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Accumulation of rare sex chromosome rearrangements in the African pygmy mouse, *Mus* (*Nannomys*) *minutoides*: a whole-arm reciprocal translocation (WART) involving an X-autosome fusion

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Abstract

Although sex chromosomes are generally the most conserved elements of the mammalian karyotype, those of African pygmy mice show three extraordinary deviations from the norm: (a) asynaptic sex chromosomes, (b) multiple sex–autosome fusions, and (c) modifications of sex determination in some populations/species. In this study we identified, in two sex-reversed females of *Mus* (*Nannomys*) *minutoides*, a fourth rare sex chromosome change: a spontaneous whole-arm reciprocal translocation (WART) between an autosomal Robertsonian pair Rb(13.16) and the sex–autosome fusion Rb(X.1). This represents one of the very few reported cases of WARTs *in natura* within mammals, and is the first one to involve sex chromosomes. Hence, this finding offers new insights into the mechanisms of chromosomal differentiation in African pygmy mice, as WARTs may have contributed to the extensive diversity not only of autosomal Robertsonian fusions, but also of sex–autosome translocations. More widely, these results provide additional support to previous studies on the house mouse and the common shrew which indirectly inferred the role of WARTs in their karyotypic evolution, and may even help to understand how the fascinating 10 sex chromosome chain of the platypus might have evolved. This accumulation of rare sex chromosome changes in single specimens is, to our knowledge, exceptional among mammals.

Introduction

African pygmy mice are very small rodents widespread throughout sub-Saharan Africa. They constitute a complex of morphologically similar species representing the most speciose subgenus (*Nannomys*) of the genus *Mus* (e.g. Musser & Carleton 2005, Veyrunes *et al*. 2006). In spite of this diversity they have been poorly studied, even though the taxonomic and karyotypic studies performed in the 1960s and 1980s hinted at their extraordinary chromosomal evolution, particularly that involving the sex chromosomes (e.g. Matthey 1966a,b, 1970, Jotterand 1972, Jotterand-Bellomo 1986, 1988). Very recently renewed interest in this subgenus has led to studies confirming the peculiar karyotypic features of this group (Castiglia *et al*. 2002, 2006, Veyrunes *et al*. 2004). In effect pygmy mice show a wide range in diploid number from 18 to 36, mostly due to the recurrent fixation of Robertsonian (Rb) fusions. Thus, chromosomal diversity in pygmy mice matches that of the house mouse *Mus musculus domesticus* (e.g. Hauffe & Pialek 1997, Garagna *et al.* 1997, Pialek *et al.* 2005, Britton-Davidian *et al.* 2005) and the common shrew *Sorex araneus* (e.g. Fredga 1996, 2003, Wojcik *et al.* 2002, Andersson *et al.* 2005). In these taxa new Rb fusions occur by two processes: *de-novo* fusion of two acrocentric chromosomes at their centromeres and WART (whole-arm reciprocal translocation), which involves an exchange of chromosomal arms between two metacentric chromosomes (see Figure 1) or between a metacentric and an acrocentric. However, in all these studies the occurrence of WARTs was inferred using indirect approaches, i.e. cladistic or phenetic reconstructions, while direct observations remained quite scarce. The first mention of a WART was described by Crocker & Cattanach (1981) in a laboratory mouse exposed to X-rays. Since then the spontaneous occurrence (in a heterozygous state) *in natura* has been reported only twice in the house mouse (Capanna & Redi 1995, Castiglia & Capanna 1999), a third report coming from the progeny of wild-derived mice (Catalan *et al.* 2000). Within mammals a fourth case has been described in a specimen of a tree shrew (*Tupaia glis*, Scandentia; Hirai *et al.* 2002). Finally, a WART between chromosomes 8 and 9 characterizes the Sumatran population of the agile gibbon *Hylobates agilis* (Van Tuinen *et al.* 1999, Hirai *et al.* 2003, 2005). In this study we report a new case from *Mus* (*Nannomys*) *minutoides*, which is the first to involve the X chromosome. In contrast to the extreme conservation of this chromosome in eutherian karyotypes (review in Marshall Graves 2006), the pygmy mouse genome exhibits three rare chromosomal features involving sex chromosomes: (a) asynaptic sex chromosomes, (b) multiple sex–autosome translocations, and (c) modifications of sex determination in some populations/species (Matthey 1966a, Jotterand-Bellomo 1981, 1988, Veyrunes *et al.* 2004, in preparation, Veyrunes 2005). Thus, the WART identified in this lineage represents a fourth rare phenomenon involving sex chromosomes.

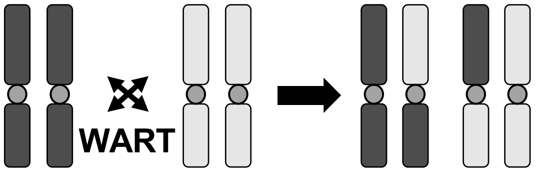

Figure 1. Schematic diagram showing a WART between two pairs of metacentric chromosomes.

This result offers new information to assess the mechanisms of chromosomal diversification in African pygmy mice, but also in other species, notably the well-studied Rb races of the house mouse and the common shrew, and may even help to understand the fascinating 10 sex chromosome system of the duck-billed platypus *Ornithorhynchus anatinus* (Rens *et al.* 2004, Grützner *et al.* 2006).

Material and methods

During a karyological survey of *Mus minutoides* from Caledon Natural Reserve (Free State, South Africa), a population known for having a particular sex determination system with XY females (Veyrunes *et al.* in preparation), six specimens were live-trapped (three females, three males) and karyotyped. Chromosome preparations were made either from bone marrow of yeast-stimulated animals, or fibroblast cell cultures established from skin biopsy following standard procedures. Identification of the chromosomes was performed by the DAPI-banding technique and Zoo-FISH analyses using *M. minutoides* chromosome-specific paints (Veyrunes *et al.* 2006), following the procedure of hybridization and detection described in Rens *et al.* (2006). Biotin-labelled probes were visualized using Cy3-avidin (1:500 dilution, Amersham). Slides were then mounted in Vectashield mounting medium with DAPI (Vector Laboratories). Images were captured using Genus software (Applied Imaging).

Results and discussion

Evidence for a heterozygous WART

Results for two of the male specimens are presented in Veyrunes *et al.* (2004). DAPI-banding of the remaining animals revealed that the third male and one female presented the same karyotype as the two previously described; i.e. they possessed nine pairs of biarmed chromosomes including both sex chromosomes ($2n = 18$), resulting from Robertsonian fusions: Rb(2.10), Rb(3.9), Rb(4.7), Rb(5.8), Rb(6.11), Rb(12.17), Rb(13.16), Rb(14.15), and Rb(X.1)(Y.1).

In this sample the males and the female all carry the same sex chromosomes, i.e. Rb(X.1)(Y.1), suggesting that a particular sex determination system is present leading to sex-reversed females (Veyrunes *et al.* in preparation). In contrast, the two further females shared a different karyotype from the preceding specimens (Figure 2). Of the 18 biarmed chromosomes present, seven pairs were common to the other specimens: Rb(2.10), Rb(3.9), Rb(4.7), Rb(5.8), Rb(6.11), Rb(12.17) and Rb(14.15), whereas four heterozygous (sub)metacentric chromosomes were observed: Rb(13.16), Rb(1.13), Rb(X.16) and Rb(Y.1).

Thus, these females shared 16 chromosomes with the other mice, and carried two newly described fusions: Rb(1.13) and Rb(X.16) (Figure 2). The results of the fluorescence *in-situ* hybridization analysis (Zoo-FISH) were non-ambiguous and confirmed the DAPI-banding analysis. The *M. minutoides* chromosome-specific probe Rb(X.1) was hybridized onto metaphases of animals carrying the two karyotypes. Specimens with the standard karyotype showed two signals (i.e. underlined): Rb(X.1) and Rb(Y.1), whereas the heterozygous females had three signals corresponding to Rb(X.16), Rb(1.13) and Rb(Y.1) (Figure 3).

Such a heterozygous karyotype can originate from two processes. First, these females may be hybrids between two parapatric chromosomal races having seven Rb fusions in common and differing by two monobrachial pairs, i.e. respectively Rb(X.1)(Y.1), Rb(13.16) in one, and Rb(X.16)(Y.16), Rb(1.13) in the other (no specimens belonging to such a race were identified in our sample). However, the exis-

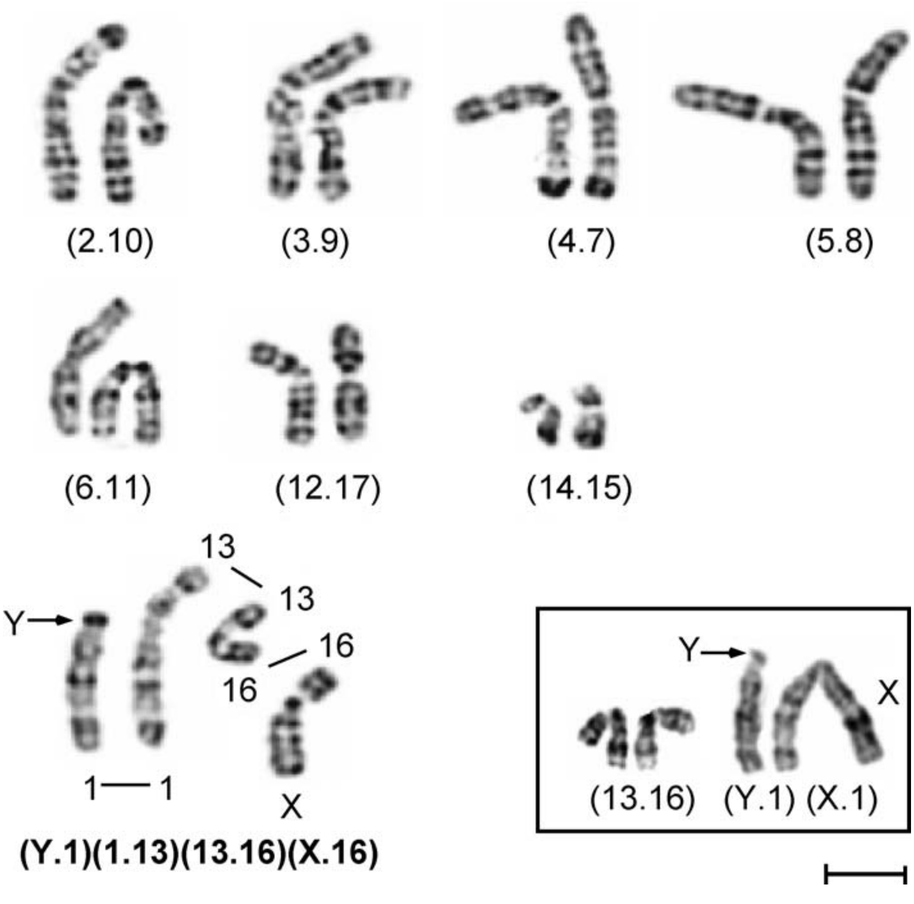

Figure 2. DAPI-banded karyotype (equivalent to a G-banded) of a XY female with a heterozygous WART between the chromosomes Rb(X.1) and Rb(13.16) resulting in four chromosomes with alternate monobrachial arm homology: Rb(Y.1), Rb(1.13), Rb(13.16), Rb(X.16). The insert shows the homozygous Rb(13.16) pair and sex chromosomes Rb(Y.1) Rb(X.1) of a male with the standard karyotype. Scale bar indicates 10 μm.

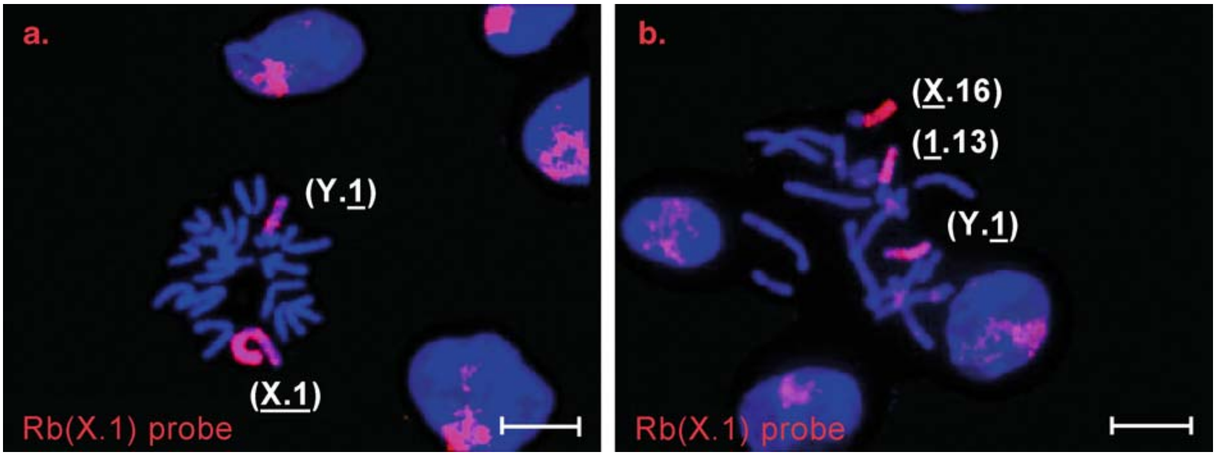

Figure 3. Fluorescence *in-situ* hybridization using the *M. minutoides* Rb(X.1) probe on (**a**) a male with the standard karyotype, and (**b**) an XY female with the atypical karyotype, showing respectively two and three signals (i.e. underlined). Scale bars indicate 10 µm.

tence of two races sharing seven of the eight autosomal fusions but not the sex chromosome translocations is not supported by a recent phylogenetic analysis indicating that Rb(X.1)(Y.1) were the first fusions to be fixed in the *M. minutoides* lineage (Veyrunes *et al.* 2005). Thus, it appears highly improbable that two such lineages evolved independently and convergently fixed seven identical autosomal Rb fusions. Moreover, the fusions Rb(X.16) and Rb(1.13) have never been identified before. Hence, the most likely interpretation is that the two females are related, and that this configuration appeared following a WART between the chromosomes Rb(13.16) and Rb(X.1) in one of their parents which transmitted the new variants, Rb(1.13) and Rb(X.16) to its offspring.

Implications for chromosomal evolution

This new report of a heterozygous WART in a wild population confirms the recurrence of WARTs *in natura*, and the potential of this event to quickly create new chromosomal variants. Furthermore, this provides additional support to the studies which highlight the role of this type of rearrangement in the karyotypic evolution of parapatric Rb races of the house mouse and the common shrew, even if evidence of its occurrence remained scarce (e.g. Hauffe & Pialek 1997, Pialek *et al.* 2005, Andersson *et al.* 2005, Britton-Davidian *et al.* 2005). In effect, all these studies argue in favour of scenarios involving WARTs over multiple Rb fissions and/or fusion events, as the former rearrangements greatly reduce the number of evolutionary steps and thus lead to more parsimonious chromosomal phylogenies. This is particularly true for the house mouse in which fissions are considered as unlikely since they require the *de-novo* formation of telomeres and the duplication of a centromere, sequences that are lost during the fusion event (Garagna *et al.* 1995, Nanda *et al.* 1995). WARTs have no such requirements since they result from the swapping of a chromosomal arm between two existing chromosomes with no change in the number or the structure of the centromeric regions.

This is the first description of a WART involving the X chromosome, and thus producing a new sex–autosome Rb fusion, Rb(X.16), which is the fifth one to be identified in African pygmy mice; the other four being Rb(X.1)(Y.1), Rb(X.7), Rb(X.12), and Rb(X.15)(Y.15) (see Veyrunes *et al.* 2004). In mammals, sex–autosome fusions are considered as one of the most deleterious chromosomal rearrangements, and as such are rare events. The reason for this is that, in addition to the usual meiotic problem of malsegregation inherent to karyotypic mutations, sex–autosome fusions generate important perturbations of gametogenesis and gene expression due to: (a) conflicting replication requirements between sex chromosome and autosome components, (b) intrusion of autosomal material into the sex body with subsequent interference with X-inactivation, and finally,

(c) the spreading of X-inactivation into the adjacent autosome, causing the silencing of the autosomal genes (reviews in King 1993, White *et al.* 1998, Ashley 2002, Dobigny *et al.* 2004). The deleterious effects of these sex chromosomal rearrangements can be overcome, however, by the addition of a large block of heterochromatin or repetitive sequences, such as telomeres, in the centromeric region of the metacentric chromosome (Veyrunes *et al.* 2004, Castiglia *et al.* 2006). These sequences thereby functionally isolate the two chromosomal components (reviewed in Dobigny *et al.* 2004).

Hence, this newly described sex–autosome Rb fusion confirms the African pygmy mice as the lineage with the greatest diversity of this type of rearrangement known so far. Such a variability suggests that specific genomic traits allowing a higher rate of appearance and/or fixation of this deleterious rearrangement may be present within the subgenus (Veyrunes *et al.* 2004, 2005). In the present study it is clear that this diversity may not result solely from independent fixations of sex–autosome Rb fusions, but also from WARTs, which may be the factor contributing to the higher rate of fixation of this rearrangement in this clade. Indeed, a WART involving an existing X-autosome translocation preserves the integrity of the additional centromeric sequences isolating the sex chromosome and autosomal compartments, thereby reducing the large disadvantage commonly associated with these rearrangements. However, for WARTs to contribute to the chromosomal diversity in pygmy mice requires that the malsegregation rates associated with the mutation be sufficiently low for fixation to occur. At meiosis, pairing of the chromosomes involved in the WART is complex. As the sex chromosomes of the African pygmy mice are asynaptic (Matthey 1966a, Jotterand-Bellomo 1981, Veyrunes 2005), a chain of four chromosomes is present with the X and Y at each extremity (Figure 4): (Y.1)(1.13) (13.16)(16.X). At the first meiotic division the alternate segregation of the chromosomes in the chain is necessary to produce balanced gametes which are of two types: Rb(Y.1) Rb(13.16) and Rb(1.13) Rb(16.X). Unfortunately, both mutant females had been autopsied long before the WART was identified, so no direct observations of the meiotic behaviour of this rearrangement were made. In its close relative, *Mus musculus*, individuals with a quadrivalent formation at meiosis have very variable fertility (subfertile to sterile in males), depending on the chromosomes involved (Forejt 1979, Gropp *et al.* 1982, Redi *et al.* 1984, Mahadevaiah *et al.* 1990), but the presence of the sex chromosomes in such a configuration has never been tested. More generally, autosomal meiotic multiples (i.e. chain or ring) often cause infertility in mammals because they interfere with meiotic progression, and those involving the sex chromosomes usually lead to even lower fertility (Grützner *et al.* 2006). Hence, except in monotremes (see below), constitutive sex chromosome chains of four or more chromosomes are extremely rare in mammals (review in Grützner *et al.* 2006), and have so far been documented in only three other lineages. Within Artiodactyla, in the genus *Gazella*, a chain of four is characteristic of some

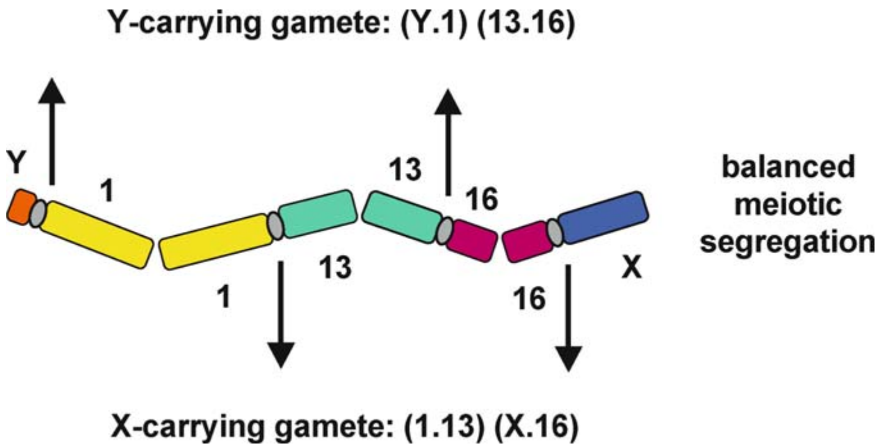

Figure 4. Schematic representation of the likely configuration of the multivalent at first meiotic division. An alternate segregation of the chromosomes is necessary to ensure the formation of balanced gametes, carrying respectively Rb(Y.1) Rb(13.16) and Rb(1.13) Rb(16.X).

species following the Rb fusions of the X and Y chromosomes with different autosomes (Vassart *et al.* 1995), and in the black muntjac *Muntiacus crinifrons*, a combination of tandem fusion, inversion and fission events involving the sex chromosomes and autosomes has contributed to the origin of a pentavalent chain at the male meiosis (Huang *et al.* 2006). Finally, within the New World Monkeys (Platyrrhini) of the genus *Alouatta*, a chain of four is apparently thought to be due a translocation between parts of an autosome and the Y chromosome (e.g. Lima & Seuanez 1991, Rahn *et al.* 1996, de Oliveira *et al.* 2002, Solari & Rahn 2005). Furthermore, in *A. fusca*, a report of an additional translocation may have led to a chain of five chromosomes (de Oliveira *et al.* 2002). But the most striking of all are the monotremes which show a sex chromosome chain of 10 chromosomes in the platypus and nine in the echidna (Rens *et al.* 2004, Grützner *et al.* 2004, 2006). The origin of the platypus chain is puzzling, and several models have been proposed to explain it, i.e. via multiple translocations between the sex chromosomes and autosomes (Rens et al. 2004), or a hybridization event between two ancestral cytotypes with different sets of Rb fusions (Ashley 2005). Both models were subsequently reinterpreted and developed (Grützner *et al.* 2006). The configuration shown in the present study, with sex chromosomes at each extremity of the chain, is described for the first time, and is reminiscent of the sex chromosome chain in the male platypus. Hence, our observations from a rodent case study may give new insights on how the fascinating chain of the platypus might have evolved.

Chromosomal changes involving the sex chromosomes most often lead to complete sterility (e.g. reviewed in King 1993). However, these two pygmy mouse specimens have an extraordinary karyotype with no less than four features involving the sex chromosomes, all of which are considered as extremely rare. These are asynaptic sex chromosomes, XY females, sex–autosome translocations and a heterozygous WART (Veyrunes 2005, Veyrunes *et al.* in preparation, this study). This accumulation of rare sex chromosomal changes in single specimens is, to our knowledge, exceptional among mammals, and makes African pygmy mice an excellent model for investigating the evolution of mammalian sex chromosomes, their plasticity, as well as the evolutionary consequences on the genome and the species.

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