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Distribution of Telomeric Sequences $(TTAGGG)_n$ in Rearranged Chromosomes of Phyllotine Rodents (Cricetidae, Sigmodontinae)

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Phyllotini · Robertsonian rearrangements · Rodents · South America · Telomeres

Abstract
Phyllotines are sigmodontine rodents endemic to South America with broad genetic variability, Robertsonian polymorphisms being the most frequent. Moreover, this taxon includes a species with multiple sex chromosomes, which is infrequent in mammals. However, molecular cytogenetic techniques have never been applied to phyllotines to elucidate their karyotypic evolution. We studied the chromosomes of 4 phyllotine species using FISH with a pantelomeric probe $(TTAGGG)_n$. *Graomys griseoflavus*, *Eligmodontia puerulus,* and *E. morgani* are polymorphic for Robertsonian translocations, whereas *Salinomys delicatus* possesses XX/XY_1Y_2 sex chromosomes. Telomeric signals were detected at both ends of all chromosomes of the studied species. In *S. delicatus* interstitial telomeric sequences (ITS) were observed in the 3 major chromosome pairs, which are equidistant from one of the telomeres in these chromosomes. These results suggest that ITS are important in the reshuffling of the highly derived karyotype of *S. delicatus*. Considering the phylogeny of phyllotines, the Robertsonian rearrangements of *G. griseoflavus*, *E. puerulus,* and *E. morgani* possibly represent chromosome fusions which have occurred independently. The pericentromeric regions of the biarmed chromosomes of these species do not contain telomeric sequences characteristic for strict fusions of recent origin, suggesting a common pattern of telomeric repeat loss during chromosomal evolution of these rodents.

Telomeres are nucleoprotein complexes located at the ends of eukaryotic chromosomes that are involved in maintaining chromosome stability and integrity, protecting them from degradation by nucleases and recombination or fusion with other chromosomes [Bolzán and Bianchi, 2006]. In vertebrates, the DNA sequence of telomeres is composed of tandem repeats of the hexamer $(TTAGGG)_n$ [Meyne et al., 1990], which can be detected by FISH with a telomeric probe [Bolzán and Bianchi, 2006]. This sequence can be located not only at the terminal regions of the chromosomes but also close to the centromere or between the centromere and the telomere, which constitute the so-called interstitial telomeric sequences (ITS) [Lin and Yan, 2008; Ruiz-Herrera et al., 2008].

It is well known that telomeric sequences are implicated in several types of chromosome rearrangements, such as Robertsonian translocations (Rb), tandem fusions, and inversions [Meyne et al., 1990; Slijepcevic,

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1998; Bolzán and Bianchi, 2006; Ruiz-Herrera et al., 2008]. These rearrangements may involve retention, multiplication, or loss of telomeric sequences, as observed in different taxa [Meyne et al., 1990; Garagna et al., 1995; Slijepcevic, 1998]. Since telomeric sequences play a fundamental role in chromosome rearrangements and evolution [Meyne et al., 1990; Slijepcevic, 1998; Ruiz-Herrera et al., 2008], the study of their distribution in different taxa is of particular interest for understanding karyotypic evolution.

The subfamily Sigmodontinae is a lineage of cricetid rodents that radiated and differentiated in South America and is composed of ~400 species distributed in 84 living genera [Patton et al., 2015]. These genera are grouped into tribes. Among them, the tribe Phyllotini is mainly distributed along the arid and semiarid landscapes of the south-central and southern of South America [Salazar-Bravo, 2015] and exhibits great chromosome variability [Spotorno et al., 2001].

In the subfamily Sigmodontinae, the use of the FISH technique with a telomeric probe has revealed the presence of terminal signals and ITS on the chromosomes of several species. In some cases, the presence of internal hybridization signals could be associated with specific chromosomal rearrangements [Fagundes et al., 1997; Viera et al., 2004; Nagamachi et al., 2013]. Despite the above studies, telomere-FISH has never been applied to metaphase spreads of species from the tribe Phyllotini, so the distribution pattern of the telomeric sequence $(TTAGGG)_n$ in these species is unknown.

In this work, we analyzed the distribution of the telomeric sequence in the chromosomes of 4 phyllotine species. One was *Salinomys delicatus* (Braun and Mares, 1995), a rare species with the lowest diploid number in the tribe and multiple sex chromosomes (XX/XY_1Y_2), which is infrequent in mammals. The other 3 species are polymorphic for Rb rearrangements. *Graomys griseoflavus* (Waterhouse, 1837) has a broad distribution of Rb polymorphisms, with chromosome numbers ranging from 2n = 33–38 and at least 3 different Rb fusions previously reported [Zambelli et al., 1994; Tiranti, 1998; Lanzone et al., 2014]. *Eligmodontia puerulus* (Philippi, 1896) has high intraspecific chromosome variability due a complex Rb system (2n = 31–37), with fixed chromosome races as well as polymorphic populations [Lanzone et al., 2011]. The fourth studied species, *E. morgani* (Allen, 1901), has a reduced karyotype within the genus and is polymorphic for only one Rb rearrangement that produces a variation from 2n = 34 to 2n = 32 [Ortells et al., 1989; Sikes et al., 1997]. Thus, all 4 studied species in the present work are phylogenetically related at the tribal level [Salazar-Bravo, 2015]. *G. griseoflavus, E. puerulus,* and *E. morgani* are the only species of the tribe Phyllotini with polymorphic Rb rearrangements. Additionally, due to the presence of a reduced karyotype with multiple sex chromosomes in *S. delicatus*, its study is of particular interest. In order to get further insights into the chromosome evolution of the tribe Phyllotini, we determined the distribution patterns of the telomeric sequence $(TTAGGG)_n$ in the above mentioned species by applying the FISH technique with a pantelomeric PNA probe on metaphase spreads.

Materials and Methods

Samples and Chromosome Preparations

Bone marrow samples from 10 individuals of different species of phyllotine rodents living in different localities of Argentina were studied. Three specimen belonged to *S. delicatus*, 1 female from Laguna del Rosario (Mendoza Province) that had 2n = 18; and 2 males, 1 from Laguna del Rosario and the other from Estancia El Tapón (Mendoza Province) with 2n = 19 and the number of autosomal arms (FNa) = 32. Four specimens of *G. griseoflavus* were from the Mendoza Province with different chromosome combinations. Localities and chromosome constitutions are as follow: Las Catitas (n = 1), a male double heterozygous with 2n = 36/FNa = 44; Luján de Cuyo (n = 2), a female with 2n = 33/FNa = 44 and another with 2n = 34/FNa = 44, both of them with 3 different Rb chromosomes; and Ñacuñán (n = 1), a female with 2n = 38/FNa = 44, exhibiting the acrocentric variants of these 3 Rb chromosomes. The studied specimens of *E. puerulus* were a male with 2n = 33/FNa = 48 and a female with 2n = 31/FNa = 48 from Abra Pampa (Jujuy Province). The specimen of *E. morgani* was from 10 km south of Las Leñas (Mendoza Province) and has 2n = 32/FNa = 32, with 2 homologous Rb metacentrics (the only biarmed chromosomes in the karyotype). Metaphase spreads were obtained using the standard hypotonic technique for bone marrow [Ford and Hamerton, 1956] with small modifications.

Fluorescence in situ Hybridization

A Cy3-conjugated PNA pantelomeric probe [Cy3-$(CCCTAA)_3$] obtained from Panagene (Korea) was used. FISH was performed according to the protocol provided by the supplier. Briefly, after pre-treatment with 3.7% formaldehyde and a solution containing 2 mg/ml proteinase K for 10 min, sample DNA was denatured at 85°C for 10 min under a coverslip in the presence of the Cy3-conjugated probe. Hybridization in a moist chamber (1 h at room temperature) was followed by 2 washes in 2× SSC 0.1% Tween 20 for 10 min at 55–60°C. Afterwards, slides were mounted on an antifade reagent containing DAPI (4,6-diamidino-2-phenylindole) as counterstain. Fluorescence microscopy was performed with a Nikon Eclipse 50i epifluorescence microscope equipped with an HBO 100 mercury lamp, a Nikon high-resolution digital color camera (DS-Ri-U3), and filters for DAPI and Cy3 (Chroma Technology Corp., Rockingham, Vt., USA).

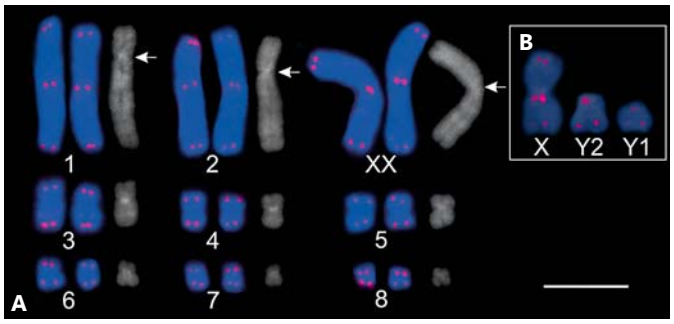

Fig. 1. Chromosomes of *S. delicatus* hybridized with the pantelomeric probe. **A** Female karyotype. **B** Detail of the sex chromosomes of males. Note the similar position of ITS in the 3 major chromosome pairs. In **A** DAPI staining is shown to identify the centromere position. Bar = 10 μm.

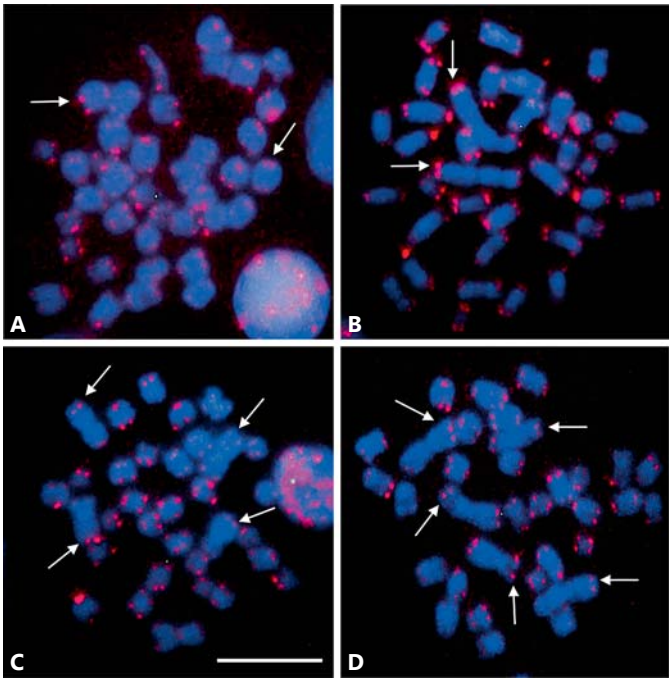

Fig. 2. In situ localization of the telomeric sequence $(TTAGGG)_n$ on metaphase chromosomes of *G. griseoflavus* with different chromosome complements. **A** Metaphase cell with 2n = 38/FNa = 44. **B** Metaphase cell from a double heterozygous individual with 2n = 36/FNa = 44. **C** Metaphase cell with 2n = 34/FNa = 44 chromosomes. **D** Metaphase with 2n = 33/FNa = 44 chromosomes. Arrows in **A** indicate the presence of telomeric signals in acrocentric chromosomes. Arrows in **B–D** indicate the presence of telomeric signals at the ends of Rb metacentric chromosomes. Bar = 10 μm.

Results

The karyotype of *S. delicatus* is composed of 2n = 18 chromosomes in females and 2n = 19 in males [due to multiple sex chromosomes (XX/XY_1Y_2)]. All autosomes and the X chromosomes are biarmed (FNa = 32) and the Y_1 and Y_2 are acrocentric. The metacentric X and the first 2 submetacentric autosome pairs are notably larger than the other chromosomes [Lanzone et al., 2011] (fig. 1). In *S. delicatus* the telomeric probe hybridized to both ends of all chromosomes. Some variations in the intensity of the signals were detected, especially among the telomeres of the small chromosomes. Additionally, ITS were observed in the 3 largest chromosomes: in the pericentromeric region of the X, near the centromere of pair 2, and in the interstitial region of the long arm of pair 1. The signals were strong in all cases and are equidistantly localized from one chromosome end in the 3 pairs (fig. 1).

G. griseoflavus is a species polymorphic for Rb rearrangements with 3 different Rb chromosomes [Lanzone et al., 2014 and literature herein]. Here, we analyzed the chromosomes of 4 selected specimens by PNA telomere-FISH. One of them possessed a karyotype with 2n = 38 chromosomes with 14 pairs of acrocentric chromosomes that gradually decrease in size (pairs 1–14) and 4 submetacentrics of medium and small size (pairs 15, 16, 17, and 18) that are constant among all the cytotypes of this species (fig. 2A). Another individual possessed a karyotype with 2n = 36 chromosomes which had 2 Rb fusions in a heterozygous state (fig. 2B). These rearrangements involved chromosomes of similar size that generated 2 large metacentrics (pairs 1 and 2). Finally, individuals with 2n = 34 (fig. 2C) and 2n = 33 (fig. 2D) were also studied, both having an extra chromosome fusion involving acrocentric chromosomes of different size that generated one pair of submetacentric chromosomes (pair 3). In the metaphases of *G. griseoflavus* analyzed in the present work, telomeres were clearly labeled with the Cy3-conjugated PNA probe, and all chromosomes (including Rb ones) of the karyotype exhibited 4 telomeric signals, 2 at each end. Differences in the intensity of telomeric signals on different chromosome arms were observed (fig. 2). No internal fluorescence signals were detected in any of the chromosomes of the specimens analyzed.

In *Eligmodontia* 2 species are polymorphic for Rb rearrangements. *E. morgani* has a predominantly acrocentric karyotype with 2n = 32–34 and FNa = 32, which is the lower FNa found within the genus. The X and Y chromosomes in this species are acrocentric. The variation in the diploid numbers is produced by a Rb fusion that generates the only biarmed chromosome in the complement with a medium size. In the homozygous individual with

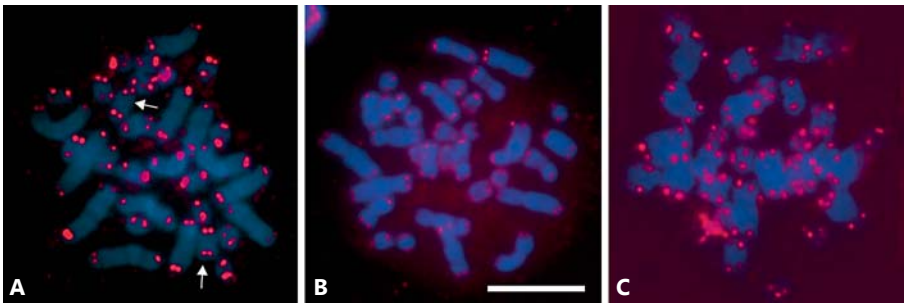

Fig. 3. Metaphase cells hybridized with telomeric probe of *E. morgani* with 2n = 32/FNa = 32 (**A**), a male of *E. puerulus* with 2n = 33/FNa = 48 (**B**), and a female of *E. puerulus* with 2n = 31/FNa = 48 (**C**). Arrows indicate the presence of telomeric signals only at the ends of Rb metacentric chromosomes. Bar = 10 μm.

2 metacentric Rb chromosomes and 2n = 32 studied in this work, the telomeric probe hybridized only at both ends of all chromosomes (fig. 3A). *E. puerulus* has high intraspecific chromosome variability due to multiple Rb translocations all with FNa = 48. The specimens studied in this work were a male with 2n = 33 (17 biarmed and 14 acrocentric autosomes, fig. 3B), and a female with 2n = 31 (19 biarmed and 10 acrocentric autosomes, fig. 3C). The X and Y chromosomes are acrocentric [Lanzone et al., 2011]. The telomeric probe hybridized to both ends of all chromosomes, and no ITS were detected in the chromosomes of the specimens analyzed (fig. 3B, C).

Discussion

In the present work, we found that all chromosomes of the phyllotine species analyzed showed telomeric signals at both ends after PNA-FISH. The presence of 4 signals on each chromosome suggests that none of them is strictly telocentric but rather acrocentric. Similar results were reported for most of the mammalian species studied so far [Nanda et al., 1995; Lizarralde et al., 2003, 2005; Mudry et al., 2007; Faria et al., 2009; Rovatsos et al., 2011], indicating that this is a common pattern for mammalian karyotypes.

Since the intensity of the PNA-FISH signal is directly correlated with the number of telomeric repeats present [Lansdorp et al., 1996], differences in the intensity of telomeric signals on different chromosome arms suggest that there are intra- and inter-chromosomal variations in telomere length within and among all the species of phyllotine rodents studied. A variable distribution in the amount of telomeric sequences in some karyotypes and among different species was also detected in other mammalian species [Meyne et al., 1990; Mudry et al., 2007; Ivanitskaya et al., 2008; Ruiz Herrera et al., 2008; Rovatsos et al., 2011].

Rb translocations are one of the more frequent chromosomal rearrangements in rodents [Patton and Sherwood, 1983]. In Rb fusions different distribution patterns of the telomeric sequences during the karyotypic evolution of vertebrates were detected: some species maintained the telomeric sequences close to the centromere of the biarmed Rb, others lost its telomeres, and some species present a combined pattern of retention and loss of telomeric sequences in different Rb chromosomes [Slijepcevic, 1998; Castiglia et al., 2002; Bolzán and Bianchi, 2006]. Considering the phylogeny of Phyllotini rodents, the Rb rearrangements of *G. griseoflavus*, *E. puerulus,* and *E. morgani* possibly represent chromosome fusions which occurred independently during their karyotypic evolution [Lanzone et al., 2011, 2014]. Thus, the presence of strong signals on both telomeres of all acrocentric variants in non-fused karyotypes and the absence of signals in the pericentromeric regions of all Rb chromosomes suggests a convergent process of telomeric repeat loss during the chromosomal evolution of these phyllotines. The loss of telomeres close to the centromeres in all Rb chromosomes was also observed in other broadly polymorphic species such as *Mus musculus domesticus* and *Suncus murinus* [Nanda et al., 1995; Rogatcheva et al., 2000].

The localization of ITS in heterochromatic and/or in pericentromeric regions of the chromosomes was reported for several vertebrate species [Meyne et al., 1990; Go, 2000; Ventura et al., 2006; Ivanitskaya et al., 2008; Ruiz Herrera et al., 2008; Rovatsos et al., 2011]. In our present work, strong ITS signals were detected in euchromatic and heterochromatic regions of the chromosomes of *S. delicatus*. This species has a constant chromosome complement which is highly derived within the tribe Phyllotini. Even more, *S. delicatus* is the only Sigmodontinae species with XY_1Y_2 sex chromosomes, which is a rare phenomenon found in mammals [Lanzone et al., 2011]. For the X chromosome, telomeric sequences were ob-

served in the pericentromeric region, which is heterochromatic and was proposed as the point of fusion between the autosome and the ancestral X chromosome [Lanzone et al., 2011]. This suggests that ITS represent the original telomere that was retained after the chromosome fusion event as previously proposed for other mammalian species exhibiting ITS in their rearranged chromosomes [Go, 2000]. The ITS observed in the X chromosome can prevent the extension of the sexual differentiation to the autosomal part in the sex trivalent [Dobigny et al., 2004]. ITS were also observed in other sex chromosomes involved in translocations such as in *Mus minutoides/musculoides* and in several species of *Taterillus* [Castiglia et al., 2002; Dobigny et al., 2004] although there are some mammalian species with rearranged sex chromosomes where ITS are absent in the X chromosomes [Mudry et al 2007; da Silva Calixto et al., 2014].

Moreover, the autosomes of *S. delicatus* exhibited non-centromeric ITS. Since heterochromatic blocks in this species were observed only in the pericentromeric regions of all chromosomes, except the Y_1 [Lanzone et al., 2011], it can be concluded that the ITS found in the autosomes are located in euchromatic regions of the chromosomes. ITS have been previously observed in euchromatic regions of some chromosomes of very few species [Meyne et al., 1990; Ventura et al., 2006; Ivanitskaya et al., 2008], indicating that this distribution pattern of ITS is very unusual. Therefore, the presence of ITS in the 2 major autosomes of *S. delicatus* is intriguing. One possibility is that ITS resulted from chromosome rearrangements other than Rb translocations, because this species must have undergone several chromosome changes to have acquired its reduced karyotype [Lanzone et al., 2011]. However, there are diverse mechanisms that might explain the origin of ITS other than chromosomal rearrangements, such as amplification and transposition of telomeric sequences [Ventura et al., 2006; Rovatsos et al., 2011]. The similar localization of ITS in the 3 major chromosomes of *S. delicatus* suggests that these sequences on the autosomes of this species could have been generated by transposition of ITS from the X chromosome to a similar region of similar-sized chromosomes. Whatever the origin of these ITS in *S. delicatus*, it indicates the existence of a complex and dynamic chromosome evolution in this species.

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Statement of Ethics

The authors have no ethical conflicts to disclose.

Disclosure Statement

The authors have no conflicts of interest to declare.

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