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Research Article

Phylogenetic relationships and karyotype evolution in the sigmodontine rodent *Akodon* (2n = 10 and 2n = 16) from Brazil

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Abstract

Comparison of G-bands from 2n = 10 and 2n = 16 karyotypes of *Akodon* revealed tandem fusions, pericentric inversions and Robertsonian rearrangement in autosomes and addition/deletion of constitutive heterochromatin in sex chromosomes. Cytochrome-b sequences indicate that the 2n = 10 karyotype is a new species and show it to be a sister taxon of the 2n = 14, 2n = 15 and 2n = 16 karyotypes. Indeed, this group shows a particular evolutionary situation in which a unique taxonomic unit based on morphological data can be detected, but, karyologically, it can be separated into two groups (2n = 14-15-16 and 2n = 10). Cytochrome-b sequences show a finer resolution, indicating that these four karyotypes represent three molecular entities (2n = 14-15, 2n = 16 and 2n = 10) that may be derived from a common ancestor with a 2n = 16 karyotype.

Key words: Akodon, cytochrome-b, G-bands, karyotypical evolution, phylogeny.

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Introduction

The Akodontini tribe encompasses about 35% of the total diversity of the extant species among 10 tribes of the subfamily Sigmodontinae of South American rodents (Smith and Patton 1993), although relationships at genera and species levels within this tribe remain uncertain.

Karyotypes have been useful in generating species classification and clarifying some systematic problems, especially those related to cryptic species within the genus *Akodon*. In *Akodon* the diploid chromosome number ranges from 2n = 9 or 10 to 2n = 52, with the majority of the members of this genus being characterized by relatively low chromosome numbers (Spotorno and Fernandez, 1976; Yonenaga *et al.*, 1976; Kasahara and Yonenaga-Yassuda, 1984; Liascovich and Reig, 1989; Svartman and Almeida, 1994; Geise *et al*., 1998; Fagundes and Yonenaga-Yassuda, 1998; Fagundes *et al.*, 1998; Silva and Yonenaga-Yassuda, 1998). Brazilian *Akodon* species with known karyotypes are as follows: *Akodon* sp. n. (2n = 9, 10); *A. cursor* (sensu Christoff, 1997) with 2n = 14, 15 and 16 (the latter diploid number has been cited as belonging to *Akodon* aff. *cursor* by Rieger *et al*., 1995, and Geise *et al*., 2001); *A. montensis* (2n = 23-26); *A. azarae* (2n = 38); *A. reinhardti* (2n = 37, 38); *A. lindberghi* (2n = 42); *A. serrensis* (2n = 46); *A. toba* (2n = 42 or 43) and *A. paranaensis* (2n = 44) (Yonenaga, 1972; Yonenaga, 1975; Yonenaga-Yassuda, 1979; Yonenaga-Yassuda *et al*., 1987; Castro, 1989; Sbalqueiro, 1989; Geise *et al*., 1996, 1998; Sbalqueiro and Nascimento, 1996; Fagundes *et al*., 1998; Silva and Yonenaga-Yassuda, 1998; Christoff *et al*., 2000).

Silva and Yonenaga-Yassuda (1998) suggested that the new 2n = 9, 10 karyotype (*Akodon* sp. n.) from Mato Grosso state in central Brazil ranks as a new *Akodon* species. This karyotype has an autosomal polymorphism in chromosome 3, which can be either an acrocentric or a submetacentric due to a pericentric inversion, and the odd diploid number (2n = 9) being caused by monosomy of the X chromosome.

The 2n = 14, 15 and 16 karyotypes have been assigned to the same taxonomic unit, *A. cursor* (Christoff, 1997; Fagundes *et al*., 1998), but based on cytochrome-b mitochondrial gene sequences Geise *et al*. (2001) argued that 2n = 16 specimens of this species from the Brazilian states of Paraná, Bahia and Minas Gerais should be recognized as being different from *A. cursor* and should be referred to as *Akodon* aff. *cursor*.

As the traditional classification of a large number of South American sigmodontine taxa remain poorly understood (Smith and Patton, 1999), chromosomal data and, more recently, mitochondrial DNA sequences (which al-

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low better identification of species and phylogeographic patterns) have provided relevant information to establish relationships among this and other groups (Smith and Patton, 1993, 1999; Myers *et al*. 1995; Da Silva and Patton 1998; Garcia 1999; Geise *et al*. 2001; Bonvicino and Moreira 2001).

In this paper we compare G-band patterns between the 2n = 10 and 16 *Akodon* karyotypes, and discuss the phylogenetic implications based on cytochrome-b sequences. Comparison of G-banded chromosomes, molecular systematics and biogeographic information provide additional data to aid our understanding of the evolutionary process as well as the present status and phylogeny of *Akodon*.

Material and Methods

Cytogenetic procedures

We used Seabright's method (1971) to obtain somatic cell G-banding patterns from 28 *Akodon* specimens with a 2n = 10 karyotype and compared the G-banded chromosomes of 2n = 10 specimens from Gaúcha do Norte in the Brazilian state of Mato Grosso and 2n = 16 (referred to as *A. cursor* by Fagundes *et al*., 1998) from the Brazilian state of São Paulo.

Sequencing procedures

Total genomic DNA from seven *Akodon* specimens with 2n = 10 (specimens MZUSP-29658, 29671, 29673, 29678, 29684, 29685 and APC-270) was extracted from muscle or liver using the Chelex (BioRad) method (Walsh *et al*., 1991). Tissues had previously been frozen in liquid nitrogen and transferred to 95% ethanol. The cytochrome-b gene was amplified by the polymerase chain reaction (PCR) with the MVZ05 and MVZ16 primer set as described by Smith and Patton (1993) and amplification confirmed by 2% agarose gel electrophoresis. The PCR products were sequenced using an ABI 377 automated sequencer using a d-Rhodamine cycle sequencing kit and the MVZ05 primer. The sequences were edited using the Sequence Navigator software (Applied Biosystems, Inc. 1994). Phylogenetic analyses under parsimony criterion were performed using the PAUP*4.0b6 program with 100 bootstrap replicates and Kimura-2-parameter distances (Kimura 1980) were also calculated.

The first 750 bp mitochondrial cytochrome-b sequences were obtained from seven *Akodon* specimens, four from Gaúcha do Norte and three from Vila Rica (both in Mato Grosso state), all specimens having been previously karyotyped. Since data indicated that these specimens share similar haplotypes we only use one specimen from each locality: the specimen MZUSP-29671 (GenBank accession number DQ631966) from Gaúcha do Norte and MZUSP-29685 (DQ631965) from Vila Rica in order to access the phylogenetic reconstruction. Other *Akodon* sequences and *Bolomys* (U03528) (*Necromys* after Smith and Patton, 1999) were obtained from GenBank, and the latter being used as the outgroup taxon. Voucher specimens with 2n = 9, 10 were deposited at the Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo state, Brazil.

Results and Discussion

Conventionally stained and banding patterns karyotypes of *Akodon* with 2n = 14, 15 and 15 have been reported by various authors (Yonenaga, 1972, 1975; Yonenaga-Yassuda, 1979); Sbalqueiro and Nascimento, 1996; Fagundes *et al*., 1998) and samples with a 2n = 9, 10 karyotype have been described by Silva and Yonenaga-Yassuda (1998).

We compared G-bands of the 2n = 10 and 2n = 16 karyotypes, as fewer steps were involved in the differentiation between these karyotypes than between 2n = 10 and 2n = 14. This analysis suggests that a similar karyotype or a diploid number higher than 2n = 16 gave rise to the lowest chromosome number of *Akodon* sp. n. (2n = 10). Diagrams of the 2n = 16 and 2n = 10 karyotypes are being shown in Figure 1.

Comparison of 2n = 10 and 16 G-banded metaphases (Figure 2) revealed the following complex chromosomal rearrangements: chromosome 1 of 2n = 10 could have derived from multiple tandem fusions of chromosomes 1 (after a pericentric inversion), 6 and 5q of a 2n = 16-like karyotype; chromosome 2 of 2n = 10 could have originated by a Robertsonian rearrangement of chromosomes 3 (after a pericentric inversion) and 4 of 2n = 16; chromosome 3 could have resulted from a tandem fusion involving chromosome 2 and probably 5p of 2n = 16; pair 4 of 2n = 10 and pair 7 of 2n = 16 were the smallest chromosomes of each complement and seemed to be totally homologous in both karyotypes. The X chromosome was larger in the 2n = 10

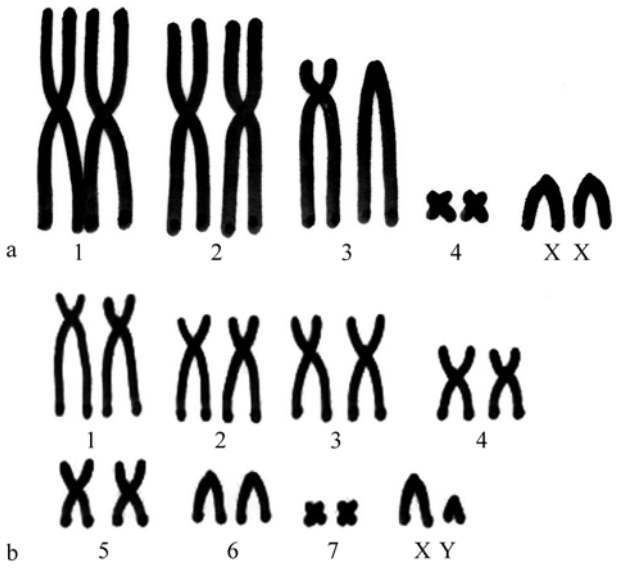

Figure 1 - Diagrammatic representation of *Akodon* karyotypes: (a) 2n = 10 with pair 3 heteromorphic. (b) 2n = 16.

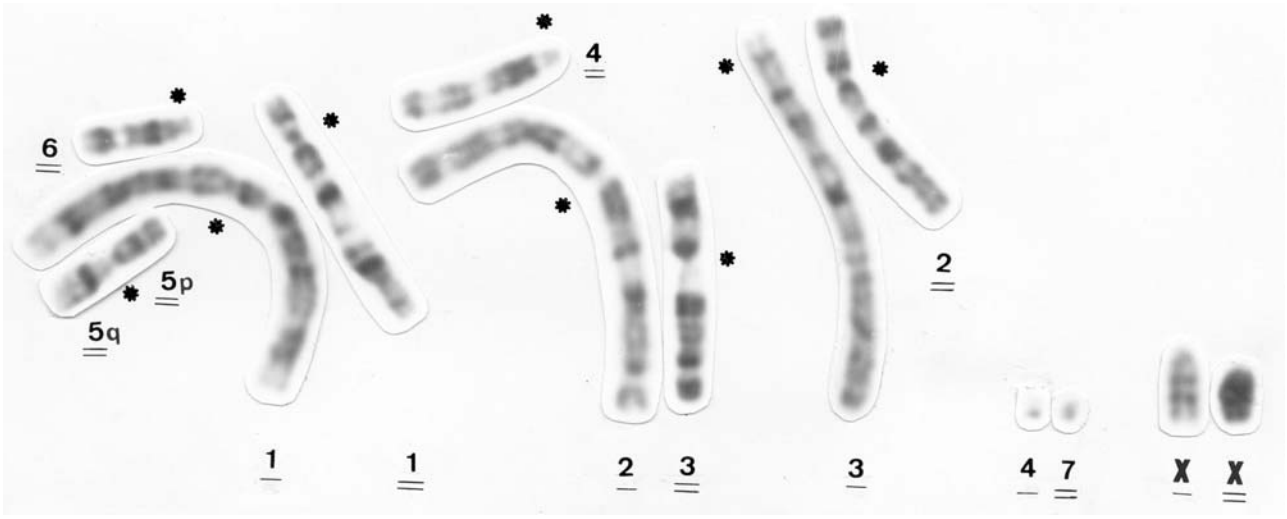

Figure 2 - Comparison of G-banded karyotypes: *Akodon* with 2n = 10 (left) and 2n = 16 (right). Asterisks indicate centromere positions.

than in the 2n = 16 karyotype due to the presence of a block of constitutive heterochromatin in the proximal region of the long arm and the Y chromosome was a minute subtelocentric whereas in 2n = 16 karyotype it was acrocentric.

Although we did not identify any homologies between the distal region of chromosome 3 of the 2n = 10 karyotype and the other components of the 2n = 16 karyotype it is possible that this sequence was lost from the ancestral 2n = 16 karyotype to give rise to the 2n = 16 karyotype and was then maintained in the 2n = 10 karyotype, although the distal region of chromosome 3 could have arisen as a result of amplification of a segment in 2n = 10 karyotype. Up to now we are not able to mention the origin, nature or function of this genetic material or if it implies difference in the fitness of the individuals. We can just mention that morphologically 2n = 10 and 2n = 16 seem to be indistinguishable (Christoff, in prep.)

Previous cytogenetic studies by Silva and Yonenaga-Yassuda (1998) revealed interstitial silver-stained nucleolar organizer regions (Ag-NORs) located at 1p and 1q, on the telomeric region of the 2p chromosome and the short arm of one pair 4 homologue of the 2n = 10 karyotype, the 2n = 16 karyotype reported by Fagundes *et al.* (1997) exhibited Ag-NORs on the telomeres of chromosome pairs 4 and 5. As far as we could detect, there was correspondence of Ag-NOR positions on the telomeric regions of both the 2p chromosome for the 2n = 10 karyotype and the 4p chromosome for the 2n = 16 karyotype. Absence of Ag-NORs on the 1p telomeres and their presence on one 2n = 10 pair 4 homologue could be due to either loss of NORs or relocation of ribosomal genes.

According to Fagundes *et al*. (1997) fluorescence *in situ* hybridization analysis (FISH) with a telomeric (TTAGGG)n probe resulted in only telomeric signals on the 2n = 16 karyotype chromosomes. Interestingly, Silva and Yonenaga-Yassuda (1998) reported conspicuous interstitial telomeric sites (ITS) on the pericentromeric region and the short arm of pair 1 and on the long arm of pair 3 of the 2n = 10 karyotype, in addition to the regular telomeric signals. However these signals detected on the 2n = 10 karyotype 1p and 3q chromosomes did not seem to be coincident with the specific positions involved in the chromosomal rearrangements. In addition, the pericentromeric signal of chromosome 1 was co-localized with pericentromeric constitutive heterochromatin, which is a highly repetitive DNA sequence. All this evidence led us to believe that much more complex rearrangements than we observe after the comparison of G-banded chromosomes had occurred during the evolutionary process which drove the differentiation of the 2n = 10 and 2n = 16 karyotypes.

Phylogenetic analyses and parsimony of cytochrome-b sequences support our previous chromosome results suggesting that the 2n = 10 *Akodon* karyotype is a new species. These animals from Gaúcha do Norte and Vila Rica (localities geographically separated by nearly 450 km) share quite similar haplotypes (Kimura-2-parameter equal to 0.002) which are grouped in a strongly supported monophyletic group (bootstrap value of 100%), reinforcing the requirement of a new taxonomic status for this species (Figure 3). Furthermore, this species is recovered as the sister group (with bootstrap support of 100%) of *Akodon* specimens with 2n = 14, 15 and 16 karyotypes, where the 2n = 16 karyotype is the sister group of 2n = 14 and 15 karyotypes. All of these three karyotypes show a common ancestor relative to other species of the *cursor*-complex, such as *A. montensis* and *A. mistax* (Figure 3).

Geise *et al*. (2001) reported a bootstrap value of 94% supporting *Akodon* with a karyotype of 2n = 14, 15 as a sister of the 2n = 16 karyotype, and referred to them as *A. cursor* and *Akodon* aff. *cursor*, respectively. After including our data (2n = 10 cytochrome-b sequences), the support for the relationships of these two taxa decreased to 72%, while

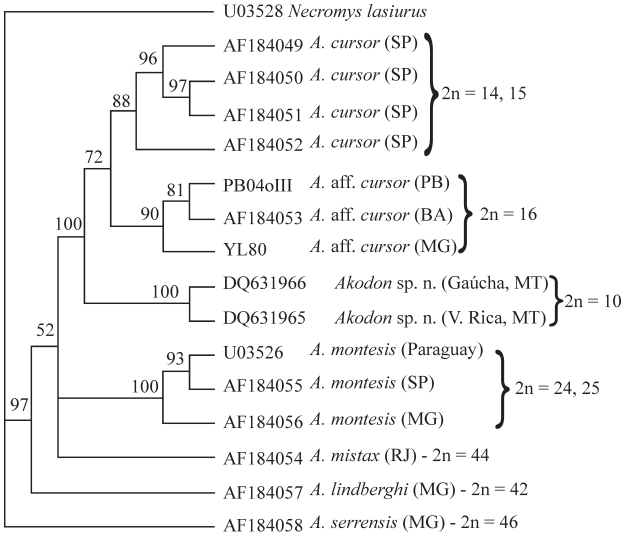

Figure 3 - Maximum parsimony majority consensus-tree (50% bootstrap) after a search with 100 replicates. Ninety-seven variable characters are parsimony uninformative and 558 are constant.

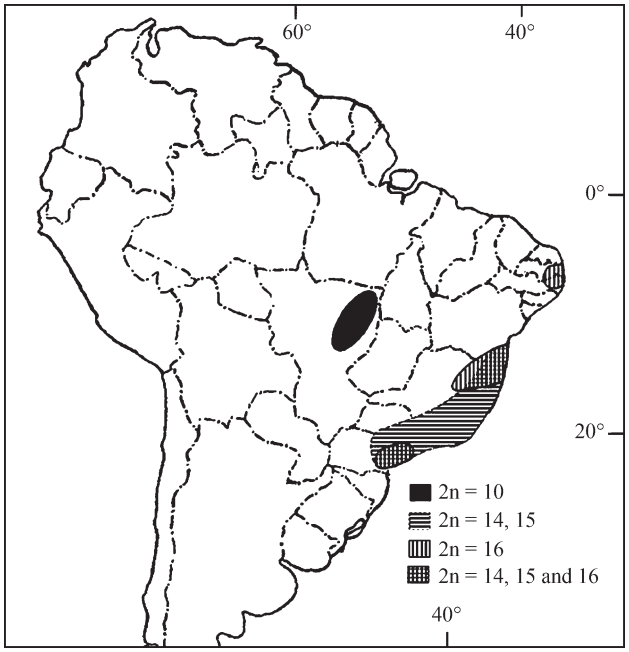

Figure 4 - Distribution of *Akodon* with 2n = 10; 2n = 14,15 and 2n = 16, summarized from Yonenaga-Yassuda (1979); Maia and Langguth (1981); Rieger *et al*. (1995); Sbalqueiro and Nascimento (1996); Fagundes *et al*. (1998); Silva and Yonenaga-Yassuda (1998); Geise *et al*. (2001).

the bootstrap values to support the 2n = 14, 15 and 2n = 16 karyotypes as monophyletic groups increased respectively to 88 and 90%.

Kimura-2-parameter (K2p) distances within and among taxa were as follow: geographic samples of the 2n = 10 karyotype differed by 0.002; 2n = 14-15 by 0.007-0.023; 2n = 16 by 0.032-0.052; and 2n = 10 differed from 2n = 14-15 by 0.053-0.062 and from 2n = 16 by 0.057-0.071; 2n = 14, 15 differed from 2n = 16 by 0.040-0.067. *Akodon montensis* differed from them by 0.090-0.113 and *Necromys lasiurus* also differed from them by 0.155-0.190 K2p.

Maia and Langguth (1981) described an *Akodon* population from the Brazilian state of Pernambuco in which all specimens had a karyotype of 2n = 16. More recently, *Akodon* specimens with a 2n = 16 karyotype have also been found in the Brazilian states of Paraíba, Minas Gerais, São Paulo, Bahia and Paraná (Figure 4) (Rieger *et al*., 1995; Sbalqueiro and Nascimento 1996; Fagundes *et al*., 1998; Geise *et al*., 2001). Regardless of the karyotype diversity in *Akodon* specimens with 2n = 14, 15 and 16 karyotypes (a total of 28 karyotypes), Christoff (1997) and Fagundes *et al*. (1998), considered these specimens as a single species (*Akodon cursor*) and explained the variation as being due to pericentric inversions in three different chromosome pairs, a complex rearrangement involving centric fusion with previous pericentric inversions of two pairs, trisomy of pair 7 and monosomy of the X chromosome. But Christoff (1997) noted that *Akodon* specimens with 2n = 14, 15 and 16 karyotypes were not distinctive taxonomically by external or cranio-dental morphology, and grouped as one unique species. However, the phylogenetic analyses of mitochondrial sequence data revealed, with relatively high support (72%), a node in which the *Akodon* specimens from São Paulo with a 2n = 14 and 15 karyotype is the sister group of the *Akodon* specimens from Paraíba, Bahia and Minas Gerais with a karyotype of 2n = 16. Moreover, according to Geise *et al*. (2001), cytochrome-b sequences of *Akodon* specimens from Una (Bahia state) with a 2n = 14-15 karyotype share more similarities to specimens with the same karyotype which were 1500 km away than to 2n = 16 karyotype specimens collected in the same locality. Therefore if the 2n = 14 and 16 karyotypes were panmictic (randomly interbreeding) there should be no reason for their mitochondrial DNA to appear so different as the results show.

Rieger *et al*. (1995) used 22 structural loci encoding 14 proteins to check genetic variability in 22 *Akodon* specimens from Paraná with 2n = 16 karyotypes, 41 specimens from Espírito Santo with 2n = 14 and 15 karyotypes and 206 specimens from the Brazilian states of Santa Catarina and three localities in the Brazilian state of Rio Grande do Sul with 2n = 24, 25 and 26 karyotypes. On the basis of phenetic and phylogenetic data, Rieger *et al*. (1995) suggested that members of the *cursor*-complex have undergone recent differentiation and that chromosomal divergence has proceeded without eletromorphic divergence. We can add here that mitochondrial sequences can identify and separate these three units plus the new species with the 2n = 10 karyotype.

It is also interesting to point out that preliminary morphometric studies (Christoff *et al*., in prep.) showed no differences between 2n = 10 karyotype *Akodon* and *A. cur-*

sor (sensu Christoff, 1997), indicating the possibility that they are cryptic species as already observed in *A. cursor* and *A. montensis* (Christoff, 1997).

It therefore seems that a special evolutionary situation exists in which a group is recognized as a unique species on the basis of morphological traits but karyologically is clearly separated into 2n = 14, 15 and 16 forms and 2n = 10, with cytochrome-b sequences indicating that the 2n = 10 karyotypes represents a well supported full species and 2n = 24 is another strongly bootstrapped species while *Akodon* with 16 chromosomes is probably a different entity distinct from *Akodon* with 2n = 14-15 chromosomes as previously hypothesized by Geise *et al*. (2001).

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