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ORIGINAL PAPER

Chromosome variability and evolution in rodents of the tribe Abrotrichini (Rodentia, Cricetidae, Sigmodontinae)

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Abstract

Rodents are a very diverse group with large chromosome variability. One of the most species rich linage in the Neotropics is the Sigmodontinae. Among them, the tribe Abrotrichini was recently defined and its taxonomy and phylogeny were mostly elucidated through molecular and morphological evidence. Meanwhile, chromosome data were only secondarily used because of fragmentary information. In this contribution, we conduct a chromosome characterization of *Abrothrix hirta*, *A. olivacea*, *A. andina*, and *Paynomys macronyx*, review the cytogenetic background of the tribe, and contrast it with molecular data. Chromosomes were analyzed by conventional and differential techniques. All *Abrothrix* species presented 2n = 52/FNa = 56, with a high similarity in the banding patterns reflecting a conserved karyotype, which does not coincide with its high molecular variability. In turn, *P. macronyx* have 2n = 54/FNa = 58–59, varying due to a heteromorphic pair of autosomes. In addition, in this last species, different morphologies of the X chromosome and the presence of B chromosomes were detected. Heterochromatin was involved in these variants. The telomeric probe in *P. macronyx* marks terminal regions of all chromosomes. B chromosomes generated strong telomeric signals. The Ag-NORs banding revealed the same patterns in *Abrothrix* and *Paynomys*. Cytogenetic data support phylogenetic relationships previously proposed and suggest that the specious genus *Abrothrix* could have retained the ancestral karyotype of the subfamily. In the tribe, the relatively conserved chromosome complement contrasts with its high molecular variability. This indicates decoupling between the rates of chromosomal and molecular divergence, as observed in other rodent lineages. In abrotrichines, chromosome evolution was slower.

Keywords Cytogenetic · Diversification · Molecular variability · Rodentia · South America

Introduction

The subfamily Sigmodontinae is one of diversified and widely distributed group of rodents in South America. The Abrotrichini, initially referred as the "Andean Clade", is one of the tribes included in this Neotropical subfamily. This tribe has its geographic distribution in the central and southern Andes in Argentina, Bolivia, Chile, and Peru, and several

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studies recover it as a monophyletic lineage (Smith and Patton 1999; D'Elía 2003; Cañón et al. 2014; Teta et al. 2016). The species of this major lineage evidence an important ecomorphologic diversification, including the occurrence of terrestrial and fossorial forms, this last being an uncommon lifestyle among sigmodontines (Patton et al. 2015).

The tribe Abrothrichini was traditionally composed by the genera *Abrothrix*, *Chelemys*, *Geoxus*, *Notiomys*, and *Pearsonomys*; most of which were previously assigned to the tribe Akodontini (Reig 1987). Molecular analyses, based on mitochondrial and nuclear sequences, have placed those genera in a separate clade with high support and consistency (Smith and Patton 1999; D'Elía 2003). More recently, Teta et al. (2016) found some inconsistent phylogenetic relationships among this group and proposed a new classification for the tribe, including *Abrothrix* (with four subgenera [*Abrothrix*, *Angelomys*, *Chroeomys*, and *Pegamys*]), *Paynomys* (to include *Chelemys macronyx*), *Chelemys* (now restricted to *C. megalonyx*), *Geoxus* (including *Pearsonomys*), and *Notiomys*. In this revision, the tribe was divided into two subtribes: Abrotrichina that groups all *Abrothrix* species and Notiomyina for all other genera (Teta et al. 2016).

At the chromosomal level, it was suggested that this lineage shares a similar 2n = 52 karyotype (Reig 1987; Liascovich et al. 1989; Spotorno et al. 1990), which was considered a synapomorphic character for the entire tribe (Smith and Patton 1999). However, during several decades, the cytogenetic data was limited to some species of the tribe, particularly those of the genus *Abrothrix* (Reig 1987; Gallardo 1982; Pearson 1984; Liascovich et al. 1989; Spotorno et al. 1990). Additional data from *Geoxus* (= *Pearsonomys*) *annectens* and *Paynomys* (= *Chelemys*) *macronyx*, based in conventional cytogenetic techniques, suggest that the abrotrichines possess a higher chromosomal variation than previously suspected (Ojeda et al. 2005; D'Elía et al. 2006).

The aim of our study is: a) to present new karyotype information of the *Abrothrix* and *Paynomys* species, b) to review chromosome data in members of the tribe Abrotrichini, and c) to contrast and discuss chromosome data with molecular information.

Materials and methods

The specimens analyzed were collected in different localities of west-central Argentina (Supplementary Fig. 1 and Supplementary Table 1), and handled followed ASM guidelines for the use of wild mammals in research (Sikes et al. 2016). Fifteen individuals of *Abrothrix* [*A. hirta* (N = 2), *A. olivacea* (N = 8), and *A. andina* (N = 5)] and nine of *Paynomys macronyx* were studied using different cytogenetic techniques. Sampling localities are shown in Supplementary Fig. 1 and Supplementary Table 1. The studied specimens, including skins, skeletons, and cellular suspensions are housed at the Mammals Collection of the Instituto Argentino de Investigaciones de Zonas Áridas IADIZA, CCT-CONICET, Mendoza (Supplementary Table 1).

Mitotic and meiotic chromosome preparations were obtained from bone marrow and testes, respectively, using standard techniques (Ford and Hamerton 1956; Evans et al. 1964). Chromosomes were stained with Giemsa (pH = 6.8). Fundamental numbers (FNa) refer only to autosomes (Patton 1967). The distribution of constitutive heterochromatin (CH, C-bands) was determined using the method of Sumner (1972). The technique of Schweizer (1980) was used for DAPI staining. Ag-NORs staining was performed with the technique proposed by Howell and Black (1980). Fluorescent in situ hybridization (FISH) was performed with a Cy3-conjugated PNA pan-telomeric probe [Cy3-(CCCTAA)3] obtained from PNABio Inc. (CA, USA), according to the protocol provided by the supplier, as previously described (Lanzone et al. 2015). The FISH technique was only performed in *P. macronyx*. Photomicrographs were obtained using an Olympus BX 50 photomicroscope, with a Sony Exwave HAD digital camera. Fluorescence microscopy was performed on 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).

In addition, we carried out an extensive review of the literature and compiled chromosomal information of abrotrichines species (Supplementary Table 2). We described the frequencies and distribution of the diploid numbers (2n) and FNa in the tribe to investigate variability in both parameters, and contrasted the chromosomal data with the phylogeny previously proposed by other authors (Cañón et al. 2014; Teta et al. 2016).

Finally, we performed basic molecular analyses of cytochrome b (cytb), Adh, βfbg, and IRBP sequences to investigate the degree of divergence in the tribe in these molecular markers. For this approach, we used some sequences of the same dataset employed by Teta et al. (2016) available in GenBank. We calculated the genetic distances for all pairwise comparisons with the MEGA 6.0 software (Tamura et al. 2013). The selected model was K2P since all DNA regions displayed Tv/Ts bias and showed relatively low genetic variability, besides that it is the most used model in molecular analyses (Supplementary Table 3).

Results

In this paper we present, for the first time, the chromosome complements of members of the tribe Abrotrichini from San Juan (*A. andina*) and Mendoza (*A. hirta*, *A. olivacea*, and *P. macronyx*) provinces in Argentina, analyzed with

conventional and differential cytogenetic techniques (Supplementary Tables 1 and 2). All specimens of *Abrothrix* studied, including samples of two different subgenera [*A.* (*Abrothrix*) *hirta*, *A.* (*Angelomys*) *olivacea*, and *A.* (*Angelomys*) *andina*] had the same 2n = 52 and FNa = 56 (Fig. 1). These complements consisted of 25 autosomes and a pair of sex chromosomes XX/XY. Among the autosomes, 22 pairs were acrocentric and three pairs were small submetacentrics. The subtelocentric X was one of the largest chromosomes in the complement, while the Y was one of the smallest chromosomes, with very small short arms, often difficult to identify. In *A. andina*, the Y chromosome was larger than in the other species (Fig. 1d). In all specimens, DAPI and C-bands were similar (Fig. 1c–g). Small pericentromeric C-bands in all autosomes and in the X chromosome were observed (Fig. 1e–g). One small biarmed pair exhibited a small interstitial C mark. The Y chromosome of all specimens was heterochromatic. However, in *A. andina*, a larger amount of CH and a DAPI neutral pericentromeric region, absent in other specimens, were detected (Fig. 1c–g).

Individuals of *Paynomys macronyx* shared a diploid number of 2n = 54, with 26 pairs of autosomes and the sex pair

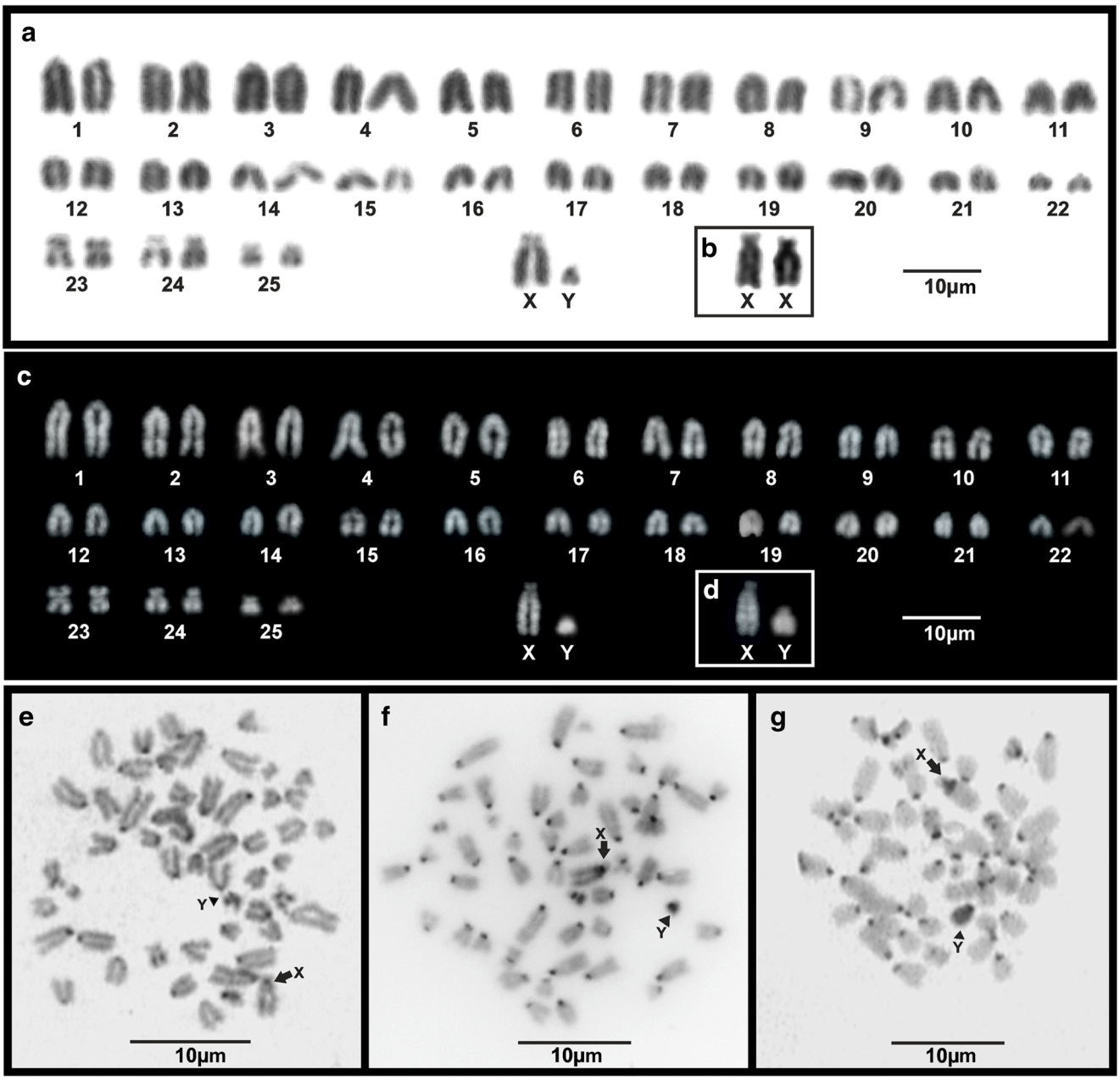

Fig 1 Chromosomal constitution of the *Abrothrix* specimens analyzed in this work. **a** Karyotype of a male of *A. olivacea* with conventional staining. **b** In frame are sex chromosomes of one female. **c** DAPI bands in chromosomes of *A. hirta*. **d** In frame are the sex chromosomes of a male of *A. andina*. **e**–**g** C-bands in *Abrothrix*: **e** *A. olivacea*, **f** *A. hirta*, **g** *A. andina*

XX/XY (Fig. 2). Among autosomes, pair one was subtelocentric and pairs 25 and 26 were small submetacentrics. The remaining autosomes were acrocentric and varied in size from large to small. In some individuals (five of nine; three males and two females), pair 8 was heteromorphic, formed by an acrocentric and a metacentric chromosome. This produced a variation in FNa between 58 and 59 (Fig. 2a, c). The biarmed homolog of this heteromorphic pair had a large amount of CH (Fig. 2h). The X chromosome also presented heteromorphism due to differences in length of its short arms, and could be submetacentric (with two different morphological variants) or acrocentric (Fig. 2D–E; Supplementary Table 2). Its short arms were completely heterochromatic (Fig. 2f–h) and variable to DAPI staining (Fig. 2c–e). The Y chromosome was one of the smallest DAPI positive acrocentrics (Fig. 2c). Supernumerary

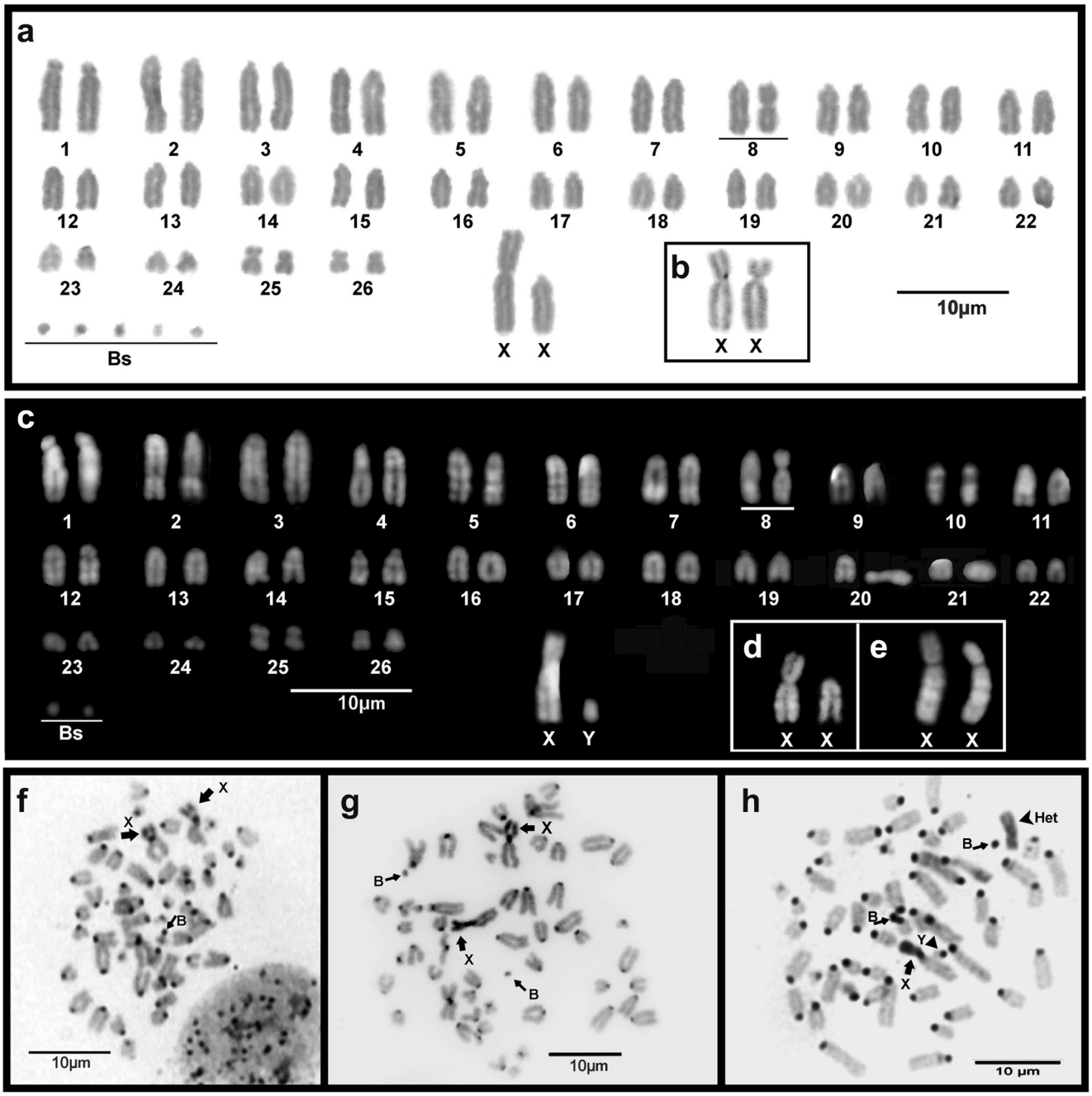

Fig 2 Chromosome complements of *Paynomys macronyx*. **a** Conventional staining in a cell form a specimen with different X chromosomes. **b** In frame is a pair of X chromosomes with other morphology from another female. **c** DAPI bands of a male. **d**–**e** Sex chromosomes of two different females. **f**–**g** C-bands of cells from two females with different number of B chromosomes. **h** C-bands in a male that carried the heteromorphic pair. Note the different number of supernumerary chromosomes among the cells

microchromosomes were detected in eight of nine individuals; the number of B chromosomes varied among individuals and among cells of the same individual (Supplementary Table 1). B chromosomes were C positive and neutral to DAPI staining (Fig. 2c, f–h). In the autosomes, the CH was concentrated in the pericentromeric regions (Fig. 2f–h). In *P. macronyx*, telomeric FISH signals were observed only at both terminal regions of each chromosome (Fig. 3a and b). Some variation in the intensity of fluorescent signals was detected at both, intra- and inter-chromosomal level. B chromosomes showed high intensity of fluorescence with the telomeric probe (Fig. 3a). In meioses, the XY pair showed the characteristic end-to-end association (Fig. 3).

The Ag-NOR technique reveled the same banding pattern in both genera. Positive marks in the short arms of two pairs of acrocentric chromosomes were observed (Fig. 3d–e). The comparison between the banding chromosome complements of both genera indicated a high degree of conservation between them; however, some differences were observed. For example, all specimens of *Abrothrix* had an extra pair of small biarmed chromosomes. Also, pair one of *P. macronys* was differentiated; the long arms appeared homologous to pair three of *Abrothrix* and vice versa, but not its short arms. The long arms of the X chromosomes were similar in banding pattern, but the short arms of *Paynomys* did not evidenced visible banding homology to any chromosome of *Abrothrix* (Figs. 1c and 2c).

Chromosome variability within the tribe

Few different chromosome complements were described for the tribe Abrotrichini, especially for the specious genus *Abrothrix* (Supplementary Table 2). All diploid numbers recorded in the tribe were even. The only autosomal polymorphism was the one described here in *P. macronyx*, and produced variation in the FNa. The sex chromosomes were variable. The Xs were always big in size and presented different morphologies (submetacentric, subtelocentric, or acro-telocentric). In only one species, *P. macronyx*, we found these variants as polymorphism. The Y chromosome could be submetacentric, subtelocentric, or acro-telocentric, but always with a small size. These morphological variations were described at intra- and inter-specific level. A constant chromosome number characterizes the *Abrothrix* species. In this genus, few variations in the FNa, due to differences in the number of small biarmed autosomes, were reported. These chromosome pairs are difficult to distinguish, and in some cases seem to correspond to differences in chromatin condensation among samples. A 2n = 44 was referred to *Abrothrix* in a simple report (Supplementary Table 2). The same occur with the mentioned diploid number of 52 for *Paynomys macronyx* and *Geoxus valdivianus*, but none of these chromosome complements were showed to corroborate the information (Supplementary Table 2).

Molecular divergence within the tribe

Molecular divergences based on cytochrome b sequences were very high among all the studied species of the tribe (Supplementary Table 3), whereas the nuclear markers showed lower levels of variability. The variation in the mitochondrial marker was in general an order of magnitude greater than in nuclear sequences. The number of substitutions found in the βFBG was superior to the one observed in the Adh; the IRBP presented the lowest variation. There was a taxonomic scaling in the genetic distances in all molecular markers

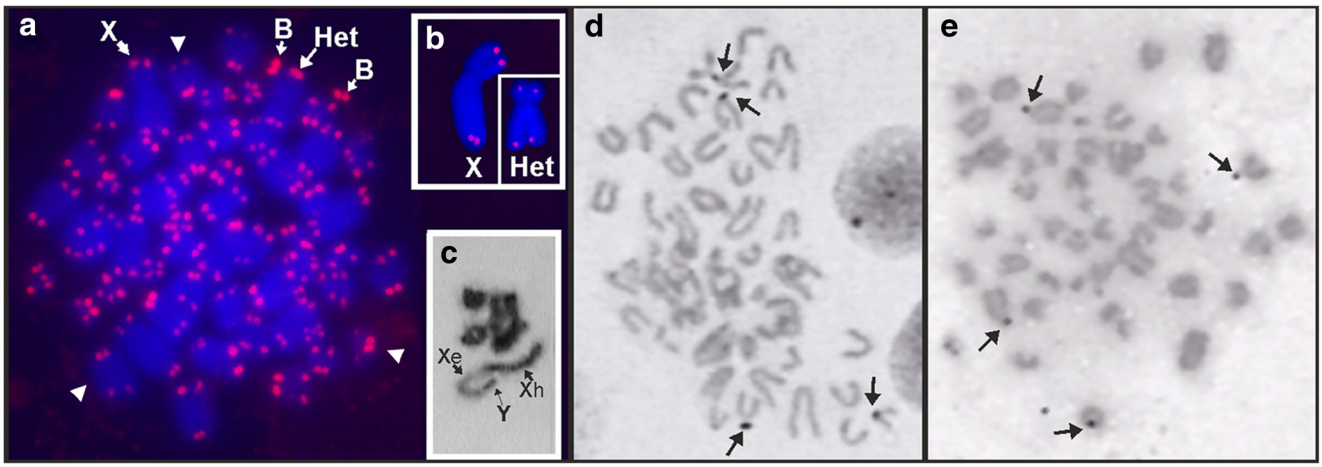

Fig 3 **a** FISH in *Paynomys macronyx* with the pantelomeric probe. The arrows indicate the X, the biarmed chromosome of the heteromorphic pair and two B chromosomes. Note the strong signals in the supernumerary chromosomes. Arrowheads indicate chromosomes with different intensity of fluorescent signals at both ends. **b** Detail of the X chromosome and the biarmed homolog of the heteromophic pair. **c** Meioses in *P. macronyx*. Detail of the sex pair in diakinesis. Xe = euchromatic arm of the X chromosomes, Xh = heterochromatic arm of the X chromosome, Y = chromosome Y. **d** NORs in *Abrothrix hirta*. **e** NORs in *P. macronyx*

analyzed. But Abrotrichina, which include all its diversity in the unique genus *Abrothrix*, displayed similar values of maximum divergence than Notiomyina, in which the comparisons encompassed three to four genera depending on the marker (Supplementary Table 3). The only exception was the βFBG, where the values of maximum divergence were similar to the maximum observed for the entire tribe.

Discussion

Earlier taxonomic assessments, mostly based on morphological evidences, placed Abrotrichini as part of Akodontini, with whom they share several morphological traits (see Reig 1987). Molecular data provided by recent studies enable the novel diagnosis of the tribe, which is strongly supported in all phylogenetic analyzes (Smith and Patton 1999; D'Elía 2003; Parada et al. 2013; Cañón et al. 2014), and is characterized by deep genetic divergences between species (see Supplementary Table 3). Cytogenetic evidence indicate a conserved 2n = 52 and FNa = 56 with minor variations in the FNa for the genus *Abrothrix*, including representatives of the four known subgenera (Bianchi et al. 1971; Gallardo 1982; Rodriguez et al. 1983; Patterson et al. 1984; Liascovich et al. 1989; Spotorno et al. 1990; Feijoo et al. 2010; present work). The morphology of the Y chromosome varies at both intra- and inter-specific level, as in others genera of sigmodontine rodents (Lanzone et al. 2016). The occurrence of a population of *Abrothrix* cf. *A. olivacea* in Comodoro Rivadavia (Chubut, Argentina) with 2n = 44 (Rodriguez and Theiler 2007) needs further confirmation. This 2n resembles the chromosome complements of some species of *Akodon*, a genus morphologically similar to *Abrothrix*, with which it can be easily confused (Teta et al. 2016 and references therein).

Due to its extensive occurrence, some authors suggest that the 2n = 52 represents a synapomorphic character for the tribe Abrotrichini (Smith and Patton 1999). The revision of the literature indicates that this 2n is shared by all *Abrothrix* species (subtribe Abrotrichina; sensu Teta et al. 2016), but not for its sister clade Notiomyina (Teta et al. 2016). This 2n is also shared by some akodontines such as *Thaptomys* and *Brucepattersonius* (Lanzone et al. 2018 and references therein), as well as by some species from other tribes, such as the Oryzomyini *Nectomys rattus* (Maia et al. 1984; Bonvicino et al. 1996), and the Phyllotini *Eligmodontia moreni* (Lanzone et al. 2016), among others. Evidences based on the chromosome painting technique, combined with molecular phylogeny, indicate that 2n = 52 is the plesiomorphic condition for the subfamily Sigmodontinae (Swier et al. 2009). This suggests that the chromosome complement of *Abrothrix* species could be very similar to that of the ancestral complement of the subfamily, which reinforces the hypothesis of chromosome stability within this genus.

There is no chromosomal data for some of the species within the Notiomyina clade (see Supplementary Table 2). However, *Paynomys* and *Geoxus* display chromosomal differentiation in the diploid and fundamental numbers, complementing and confirming previous observations (Ojeda et al. 2005; D'Elía et al. 2006; present work). Considering the 2n = 52 ancestral for the tribe, these species show an increase in the 2n and FNa, which can be distinctive for the subtribe. Phylogenetic analyzes, based on molecular and morphological characters, showed that *Pearsonomys* and *Geoxus* are congeneric forms (Smith and Patton 1999; D'Elía et al. 2006; Teta et al. 2016). This relationship is also supported by chromosome data, because both taxa share very similar chromosome complements (D'Elía et al. 2006; Supplementary Table 2). Pearson (1984) described a 2n = 52 for *Geoxus valdivianus*, indicating that this 2n was identical- or almost- to that of *P. macronyx*. However, none of these chromosome complements were exhibited to corroborate the information and may represent errors in the literature.

To accommodate the taxonomy with the evolutionary history of the taxa recovered in the phylogenetic trees, Teta et al. (2016) named a new genus, *Paynomys*, to include *Chelemys macronyx*, which in turn do not form a monophyletic group with *C. megalonyx* (the type species of the genus *Chelemys*). Unfortunately, the karyotype of *C. megalonyx* is unknown. On the other hand, *P. macronyx* not only differs from all other abrotrichines in terms of their 2n and FN, but also differs in the presence of B chromosomes, which varies at intra- and inter-population levels (Ojeda et al. 2005 and data cited there; present work). Other chromosome characteristics, apparently unique in *Paynomys* within abrotrichines, are the polymorphism in the X chromosome and the occurrence of a medium sized chromosome almost completely heterochromatic. All these differential chromosomal characteristics support the inclusion of *P. macronyx* in its own genus.

The karyotypes of *Paynomys* and *Geoxus* are morphologically very similar, supporting their close relationship. *Geoxus annectens* and *P. macronyx* share a pair one subtelocentric and a submetacentric X chromosome (Ojeda et al. 2005; D'Elía et al. 2006; present work). In all *Abrothrix* species, pair one is acrocentric and the X is subtelocentric. Thus, chromosome characteristics support the differentiation of both major clades within Abrotrichini.

Species within the tribe Abrotrichini have low chromosome variability. Several taxa share the same complement, and the ranges of variation in the 2n and FNa are narrow. In addition, species diverging in the 2n and FNa were very similar in DAPI, C, and Ag-NOR banding pattern, which indicate conservation in most chromosomes pairs. However, the divergence among cytochrome b sequences within the abrotrichines is high, compared with that of most rodent species (Baker and Bradley 2006), indicating uncoupling between the rates of chromosomal and mitochondrial evolution.

In the case of abrotrichines, chromosome evolution appears to be slower than molecular one in the mitochondrial genome. This incongruence between cytogenetic and molecular evidence was also observed in some other rodents, where chromosome evolution appeared accelerated compared with a low molecular divergence (Buschiazzo et al. 2018). On the other hand, molecular divergences in the nuclear sequences were low, as observed in other rodents (D'Elía 2003; Steppan et al. 2007), regardless of its chromosome variability. The βFBG was the marker with the highest number of substitutions, which was also observed in other taxa (Henson and Bradley 2009; Machado et al. 2014). However, there are different combinations of molecular markers used in different works, especially from the nuclear genome, which prevent broader comparisons among sigmodontines.

Chromosomes in *P. macronyx*

This species is very peculiar among rodents, since it possess three chromosome variations that are uncommon to this group. *Paynomys macronyx* has B chromosomes, heterochromatic variations of the X chromosome, and a heteromorphic pair of autosomes. However, FISH signals were observed only at the ends of all chromosomes. Some variations in the intensity of signals in some autosomal pairs were observed, but not in the chromosomes that present polymorphic variants. This suggests that telomeric sequences are not related to the chromosomal modifications detected in *Paynomys*. Strict telomeric signals are also common in some sigmodontines displaying chromosome rearrangements (Lanzone et al. 2015). However, in the B chromosomes, signals were very strong, suggesting that they are composed in a large proportion of telomeric sequences. Additional telomeric repeats were also recorded in several B chromosomes of other mammals (Vujošević et al. 2018).

Supernumerary chromosomes are infrequent in mammals, with most descriptions in the literature belonging to rodents from the superfamily Muroidea (Palestis et al. 2004; Vujošević and Blagojević 2004; Vujošević et al. 2018). In general, these chromosomes are heterochromatic, as observed in *P. macronyx*, but they are found in low frequencies within populations (Palestis et al. 2004; Vujošević and Blagojević 2004). Some exceptions are that of *Trinomys iheringi*, where dot-like B chromosomes were observed in all individuals (Fagundes et al. 2004), plus that of some species of *Nectomys* in which several variants of supernumerary chromosomes were found in high frequency in some populations (Maia et al. 1984). Also, in two *Apodemus* species, *A. peninsulae* and *A. flavicollis*, Bs were found in almost all populations, in frequencies reaching 100 percent in the former species (Kartavtseva and Roslik 2004; Wójcik et al. 2004). In *P. macronyx*, these chromosomes were also dot-like and unstable, producing mosaicism in somatic cells in all specimens. In a review of Brazilian rodents carrying B chromosomes, it was reported that *Akodon montensis*, *N. squamipes*, *Oligoryzomys flavescens*, *Proechimys* sp., and *T. iheringi* presented mosaicism; but except for *Trinomys*, in all the other species this mitotic instability was observed only in some individuals (Fagundes et al. 2004; Silva and Yonenaga-Yassuda 2004). The high frequency of these chromosomes in *P. macronyx* and their instability suggest that they are in an early evolutionary stage of accumulation (Camacho et al. 2000), at least in the studied region.

Another unusual variation observed in *P. macronyx* is the polymorphism of the X chromosome (Fredga 1970, 1988; Paresque et al. 2007). These variations are due to differences in the length of its short arms, which are heterochromatic, as in *N. squamipes* (Maia et al. 1984) and *O. nigripes* (Paresque et al. 2007). Also, the occurrence of a mostly heterochromatic medium sized autosome is a rare cytogenetic feature. Intriguingly, a similar case was described in the phyllotine *Phyllotis xanthopygus*, from a population of the same geographic region as that of *P. macronyx* described here (Labaroni et al. 2014).

In *P. macronyx*, the CH content was higher than in the studied species of *Abrothrix*. Not only the pericentromeric blocks were bigger, but also larger amounts of CH in the X chromosome and in one autosome were detected. The occurrence of a large variability in the amount of CH in the X chromosomes, in addition to the presence of B chromosomes in high frequency, was also detected in *N. squamipes* (Maia et al. 1984). This suggests some relationship between the accumulation of CH in the standard complement, especially in the variable short arms of the X, and the presence of supernumerary chromosomes in these species. The relation between sex chromosomes and the origin of supernumerary chromosomes was demonstrated in some species (Karamysheva et al. 2002; Silva and Yonenaga-Yassuda 2004; Vujošević and Blagojević 2004; Rajičić et al. 2017), and seems to be the case for *P. macronyx*.

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