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Morphology and chromosomes of *Tatera* Lataste 1882 (Rodentia Muridae Gerbillinae) in West Africa

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In a sample of the genus *Tatera* Lataste 1882 from West Africa (Benin and Burkina Faso), we analyzed the cranial and dental morphology and the karyotype (G, R, C and NOR banding). The cranial morphology confirms the attribution of this sample to *Tatera kempi* Wroughton 1906. An analysis of the dental morphology was also performed but it seems not to offer diagnostic traits. The karyotype described in the present work for *T. kempi* is comparable with that described for *T. hopkinsoni* Thomas 1911, supporting the synonymy of these two taxa. In contrast, the karyological results clearly discriminate *kempi* from both *guineae* and *nigrita*, the latter currently considered a synonym. In the karyotype of *T. kempi*, we found a polymorphism of a small chromosome, which occurs in the three situations: metacentric/metacentric, metacentric/acrocentric and acrocentric/acrocentric. A similar polymorphism was described for *hopkinsoni*. The banding shows that the variation of the morphology of the X chromosome in *Tatera* is related to a pericentric inversion.

KEY WORDS: *Tatera*, rodents, chromosomes, taxonomy, West Africa, evolution.

INTRODUCTION

The systematic status of the genus *Tatera* Lataste 1882 is currently very controversial. The taxonomy of the West African taxa (Senegal to Nigeria) is particular-

ly complex, with six species described, i.e. *T. valida* Bocage 1890, *T. gambiana* Thomas 1910, *T. kempi* Wroughton 1906, *T. hopkinsoni* Thomas 1911, *T. nigrita* Wroughton 1906, *T. guineae* Thomas 1910. Recently, Musser & Carleton (1993) considered *T. guineae*, *T. kempi* (syn. *hopkinsoni* and *gambiana*) and *T. valida* (syn. *nigrita*) to be valid species. However, on the basis of morphological traits, a preceding revision (Davis 1975) includes all the Western taxa, as synonyms, in a complex of species, the "valida" group, contrasting them to the more eastern species, combined in the "robusta" group.

Since the early 1970s, karyological studies have highlighted a complex situation.

In the present state of knowledge, it is more important to characterize the populations by means of the largest possible number of biological parameters (morphological, genetic, molecular, etc.) rather than to give a definitive taxonomic position to them. The latter must follow a complete revision of the genus.

In this study, we investigate the karyology of a sample of specimens, deriving from Benin and Burkina Faso, attributable to the "valida" group. We also study their cranial and dental morphology, since this is the basis of a preliminary classification.

MATERIAL AND METHODS

We examined 15 specimens (7 females and 8 males) of the genus *Tatera* Lataste 1882, one from Ouagadougou (Goden), Burkina Faso, and 14 from different sites in Benin (Table 1). All the specimens were used for the morphometric analysis and 12 of them were used for the cytogenetic analysis.

The specimens were divided into four age-classes (A, B, C, D) according to Beg et al. (1975) for *Tatera indica*, modified by Bates (1985). It is based on the degree of development of the supraorbital crests and the degree of dental wear.

Table 1.

Specimen code, sex, locality, latitude and longitude, and habitat.

Specimen	Sex	Locality	Latitude and Longitude	Habitat
B15	♂	Toffò, Benin	7°60'N – 2°07'E	Crops
B23	♂	Toffò, Benin	7°60'N – 2°07'E	Crops
B28	♀	Toffò, Benin	7°60'N – 2°07'E	Crops
B49	♀	Atcherigbè, Benin	7°03'N – 2°06'E	Forest
B50	♀	Settò, Benin	7°31'N – 2°06'E	Crops
B52	♀	Settò, Benin	7°31'N – 2°06'E	Crops
B68	♀	Atcherigbè, Benin	7°03'N – 2°06'E	Forest
B74	♂	Tanougou, Benin	11°20'N – 1°29'E	Fallow field
B75	♂	Tanougou, Benin	11°20'N – 1°29'E	Arid savanna
B79	♂	Tanougou, Benin	11°20'N – 1°29'E	Arid savanna
B81	♀	Tanougou, Benin	11°20'N – 1°29'E	Arid savanna
B87	♂	Settò, Benin	7°31'N – 2°06'E	Crops
B93	♂	Settò, Benin	7°31'N – 2°06'E	Crops
B94	♀	Settò, Benin	7°31'N – 2°06'E	Crops
BKF7	♂	Goden, Burkina Faso	12°26'N – 1°22'W	Arid savanna

The morphology of the first lamina of M_1 was also considered a trait that exhibits marked variability and is considered a useful diagnostic character (BATES 1988).

We measured some cranial dimensions on each animal: Greatest skull length (GSL), Condylobasal length (CBL), Nasal length (NL), Interorbital constriction (IC), Zygomatic width (ZW), Greatest skull width (GSW), Maxillary cheek teeth row length (MCL), Tympanic bulla length (TBL), Diastema length (DL). The values obtained were compared with those in the literature for *T. nigrita* (TRANIER 1974). The significance of the differences was tested statistically (Table 3).

The material is preserved in the Collection of Rodents of the Museum of Comparative Anatomy "B. Grassi", University of Rome "La Sapienza".

The study of the karyotypes was performed on somatic metaphases prepared from brief cultures of bone marrow cells, according to the standard procedure of HSU & PATTON (1969), and from cultures of fibroblasts obtained from cutaneous biopsy performed on the ear of the anesthetized animals (STANYON & GALLENI 1991) and treated with an antimitotic in vitro. The slides were prepared with the common techniques of air-drying (MOORHEAD et al. 1960). The meiotic preparations were obtained from the testicles following the standard procedure of EVANS et al. (1964). The nucleolar organizer regions (NOR) were revealed by the silver impregnation technique (HOWELL & BLACK 1980). G bands were obtained with the method of SEABRIGHT (1971), slightly modified; C banding was according to BICKHAM (1979). The R banding was obtained with the BSG (basic-saline-giemsa) method (KANDA 1976), modified in the scan times and temperature. The figures obtained with the latter method were used for comparison with the R-banding karyotypes of *T. nigrita* and *T. guineae* (BENAZZOU et al. 1984). For staining with Chromomycin A_3 (CMA_3), we used the protocols of FERRARO & LAVIA (1983) and SCHWEIZER (1980), slightly modified.

The diploid number (2n) and the number of autosomal arms (AFN) were determined on photographic enlargements (2000 ×) of at least 20 metaphases per animal.

RESULTS

Morphological characterization of the sample

The values of the cranial measures for the specimens of *T. kempi*, arranged per age-class (A = elderly individuals to D = very young individuals), are reported in Table 2. The traits that reach their maximal development at an early age (IC, MCL, TBL) have more constant values, even in particularly young specimens (class D). The values of these traits and of GSL were compared with the values of the same traits in the three groups of the population of *T. nigrita* (TRANIER 1974) from Chad, characterized by a chromosomal polymorphism on the X chromosome (Table 3).

Only the maxillary cheek teeth row length is significantly greater in *T. kempi* than in the three groups of *T. nigrita* (Student's t test, $P < 0.01$). There are no significant differences among the groups for IC and TBL, while GSL is significantly different only in the *T. nigrita* group from Bekao (Table 3).

Examination of the morphology of the first lamina of M_1 reveals that 6 of the 15 specimens show a clear opening facing posteriorly, 7 have no opening and 2 have an opening facing anteriorly (Fig. 1). The various morphologies do not seem to be related to age or to the karyotype of the specimens. This character has been used by BATES (1988) as a diagnostic trait to distinguish two subspecies of *Tatera valida*: *T. v. valida* and *T. v. kempi*. However, this is not confirmed by the specimens examined in the present study.

Table 2.

Cranial measurements (mm).

Specimen	Age Class	CBL	GSL	DL	NL	MCL	TBL	GSW	ZB	IC
B15	A	38.5	41.5	12	17	6.5	11	16.5	21	8
B93	A	40	42	12	17	7	11	16	21	7
B50	B	39.5	42.5	12	17.5	6.5	11	16.5		6.5
B68	B	38.5	41	12	17	7	11.5	16	20.5	6
B28	C	30.5	33	9	12	6.5	9.5	16		6.5
B49	C	34	37	10	15	7	10	16	18.5	6
B74	C	33	36	9.5	13.5	7	10	16	19	6
B75	C	32.5	35	8	13.5	7	9.5	15		6
B79	C	35.5	38.5	10	15	6.5	11	16	19	7
B81	C	33	36	9.5	14	6.5	10	15	18	6
B87	C	37	39	10.5	16	7	10.5	15.5	21	7
B94	C	34.5	36.5	10	15	7	10.5	16	19	6.5
BKF7	C	36	38.5	10.5	15	6.5	11	16	20	6.5
B23	D	28	30.5	8	12.5	7	9	13.5		6
B52	D	34	36.5	10	14.5	6.5	10.5	15		6

GSL = Greatest skull length, CBL = Condylobasal length, NL = Nasal length, IC = Interorbital constriction, ZW = Zigomatic width, GSW = Greatest Skull width, MCL = Maxillary cheek teeth row length, TBL = Tympanic Bulla length, DL = Diastema length.

Table 3.

Mean ± standard deviation of some cranial measurements (mm) of *T. kempi* and *T. nigrita* from Chad (Tranier 1974) and significant differences in skull measurements between samples (Student's t test).

	T. kempi Present paper X acrocentric	*T. nigrita* (A) Moundou X biarmed	*T. nigrita* (B) Moundou X acrocentric	*T. nigrita* (C) Bekao X acrocentric	*T. kempi* vs *T. nigrita* (A)	*T. kempi* vs *T. nigrita* (B)	*T. kempi* vs *T. nigrita* (C)
GSL	37.6 ± 3.38	39.73 ± 1.37	40.18 ± 2.01	40.87 ± 1.44	$P < 0.05$	$P < 0.05$	$P < 0.01$
IC	6.47 ± 0.58	6.76 ± 0.33	6.89 ± 0.41	6.68 ± 0.10	$P > 0.05$	$P < 0.05$	$P > 0.05$
MCL	6.77 ± 0.26	6.25 ± 0.04	6.29 ± 0.31	6.30 ± 0.35	$P < 0.01$	$P < 0.01$	$P < 0.01$
TBL	10.40 ± 0.71	10.76 ± 0.59	10.72 ± 0.42	10.89 ± 0.33	$P > 0.05$	$P > 0.05$	$P < 0.05$

GSL = Greatest skull length, IC = Interorbital constriction, MCL = Maxillary cheek teeth row length, TBL = Tympanic Bulla length.

Cytogenetic characterization of the sample

All the specimens of *Tatera* examined present 2n = 48, while the AFN varies from 62 to 64 (Fig. 2, Table 4). A preliminary report on Benin specimens was presented by our group (Codjia et al. 1994). The most commonly observed karyotype is composed of 9 pairs of biarmed chromosomes and 14 pairs of acrocentrics (AFN = 64). The X chromosome is acrocentric and is the largest of all; the Y chromosome is of medium size, submetacentric and barely distinguishable from the metacentric autosomes of equal size. The characterization by R and G banding allows a precise

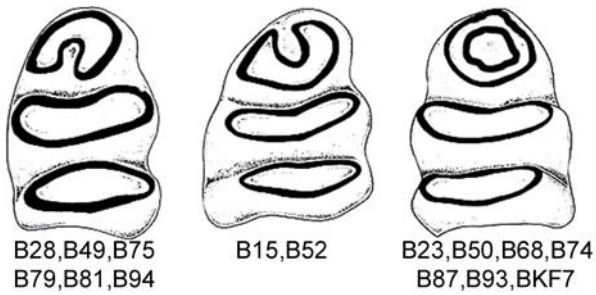

Fig. 1. — Morphology of first lamina of M_1.

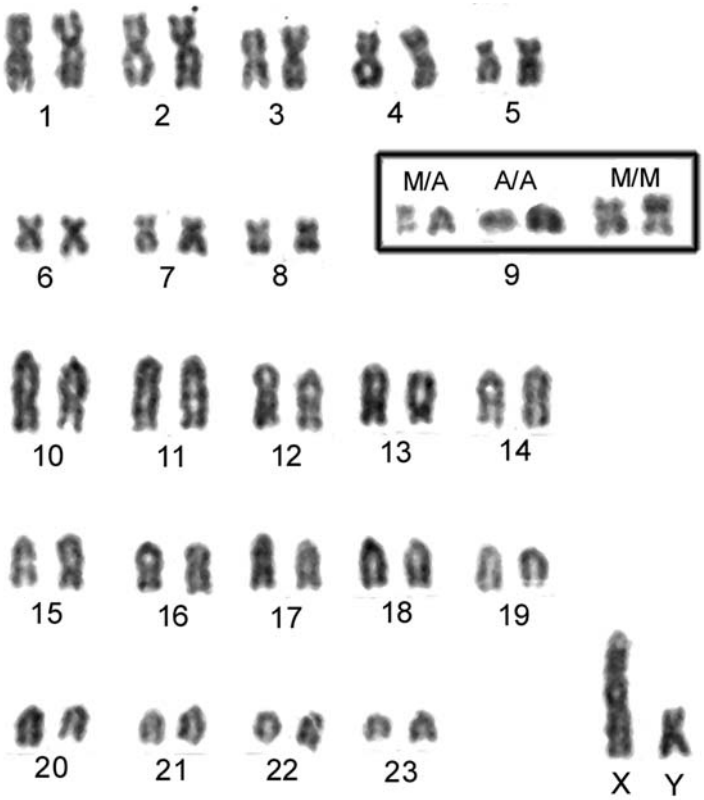

Fig. 2. — Karyotype of *T. kempi*, 2n = 48 (♂) from Settò (Benin). In the box the three polymorphic variants (M/A = metacentric/acrocentric, A/A = acrocentric/acrocentric, M/M = metacentric/metacentric.

identification of the largest chromosomes (Fig. 3). In the meiotic diakineses, it is possible to observe 23 bivalents, corresponding to the autosomes, and one bivalent sexual that frequently appears precociously disjunct.

Table 4.

Fundamental number (AFN) variability observed in the 12 specimens analysed.

Specimens	2n	no. Biarmeds	no. Acrocentrics	AFN	X	Y
B15	48	18	28	64	A	SM
B23	48	17	29	63	A	SM
B28	48	18	28	64	A	—
B50	48	16	30	62	A	—
B52	48	16	30	62	A	—
B68	48	16	30	62	A	—
B79	48	18	28	64	A	SM
B81	48	17	29	63	A	—
B87	48	18	28	64	A	SM
B93	48	18	28	64	A	SM
B94	48	18	28	64	A	—
BKF7	48	18	28	64	A	SM

A = acrocentric, SM = submetacentric.

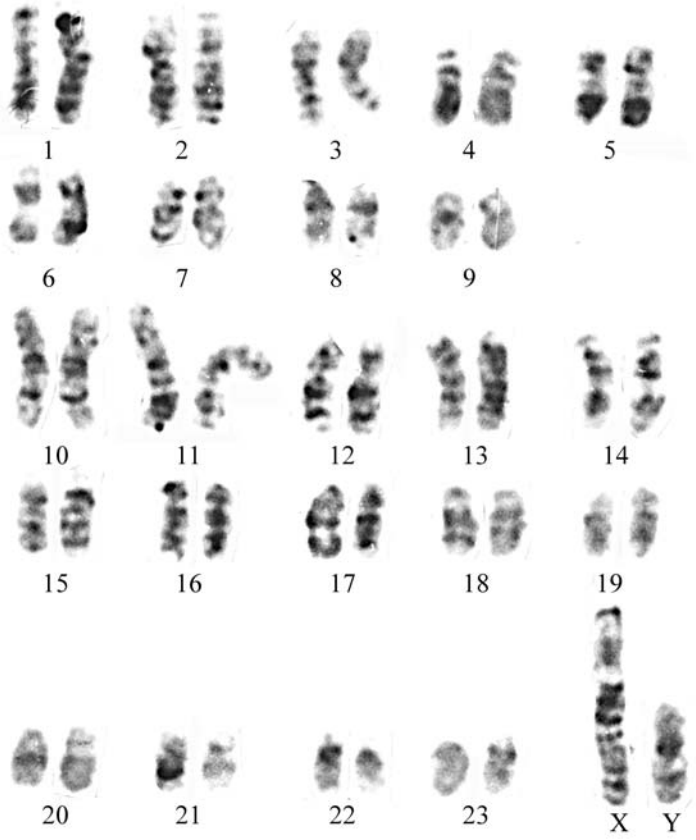

Fig. 3. — G banded karyotype of *T. kempi* (♂) from Settò (Benin).

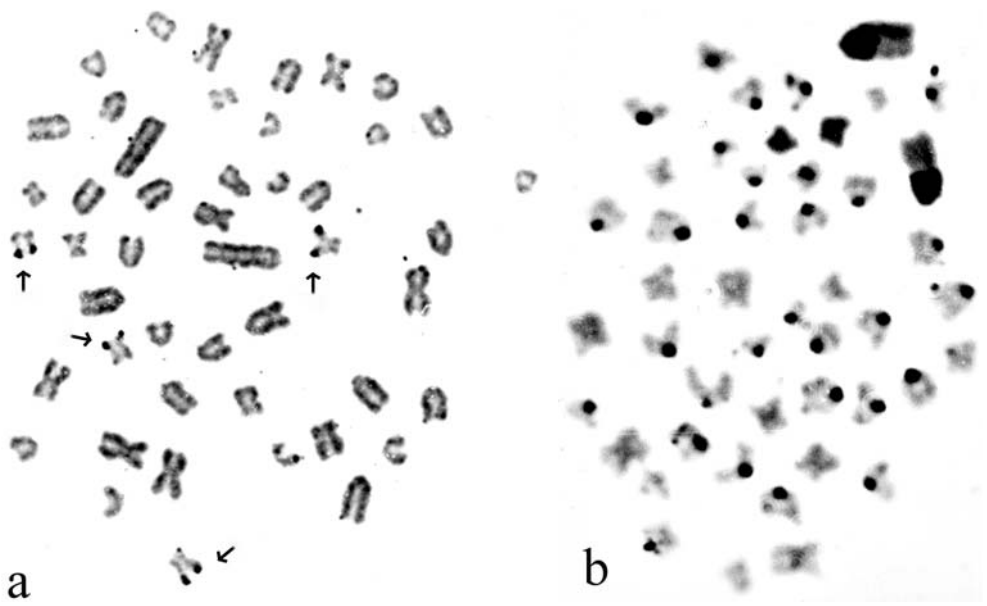

Fig. 4. — (a) NOR of *T. kempi*; (b) C bands of *T. kempi*.

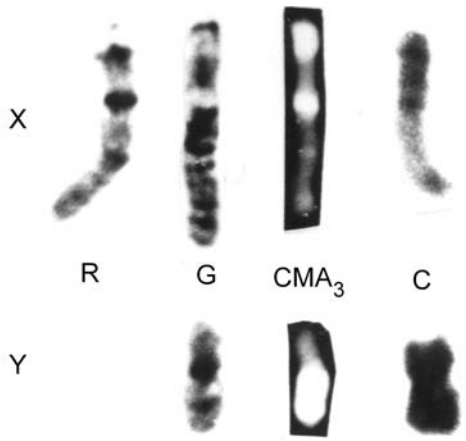

Fig. 5. — Heterochromosomes of *T. kempi* after R, G, C and CMA_3 banding.

There is a polymorphism of the smallest pair of biarmed chromosomes (no. 9). Of the 12 animals examined, three present the acrocentric/acrocentric situation (AFN = 62) and two present the acrocentric/metacentric structural heterozygote situation (AFN = 63).

The maximum number of contemporaneously active NOR is four in all animals. The nucleolar regions (Fig. 4a) are located in a telomeric position on two pairs of small metacentric chromosomes in all the specimens.

C banding (Fig. 4b) reveals regions of constitutive heterochromatin particularly evident at the centromere of all the acrocentric chromosomes, while most of the biarmed chromosomes do not present C-positive bands. In the meiotic figures, one can clearly observe only one completely heterochromatic bivalent in preparations treated with barium hydroxide.

The X chromosome (Fig. 5) shows a broad heterochromatic band in the pericentromeric region, which extends for about 1/3 of the entire chromosome. After R banding and CMA_3 staining, the same region presents two large, very intense bands, while the distal region shows a series of small bands of weak intensity. G banding reveals instead a series of bands that extend for the whole chromosome and, in the proximal region, in correspondence to the R-negative bands.

The Y chromosome (Fig. 5) has a submetacentric morphology and is entirely C-positive. The CMA_3 staining highlights an intense band on the long arm. After treatment with trypsin, the Y chromosome shows an intense G band at the centromere and a thinner band on the long arm.

DISCUSSION

Chromosomes and taxonomy

According to morphometry, this West African sample is assigned to the valida group. However, the attribution to one species presents difficulties due mainly to the facility with which new species and synonymies have been assigned in the past on the basis of inconclusive traits. On the basis of metric traits, it seems possible to attribute these animals provisionally to *Tatera kempi*, in anticipation of future research that will provide new karyological and molecular data useful for an understanding of the complex genetic structure of the rodent populations in this area of Africa.

The karyological comparison with the published data for other species of the West African valida group indicates a close cytotaxonomic affinity, due to a high number of conserved chromosomes. However, it also shows that the genomes of the samples of *Tatera* have undergone a series of complex rearrangements. Some of these could potentially have given rise to new cryptic species, while others have been assimilated and conserved in the populations, determining intraspecific polymorphisms. All of this can cause great confusion with regard to taxonomic attributions.

We made a precise comparison of the R banding pattern of our sample with those of both a sample of *T. nigrita* from the Central African Republic (2n = 48, AFN = 62) with a submetacentric X chromosome and a sample of *T. guineae* from Burkina Faso (2n = 50, AFN = 64) (Benazzou et al. 1984). There is an evident banding homology for 14 pairs of autosomes (Fig. 6), which represents a marked karyological symplesiomorphy. For other chromosomes, these correspondences are not evident because of the chromosomal transformations that characterize each karyotype. Greater correspondences are observed between the autosomes of *T. kempi* and *T. nigrita* than between those of *T. kempi* and *T. guineae*.

The X chromosome is acrocentric in *T. kempi* and submetacentric in *T. nigrita* from Central African Republic. Analysis of the banding pattern shows that a pericentric inversion is responsible for this change. In fact, the long arm of the submetacentric X chromosome of *T. nigrita* corresponds to the distal 2/3 of the acrocentric X chromosome of *T. kempi*, while the remaining 1/3 corresponds to the

short arm of the X chromosome of *T. nigrita*. The large submetacentric X chromosome of *T. guineae* shows an entire heterochromatic arm strongly stained with R bands. The differences from the X chromosome of *T. kempi* are evident and it is not easy to identify homologous regions.

The Y chromosome of *T. nigrita* is a small submetacentric, while that of *T. kempi* is a medium-sized submetacentric. The R banding patterns are not comparable.

These results tend to highlight a clear difference between *nigrita* and *kempi*, once believed to be valid synonyms. For now, we can only support the proposed elevation of *T. kempi* to the rank of species in the valida group (MUSSER & CARLETON 1993). It remains to be clarified whether the karyotype described for *T. nigrita* can also be attributed to other forms of *T. valida*, i.e. *beniensis*, *benvenuta*, *liodon*, *taborae*, etc., in which case it would constitute the fundamental karyotype of this species.

Polymorphism in T. kempi

The diploid number (2n = 46) of a sample from Guinea (GAUTUN et al. 1986), attributed to *T. kempi* but reported without other information about the karyotype, can be seen as the result of processes of Robertsonian speciation, which are well known in other rodents. However, the observation of a varying diploid number is not exceptional in the genus *Tatera*; in a sample of *T. nigrita* from Chad (TRANIER 1974), the number of chromosomes varied from 48 to 50.

The variability in the ratio of acrocentric and metacentric chromosomes does not seem to be related to the different geographical origins of the *T. kempi* samples studied. It is probably due to non-Robertsonian chromosomal rearrangements, which are rather common in heterochromatic chromosomal regions. This variability in *T.*

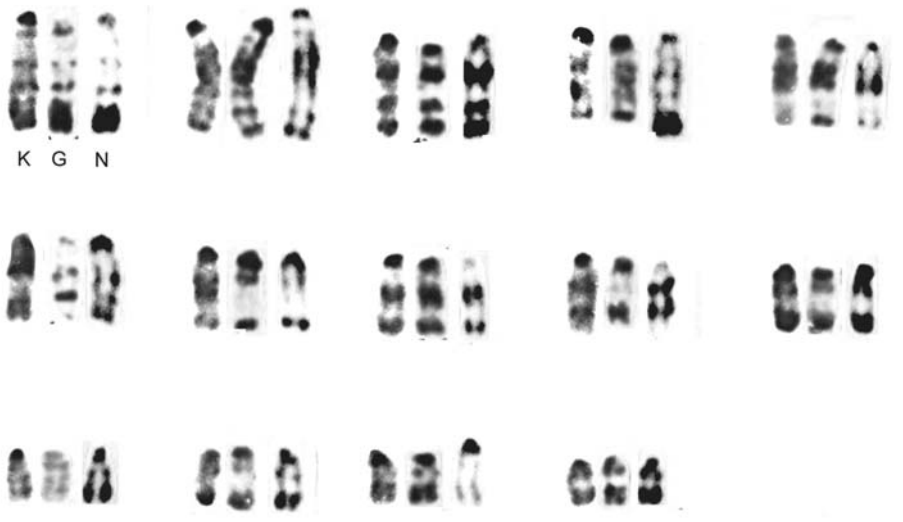

Fig. 6. — Homologous chromosomes (R banding): *T. kempi* at left (K), *T. guineae* (BENAZZOU et al. 1984) at center (G) and *T. nigrita* (BENAZZOU et al. 1984) at right (N).

kempi is determined by the polymorphism of a pair of autosomes, probably the one that appears entirely C-positive in the karyotype and in the meiotic figures, which presents a biarmed morphology and can be either homozygous or heterozygous.

The karyotype observed in our sample of *T. kempi* is morphologically very similar to that described by MATTHEY & PETTER (1970) for a sample of *T. hopkinsoni* (2n = 48, AFN = 62-64) from Burkina Faso. Indeed, the animals attributed to *T. hopkinsoni* show the same chromosomal number as our samples from Benin and the same acrocentric morphology of the X chromosome. Moreover, in *T. hopkinsoni*, there is the same variability in the number of biarmed chromosomes as in *T. kempi*. However, the morphology of the Y heterochromosome is very different: in our animals it is submetacentric, while in *T. hopkinsoni* it appears acrocentric. In all previous systematic revisions, *T. hopkinsoni* has been placed in synonymy with *T. kempi*, both when *kempi* was considered a good species (MUSSER & CARLETON 1993) and when it was considered synonymous with (DAVIS 1975) or a subspecies of *T. valida* (BATES 1988). Our results confirm this attribution.

Morphology of the X chromosome in Tatera

Another point that deserves thorough discussion is the presence of an acrocentric X chromosome in *T. kempi*. In fact, in almost all species of the genus *Tatera*, and in species of other genera of Gerbillinae, the X heterochromosome appears biarmed, while only *T. hopkinsoni* and two subpopulations of *T. nigrita* from Chad show an acrocentric X (TRANIER 1974).

The comparison with the data in the literature lead us to hypothesize, in agreement with TRANIER (1974), that a pericentric inversion, probably followed by other mechanisms of chromosomal transformation, is the basis of the transformations of the X chromosome of *Tatera*. Other authors (MATTHEY & JOTTERAND 1972, WASSIF 1977, VIEGAS-PÉQUIGNOT et al. 1982) have shown that, in the Gerbillinae, the X chromosome has undergone a series of complex transformations following inversions, translocations, fusions and, perhaps, centromeric inactivations.

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