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B chromosomes in Brazilian rodents

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Abstract. B chromosomes are now known in eight Brazilian rodent species: *Akodon montensis, Holochilus brasiliensis, Nectomys rattus, N. squamipes, Oligoryzomys flavescens, Oryzomys angouya, Proechimys* sp. 2 and *Trinomys iheringi*. Typically these chromosomes are heterogeneous relative to size, morphology, banding patterns, presence/absence of NORs, and presence/absence of interstitial telomeric signals after FISH. In most cases, Bs are heterochromatic and late replicating. Active NORs were detected in two species: *Akodon montensis* and *Oryzomys angouya*. As a rule, Bs behave as uni or bivalents in meiosis, there is no pairing between Bs and autosomes or sex chromosomes and also their synaptonemal complexes are isopycnotic with those in A chromosomes.

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Occurrence of B chromosomes in Brazilian rodents

In 1982, Jones and Rees reported B chromosomes in over a thousand species of plants and more than 260 animal species. From a total of 22 species of vertebrates, 19 were mammals with 12 species of rodents represented. Volobujev (1981) listed 18 species of rodents within the "B-chromosome system of the mammals", which included three Brazilian species: *Akodon* sp., *Proechimys iheringi* and *Oryzomys* sp. More than twenty years after Volobujev's review, the number of species with Bs is certainly higher than that previously reported.

Concerning Brazilian rodents, up to 1984, Kasahara and Yonenaga-Yassuda had compiled karyotypes of about 60 Brazilian species within the order Rodentia, recognizing six B-carrier species. Currently, about 140 species belonging to the families Muridae, Echimyidae, Caviidae, Ctenomyidae, Dasyproctidae, Hydrochaeridae were summarized in a cytogenetic compilation (Silva et al., 2004), including eight species harboring B chromosomes: *Akodon montensis* (2n = 24 + 0–2B), *Holochilus brasiliensis* (2n = 56 + 0–2B), *Nectomys rattus* (2n = 52 + 0–3B), *N. squamipes* (2n = 56 + 0–3B), *Oligoryzomys flavescens* (2n = 64 + 0–2B), *Oryzomys angouya* (2n = 58 + 0 or 2B), *Proechimys* sp. 2 (2n = 26 + 0–1B) and *Trinomys iheringi* (2n = 60 + 1–6B) (Table 1). It implies that about 5.7% of Brazilian rodents probably bear B chromosomes, a figure slightly larger than the 3.3% estimated for mammals in general (Vujocevic and Blagocevic, 2004).

Considerations on B chromosomes of Brazilian rodents

Characteristically in mammals, B chromosomes neither promote phenotypic alterations nor affect fitness of the individuals (Jones and Rees, 1982). By contrast, in plants for example, increasing numbers of Bs results in loss of vigor, reflected by delay in seed germination and the onset of flowering (Jones and Rees, 1982). In the parasitic wasp genus *Nasonia*, the paternal sex-ratio (PSR), a B chromosome, causes all-male offspring (Werren, 1991) and, in the fungus *Nectria haematococca*, Bs confer resistance against toxins (Miao et al., 1991). Similarly, chiasma frequency in A chromosomes can also be affected (Volobujev, 1981).

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Table 1. Occurrence of B chromosomes in Brazilian rodents

Species	No. of Bs	Locality (states)	B chromosome characteristics	References
Akodon montensis (2n = 24)	0	São Paulo, Rio de Janeiro		Cestari and Imada, 1968 Geise et al., 1998
	0, 1, 1/2[a]	São Paulo	Medium submetacentric: uniformly G-banded, uni or bivalent	Kasahara, 1978
	0, 1, 2	Santa Catarina, Rio Grande do Sul	Medium submetacentric: BG proximal in the long arm, slightly C-banded	Christoff, 1991
	0, 1	São Paulo	Medium submetacentric: late replicating; slightly heterochromatic, univalent in meiosis; SC do not exhibit distinct behavior in relation to the autosomes; NORs in both ends of both arms	Assis et al., 1978 Yonenaga-Yassuda et al., 1992 Fagundes, 1993, 1997
	0, 1, 2	Rio Grande do Sul	Submetacentric: slightly C-positive, uni or bivalents in meiosis NORs in both ends of both arms	Castro, 1989
Holochilus brasiliensis (2n = 56)	0, 1, 2	Maranhão	Large submetacentrics with different sizes: almost entirely G-positive; two strong C-positive blocks in the pericentromeric region of both arms; late replicating Absence of NORs	Freitas et al., 1983; Yonenaga-Yassuda et al., 1987
			Large metacentric, two strong C-positive blocks in the pericentromeric region of both arms; late replicating Absence of NORs	Present review
Nectomys rattus (2n = 52)	0, 1, 2, 3	Pernambuco	Medium metacentric: totally heterochromatic; Absence of NORs Small acrocentric: heterochromatin distal in the long arm; Absence of NORs	Furtado, 1981 Maia et al., 1984
	0	Paraíba, Amazonas, Pará, Maranhão, Piauí, Mato Grosso do Sul, Brasília (D.C.)		Zanchin, 1988 Yonenaga-Yassuda et al., 1988 Svartman, 1989 Bonvicino et al., 1996
	1	Mato Grosso	Large subtelocentric: almost totally heterochromatic, except for the short arm; proximal G-positive band in the long arm; late replicating; FISH: absence of interstitial telomeric sites (ITS); Absence of NORs	Silva and Yonenaga-Yassuda, 1998
	0, 1	Tocantins	Medium submetacentric: totally heterochromatic; Absence of NORs	Lima, 2000
Nectomys squamipes (2n = 56)	0, 1	Pernambuco	Acrocentric (size not mentioned); Absence of NORs	Yonenaga, 1972 Freitas, 1980
	0, 1, 2, 0/1[a]	São Paulo	Medium submetacentric and one larger-sized submetacentric; heterochromatin in the long arm and pericentromeric regions or C-band in the middle long arm; Absence of NORs	Furtado, 1981 Maia et al., 1984
	0, 1, 2, 3	Rio de Janeiro	Medium submetacentric and one submetacentric smaller than the medium-sized; Absence of NORs	
	0, 1, 2	Rio Grande do Sul	Medium submetacentric: very light C-banding in the entire long arm or spreads over the long arm and pericentromeric regions; Absence of NORs	
	0, 1, 2	Paraná	Not mentioned	Sbalqueiro et al., 1986 Bossle et al., 1988
	0, 1, 2, 3	Rio Grande do Sul, Bahia, Espírito Santo	Bahia and Rio G. Sul: submetacentric and subtelo/submetacentric; Espírito Santo: subtelo/submetacentric	Zanchin, 1988
	0, 1, 2	São Paulo	Medium submetacentric different sizes; C-band interstitial in the long arm; G-negative band in the proximal region of the long arm; late replicating; Absence of NORs	Yonenaga-Yassuda et al., 1988
	0	São Paulo, Minas Gerais, Rio de Janeiro, Mato Grosso do Sul, Bahia		Bonvicino et al., 1996
	0, 1	São Paulo	Medium submetacentric: C banding in the long arm; almost all G-positive, except for the proximal G-negative band in the long arm; late replicating; FISH: a strong block of telomeric band in the proximal region of the long arm; univalent; synaptonemal complexes (SC) do not exhibit distinct behavior in relation to the autosomes; Absence of NORs Medium acrocentric: heterochromatic block distal in the long arm; G-positive band distal in the long arm; early replicating, except for a tiny proximal band; FISH: absence of interstitial telomeric sites (ITS); Absence of NORs	Silva and Yonenaga-Yassuda, 1998

Table 1 (continued)

Species	No. of Bs	Locality (states)	B chromosome characteristics	References
Oligoryzomys flavescens (2n = 64)	0, 2	São Paulo	Minute submetacentrics: heterochromatics; behave as bivalents in the meiosis of individuals with 2n = 66	Yonenaga et al., 1976 Kasahara, 1978 Kasahara and Yonenaga-Yassuda, 1984
	0, 1, 2, 0/1[a]	Paraná, Rio Grande do Sul	Small acrocentrics: heterochromatics less intensely stained than the pericentromeric blocks of A chromosomes; univalent in meiosis of individuals with 2n = 65 Absence of NORs	Sbalqueiro et al., 1991
	0	Tocantins		Lima, 2000
Oryzomys angouya (2n = 58)	0	São Paulo		Almeida, 1980
	0	Espírito Santo, Rio Grande do Sul		Zanchin, 1988
	0, 2	São Paulo	Minute metacentrics: heterochromatic, G-positive NORs in both ends of both arms	Silva, 1994 Present paper
	0	Rio de Janeiro		Geise, 1995
Proechimys sp. 2 (2n = 26)	0, 1, 0/1[a]	Pará	Minute acrocentric: heterochromatic, univalent	Barros, 1978
Trinomys iheringi (2n = 60)	1, 2, 3, 4, 5, 2/3[a]	São Paulo	Minute chromosomes: heteromorphic in size, non-heterochromatics; they do not present late replication Absence of NORs	Yonenaga 1972, 1975 Souza, 1981 Kasahara and Yonenaga-Yassuda, 1984 Yonenaga-Yassuda at al., 1985
	2, 3, 4, 5, 6	São Paulo	Minute chromosomes: non-heterochromatics, they do not present late replication; uni or bivalent in meiosis Absence of NORs	Fagundes, 1993

[a] Indicates mosaicism. Other kinds of variation in diploid number were also reported in some species, but we just consider here those related to B chromosomes.

Comparative analysis between B chromosome-bearing specimens and non-carriers in the Brazilian rodent *Akodon montensis* evidenced neither morphological alteration nor differences in cranial measurements of both B carriers and non-carrier individuals (Christoff, 1991). As summarized in Table 1, 2n = 24 is the standard karyotype for this species and one or two medium-sized submetacentric Bs were reported as uniformly G-banded, slightly C-banded, late replicating and bearing NORs. Compiled data from studies performed by Kasahara (1978), Castro (1989), Christoff (1991), Fagundes (1993) and Geise et al. (1998) revealed a total of 238 specimens with no B chromosomes (69.32%) – including one specimen with 23/24 that lost the Y in cells with 23 chromosomes and five with 2n = 23 due to monosomy of sex chromosome (2n = 23, X0) – 99 with 1B (28.13%); 8 with 2B (2.27%) and one being 1B/2B mosaic (0.28%).

Studies in *Holochilus brasiliensis* using 5-BrdU in cell cultures in order to evaluate the influence of 0, 1 or 2Bs on sister chromatid exchanges (SCE) rates revealed that neither specimens with 1B nor those with 2B exhibited significant differences in SCE rates relative to animals with 0B, suggesting that the number of SCEs was not affected by the presence of one or two Bs (Silva, unpublished data) (Fig. 1).

In the literature, cytogenetic data are available for seven specimens of *H. brasiliensis*. Two males and one female (2n = 56) lacked B chromosomes, three females carried a single B (two of them resulting from a cross between a 1B female and a 0B male) and one male carried two B chromosomes. Bs were of two different types, both being large submetacentrics but one of them was larger than the largest A chromosome (Yonenaga-Yassuda et al., 1987). Differential staining after C-banding showed two C-positive blocks proximal in the pericentromeric region in both arms with the remaining chromosome regions showing an intermediate intensity staining (Table 1).

B chromosomes in *Nectomys rattus* and *N. squamipes* were medium and large sized chromosomes which varied in morphology and differential staining (C, G and R banding patterns) but they have never been shown to carry NORs (Table 1).

By contrast, minute or small supernumerary chromosomes have been reported in *Oligoryzomys flavescens, Oryzomys angouya, Proechimys* sp. 2 and *Trinomys iheringi* (Table 1).

In *Oligoryzomys flavescens* (2n = 64), one or two Bs have been found (Table 1). In total, 35 individuals had no Bs (57.38%), 9 showed 1B (14.75%), 14 carried 2B (22.95%) and 3 were 0B/1B mosaics (4.92%).

Compilation of the available data in *Oryzomys angouya* revealed 26 individuals lacking Bs (25 with 2n = 58 and one with 2n = 57 due to a Robertsonian rearrangement involving two autosome acrocentrics) and one with two minute Bs (Fig. 2) (Table 1). These chromosomes were slightly heteromorphic in size, heterochromatic, G-positive although less intensely stained than the darker bands (Fig. 3) and NOR carrier at the ends of both arms (Fig. 4).

Proechimys sp. 2 showed 2n = 26 in two specimens, 2n = 26 + 1B in two individuals; and 2n = 26/26 + 1B in four specimens (Table 1). Animals with B chromosomes were no longer collected in nature thus representing a unique record in 25 years. According to Barros (1978), the mosaic 2n = 26/27 was a result of loss of the B chromosome during somatic divisions due to its instability.

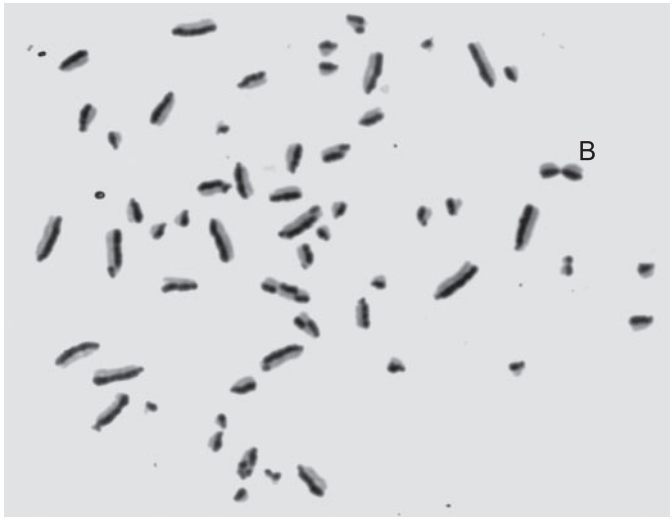

Fig. 1. Metaphase showing SCE (sister chromatid exchange) in *Holochilus brasilensis* (2n = 56 + 1B). B is indicated.

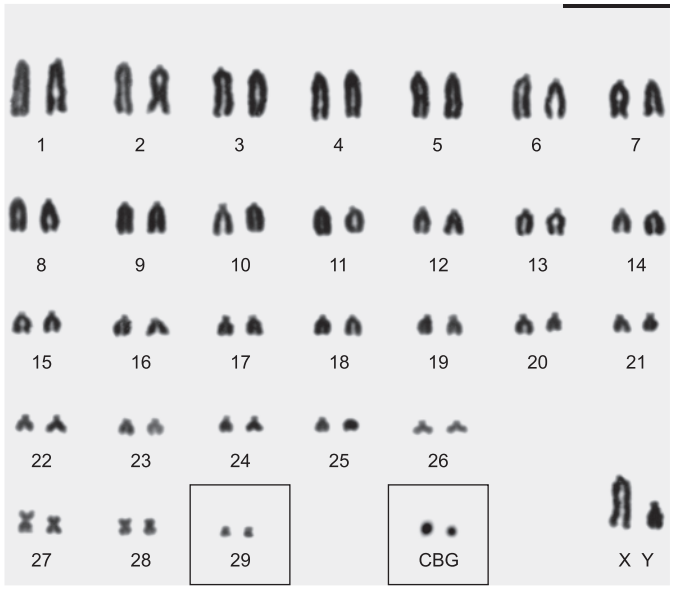

Fig. 2. Conventionally stained karyotype of *Oryzomys angouya* (2n = 60). Minute metacentrics, indicated as chromosomes 29, are B chromosomes. Heterochromatic pattern of these chromosomes is exhibited in the square (CBG = C-banding pattern): note heteromorphism in size of heterochromatic blocks. Bar = 10 μm.

In *Trinomys iheringi*, 2n = 60 is supposed to be the standard chromosomal complement although animals with this diploid number have never been found: all sampled specimens showed at least one B chromosome (Table 1). Kasahara and Yonenaga-Yassuda (1984) found 2n = 61 to 65 and 2n = 62/63. The variation in the diploid number was suggested to be due to the presence of one to five minute supernumeraries regularly with the same size (however heteromorphism was detected in one specimen). The 2n = 62/63 karyotype represents a mosaic showing intraindividual variation for B chromosome number presumably due to B mitotic instability (Table 1). Data summarized from Kasahara and Yonenaga-Yassuda (1984), Yonenaga-Yassuda et al. (1985) and Fagundes (1993) reveal five animals with 2n = 61 (22.73%); five with 2n = 62 (22.73%); four with 2n = 63 (18.18%); four had 2n = 64 (18.18%); two presented 2n = 65 (9.1%), one with 2n = 66 (4.54%) and one was a mosaic with 2n = 62/63 (4.54%), all of them from the state of São Paulo. Maintenance of this polymorphism was explained due to the existence of accumulation mechanisms in the gametogenesis process (Yonenaga-Yassuda et al., 1985). But we cannot be confident that these extra chromosomes are Bs until individuals with 60 chromosomes are found which demonstrates the dispensability of the supernumerary chromosomes.

More recently, B chromosomes in non-Brazilian rodents have been molecularly explored by fluorescence in situ hybridization, microdissection and sequencing methodologies. Karamysheva et al. (2002), for instance, performing microdissection followed by DOP-PCR and painting metaphases with the generated probes from B chromosomes in the Korean field mouse *Apodemus peninsulae*, found that all B chromosomes contained a large amount of repeated DNA sequences equivalent to the pericentromeric regions of all autosomes and non-centromeric C-blocks of the sex chromosomes.

Molecular approaches were also reported in the Brazilian water rat *Nectomys squamipes*. In situ hybridization with telomeric probes $(TTAGGG)_n$ revealed the presence of a strong interstitial block of these sequences in the submetacentric B (Silva and Yonenaga-Yassuda, 1998). Microdissection of the submetacentric B, followed by DOP-PCR and painting metaphases with the generated probes, showed hybridization with the constitutive heterochromatin of the short arms of the X chromosomes, which is considered a specific category of constitutive heterochromatin (Silva et al., unpublished data), although meiotic data confirmed that Bs behave as uni or bivalents: they were never found paired with autosomes or sex chromosomes. B synaptonemal complex (SC) neither shows peculiar behavior nor exhibits differences of staining when compared to those of A chromosomes. Remarkable heterogeneity in the composition of B chromosomes in samples of *N. rattus* and *N. squamipes* was reflected by localization of telomeric sequences, variability of amount and distribution of constitutive heterochromatin, size and morphology (Silva and Yonenaga-Yassuda, 1998) (Table 1).

Heterogeneous constitution and nature of different Bs have also been evidenced in the harvest mouse *Reithrodontomys megalotis*: these chromosomes share euchromatic arms, heterochromatic centromeric regions, absence of hybridization of the ribosomal gene probes, hybridization to LINE probes, telomeric sequences in both ends. However, the differences were concerned with the reduced amount of C-positive material in the smallest B and hybridization of the centromeric heterochromatin (pMeg-1) probe only in the largest B (Peppers et al., 1997).

A similar situation seems to be common in other groups of vertebrates. McQuade et al. (1994), for example, microdissected and amplified B chromosome DNA from a marsupial genus *Petauroides* and observed homologies between supernumeraries and centromeric regions of all autosomes, although

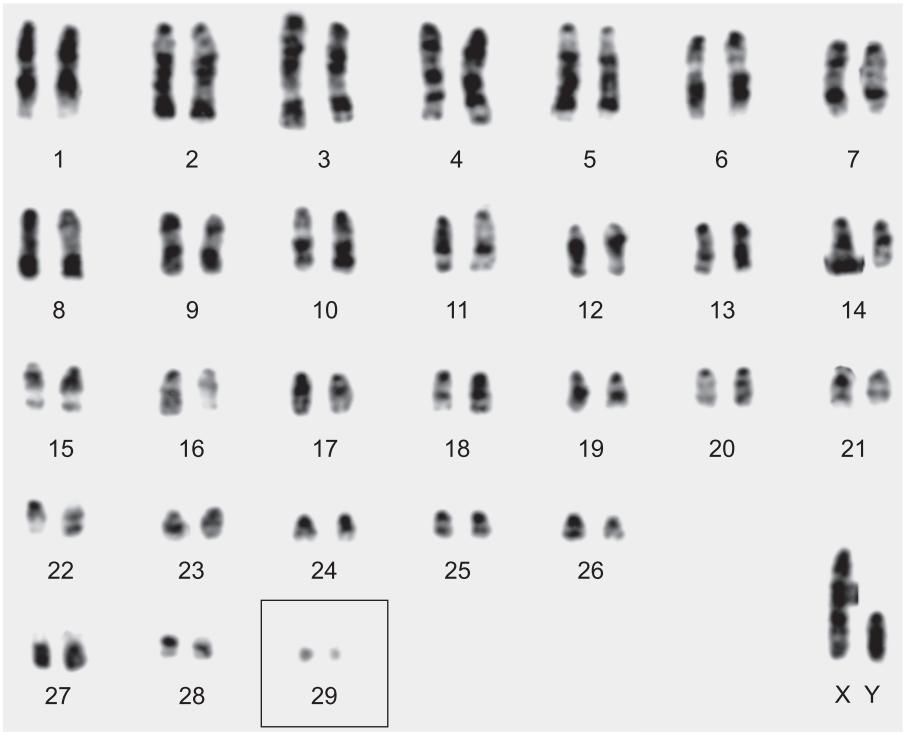

Fig. 3. GTG-banding pattern of *Oryzomys angouya* (2n = 60). B chromosomes are indicated in the square.

these chromosomes showed exclusive composition and heterogeneous DNA sequences. In *Nyctereutes procyonoides*, the raccoon dog, telomeric $(TTAGGG)_n$ sequences were also found to be distributed in the supernumeraries (Wurster-Hill et al., 1988).

Constitutively, B chromosomes are also composed of euchromatin. Empirical data reveal that these chromosomes are not necessarily inert and that chromatin structure or repression by genes on A chromosomes may cause their inactivity instead of the methylation process (López-Léon et al., 1995).

Ribosomal DNA was detected in several organisms (e.g. Assis et al., 1978; Wurster-Hill et al., 1986; Cabrero et al., 1987; Green, 1990; López-León et al., 1991; Yonenaga-Yassuda et al., 1992; Stitou et al., 2000). Two Brazilian species of rodents, *Akodon montensis* and *Oryzomys angouya,* carry Bs with active NORs in some individuals. Nucleolar organizer regions have also been described in *Rattus rattus* by Stitou et al. (2000), who suggested that the accessory chromosomes have originated from one of the smaller NOR-carrying chromosome pairs, and in the course of evolution, repetitive sequences invaded the supernumerary and NORs were inactivated by heterochromatinization and methylation.

Regarding mechanisms of origin and evolution of B chromosomes, the most accepted hypothesis suggests that a new chromosome originates due to non-disjunction or other kind of rearrangement followed by gradual modification of this chromosome because of successive mutations and structural modification until there is a complete loss of homology and capacity to pair with the original A chromosome (Volobujev, 1981; Vujosevic and Zivkovic, 1987; Beukeboom, 1994).

Green (1990) suggested that structural differences between B and A chromosomes were the result of mechanisms for divergence similar to that observed for Y chromosomes, given that some regions have weak selective pressure and evolve quickly from one generation to another. This hypothesis was supported by studies in maize in which recently originated B chromo-

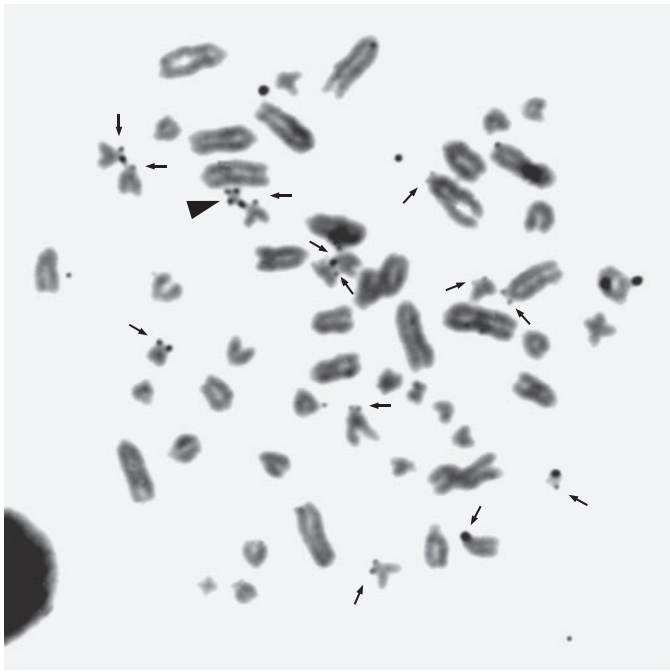

Fig. 4. Total of 15 Ag-NORs (arrows) of *Oryzomys angouya* (2n = 60), including NORs in both telomeres of one minute supernumerary (arrow head).

somes become more heterochromatic in successive generations (Peeters et al., 1985).

Camacho et al. (1997) suggested that Bs may evolve towards neutrality by losing both drive and effects on carrier fitness, but the B chromosome polymorphism may persist in natural populations because new parasitic B variants may appear and replace the near-neutral B, which would otherwise be condemned to extinction.

Most studies focusing on B chromosomes in Brazilian rodents are related to their structure and composition. Origin and evolution of these chromosomes still remain unclear, however in the light of the present review intriguing questions emerge and should be considered.

Regarding the pair of species *Nectomys squamipes* and *N. rattus,* the question is: have these chromosomes originated separately in each species or have they had a common ancestry and diverged separately in each species?

Similarly, the presumptive B chromosomes in *Trinomys iheringi* demand additional research. They are non-heterochromatic minute chromosomes showing early replication which appeared in all 22 animals collected in different years and different seasons. The theoretical basic diploid number, 2n = 60, has never been found in nature (Kasahara, 1978; Kasahara and Yonenaga-Yassuda, 1984; Fagundes, 1993). Then, what do the euchromatic and early replicating supernumeraries really mean in the evolutionary history of this species? The possibility also remains that they are not dispensable, since no individuals lacking them have been hitherto found, so that they could even be incipient A chromosomes.

We believe that the question about *Nectomys* should be investigated by the association of phylogeographical and molecular studies since the ancestral condition of these chromosomes could be checked out in the pair of species; and in *Trinomys iheringi*, molecular approaches using FISH, microdissection and DNA sequencing will probably help to figure out the nature of those euchromatic dot-like supernumeraries. A more extensive sampling and performing controlled crosses could also help to test the dispensability of the minute chromosomes, by trying to find individuals lacking them. And, finally, the origin of NORs in *Akodon montensis* and *Oryzomys angouya* remains an important point to be investigated.

It is also important to stress here that many Brazilian regions still need to be surveyed. Therefore the present knowledge of the number of B-carrier rodent species may be an underestimation reflecting our scarce knowledge of the Brazilian biodiversity.

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