjon 1996), are a medium-sized submetacentric and a small metacentric, respectively (Fig. 6). These data, confirmed by banding analysis (Dobigny unpubl.), are in agreement with those published for Senegal (Matthey and Jotterand 1972). The distribution of *T. pygargus* is thus extended 2000 kms eastwards.

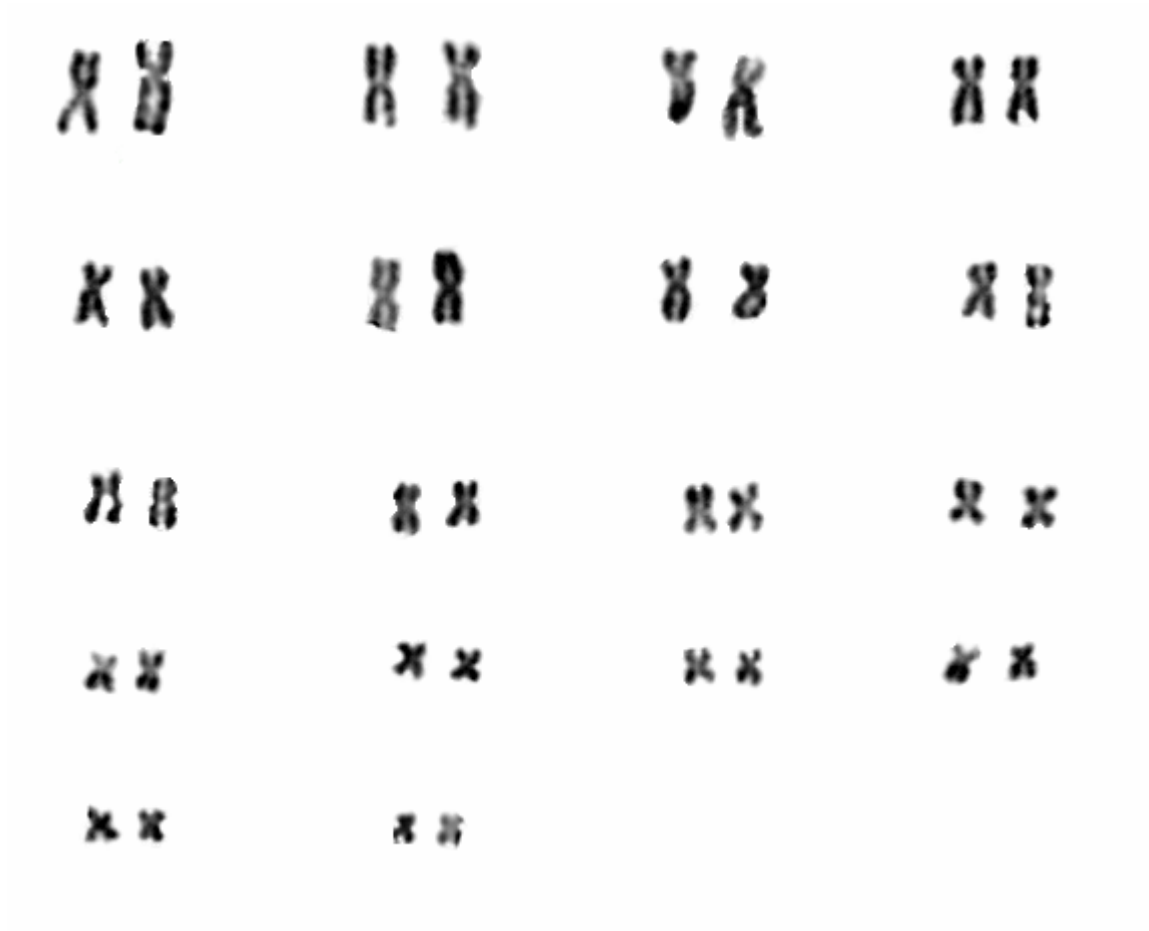
Taterillus petteri Sicard, Tranier and Gautun, 1988

We trapped no specimens of *Taterillus petteri*, but 4 individuals from the surroundings of Niamey were karyotyped by Tranier (1974), displaying 2N=18/19 chromosomes, and NFa=25 to 29. They were caught in sandy areas on the western side of Niger River, and could be confined to the Niger river loop (Sicard, Tranier and Gautun 1988).

Taterillus sp.

A new cytotype of *Taterillus* has been found in the Sahelian area of Diffa district, mainly along the Komadougou river (12b, 12d, 13a, 32a) and is characterized by 2N=24 in females and 25 in males (n=6). The

Figure 5 : Karyotype of a female *Tatera* sp. ($2N=36 / NFa=68$).



autosomes are all metacentric (NFa=44) and the sexual chromosomes are submetacentric (Fig. 7). The sex trivalent in males confirms that this form belongs to the West African complex of *Taterillus* species, characterised by the XY₁Y₂ sexual formula (Volobouev and Granjon 1996). This karyotype is quite well differentiated from the other species known for the genus (banding data; Dobigny *et al.* 2002a).

Acomyinae

Acomys airensis Thomas and Hinton, 1921

Several specimens of *A. airensis* were sampled in quite different environments throughout a large area from the Sahelian and Saharan areas including Aïr (3a, 3b, 8, 10b, 20b, 40b, 54a) where it has already been karyotyped (Tranier 1975b). Their karyotypes were all characterized by 2N=42, and NFa=66 (n=8; data not shown), except for one specimen from Fachi having 2N=46 chromosomes (NFa=66). This variation, suggesting the occurrence of a Roberstonian polymorphism, remains in agreement with the data previously published for Adrar des Iforas, Mali (2N=44 and 46; Dobigny *et al.* 2001b), and other specimens of Niger from Aïr (Tranier 1975b), Karma (13°39N, 1°51E) and Hamdara (13°49N, 9°47E) (2N=41 to 43; Volobouev unpubl.; see Barome 1998).

Acomys sp.

Two spiny mice were caught in rocky sites of the Sudanian zone (near Tamou, 12°45N 2°10E, and Gouroubi, 12°52N, 2°21E). Their karyotype (Britton-Davidian, Catalan, Poteau in litt.) was characterized by 66 chromosomes, all autosomes being acrocentric, except for a large metacentric pair (NFa=66). The X and Y chromosomes are a large and a very small acrocentric, respectively. This chromosomal morphology has already been observed in Wayen, Burkina-Faso (Volobouev unpubl.), but no name is available for this species to date. This form has never been found on the left bank of the Niger river, where only *A. airensis* has been trapped, at least in Niger.

Cricetomyinae

Cricetomys gambianus Waterhouse, 1840

Cricetomys gambianus was trapped in Niamey and Kojimairi (38a, 32b), but is probably present in all the Sahelian and Sudanian areas (animals caught, observed or described from Kollo, Afolé, Dogondoutchi, Babangata, Niamey area, Diffa, etc ...), generally close to human settlements. This large-sized rodent seems to be naturally present in a wide zone south of the country, but may subsist further North in drier areas where it survives in gardens or fields (e.g. Kojimairi). Two young specimens of the same litter captured near Niamey were karyotyped. Preparations are of very poor quality but the diploid number may range from 79 to 80, with a NFa probably reaching 82. The X and Y chromosomes may be respectively acrocentric and submetacentric (data not shown). That would be in agreement with previously published data for Senegal where an animal with 2N=80 chromosomes (NF=86) was studied (Granjon *et al.* 1992). These results and other analyses from Benin (2N=82; NFa=88; X large submetacentric; Codjia *et al.* 1994) as well as on a specimen of unknown origin (2N=78; Matthey 1953, quoted by Granjon *et al.* 1992) suggest that chromosomal variation occurs in *C. gambianus* deserving further studies.

CTENODACTYLIDAE

Massouteria mzabi (Lataste, 1881)

Goundis were caught by hand in rocky areas of Aïr (40b). This species is found in almost all the rocky areas of the Central Sahara (Hoggar, Algérie, cf. Kowalski and Rzebik-Kowalska 1991; Adrar des Iforas, Mali, cf. Dobigny *et al.* 2001a; Aïr, cf. Giazzi 1996; this study). Previous chromosomal data was only available for female *M. mzabi* (George, 1985). We could karyotype two specimens characterized by 2N=36 chromosomes, NFa=68, all autosomes being meta- or submetacentric (George, 1985). The gonosomes X and Y are respectively a medium-size submetacentric and a very small acrocentric (Fig. 8).

DIPODIDAE

Jaculus jaculus (Linnaeus, 1758)

The jerboa *Jaculus jaculus* is supposed to be characteristic of Saharan sandy habitats, but specimens were noted southwards down to north-east Nigeria (Happold 1987). In Niger, it was trapped or its presence was observed in Sahelian and Saharan localities such as Aïr, the Dilia valley, Djado and Ténéré desert, but also throughout all the Sahelian and Sudanian areas, to south of Niamey. It was also mentioned in the W National Park, near the Benin border (Poché 1976; data confirmed by game rangers). Two animals from Aïr and

Figure 6 : Karyotype of a male *Taterillus pygargus* (2N=23 / NFa=40).

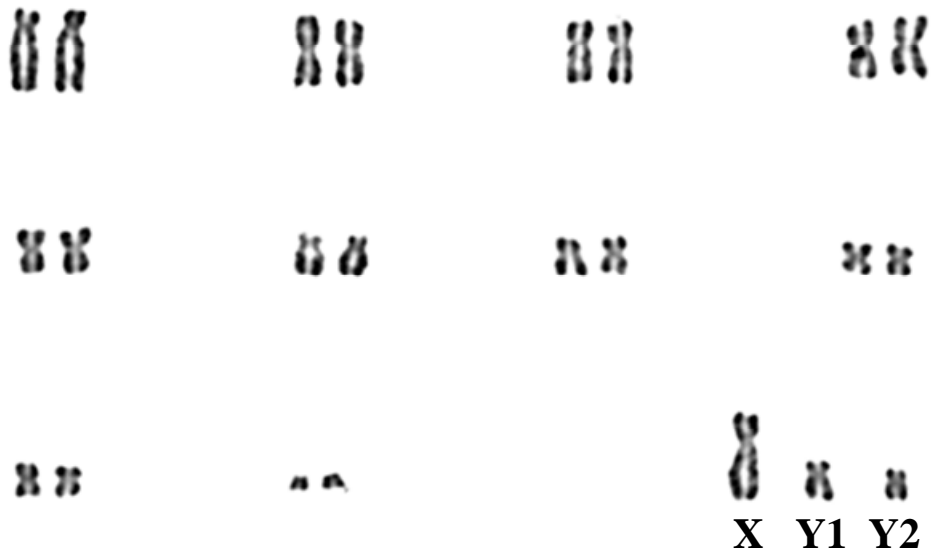
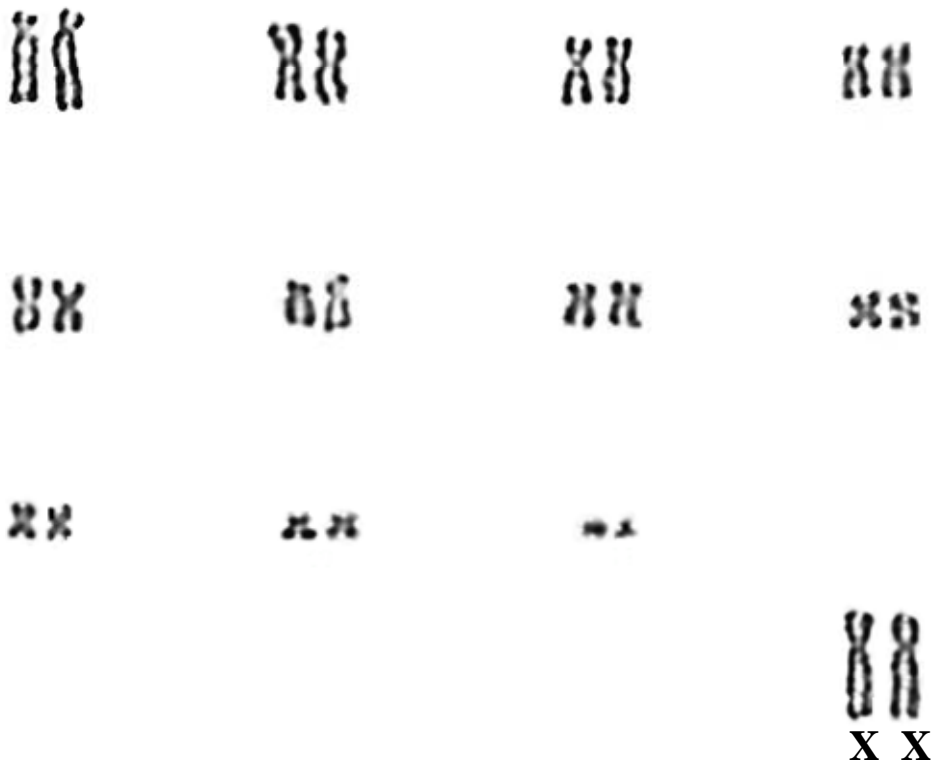


Figure 7 : Karyotype of a female *Taterillus* sp. ($2n=24$ / $NFa=44$).



Babangata (6d, 27b) were karyotyped, but the very low quality of the preparations only permitted to unambiguously determine the diploid number, i.e. $2N=48$ (data not shown).

HYSTRICIDAE

Hystrix cristata Linnaeus, 1758

The presence of the African porcupine was identified by tracks and characteristic dorsal hairs in several sites of the Sudanian (Poché 1976) and Sahelian areas, and in the Air. Karyotyping of this animal was not attempted.

MYOXIIDAE

Graphiurus cf. *parvus* (True, 1893)

A single specimen of *Graphiurus* from Kollo (33b) was studied. Due to the low quality of the preparation, only the diploid number could be determined with certainty: $2N=70$ (data not shown). The taxonomic situation and geographic distributions of species within the genus *Graphiurus* are quite unclear and still in need of extensive revision (cf. Schlitter, Robbins and Williams 1985). Following Genest-Villard (1978) and Schlitter *et al.* (1985), we provisionally refer our specimen to *G. parvus* on morphological and geographical basis.

SCIURIDAE

Xerus erythropus Desmarest, 1817

Ground squirrels are very frequent and are found throughout Niger, to the exclusion of the most arid areas. We observe them in many places all over the anthropised Sahelian area, in the Dilia valley, and in the Air massif. They were mentioned in the W National Park (Poché 1976). One specimen was karyotyped (34), and, in spite of the poor quality of the preparation (Fig. 9), could be unambiguously characterized by $2N=38$. The NFA is at least 68 as most of the autosomes are meta- or submetacentric, except for two small pairs that may be acrocentric. The X and Y chromosomes are a submetacentric and a small acrocentric, respectively.

DISCUSSION

Cytotaxonomy and α -systematics implications

Beyond the description – at least partial - of new chromosomal data for four species (*Gerbillus nancillus*, *Graphiurus* cf. *parvus*, *Massouteria mzabi* and *Xerus erythropus*), this cytotaxonomical survey enabled us to report a chromosomal form never described before, i.e. *Taterillus* sp.. Moreover, three previously described but as yet not attributed cytotypes are confirmed and most likely deserve a species status : *Acomys* sp., *Mastomys* sp. and *Tatera* sp..

Acomys sp. from Burkina-Faso with the same standard karyotype as the one found in Niger has already been referred (Barome 1998) to *A. cf. gautuni* but this name is not valid as no formal description has been provided yet.

The karyotype of *Mastomys* sp. has already been described under the provisional acronym MER-2 (Volobouev *et al.* 2001). This karyotype is sufficiently divergent from the other chromosomal forms known in the genus to presumably ensure reproductive isolation, i.e. to characterise a different and good biological species (Volobouev *et al.* 2001). We here propose to provisionally refer the multimammate rats of Northern Niger to *M. kollmannspergeri*, first described as a subspecies of *M. natalensis* by Petter (1957). This description was based on specimens “with a silky fur” (Rosevear 1969, p.425) from « Titintarat » (i.e., « Tchet-en-Taghat », on the French IGN map of Air, 1:500 000) (Rosevear 1969, p. 430), « 150 kms north of Agadez » (Petter 1957) and « near the wells of Tedjidda-n-Tesemt » (i.e., « Teguidda-n-Tessoumt ») (Rosevear 1969, p. 423). These localities are close to the trapping sites of our *Mastomys* sp., and the area is very homogeneous from an ecological point of view, i.e. a very wide, clayey and seasonally herbaceous-covered plain. However, our taxonomic proposal needs further morphological analyses before a definitive conclusion can be reached.

At the moment, the genus *Tatera* clearly requires a thorough systematic revision (Granjon *et al.* in prep.). Many names have been proposed for both species and subspecies, and many of them from specimens trapped in Central Africa (Ellerman 1941). As a consequence, precise morpho-anatomical comparisons with type specimens and a wide-ranging cytotaxonomical survey of this genus in West, Central and East Africa are needed before definitive conclusions can be drawn. Nevertheless, it seems reasonable to provisionally refer our *Tatera* sp. to *T. robusta* (for further details, see Granjon and Dobigny submitted).

Figure 8 : Karyotype of a male *Massouteria mzabi* (2N=36 / NFa=68).



Figure 9 : Karyotype of a male *Xerus erythropus* (2N=38 / NFa>68).



The same kind of problem exists for *Taterillus* sp.. As the genus appears to contain many sibling species (Dobigny *et al.* 2002b), including several ones probably still to be discovered (Tranier 1974; Volobouev and Granjon 1996). This has led to great taxonomic confusion, resulting in many names now lapsing into synonymy (Musser and Carleton 1993). Some of the latter could be used to name specimens trapped in the surroundings of Lake Chad, such as those described here, but further investigations are needed.

Cytotaxonomy and rodent biodiversity in Niger

Once again, this work supports the usefulness of cytotaxonomical techniques for small mammal inventories involving complex of sibling species (Petter 1971; Volobouev *et al.* 2001; Dobigny *et al.* submitted). Indeed, without karyotyping, several taxa would not have been determined unambiguously, and could have been misidentified (e.g., *Gerbillus pyramidum* and *G. tarabuli*, *Taterillus gracilis*, *T. pygargus* and *T. petteri*, *Tatera gambiana*, *Mastomys erythroleucus* and *M. natalensis*, *Mus (N.) haussa*, *Acomys airensis*). *Taterillus* from Tamaya represent the best example. They were referred to *T. arenarius* by Robbins (1974) on morphological criteria, and were shown to belong to *T. pygargus* by our survey (same site, GPS coordinates given in Robbins 1974). Moreover, several species would have been indisputably overlooked, such as *Arvicanthis* sp., *Taterillus* sp., and probably *Mastomys* sp. and *Tatera* sp.. Had the chromosome analysis not been performed, the number of species that would have been omitted from this inventory can be estimated to be as many as nine (in the genera *Tatera*, *Mastomys*, *Taterillus*, *Acomys*, *Arvicanthis*), i.e. 23.1% of the specific biodiversity of rodents in Niger.

This first inventory of rodents from Niger comprises at least 18 genera and 34 species. If data from the literature for species such as *Heliosciurus gambianus*, *Funisciurus anerythrus*, *Thryonomys swinderianus* (mentioned from the W National Park; Poché 1976), *Psammomys obesus* and *Meriones libycus* (mentioned from the Aïr; see Giazzi 1996, p. 523 and 541) are taken into account, a list with a total of 22 genera and 39 species is reached. Gerbilline and murine rodents each represent 27.2% of the generic diversity (6 genera) and 46.2% (18 species) and 25.6% (10 species) of the specific diversity, respectively.

Biogeographical patterns

This work can be added to that already available for the other African countries (e.g., review in Happold 1987, p.297 and 298; Gautun *et al.* 1985; Duplantier and Granjon 1992; Duplantier *et al.*, 1997; Robbins and Van der Straeten 1996; Mess and Krell 1999). Such large data sets are valuable for defining biogeographical areas, and for studying their dynamics and evolution. In such a framework, our survey shows that the distribution of most of the species only partially follow the major areas previously defined (White 1986; Saâdou 1991; cf. Poilecot 1999). Based on species distributions, we would rather tentatively assign the inventoried taxa in Niger as follows :

1) The southernmost area of Niger, receiving more than 700 mm average rainfall (rather than 600 mm as previously defined for the typical Sudanian area *sensu* White 1986), shelters species characteristic of moist habitats, bushy savannahs and open forests, i.e., *Arvicanthis ansorgei*, *Lemniscomys zebra*, *Heliosciurus gambianus*, *Funisciurus anerythrus* and *Thryonomys swinderianus*.

2) A wide area is inhabited by both wide-ranging species (i.e., distribution of which overlaps several biogeographical zones) and peri-Saharan ones. This area is largely overlapping both northern Sudanian (rainfall superior to 700 mm) and Sahelian zones till 200 mm, and often including the Aïr massif and Saharan oases. *Taterillus gracilis*, *T. pygargus*, *G. nigeriae*, *Acomys airensis*, *Arvicanthis niloticus*, *Mastomys erythroleucus*, *M. natalensis*, *Myomys daltoni* and *Cricetomys gambianus* can be found in habitats ranging from the "moist" Sudanian to the dryer Sahelian zones. The peri-Saharan species often reach the sandy areas of the Aïr massif, and sometimes survive in Saharan oases by becoming commensal. Here can be placed *Mastomys* sp., *Gerbillus henleyi*, *G. pyramidum*, *G. tarabuli*, *G. nanus*, *G. nancillus* and *Taterillus* sp. (2n=24/25).

3) A typical Saharan area, characterized by *Gerbillus gerbillus* which does not seem to be present southwards.

4) An area confined to mountainous massifs such as the Aïr massif, where *Gerbillus campestris* and *Massouteria mzabi* seem to inhabit rocky habitats only.

5) Some species that are probably strictly commensal, whatever the areas, and that correspond to imported taxa, probably because of human activities, i.e., *Mus musculus* and *Rattus rattus*.

Hystrix cristata, *Jaculus jaculus*, *Xerus erythropus* and *Desmodilliscus braueri* are the only species found and/or observed in almost all the areas, from the Sudanian, the Sahelian and the mountainous Saharan ones (*J. jaculus* is also found in the typical Saharan zone). It is obvious that a larger sample could result in a change of category for some species, but these 5 main biogeographical groups seem rather coherent. Some taxa could not be attributed to any definite category, the data for Niger being too sparse (i.e., *Acomys* sp., *Meriones crassus*,

Tatera gambiana and *Tatera* sp., *Taterillus petteri*, *Mus haussa*, *Graphiurus* cf. *parvus* ; see Giazzi, 1996 for *M. libycus* and *Psammomys obesus*).

From a global point of view, the group 1 (in the Sudanian area receiving less than 700 mm rainfall) appears to be the most precisely defined by the rodent fauna, with at least five species characteristic of this zone. On the contrary, the specific distributions do not support a zoological distinction between Northern and Southern Sahel as defined by White (1986). Moreover, our group 2 contains some species usually recognized as “Sahelian” or “Sahelo-Saharan” species, but present quite southward in Niger (e.g., *Gerbillus nigeriae* in the Sudanian area). This southernmost extension is clearly illustrated by *Jaculus jaculus*, usually considered as a typically Saharan species, and which has also been found in the typical Sudanian area (“W” National Park). This may be explained by the ongoing desertification of this part of Africa, as already suggested on the basis of rodents inventories in Burkina-Faso (Maddalena *et al.* 1988), Senegal (Duplantier, Granjon and Bâ 1991) and Chad (Granjon and Dobigny submitted). For instance, the drastic impact of recent rainfall decrease (30% in the West African Sahel during the last 25 years ; Mouchet 1998) and agricultural activities on Sahelian habitats may lead to a rapid transformation to an environment which is less favorable to Murinae. These latter are known to be very competitive rodents but not particularly adapted to subdesertic conditions compared to Gerbillinae. Their increasing scarcity (except in human settlements) could explain the gerbil colonisation of these sandy habitats.

On the contrary, some adaptative strategies such as commensalism permit the colonization by a few species of unusual northern areas, where they would probably not survive in natural conditions (e.g., *Acomys airensis* and *Gerbillus pyramidum* in the oasis of Fachi, *Gerbillus nanus* in Bilma). Human migrations and exchanges of associated goods could be responsible for such expansions.

As for East-West difference, most of the taxa inventoried in Niger are usually spread throughout their respective latitudinal bioclimatical domains and no longitudinal cline could be observed. The relative ecological homogeneity of the Sahelian and Sudanian areas probably explain these large east-west continuous distributions.

Finally, the case of the Air massif is particularly interesting. It has already been suggested that Saharan mountainous massifs act as Sahelian refuges in the Sahara desert (e.g., Adrar des Iforas, Mali) (Dobigny *et al.* 2001a). This hypothesis is supported by morphological and biochemical differences in the wild millet, *Pennisetum glaucum*, from Air and some southernmore Sahelian localities (Tostain 1993). This massif shelters both typical Sahelian and Saharan species (e.g. plants, White 1986). But in most of them, no continuity is observed in their distribution between the Air and the Sahel, as is the case for large mammals such as *Erythrocebus patas* and *Papio cynocephalus* (Poilecot 1996). However, it is obvious that such animals are not good biogeographic indicators because they are quite sensitive to human pressure (e.g. hunting, competition with cattle, etc ...). They were present but have recently disappeared from the very populated Sahelian zone, although they have sometimes remained in the more unaccessible parts of the massif (Poilecot 1996), thus providing a biased pattern of isolation. As another evidence, these primates are present in the southern part of the Niger, but only in the W National Park where they are protected. On the contrary, small mammals communities, when not commensal, may be less influenced by human activities in this precise case. And the present study suggests a possible continuity between Sahel and the Air massif for some taxa that are usually absent of the Saharan area (e.g., *Xerus erythropus*, *Hystrix cristata*, maybe *Mastomys* sp.). The contact of the two kind of faunas, namely the Saharan and Sahelian ones, may rather be explained by a simple transition, thus suggesting the Air is a continuous “extension” of Sahel inside the desert, contrary to what was observed in northern Mali (Dobigny *et al.* 2001a). More extensive sampling and molecular studies on several model species would be of great interest to estimate the genetic differentiation between the faunas of the Sahel area and the Air massif, thus testing their level of isolation.

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Annexe : Localities and sites of capture. The numbers are those reported on the map (Fig. 1). SA, MSA, NSA, SSA and SuA are for Saharan, Mountaneous Saharan, Northern Sahelian, Southern Sahelian and Sudanian areas, respectively, as defined following White (1986) and Saâdou (1991) (see text).

N°	Localities, sites	Biogeographic Zone	GPS	Date	Habitats
1	Achegour	SA	19°01N 11°43E	July	Sandy soil
2	Afolé	SSA	13°10N 4°05E	December	Millet field, sandy soil
3a	Agadez, Alaghsas	SA	16°58N 7°59E	July, August	Gardens, sandy soil
3b	Agadez, Indoudou		17°09N 8°09E	Idem	Gardens, sandy soil
4	Amzeguer	SA	17°13N 9°14E	July	Sable
5a	Ayorou, village	NSA	14°44N 0°55E	January	Urban area
5b	Ayorou, millet field		Idem	Idem	Town surroundings, sand
6a	Babangata, Soungamé	SuA	12°55N 2°24E	August	Huts, Niger riverside
6b	Babangata, huts		idem	Idem	Huts
6c	Babangata, fields		idem	Idem	Millet fields, sandy soil
6d	Babangata, clay		idem	Idem	Village surroundings, clayey-sandy soil
7	Baga	SSA	14°55N 5°25E	April	Waste land, indurated sandy soil
8	Bagzane mounts	MSA	17°31N 8°39'E	August	Granit rocks
9	Bani Bangou	NSA	14°58N 2°41E	February	Millet fields, sandy soil
10a	Batchintoulou n°1, village	SSA	14°22N 3°23E	September	Huts
10b	Batchintoulou n°1, millet field		Idem	Idem	Town surroundings, sandy soil
11	Bilma	SA	18°41N 12°55E	July	Huts, sandy soil
12a	Bosso, garden	NSA	13°41N 13°18E	April	Garden, clayey soil
12b	Bosso, Komadougou		idem	Idem	Dry riverbed of Komadougou, clayey-sandy soil
12c	Bosso, fields 1		13°41 13°17E	Idem	Millet field, sandy soil
12d	Bosso, fields 2		13°37N 13°18E	Idem	Millet field, with bushy monticule, sandy soil
13a	Chétimari, field	NSA	13°11N 12°23E	April	Store in millet field, sandy soil
13b	Chétimari, CBLT		13°11 12°33E	August	Village, Komadougou riverside, clayey soil
13c	Chétimari, clay		Idem	April	Clayey soil
14	Dakoro	NSA	14°30N 6°46E	April	Millet field, sandy soil
15	Damagaram Takaya	SSA	14°06N 9°26E	April	Millet field, sandy soil
16a	Dilia valley, Lagane	NSA	14°54N 12°31E	April	Gramineous-covered sandy dune
16b	Dilia valley, Dugulé		15°01N 12°28E	Idem	Gramineous-covered sandy dune
17	Djado	MSA	21°03N 12°14E	January	Sandy soil
18a	Djirataoua, field	SSA	13°21N 7°08E	August	Millet and niebe field, sandy soil
18b	Djirataoua, Magia		idem	Idem	Irrigated area of the Magia river, clayey soil
19	Dogondoutchi	SSA	13°38N 4°02E	December	Millet field, sandy soil
20a	Fachi, gardens	SA	18°07N 11°35E	July	Huts, sandy soil
20b	Fachi, huts		Idem	Idem	Gardens, sandy soil
21	Gani	NSA	16°33N 7°08E	July	Nomad settlement, sandy-clayey soil
22	Garbey	NSA	14°51N 2°41E	February	Millet field
23	Gaya	SuA	11°52N 3°27E	?	?
24	Guidam Roumji	SSA	13°39N 6°41E	April	Millet field, sandy soil
25	Guidam Gajéré	NSA	14°17N 7°47E	May	Millet field, sandy soil
26	Guileyni	SuA	13°26 2°42E	March	Surroundings of well, sandy soil
27a	Gougaram, village	MSA	18°33N 7°47E	November	Surroundings of village, graveled soil, granit rocks
27b	Gougaram, sand		Idem	Idem	Sandy soil
28	Gouré	NSA	14°03N 10°13E	April	Millet field, sandy soil
29	Iférouâne valley	MSA	18°56N 8°15E	November	Bushy sandy plain
30a	I'n Jitane, site 1	SA	17°14N 7°07E	November	Sandy rounds inside a clayey plain
30b	I'n Jitane, site 2		17°12N 7°06E	Idem	Fine-graveled clayey plain with shrinkage cracks
30c	I'n Jitane, site 3		17°05N 7°27E	Idem	Granit rocks and sandy valley
31	Keita	SSA	14°46N 5°47E	November	Manioc field
32a	Koji Mairi, village	NSA	13°24N 11°05E	April	huts
32b	Koji Mairi, gardens		Idem	Idem	Depression, manioc field
33a	Kollo	SuA	13°21N 2°17E	All along the year	Fallow field, sandy soil
33b	Kollo, henhouse		Idem	May	henhouse
33c	Kollo, INRAN		13°22N 2°14E	November	Fallow field, sandy soil
34	Koré-Maïroua	SuA	13°15N 3°55E	April	Sandy soil
35a	La Tapoa, site 1	SuA	12°31N 2°25E	February	Savannah, clayey lowlands
35b	La Tapoa, site 2		12°29N 2°23E	Idem	Fine-gravelled plateau
35c	La Tapoa site 3		12°32N 2°19E	Idem	Millet field, sandy-clayey soil
36	Mayahi	SSA	13°55N 7°30E	May	Millet field, sandy soil
37a	N'guigmi, garden	NSA	14°15N 13°06E	April	Gardens, clayey soil
37b	N'guigmi, airport		14°15N 13°09E	Idem	Millet field, sandy soil
37c	N'guigmi, lake		14°11N 13°06E	Idem	Ridge of Lake Chad, sandy to sandy-clayey soils
38a	Niamey, houses	SSA	13°32N 2°06E	All along the year	Urban area
38b	Niamey, university		13°30N 2°06E	May, july, october	Urban area, fallow field
39a	Oleleoua, provisory pool	NSA	14°31N 8°36E	April	Edges of a dry waterhole, sandy-clayey soil
39b	Oleleoua, fallow land		Idem	Idem	Sandy and bushy soil

Annexe : Localities and sites of capture (continued)

40a	Ourou, gardens	MSA	19°10N 7°58E	November	Gardens, sandy-clayey soil
40b	Ourou, rocks		Idem	Idem	Surroundings of village, granit rocks
40c	Ourou, sand		Idem	Idem	Sandy soil
41	Sadoré	SuA	13°14N 2°17E	March	Fallow field, sandy soil
42	Soly	NSA	14°45N 7°30E	July	Millet field, sandy soil
43	Soumat	NSA	14°57N 2°43E	February	Millet fields, sandy soil
44a	Tamaya, site 1	NSA	15°45N 6°37E	July	Clayey-sandy soil and indurate sandy soil
44b	Tamaya, site 2		15°45N 6°39E	Idem	Sandy-clayey soil
45a	Tanout, field	NSA	14°57N 8°53E	August	Thorny millet field, sandy soil
45b	Tanout, millet store		idem	Idem	Stores in thorny millet field, sandy soil
46a	Tara, village	SuA	11°50N 3°20E	October	Huts
46b	Tara, rice cultures		idem	Idem	Irrigated rice cultures
46c	Tara, sand		Idem	Idem	Millet field, sandy soil
47	Tasker	NSA	15°04N 10°42E	October	Sandy soil
48a	Teguidda'n Tessoumt, site 1	SA	17°27N 6°42E	November	Granit rocks and sandy valley
48b	Teguidda'n Tessoumt, site 2		17°25N 6°47E	Idem	Fine-graveled and sandy-clayey plain
49	Tessaoua	SSA	13°45N 8°00E	August	Millet field, sandy soil
50a	Tera, field	SSA	14°N 0°14E	September	Millet field, sandy soil
50b	Tera, Foneko		14°16N 0°44E	Idem	Sandy soil
50c	Tera, Dingaba		14°02N 0°50E	Idem	Millet field, sandy soil
51a	Termit Dolé, sand	MSA	15°38N 11°31E	October	Sandy soil
51b	Termit Dolé, rocks		Idem	Idem	Rocky montains with small sandy areas
52	Tiraouène	SA	19°15N 6°14E	October	Non inhabited oasis, sandy soil
53	Tokaye	SuA	13°12N 2°21E	?	?
54a	Tondibia, granit pit	SSA	13°34'N 2°01'E	August	Millet fiels, next to a granitpit, sandy soil
54b	Tondibia, rice field		Idem	Idem	Next to rice fields, clayey soil
55a	Toukounous, village	SSA	14°30N 3°14E	September	Village surroundings, sandy soil
55b	Toukounous, dune		Idem	Idem	Sand dune
55c	Toukounous, ranch		Idem	Idem	Sandy soil, graminaceous dense-covered