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Cytogenetics of a new cytotype of African *Mus* (subgenus *Nannomys*) *minutoides* (Rodentia, Muridae) from Kenya: C- and G- banding and distribution of $(TTAGGG)_n$ telomeric sequences

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Abstract

We present the results of a cytogenetic study on *Mus* (*Nannomys*) *minutoides* from Kenya by means of C- and G-banding and *in-situ* fluorescence hybridization (FISH) to localize the telomeric sequences. The karyotype is characterized by the occurrence of several Rb chromosomes Rb(1.X), Rb(1.Y). Rb(2.17), Rb(3.13), Rb(4.10), Rb(5.11), Rb(6.7), Rb(8.12), the last five not yet described for this species. This finding suggests a high level of chromosomal diversification, which means it is possible to consider this cytotype as a new, well-differentiated, chromosomal lineage within the subgenus. The C-banding of the metaphases illustrated conspicuous blocks of centromeric heterochromatin at the paracentromeric regions of all telocentric chromosomes. Centromeric heterochromatin is not visible on all biarmed chromosomes. Following hybridization with telomeric probes, bright interstitial telomeric sequence (ITS) fluorescence signals are evident at the pericentromeric area of all Rb chromosomes, with the exception of Rb(2.17). Considering the localization of the C-positive heterochromatin and of the telomeric sequences, the events leading to the Kenyan cytotype from an all-telocentric condition probably included two steps: first, fusion without loss of heterochromatin and pericentromeric telomeric sequences; second, the reduction of the C-positive satellite DNA followed by the amplification of telomeric sequences in the C-negative paracentromeric region of Rb chromosomes. The presence of a single Rb(2.17) without ITS indicates possible variations of this mechanism.

Introduction

The African pygmy mice, subgenus *Nannomys* Peters, 1876 (subgenus *Mus*) constitute a species assemblage occurring in a wide range of terrestrial habitats throughout sub-Saharan Africa (Musser & Carleton 2006). The subgenus is the most speciose within the genus *Mus*, comprising 18 recognized species according to the latest checklist (Musser & Carleton 2006). However, recent analyses based on the sequence of the mitochondrial cytochrome *b* gene and on the karyotype suggested an even higher diversity (Castiglia *et al.* 2002, Veyrunes *et al.* 2004, 2005).

The role and the evolutionary importance of chromosomal polymorphism in *Nannomys* was first

shown by Matthey (1966, 1970), who revealed by means of standard staining techniques extensive karyotype variation within and among species. The successive development of banding techniques (i.e. G- and C-) made it possible to identify chromosomal rearrangements showing the occurrence of complex patterns of karyotype evolution. Chromosomal mutations include Robertsonian (Rb) translocations between autosomes Rb(a.a) or between autosomes and sex chromosomes Rb(X.a) and Rb(Y.a), tandem fusions, pericentric inversions, heterochromatin addition–deletions and deletions of parts or of the entire X chromosome (Jotterand-Bellomo 1984, 1986, Aniskin *et al.* 1998, Castiglia *et al.* 2002, Veyrunes *et al.* 2004).

Sex chromosome–autosome translocations are of particular interest in *Nannomys* because this kind of rearrangement is uncommon in other mammal lineages, probably because they are highly deleterious when in a heterozygous condition (Ashley 2002). Thus, this kind of fusion constitutes a reliable phylogenetic marker to detect common ancestry (Veyrunes *et al.* 2004, 2005).

Within *Nannomys*, four different karyotype lineages have been identified, each one characterized by different autosomes fused with sex chromosomes. These four lineages correspond to the following four different species: *M. minutoides* Smith, 1834, with Rb(X.1) and Rb(Y.1); *M. musculoides* Temminck, 1853, with Rb(X.7) and Rb(Y.7); *M. oubanguii* Petter and Genest, 1970, with Rb(X.15) and Rb(Y.15); *M. triton* (Thomas, 1909), with Rb(X.12) and Rb(Y.12).

M. minutoides is one of the most widespread species and the Rb(X.1) and Rb(Y.1) fusions have been found in South Africa, Central African Republic, Ivory Coast, and Zambia (Jotterand-Bellomo 1986, Castiglia *et al.* 2002, Veyrunes *et al.* 2004). There is also a further karyotypic differentiation in this lineage, resulting in the occurrence of six different cytotypes characterized by different autosome–autosome fusions (Table 1). The number and distinctiveness of the different Rb fusions varies, with only one fusion found in the Central African Republic and Ivory Coast, and up to eight fusions found in South Africa.

The high number and variety of chromosomal rearrangements found in *Nannomys* represent a good animal model to study genomic structural changes at a molecular level. Telomeric sequences are predominantly found at the physical ends of vertebrate chromosomes. Therefore, they can represent an appropriate tool to reconstruct the path of karyotypic rearrangements involving chromosomal ends during evolution, as for example for Rb translocation (e.g. *M. m. domesticus*, Garagna *et al.* 1995; *Sorex araneus*, Zhdanova *et al.* 2005) and tandem fusions (e.g. *Taterillus* sp., Dobigny *et al.* 2003). Telomeric sequences also occur at non-telomeric sites, known as interstitial telomeric sites (ITS). The most common ITS occur at the pericentric region of chromosomes (Meyne *et al.* 1990, Garagna *et al.* 1997, Metcalfe *et al.* 1998). In *M. minutoides* from Zambia we found ITS in metacentric chromosomes that may represent remnants of telomeric sequences retained near the centromere of Rb metacentrics (Castiglia *et al.* 2002). However, in other well-known cases, telomeric sequences are not retained at the centromeres after Rb fusion, as in *Mus musculus domesticus* (Garagna *et al.* 1995, Nanda *et al.* 1995) and in *Suncus murinus* (Rogatcheva *et al.* 2000).

In this paper we present the results of a cytogenetic study of specimens of *M. minutoides* from Kenya by means of C- and G- banding and of *in-situ* fluorescence hybridization (FISH) to locate the telomeric sequences along the chromosomal arm. We found that the karyotype of these specimens is characterized by Rb rearrangements not previously described for this species. Therefore, they indicate a further diversified karyotype lineage. Furthermore, these new Rb chromosomes show telomeric sequences localised at the pericentromeric regions.

Materials and methods

Three males were collected from two localities in Kenya, i.e. Nairobi (01°16′ S–36°49′ E) and Rongai (00°10′ S–35°51′ E), both in a mosaic of East African evergreen bushland and secondary *Acacia* wooded grassland (Figure 1). Specimens were live-trapped and transported to the Kenyatta University (Nairobi) for karyotyping. Chromosome preparations were obtained from bone marrow following Hsu & Patton (1969).

Fixed cell suspensions were then transported to the University of Rome where slides were prepared according to the standard air-drying technique. G-bands were produced with trypsin following the protocol of Seabright (1971). The identification of chromosomes was made according to the standardi-

Table 1. List of the known Robertsonian translocations found in *Mus minutoides*, and geographic origin. In all these cytotypes the sex chromosomes are fused with autosome pair number 1

	Robertsonian fusion												
Locality	2	3	4	5	6	8	9	10	11	12	13	15	Reference
Calendon Reserve (RSA)	2.10	3.9	4.7	5.8	6.11				14.15	12.17	13.16		Veyrunes *et al.* (2004)
Stellenbosch (RSA)	2.13	3.9	4.7	5.8	6.11			10.14		12.17		15.16	Veyrunes *et al.* (2004)
Kuruman (RSA)													Veyrunes *et al.* (2004)
Mutanda, Solwezi (Zambia)	2.7	3.12	4.5		6.8		9.16*						Castiglia *et al.* (2002)
Ivory Coast	2.17*												Jotterand-Bellomo (1986)
Central African Republic		3.7											Jotterand-Bellomo (1986)
Rongai, Nairobi (Kenya)	2.17	3.13	4.10	5.11	6.7	8.12							Present data

*Indicates Rb fusions occurring in polymorphic condition.

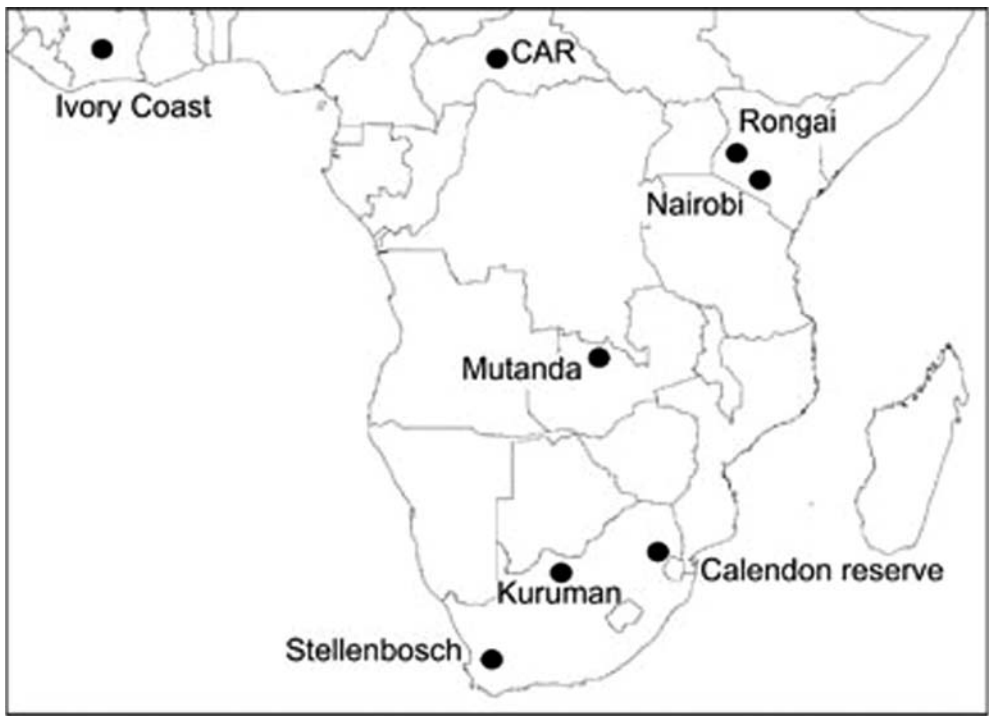

Figure 1. Map of Africa with the locations of the *M. minutoides* cytotypes investigated so far (see Table 1 for the description of the cytotypes in the different localities).

zation proposed by Jotterand-Bellomo (1986). The heterochromatic portion of the genome was identified by C-banding using 5% barium hydroxide (Sumner 1972). Metaphases were acquired using a Photometrics Sensys 1400 digital camera.

FISH was performed using an FITC-labeled $(C_3TA_2)_3$ peptide nucleic acid (PNA) probe (PerSpective Biosystems, USA) following Lansdorp *et al.* (1996). Slides were examined with an Olympus Provis fluorescence microscope and separated FITC-TRITC images were taken with a Photometrics CH-350/A camera controlled by IP Lab (Scananalytics, Inc.) and merged using IP Lab and ADOBE Photoshop softwares.

In order to evaluate the extent of the telomeric signals at different chromosomal localizations, four well-spread metaphases were analyzed with IMAGEJ 1.35S software. The areas of the telomeric sequences for each chromosome were calculated as a percentage of the entire area of each metaphase.

Specimens are stored at the Museo di Anatomia Comparata, Università di Roma 'La Sapienza' (Rongai: KE106; Nairobi: KE111, KE144).

Results

All the specimens shared the same chromosomal complement, i.e. 2n = 22 and FN = 36 (Fundamental Number) (Figure 2). The karyotype includes seven pairs of biarmed chromosomes and four pairs of telocentric chromosomes. The sex chromosomes are fused with the autosomal pair number 1, i.e. Rb(1.X), Rb(1.Y). The six pairs of metacentric autosomes were identified by G-banding as follows: Rb(2.17), Rb(3.13), Rb(4.10), Rb(5.11), Rb(6.7), Rb(8.12) (Figure 2a; Table 1).

The C-banding analysis of the metaphases shows the occurrence of conspicuous blocks of centromeric heterochromatin at the paracentromeric regions of all telocentric chromosomes. There is further occurrence of a heterochromatic short arm in one large submetacentric, i.e. Rb(Y.1). This arm corresponds to the Y chromosome (Castiglia *et al.* 2002, Veyrunes *et al.* 2004). Centromeric heterochromatin is not visible on all biarmed chromosomes (Figure 2b).

Hybridization with telomeric probes showed, as expected, signals at the telomeric ends of each

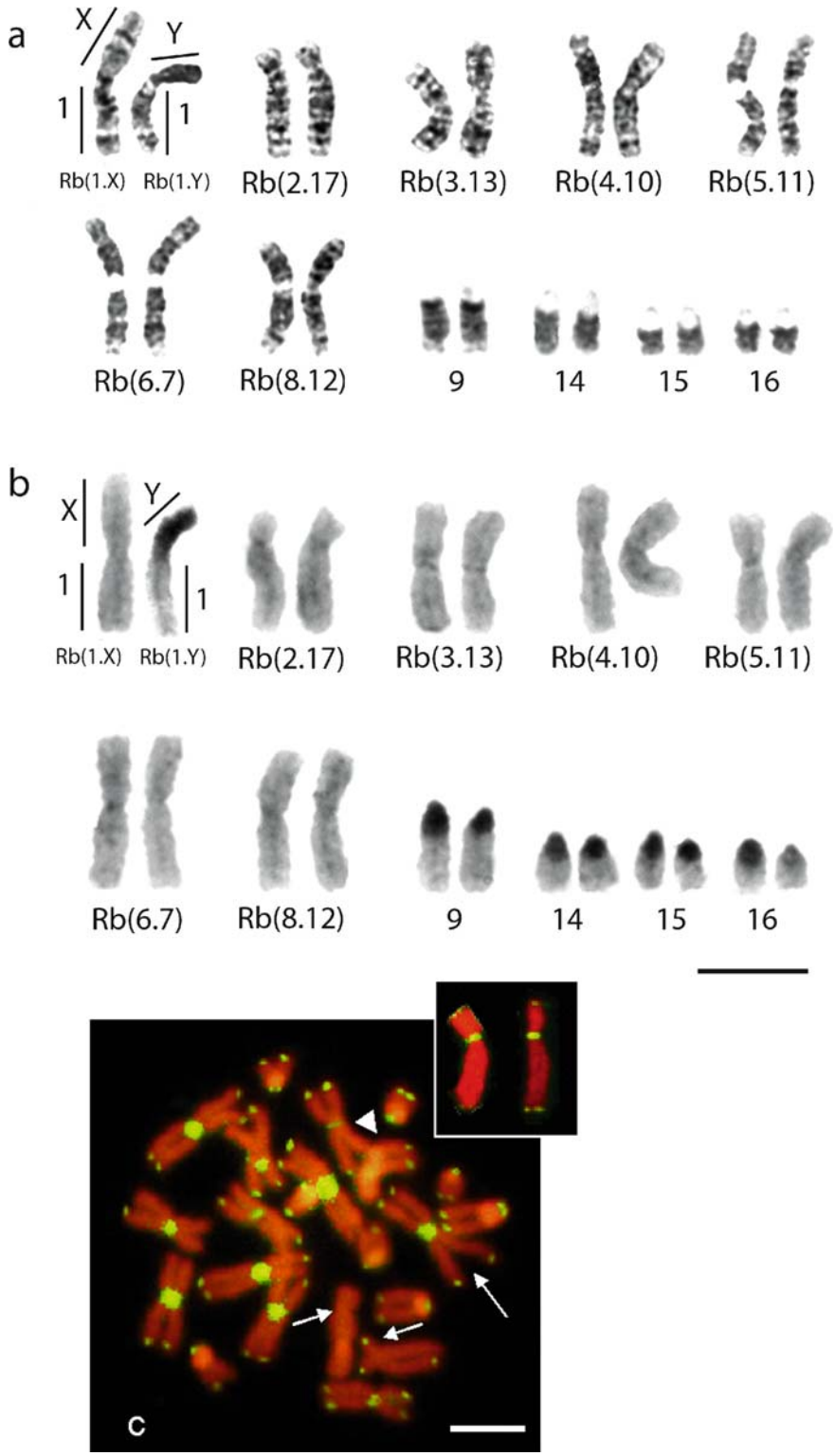

Figure 2. The karyotype of a male *M. minutoides* from Rongai (Kenya). (**a**) G-banding; numbers indicate chromosomal arms according to Jotterand-Bellomo (1986); (**b**) C-banding; (**c**) *in-situ* hybridization with the $(TTAGGG)_n$ probe; arrows indicate the absence of telomeric sequences at the centromeres of the two Rb(2.17). Arrowhead indicates Rb(Y.1). Long arrow indicates the Rb(X.1). In the box two Rb(Y.1) from different plates are shown (scale bars = 10 μm).

chromosome (Figure 2c). Telomeric sequences clearly do not occur in the large blocks of paracentromeric heterochromatin of telocentric chromosomes. Bright ITS fluorescence signals occur at the pericentromeric region of all metacentric chromosomes of *M. minutoides*, with the exception of Rb(2.17), which does not show any hybridization signal. Rb(2.17) chromosomes are identifiable because they are the only submetacentrics present in the karyotype (Figure 2a,b) which do not show any ITS (Figure 2c). ITS fluorescence signals are also visible at the centromeres of Rb(1.Y) (identifiable as the only unpaired submetacentric chromosomes with ITS) and Rb(1.X) (identifiable as the largest chromosome of the complement) (Figure 2c).

The measurement of the telomeric and ITS hybridization signals showed no differences between proximal (mean 1.7% of the total area, range 0.8–3.2%) and distal (mean 1.2%, range 0.6–2.1%) telomeres of telocentric and metacentric (mean 1.5%, range 0.5–2.5%) chromosomes. In Rb(1.Y) and in four of the Rb autosomes the area of the ITS is about 50% more (mean 2.3%, range 1.3–3.4%) than that of the telomeres whereas in the other six Rb autosomes and in the Rb(1.X) it is about four times (mean 6.2%; range 4.0–9.9%).

Discussion

On the basis of the characteristic Rb sex chromosomes, the specimens have been ascribed to the *M. minutoides* lineage, according to Veyrunes *et al.* (2004). Out of the six autosomal fusions found in this cytotype, five have never been described for *N. minutoides* (Table 1). Rb(2.17) was previously found in a polymorphic condition in specimens of *M. minutoides* from the Ivory Coast (Jotterand-Bellomo 1986); Rb(4.10) was found in *M. oubanguii*, a species from the Central African Republic (Jotterand-Bellomo 1986).

The occurrence of large blocks of heterochromatin in the telocentrics contrasts with their absence in the metacentrics. A similar pattern is also present in the specimens from Zambia, but the heterochromatic blocks present in the telocentrics were smaller (Castiglia *et al.* 2002). Large heterochromatic pericentromeric regions have also previously been reported in *M. setulosus* Peters, 1876 (Jotterand-Bellomo 1984) and *M. mahomet* Rhoads, 1896 (Aniskin *et al.* 1998); these species have an 'all-telocentric' karyotype and therefore may represent the ancestral chromosomal condition for the entire subgenus.

Considering the localization of the C-positive heterochromatin and of the telomeric sequences, the sequence of events in chromosomal rearrangement from an 'all-telocentric' condition to the Kenyan karyotype may have included the maintenance of heterochromatin after fusion and a subsequent reduction of the C-positive satellite DNA in the metacentric chromosomes. This scenario agrees with the hypothesis of telomeric sequence maintenance after Rb fusion followed by their amplification in C-negative paracentromeric regions. In fact, all but one of the metacentric chromosomes of *M. minutoides* show ITS fluorescence signals at the pericentromeric regions.

The occurrence of Rb(2.17) without ITS is worthy of note. Two hypotheses regarding this aspect can be formulated: first, a loss of telomeric sequences during Rb fusion, as observed in *M. m. domesticus* (Garagna *et al.* 1995, Nanda *et al.* 1995); second, and alternatively, a loss or modification of ITS through time, after the fusion event. However, the fact that Rb(2.17) is the only Rb shared by two localities of *M. minutoides* (out of a total of seven populations sampled) (Table 1) would support the latter hypothesis. It could be hypothesized that this chromosome represents an ancient fusion, retained in the two populations, in which the amount of ITS was reduced over time.

The loss of telomeric sequences at the centromere of 'old' Rb chromosome has been recently suggested in *Sorex araneus*. In this species, fewer signals occur at the centromeres of those metacentrics that were formed earlier during the evolution of the species, while paracentromeric ITS are present in the metacentrics of a more recent origin (Zhdanova *et al.* 2005).

The expansion of telomeric sequences at ITS of several different Rb chromosomes in *M. minutoides* suggested the occurrence of concerted evolution (for a review see Liao 1999). This amplification can be due to the absence of those well-known functional constraints that act on the functional telomeres (Fajkus *et al.* 2005). A similar pattern of amplification of paracentromeric ITS in metacentric chromosomes has also been found in *Micouerous demerare* (Pagnozzi *et al.* 2000) and in species of the genus

Eulemur (Garagna *et al.* 1997). In all these cases ITS colocalize with the C-positive heterochromatin. A peculiar characteristic of *M. minutoides* is that different degrees of amplification of ITS have been found in the two different chromosomal cytotypes typed for telomeric sequences so far (Castiglia *et al.* 2002 and present study). Moreover, ITS do not colocalize with the C-positive heterochromatin. A finer characterization of paracentromeric areas in different cytotypes of *M. minutoides* will help to understand if a relationship exists between the molecular structure of paracentromeric areas of telocentric chromosomes and the differential amplification of the ITS sequences in Rb metacentric chromosomes.

A peculiar feature of the Rb fusions identified in the pygmy mice is represented by the occurrence of four different X-autosome Rb fusions (see Introduction). Such rearrangements are known for their highly deleterious effects on gene expression and gametogenesis in mammals, due to the differential inactivation and replication requirements of the X and autosome genomes (Ashley 2002).

In *M. musculoides* the C-banding showed a large pericentromeric block on the X chromosome arm of Rb(X.7) (Veyrunes *et al.* 2004). Although in other *M. minutoides* taxa no C-staining was observed in the two arms of Rb(X.1) (Jotterand-Bellomo 1986, Castiglia *et al.* 2002, Veyrunes *et al.* 2004), ITS were found at the centromeric regions in the samples from Kenya and Zambia (Castiglia *et al.* 2002 and present study). The peculiar Rb(X.1) of *M. minutoides* may represent a good chromosome model for the study of the spreading of the X-chromosome inactivation. Several authors (Viegas-Pequignot *et al.* 1982, Ratomponirina *et al.* 1986, Jaafar *et al.* 1993, Dobigny *et al.* 2004) have proposed that the occurrence of large heterochromatic blocks between the original X and the translocated autosome operates as a boundary preventing X-inactivation from spreading to the autosomal segment, and that this also allows an independent regulation of the replication timing on both the sexual and autosomal arms.

This new cytotype represents a well-differentiated chromosomal lineage within *M. minutoides*. The characteristics of the karyotype of the different lineages described so far suggest the occurrence of two highly reproductively isolated groups of cytotypes in *M. minutoides*, one that comprises the cytotypes from South Africa and the other all the remaining ones (Veyrunes *et al.* 2004). In this respect the evaluation of the fertility of the hybrids derived from the different cytotypes described will allow us to define the role played by chromosomal rearrangements in the establishment of reproductive barriers leading to the formation of chromosomal races or species (King 1993).

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