Hereditas 127: 217–229 (1997)

New karyotypes of two related species of *Oligoryzomys* genus (Cricetidae, Rodentia) involving centric fusion with loss of NORs and distribution of telomeric $(TTAGGG)_n$ sequences

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Silva, M. J. de J. and Yonenaga-Yassuda, Y. 1997. New karyotypes of two related species of *Oligoryzomys* genus (Cricetidae, Rodentia) involving centric fusion with loss of NORs and distribution of telomeric $(TTAGGG)_n$ sequences. — *Hereditas 127*: 217–229. Lund, Sweden. ISSN 0018-0661. Received February 4, 1997. Accepted August 7, 1997

Comparative cytogenetics studies based on conventional staining, CBG, GTG, RBG-banding, Ag-NOR staining, fluorescence in situ hybridization (FISH) using telomere probes, length measurements, and meiotic data were performed on two related but previously undescribed cricetid species referred to as *Oligoryzomys* sp. 1 and *Oligoryzomys* sp. 2, respectively, from Pico das Almas (Bahia: Brazil) and Serra do Cipó (Minas Gerais: Brazil). *Oligoryzomys* sp. 1 had $2n = 46$ and *Oligoryzomys* sp. 2 had $2n = 44$, 44/45. Our banding data and measurements as well as FISH results support the hypothesis that the difference between the diploid numbers occurred by centric fusion events. The karyotypes had conspicuous and distinguishable macro- and micro-chromosomes, and we suppose that the largest pairs (1, 2, and 3) have evolved from a higher diploid number because of successive *tandem* fusion mechanisms.

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Within the rodents, the New World Cricetidae have been separated into two subfamilies: Sigmodontinae, which is found basically in South America, and Neotominae in North America. The South American subfamily is subdivided into seven tribes. Among them, the Oryzomyini is a complex Neotropical cricetid group, which consists of a variable number of genera, subgenera, and species (TATE 1932; HERSHKOVITZ 1996; HAIDUK et al. 1979; REIG 1986).

Oligoryzomys was described as a subgenus of *Oryzomys* and is usually recognized as such, or accepted as a full genus. CARLETON and MUSSER (1989) accepted *Oligoryzomys* as a genus, based on a small body size, small ears, a long tail and feet, a small skull, a short rostrum, interorbit smooth and hourglass shape, the lack of a sphenofrontal foramen and squamosal-alisphenoid groove (but with stapedial foramen) and opisthodont incisors. They recognized 15 species distributed in five groups: (1) **nigripes**, which includes *Oligoryzomys nigripes*, *Oligoryzomys eliurus*, *Oligoryzomys destructor*, *Oligoryzomys longicaudatus*, and *Oligoryzomys delticola*; (2) **flavescens**, which includes *Oligoryzomys flavescens*, and the three following undescribed species: *Oligoryzomys* sp. A (from Serra do Caparaó: state of Minas Gerais: Brazil), *Oligoryzomys* sp. B (from several localities in the Bolivian and Peruvian Andes), and *Oligoryzomys* sp. C (from Altiplano of southern Peru); (3) **fulvescens**, which includes *Oligoryzomys fulvescens*, *Oligoryzomys arenalis*, and *Oligoryzomys vegetus*; (4) **microtis**, represented by *Oligoryzomys microtis*; and (5) **andinus**, which includes *Oligoryzomys andinus* and *Oligoryzomys chacoensis*. Later, MUSSER and CARLETON (1993), without reference to species groups, included in *Oligoryzomys* three other species: *Oligoryzomys griseolus* from Venezuela and Colombia, *Oligoryzomys magellanicus* from South Patagonian Chile and Argentina, including Tierra del Fuego, and *Oligoryzomys victus* from Saint Vincent: Lesser Antilles.

The status and relationships of many species of the tribe are dubious and karyological information has proved to be an important tool to clarify the systematics of this complex group.

In this paper, we accept *Oligoryzomys* as a genus according to CARLETON and MUSSER (1989). The diploid number in this group ranges from 52 in *Oligoryzomys* aff. *eliurus* described as *Oryzomys* aff. *eliurus* (FURTADO 1981; MAIA et al. 1983; ALMEIDA et al. 1984) to $2n = 68$ in *Oligoryzomys longicaudatus* and *Oligoryzomys* cf. *flavescens*, described respectively as *Oryzomys longicaudatus* (GARDNER and PATTON 1976) and *Oryzomys* cf. *flavescens* (ESPINOSA and REIG 1991). The cytogenetic data in *Oligoryzomys* have shown numerical and structural rearrangements, including both autosomal and sex chromosomes variations.

In this report we describe the karyotypes of two related but hitherto undescribed species, herein referred to as *Oligoryzomys* sp. 1 and *Oligoryzomys* sp. 2. The chromosome number of the two species, $2n = 46$ and $2n = 44$, 44/45, respectively, were determined by conventional staining, CBG, GTG, RBG-banding, Ag-NOR, and fluorescent in situ hybridization

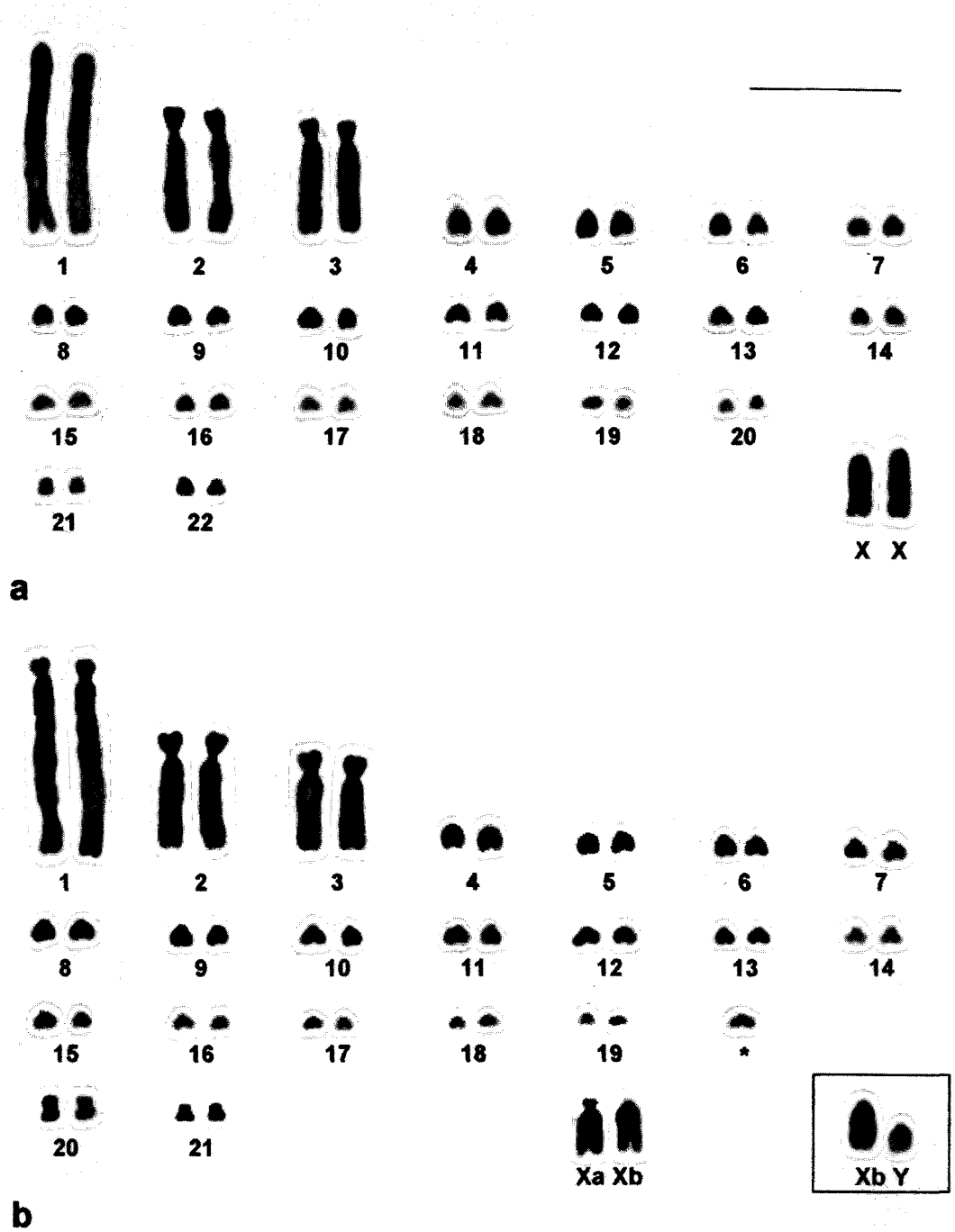

Fig. 1a and b. Karyotypes after conventional staining. **a** *Oligoryzomys* sp. 1, female with 2n = 46. **b** *Oligoryzomys* sp. 2, female with 2n = 44/45; (*) represents the extra chromosome. Inset: XbY sex chromosomes. Bar = 10 μm.

(FISH) of telomeric probes. Meiotic data and chromosome length measurements are also provided.

MATERIAL AND METHODS

Cytogenetical analysis was carried out on two females of *Oligoryzomys* sp. 1 collected at Pico das Almas (13°33′S, 41°56′W), state of Bahia and on one female and two males of *Oligoryzomys* sp. 2 from Serra do Cipó (19°18′S, 43°35′W), state of Minas Gerais. These two regions are geographically separated by nearly 800 km and situated in disjuncted areas known as "campos rupestres" along the Espinhaço mountains of eastern Brazil.

The specimens are deposited at the Museu de Zoologia da Universidade São Paulo (MZUSP) col-

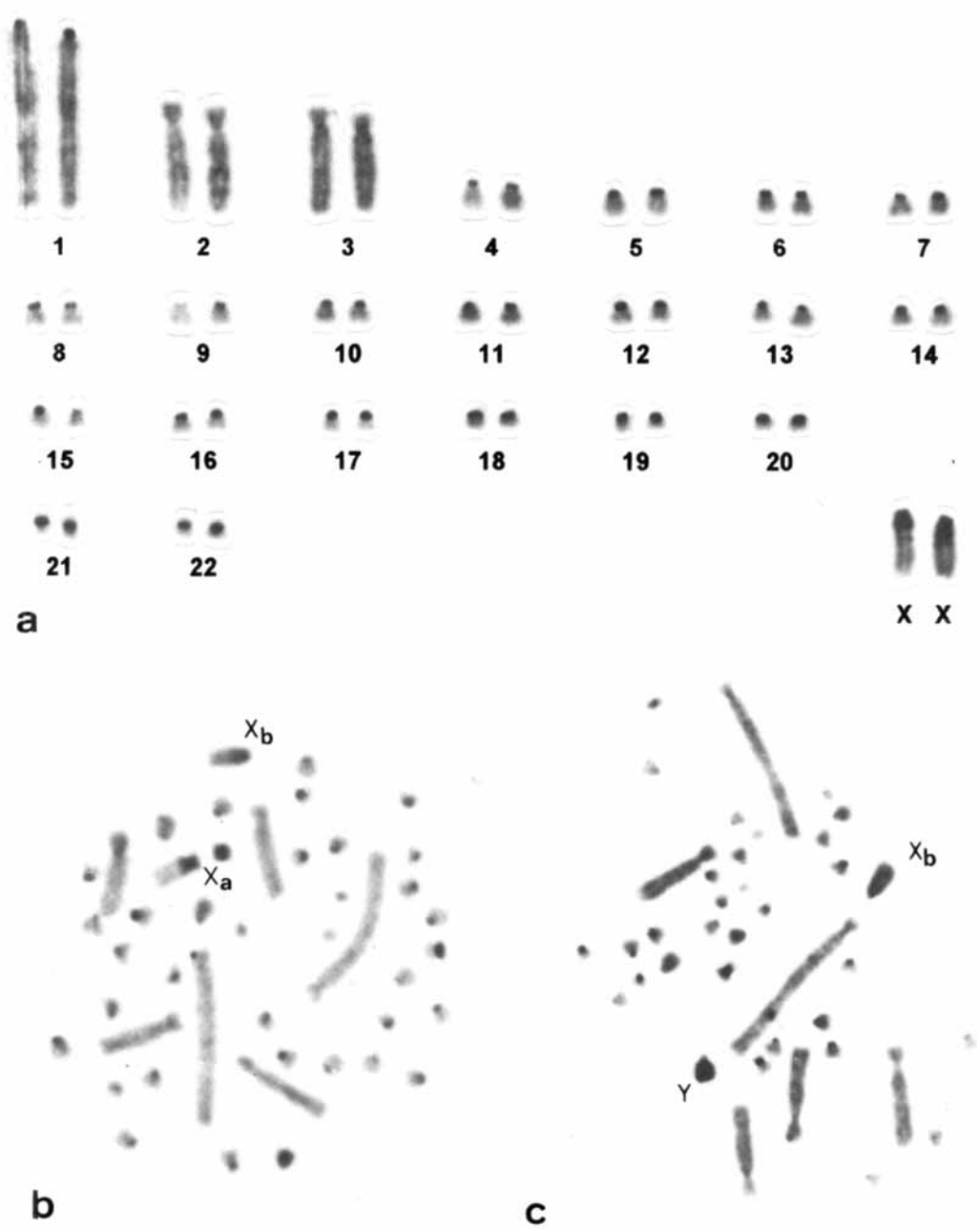

Fig. 2a–c. CBG-banding pattern. **a** *Oligoryzomys* sp. 1, female with 2n = 46. **b** Metaphase of *Oligoryzomys* sp. 2, female with 2n = 44/45. **c** Partial metaphase of *Oligoryzomys* sp. 2 male.

lection (*Oligoryzomys* sp. 1: numbers MZUSP 29015 and 29016; *Oligoryzomys* sp. 2: numbers MZUSP 27423, 29013, and 29014).

Chromosomal preparations were obtained in vivo from bone marrow and spleen and in vitro from fibroblast culture, using methods of ALMEIDA and YONENAGA-YASSUDA (1985). Meiotic analysis was performed on testis cells following the procedure described by EICHER (1966). CBG, GTG-banding patterns and Ag-NORs were produced using routine cytogenetics techniques. RBG-bandings were obtained after in vitro 5-BrdU incorporation (DUTRILLAUX and COUTURIER 1981). Analyses of synaptonemal complex (SC) were obtained according to LOIDL et al. (1991). Chromosome length measurements were calculated as a percentage of the length of the female haploid set in a minimum of 15 metaphases.

Fluorescence in situ hybridization using 3′ biotinylated telomere sequence $(TTAGGG)_n$ as a probe was performed on metaphases of both species following the Oncor's protocols (catalog number P5097-DG.5). Hybridization signals were detected by incubation

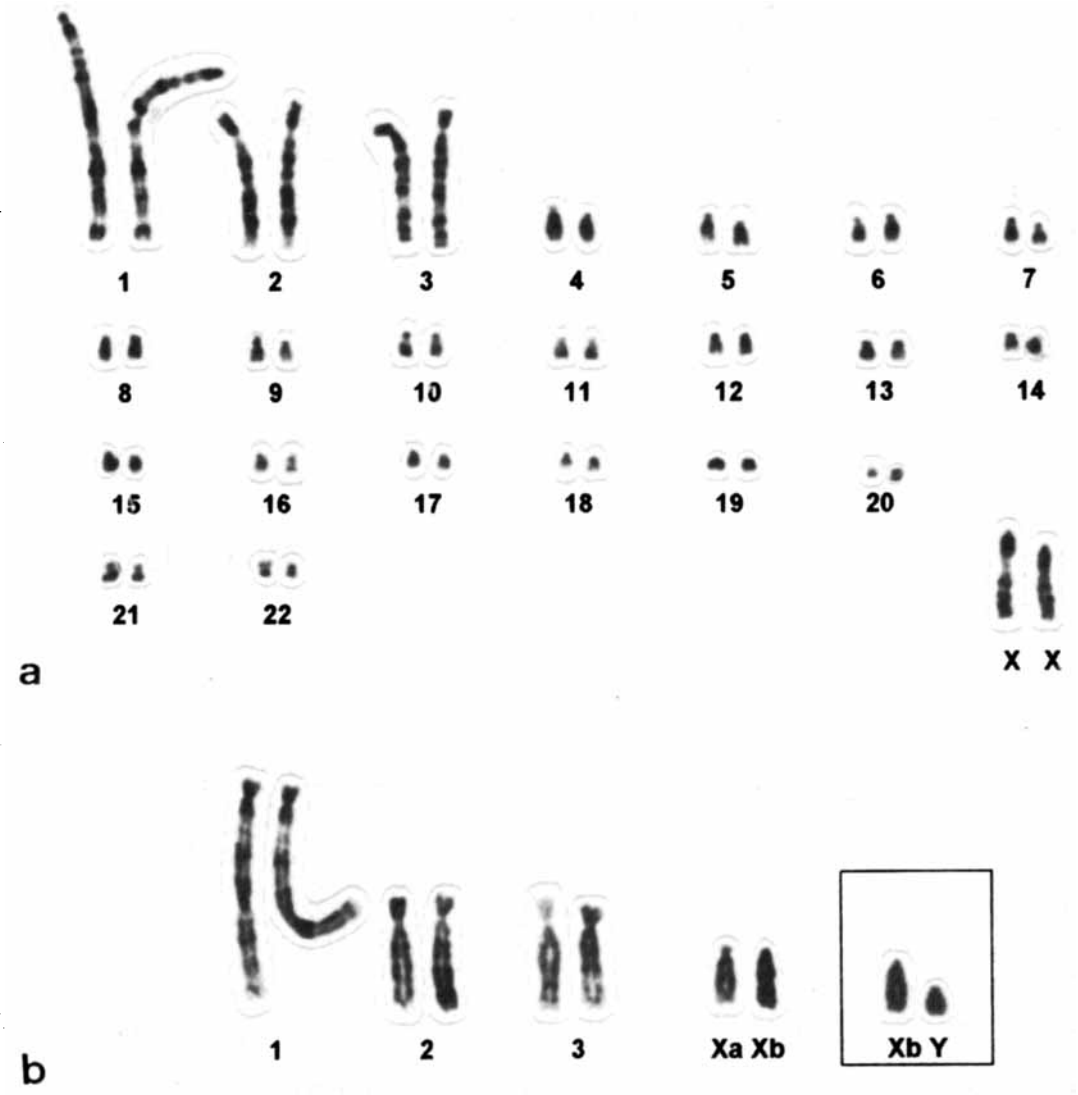

Fig. 3a and b. GTG-banding pattern. **a** *Oligoryzomys* sp. 1 with 2n = 46. **b** Partial karyotype of *Oligoryzomys* sp. 2 with pair 1, 2, 3, and XaXb. Inset: XbY.

with fluorescein isothiocyanate (FITC)-labeled anti-digoxigenin, and the slides were counterstained with propidium iodide in fluorescence antifade solution. Chromosome signals were shown using a Zeiss Axiophot microscope equipped with a FITC filter and photographed using Ektachrome 400 (Kodak) color slide film.

RESULTS

Banding data

Oligoryzomys sp. 1 (2n = 46, FN = 52). — Autosomes were composed of macro- and micro-chromosomes (three large and 19 small pairs): pair 1 was acrocentric; pairs 2 and 3 were subtelocentrics; pairs 4 to 20 were acrocentrics graded by size; pairs 21 and 22 were small metacentric and submetacentric chromosomes, respectively. This type of karyotype is not frequently encountered among mammals. The X chromosome was a medium-sized acrocentric that has a distinctive morphology (Fig. 1a). C-banding revealed constitutive heterochromatin at pericentromeric regions in all autosome pairs except pairs 2 and 3. The X chromosome exhibited a large heterochromatic block in the proximal region and a much smaller interstitial band in the long arm (Fig. 2a). GTG- (Fig. 3a) and R-banding pattern provided the precise identification of the three largest autosomal pairs and the X chromosomes. Ag-NORs analysis revealed inter- and intra-individual variability, and the number per cell varied from five to 12. They were located on short arm regions of the small acrocentrics and the short arm of the acrocentric pair 1 (Fig. 5a).

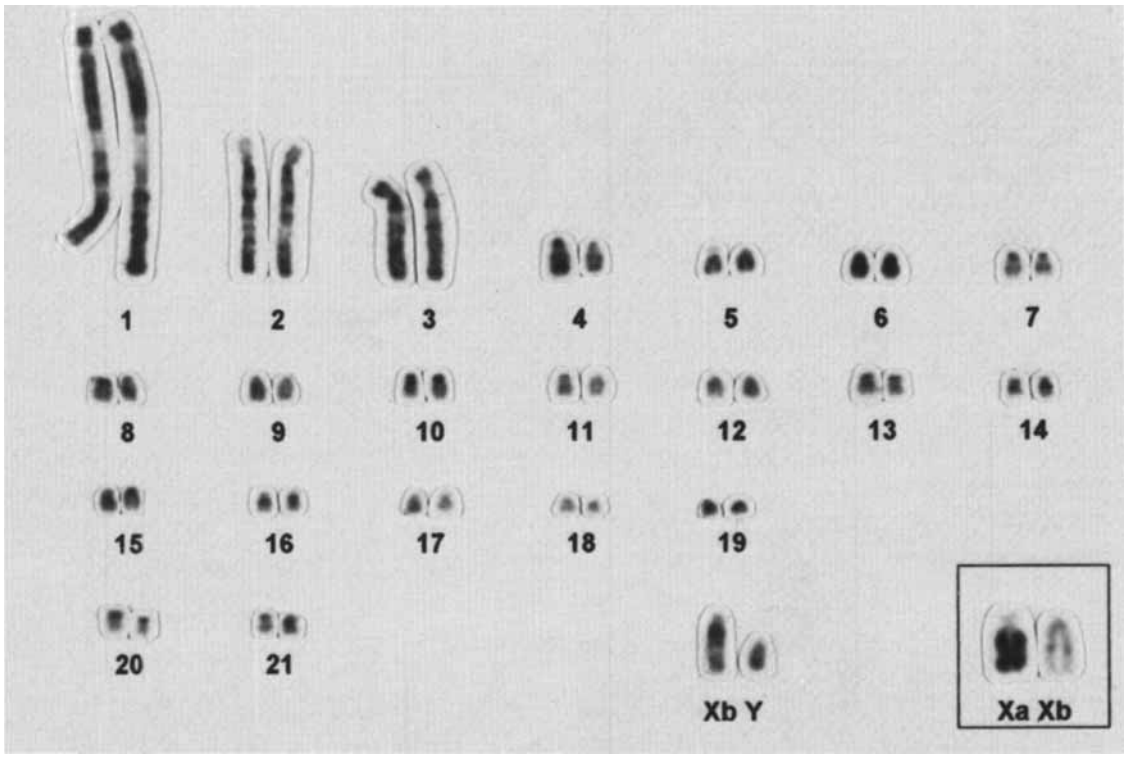

Fig. 4. RBG-banding pattern after BrdU incorporation of *Oligoryzomys* sp. 2 male with 2n = 44, including XbY. Inset: early Xa and late Xb.

Fig. 5a and b. NOR-bearing chromosomes. **a** *Oligoryzomys* sp. 1 with 11 Ag-NORs, including the macro-chromosome acrocentric pair 1 and one association between two small autosomes. **b** *Oligoryzomys* sp. 2 with six Ag-NORs showing one association of two small acrocentrics.

Oligoryzomys sp. 2 (2n = 44, FN = 52; 2n = 44/45, FN = 52/53). — Two males of *Oligoryzomys* sp. 2 had 2n = 44 and FN = 52 and the female (mother of the both males) had 2n = 44 from bone marrow cells, but 2n = 45 (FN = 53) in about 74 % of fibroblast culture cells. This mosaicism was caused by a single small acrocentric in the 2n = 44 karyotype.

The 2n = 44 karyotype consisted of three large and 18 small autosome pairs: 1, 2, and 3 were large subtelocentrics; pairs 4 to 19 were small acrocentrics graded in size, and pairs 20 and 21 were, respectively, small metacentric and submetacentric chromosomes. Two morphologically medium-sized X chromosomes were recognized in the female: a subtelocentric (Xa) and an acrocentric (Xb). The Xb form was found in both of the males. The Y chromosome was a small acrocentric (Fig. 1b). C-banding pattern showed constitutive heterochromatin at all pericentromeric regions. Pair 1, 2, and 3 did not show any constitutive heterochromatin. The Xa presented a proximal C-band block, which extended to the whole short arm; the Xb exhibited a pericentromeric and an interstitial proximal heterochromatic band (Fig. 2b). Chromosome Y was entirely heterochromatic (Fig. 2c). The G-banding pattern allowed the precise identification of the three largest autosomal pairs, X and Y chromosomes (Fig. 3b). RBG-banding pattern served to recognize the majority of the autosomes, both late and early replicating X and the Y chromosome (Fig. 4). Analysis of 23 metaphases after 5-BrdU incorporation in the female, demonstrated about 91 % of preferential inactivation of Xb chromosome. Ag-

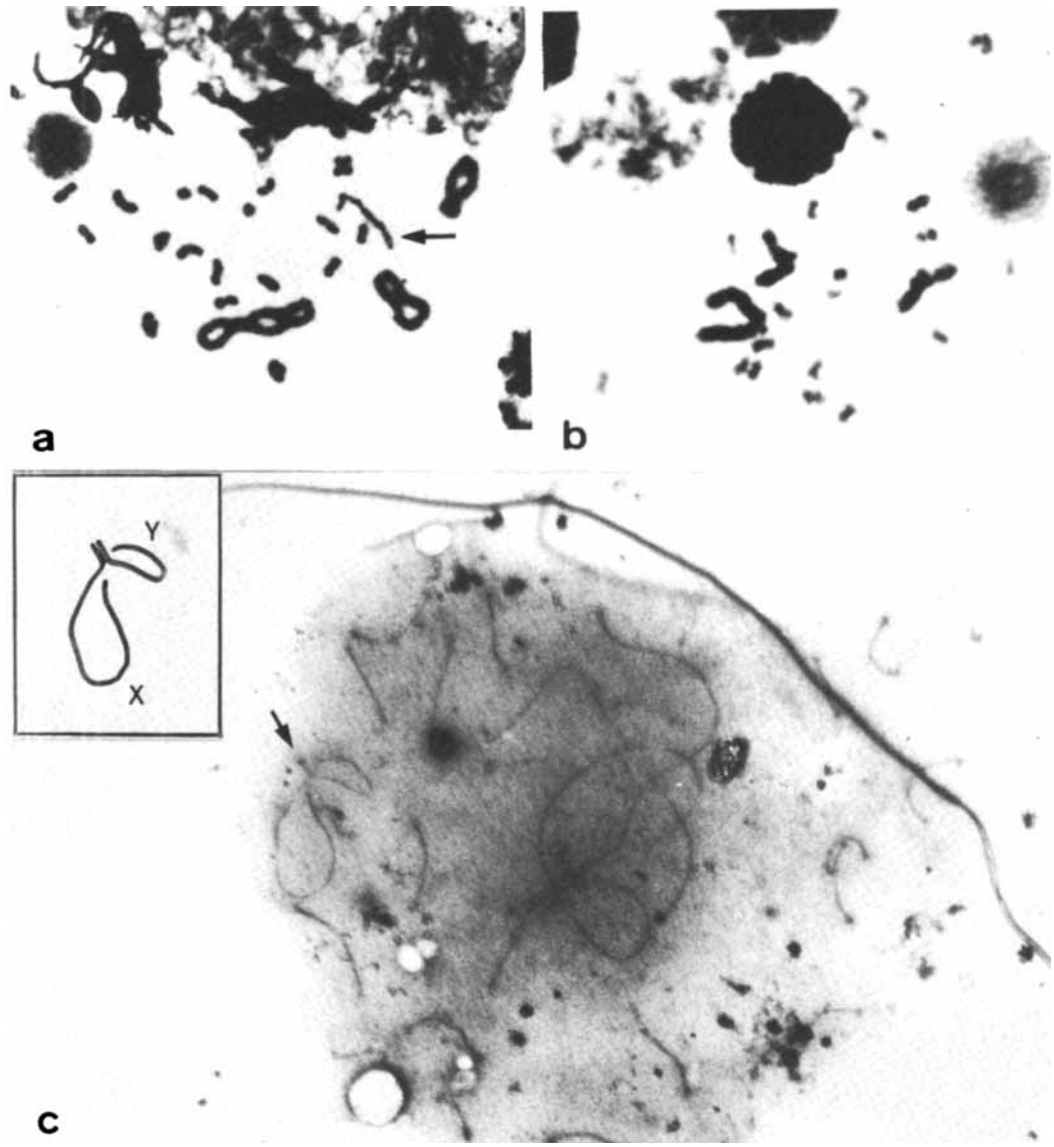

Fig. 6a–c. Meiotic cells of *Oligoryzomys* sp. 2 male. **a** Diplotene with 22-bivalents, including the end-to-end associated sex chromosomes (arrow). **b** Metaphase II with 22 chromosomes. **c** Electron micrograph of a spread pachytene spermatocyte in which a schematic representation of the sex chromosome XbY (arrow) is showed inset (× 3000).

NORs were multiple and located exclusively on the short arms of small acrocentrics; the number ranged from 2 to 9 (Fig. 5b).

Meiotic data

Meiotic analysis was performed in *Oligoryzomys* sp. 2 males. In diplotene cells, 21 autosomal bivalents could be identified plus an end-to-end associated sex pair (Fig. 6a). Metaphases II showed 22 chromosomes (Fig. 6b). Synaptonemal complex analysis revealed that the onset of autosomal synapses could be observed at either one or two ends or interstitial segment. At the late-zygonema/early-pachynema, pairing of small chromosomes was completed before the total synapses of the largest axes occurred. The X and Y synaptic initiation was observed from the telomeric end of both. Heteropycnosis of unpaired SC axes was not observed (Fig. 6c). End plaques were darkly stained and included autosomal and X-Y synaptonemal complexes.

Fluorescence in situ hybridization (FISH)

Fluorescence in situ hybridization (FISH) using a telomeric probe was used to shed light on the mechanism of rearrangements involved in the differentiation of the two karyotypes ($2n = 46$ and 44).

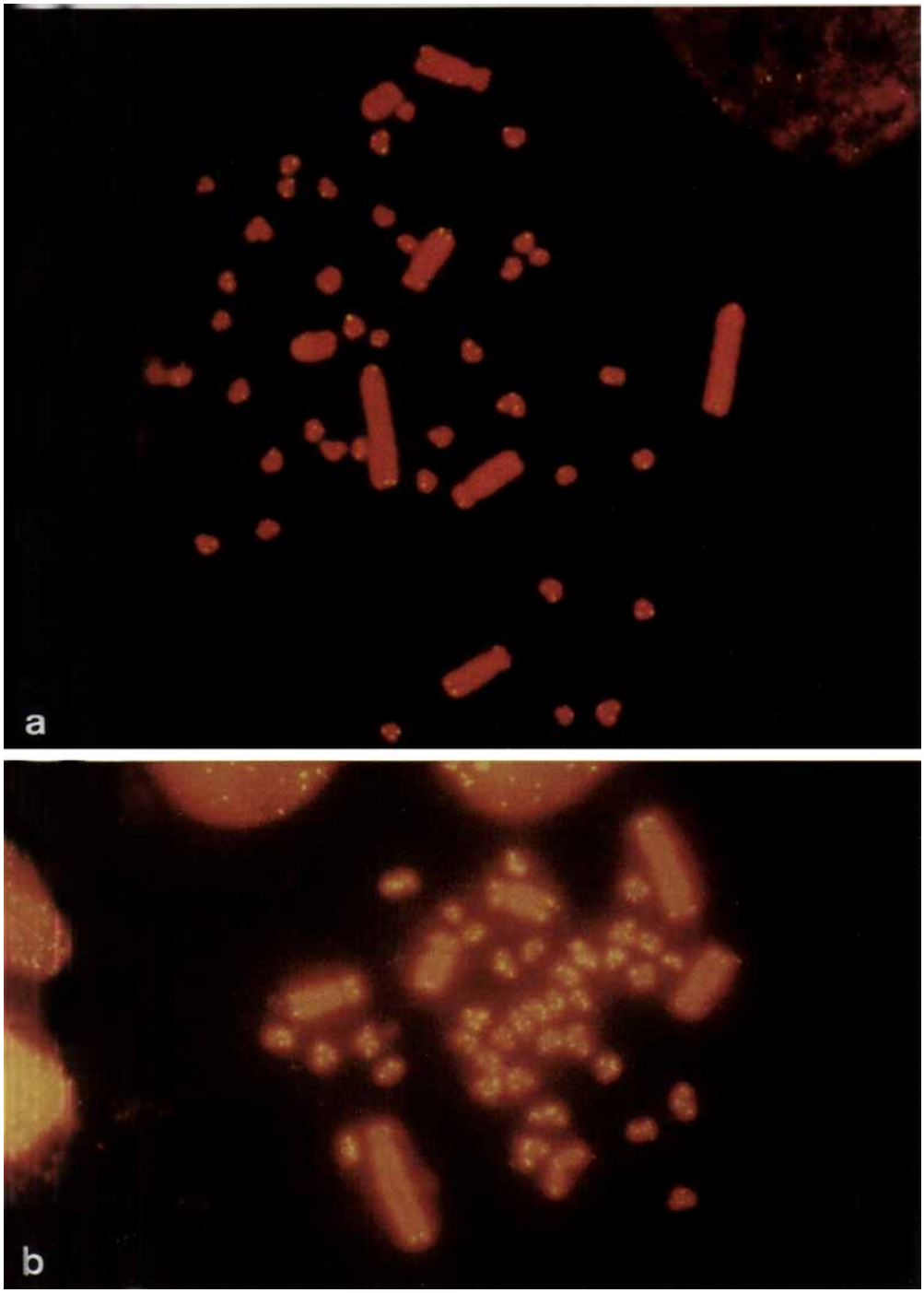

Fig. 7a and b. In situ hybridization with telomeric $(TTAGGG)_n$ probe on mitotic chromosomes. **a** *Oligoryzomys* sp. 1, female with $2n = 46$. **b** *Oligoryzomys* sp. 2 with $2n = 44$.

Telomere signals were observed at both ends of all the chromosomes including the sex chromosomes in both species (Fig. 7).

Length measurements

Chromosomal length measurements were performed to obtain the relative percent that each chromosome represents in the haploid set, including X because these two karyotypes demonstrated a very interesting size distribution with a remarkable difference between the three largest pairs and the smaller autosomes (Table 1). The largest pairs (1, 2, and 3) of *Oligoryzomys* sp. 1 ($2n = 46$) represented about 43.04 % of the haploid set. The X chromosome was a medium-

Table 1. *Relative size of the chromosomes in percentage of the haploid set, including the X, of the Oligoryzomys sp. 1 (*) and Oligoryzomys sp. 2 (**)*

Species	Chromosome pair							
	1	2	3	Small acrocentrics	21* or 20**	22* or 21**	X	Y
Oligoryzomys sp. 1	18.74	12.40	11.90	3.95 to 1.80	2.78	2.70	7.54	–
Oligoryzomys sp. 2	24.78	13.31	12.21	3.68 to 1.32	3.37	2.47	6.13	3.73

sized acrocentric representing 7.5% of the haploid set. On the other hand, the three largest pairs of *Oligoryzomys* sp. 2 (2n = 44) corresponded to 50.30% of the haploid set. X chromosomes represented 6.13% of the haploid set, and the Y was a small acrocentric (3.73%). Table 1 demonstrates that the difference between 50.3% and 43.0% of the largest pairs is due to the very large size of pair 1 of *Oligoryzomys* sp. 2.

Comparative cytogenetic analysis

The karyotypes of *Oligoryzomys* sp. 1 and *Oligoryzomys* sp. 2 are morphologically similar, differing in diploid number due to Robertsonian rearrangement. Mosaicism with 2n = 44, 45 was probably due to an artifact of rearrangements in fibroblasts culture cells. These karyotypes are unequivocally conspicuous and infrequent among the oryzomyines because the chromosomes can be separated in macro- and micro-chromosomes.

GTG and RBG comparative analysis demonstrated complete homology between the long arm of subtelocentric pair 1, pairs 2, and 3 in *Oligoryzomys* sp. 2, and the respective pairs of *Oligoryzomys* sp. 1. There was a heterochromatic block on acrocentric pair 1 in *Oligoryzomys* sp. 1, whereas there was no heterochromatin on the pair 1 of *Oligoryzomys* sp. 2. The NORs were multiple and located on the short arm regions of small acrocentrics in both species. They were also located on short arm regions of pair 1 of *Oligoryzomys* sp. 1 (Fig. 8). FISH approach showed only telomeric signals in both species, and length measurements showed size differences in pair 1 (which was largest in *Oligoryzomys* sp. 2) and in the X chromosomes (which were largest in *Oligoryzomys* sp. 1). The sex chromosomes of *Oligoryzomys* sp. 2 are smaller than those of *Oligoryzomys* sp. 1 due to the presence of blocks of heterochromatin in the latter.

DISCUSSION

It is likely that centric fusion is responsible for differences in diploid number between *Oligoryzomys* sp. 1 (2n = 46) and *Oligoryzomys* sp. 2 (2n = 44). This notion is supported by: (I) the presence of one small additional pair of acrocentrics in *Oligoryzomys* sp. 1; (II) the differences in size between pair 1, which is acrocentric in *Oligoryzomys* sp. 1 and subtelocentric in *Oligoryzomys* sp. 2; (III) the presence of constitutive heterochromatin in the pericentric region of pair 1 in *Oligoryzomys* sp. 1 (it was absent in *Oligoryzomys* sp. 2); (IV) the presence of Ag-NORs in the acrocentric pair 1 on the short arm region; (V) the similar G- and R-banding patterns between the acro-

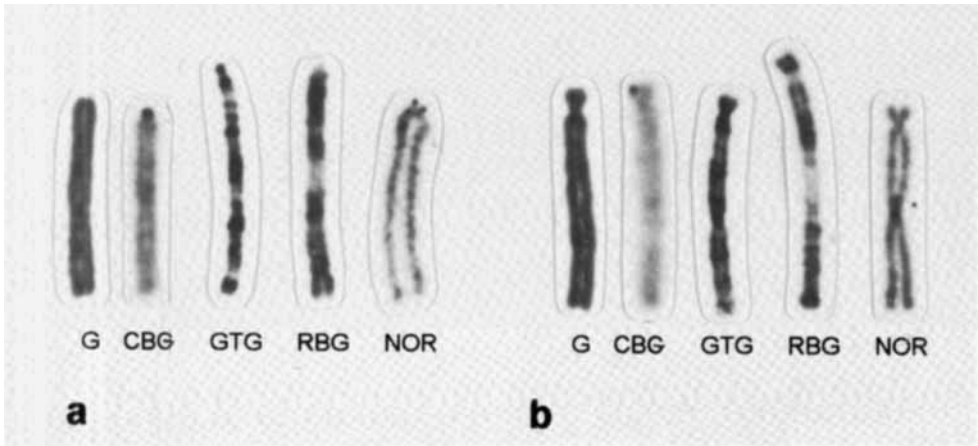

Fig. 8a and b. Macro-chromosome pair 1 after Giemsa staining (G), CBG, GTG, RBG-banding and Ag-NOR staining, respectively. **a** *Oligoryzomys* sp. 1. **b** *Oligoryzomys* sp. 2.

centric pair 1 and the long arm of the subtelocentric chromosomes; and (VI) presence of telomeric signals only at the ends of all chromosomes after FISH with telomeric probes. Thus, we suggest that the centric fusion occurred with the loss of pericentromeric, nucleolus organizer and telomeric sequences. The alternative hypothesis of centric fission would require the acquisition of those specific sequences in order to derive the 2n = 46 karyotype. Also, numerous cytogenetic studies describe Robertsonian fusions as a much more common phenomenon of karyotype evolution in many rodent species (GARDNER and PATTON 1976).

Sex chromosome polymorphism represents an evident characteristic of the Oryzomyini group and in the majority of the cases, the variations are caused by addition/deletion of constitutive heterochromatin (SILVA 1994; ALMEIDA and YONENAGA-YASSUDA 1991; SVARTMAN and ALMEIDA 1992). The intra-individual heteromorphism of the X chromosome in *Oligoryzomys* sp. 2 was the result of a pericentric inversion, since there was no size variation. On the other hand, *Oligoryzomys* sp. 1 demonstrated that both X acrocentrics were larger than that of *Oligoryzomys* sp. 2, and the interspecific variation was the result of deletion of constitutive heterochromatin.

One remarkable characteristic of the karyotypes of *Oligoryzomys* sp. 1 and *Oligoryzomys* sp. 2 is the conspicuous difference between macro- and microchromosomes. Our FISH data did not show interstitial telomeric bands (ITBs) in the three largest pairs (1, 2, and 3) of *Oligoryzomys* sp. 1 and *Oligoryzomys* sp. 2, which could be derived from successive *tandem* fusion from a higher diploid number karyotype. It is possible that telomeric sequences were lost from the original chromosomes before several fusion events took place or, these sequences are not large enough to be detected by our present methods of hybridization.

Some data from other vertebrates showed relatively large blocks of $(TTAGGG)_n$ at non-telomeric positions in some species in addition to telomeric sites (MEYNE et al. 1990; WILEY et al. 1992; LEE et al. 1993; NANDA and SCHMID 1994). These data support the hypothesis that ITBs may be remnants of chromosome rearrangements. On the other hand, studies in *Okapia johnstoni* (VERMEESCH et al. 1996) as well as in *Mus musculus* (NANDA et al. 1995) revealed no interstitial telomere sites with chromosomal rearrangements.

Several cytogenetic studies in *Oligoryzomys* have shown the occurrence of chromosomal rearrangements as pericentric inversion, sex chromosomes polymorphism, and supernumerary chromosomes. In Table 2 we summarize karyotype and chromosomal variations found in *Oryzomys* species, which now based on the systematics of CARLETON and MUSSER (1989) are considered as *Oligoryzomys*.

In the **nigripes** group, *Oligoryzomys nigripes* and *Oligoryzomys delticola* have 2n = 62, and a similar karyotype is found in almost all the specimens studied (Table 2). Comparative analysis between these karyotypes demonstrate the same diploid number, banding pattern, and rearrangements. Based on these data we believe that different names had been given for the same species, i.e., both these species represent the same taxonomic entity.

MUSSER and CARLETON (1993) argued that *Oligoryzomys eliurus* could be conspecific with *Oligoryzomys nigripes*. Even though the chromosome number (2n = 62) is the same, the karyotypes of *Oligoryzomys nigripes* is not similar to that of *Oligoryzomys eliurus* and *Oligoryzomys* aff. *eliurus* (Table 2). SVARTMAN (1989) suggested that the samples with 2n = 62 identified as *Oligoryzomys eliurus* and *Oligoryzomys* aff. *eliurus* should be considered the same taxonomic entity (*Oligoryzomys eliurus*) and that *Oligoryzomys* aff. *eliurus* with 2n = 52 represent a cryptic species from *Oligoryzomys* aff. *eliurus* with 2n = 62, because they are morphologically indistinguished (MAIA 1988).

Some of samples originally identified as *Oligoryzomys longicaudatus* actually demonstrated five different diploid numbers. Furthermore, the populations of this species from Tierra del Fuego and Rio Negro and populations of *Oligoryzomys I. philippii* from Valdivia with 2n = 56 were recognized, respectively, as *Oligoryzomys magellanicus* and *Oligoryzomys longicaudatus* (GALLARDO and PALMA 1990). Populations of *Oligoryzomys longicaudatus* with 2n = 64, described by GARDNER and PATTON (1976), were considered as *Oligoryzomys microtis* by MUSSER and CARLETON (1993) (Table 2).

MUSSER and CARLETON (1993) considered the specimens referred to *Oligoryzomys fornesi* by MYERS and CARLETON (1981) as *Oligoryzomys microtis* (Table 2).

Regarding the **flavescens** group, SBALQUEIRO et al. (1991) argued that the diploid number difference found in *Oligoryzomys flavescens* from Uruguay, Argentina, and Brazil (2n = 64 to 66) can be explained by supernumerary chromosomes.

In addition, three different karyotypes were found in *Oligoryzomys fulvescens* (assuming *Oligoryzomys delicatus* = *fulvescens*). The difference between 54 and 60 was explained by the inclusion of three additional small acrocentric pairs (Table 2).

Based on karyotypic and distributional data, we suggest that *Oligoryzomys* sp. 1 and *Oligoryzomys* sp. 2 reported in this paper, can be placed in the **nigripes**

Table 2. *Karyotypic data on rodents of the genus Oligoryzomys. Group 1 = **nigripes**; group 2 = **flavescens**; group 3 = **fulvescens**; group 4 = **microtis**; and group 5 = **andinus***

Group	Species	Locality	2n	FN	Rearrangement	Reference
1	*Oligoryzomys nigripes*	São Paulo, Rio de Janeiro (Brazil)	62	80, 81, 82	pericentric inversions of pair 3,4,8; X and Y polymorphism	ALMEIDA and YONENAGA-YASSUDA 1991; SILVA 1994
		Bahia, Espírito Santo, Rio Grande do Sul (Brazil)	62	78, 80, 81, 82	pair 2, 3 and 4 with pericentric inversion and sex pair polymorphism	ZANCHIN 1988
		Epírito Santo (Brazil)	61		loss of one sex chromosome	
		Rio de Janeiro, Minas Gerais (Brazil)	62	82		GEISE 1995
		Paraguay	62	80		MYERS and CARLETON 1981
	Oligoryzomys delticola	Buenos Aires (Argentina)	62	82	pericentric inversion of pair 21	ESPINOSA and REIG 1991
		Maldonado, Paysandu, Colonia,	62	80	pericentric inversion of pair 3;	BRUM-ZORRILLA et al. 1988
		Durazno (Uruguay)	60	76	inversion, deletion and loss of chromosomes	
		Paraná, Rio Grande do Sul (Brazil)	62	79, 80, 81, 82	pericentric inversion of pair 3 and, eventually, pair 10; sex chromosomes polymorphism	SBALQUEIRO 1989
	Oligoryzomys eliurus	Brasília (Brazil)	62	64		SVARTMAN 1989
	Oligoryzomys aff. *eliurus*	Pernambuco (Brazil)	52	68	X chromosome polymorphism	FURTADO 1981; MAIA et al. 1983;
			62	64		ALMEIDA et al. 1984
	Oligoryzomys magellanicus	Rio Negro (Argentina)	56	64	pericentric inversion and	ESPINOSA and REIG 1991, referred to
		Tierra del Fuego (Argentina)	56	66	X morphological variation	*Oligoryzomys longicaudatus*
		Tierra del Fuego (Argentina)	54			GALLARDO and PALMA 1990
	Oligoryzomys longicaudatus	Peru	68	74 or 76		GARDNER and PATTON 1976
			60	76		
		Venezuela	62	74 or 76		
		Valdivia (Chile)	56	70	X polymorphism	GALLARDO and GONZÁLEZ 1977, referred to *Oligoryzomys l. philippii*
	Oligoryzomys cf. *longicaudatus*	Jujuy, Tucumán (Argentina)	58	74		ESPINOSA and REIG 1991
2	*Oligoryzomys flavescens*	Buenos Aires, Córdoba (Argentina)	66	68	supernumerary chromosome and Y polymorphism	ESPINOSA and REIG 1991
			67			
		Boca Cerrada, Punta Lara (Argentina)	66	70	autosomal pair 3 and Y polymorphism	BRUM-ZORRILLA et al. 1988

Table 2 (continued).

Group	Species	Locality	2n	FN	Rearrangement	Reference
		Montevideo, Colonia, Maldonado,	66	68, 70		BRUM-ZORRILLA et al. 1988
		Artigas, Fray Bentos, Canelones (Uruguay)	64	66	pericentric inversion	
		Paraná, Rio Grande do Sul (Brazil)	64–66	66–68		SBALQUEIRO et al. 1991
			64/65	66/67	supernumerary chromosome	
	Oligoryzomys cf. *flavescens*	Jujuy, Tucumán (Argentina)	66–68	68–70	X and Y polymorphism	ESPINOSA and REIG 1991
3	*Oligoryzomys fulvescens*	Costa Rica	54	68		GARDNER and PATTON 1976
		Guatemala	60	74	X polymorphism	HAIDUK et al. 1979
		Venezuela	60	72		KIBLISKY 1969, referred to *Oligoryzomys delicatus*
		Suriname	60, 64			BAKER et al. 1983 referred to *Oligoryzomys delicatus*
4	*Oligoryzomys microtis*	Paraguay	62	64	X polymorphism	MYERS and CARLETON 1981, referred to *Oligoryzomys fornesi*
			64–66	66–68		
		Peru	64	66		GARDNER and PATTON 1976, referred to *Oligoryzomys longicaudatus*
5	*Oligoryzomys andinus*	Peru	60	70		GARDNER and PATTON 1976
	Oligoryzomys chacoensis	Paraguay	58	74		MYERS and CARLETON 1981

or the **flavescens** group, but taxonomic revision will be necessary before it is possible to clarify the position of these species into the groups that were described by CARLETON and MUSSER (1989).

ACKNOWLEDGEMENTS

We are grateful to Dr. Miguel T. Rodrigues and Dr. James Bogart for their valuable comments and suggestions on the manuscript; to Dr. Miguel T. Rodrigues, Pedro L. B. da Rocha and Gabriel Skuk for collecting the specimens. We are also indebted to Dr. Ângela M. Vianna-Morgante and Msc. Ana Carolina C. Barbosa for FISH assistance; to Miriam Romeo Silva, Cristina M. Barnabé and Dr. Tien Hsi Chu for technical assistance. This work was supported by CNPq, CAPES, FAPESP and FINEP.

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