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Genetic studies in representatives of genus *Rhipidomys* (Rodentia, Sigmodontinae) from Brazil

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Karyotypic polymorphism of five taxa of the rodent genus *Rhipidomys* from the Brazilian Amazon and Cerrado biomes was analysed. *Rhipidomys nitela* Thomas, 1901 from Amazon has 2n = 48, FN = 68. The other species, all have 2n = 44, but can be separated into two groups, one with high FNs (76, 80) and the other with low FNs (48, 52). Two cytotypes of *R. mastacalis* (Lund, 1840) with high FNs were trapped in four localities of the Cerrado, showing 19 and 17 biarmed autosomes, respectively. A low FN (48) was observed in *R. leucodactylus* (Tschudi, 1844) in two localities of the Cerrado and FN = 52 in one locality in the Cerrado and the Amazon. All taxa with 2n = 44 have a medium-sized acrocentric X chromosome and a small Y. *Rhipidomys nitela* is different from the species with 2n = 44 by presenting a heterochromatic short arm of the X chromosome. In all karyotypes analysed, the nucleolus organizer regions were located in the short arms of two to six pairs and the $(T_2AG_3)_n$ telomeric probes hybridized *in situ* in both the short and long arms of all pairs of the karyotypes.

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Key words: *Rhipidomys*, Cerrado, Amazon, *in situ* hybridization, DNA microsatellite

Introduction

Rhipidomys is a widely distributed Neotropical tree rat, ranging from eastern Panama, Guianas, Venezuela, Colombia, Ecuador, and Peru to southern Bolivia, northwestern Argentina and north, central and eastern Brazil (Musser and Carleton 1993). The majority of authors include *Rhipidomys* in the thomasomyine group of the Sigmodontinae subfamily of the New World murids (Hershkovitz 1966, Cerqueira 1982, Carleton and Musser 1989, Gardner 1989, Voss 1993, Steppan 1995). It is a speciose genus with a confused taxonomy, which was recently revised

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by Tribe (1996). The proposed number of species ranges from 5 (Cabrera 1961), 7 (Honacki *et al*. 1982), 9 (Reig 1984), 14 (Musser and Carleton 1993), to 18 (Tribe 1996).

Cytogenetic studies performed in one species from Colombia (Gardner and Patton 1976), 2 from Venezuela (Aguilera *et al*. 1994), and in 8 from Brazil (Zanchin *et al*. 1992, Svartman and Almeida 1993, Silva and Yonenaga-Yassuda 1999), showed that, with the exception of one, all species of this genus have the same diploid number (44), apparently differing among themselves only by the number of biarmed elements they carry (autosomal arms numbers ranging from 48 to 74).

In this paper we report the 2n = 48 karyotype of *R. nitela* Thomas, 1901 from Amazon, and 4 other *Rhipidomys* karyotypes with 2n = 44, 2 of them with high and 2 of them with low autosomal arm numbers, trapped in the Brazilian biomes of Amazon and Cerrado. We are also describing the results of the *in situ* hybridization analysis made in these 5 species with the telomeric probe $(T_2AG_3)_n$.

Material and methods

Twenty-seven specimens (22 karyotyped) of 5 taxa trapped in 7 localities of the Brazilian territory were examined (Fig. 1, Tables 1 and 2). Skins and skulls were deposited in the Mammals Collection of the Museu Nacional, Rio de Janeiro. Voucher specimen numbers are in the Appendix.

Metaphase plates were obtained from bone marrow according to the technique of Baker *et al*. (1982). C-banding, NOR and G-banding were performed employing the methods of Sumner (1972), Howell and Black (1980) and Seabright (1971), respectively. In the case of the G-bands (data not shown), due to a problem in preparing the cellular suspensions in the field, they were useful only to detect the occurrence of pericentric inversions in the largest pairs of the karyotype. The hybridization process of the telomeric sequence $(T_2AG_3)_n$ was done using the Oncor (Gaithersburg, MD) "all human telomeres" probe stained with digoxigenin according to the manufacturer's protocol, except for the temperature of post-hybridization washing being lowered to 68°C. Detection was performed using FITC anti-digoxigenin and propidium iodide as counterstaining. Kodak Ektachrome, ASA 400 film was used in the photomicrographs.

Eleven sets of microsatellite DNA primers designed for *Rattus* (R12, R47, R65, R69, R75, and R97 designed by Serikawa *et al*. 1992) and *Mus* (M13, M23, and M49, and ATP, and KRT, according Love *et al*. 1990 and Santos *et al*. 1995) were amplified by heterologous PCR in five species (four taxa as described in Lima-Rosa *et al*. 2000, plus *R. nitela* of this work).

Results

The results of the analysis performed in the genus *Rhipidomys* in this study and those described in the literature are presented in Table 2. *Rhipidomys nitela* was the only species of the genus that did not present a diploid number of 44. Its 48 chromosomes include 11 and 12 biarmed and acrocentric autosomal pairs, respectively. The X chromosome is a large submetacentric (size between pairs 1 and 2), and the Y chromosome a small acrocentric (Fig. 2a). All the other species analysed presented 2n = 44 and an acrocentric sexual pair, with the X chromosome being medium sized and the Y chromosome small. They differ by their autosomal arms

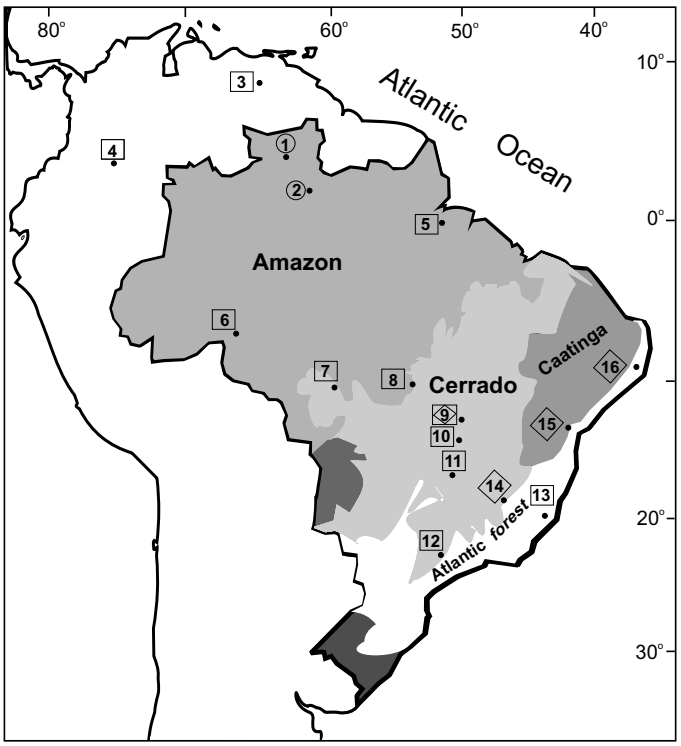

Fig. 1. Collection points: 1 – Surumú, Roraima state; 2 – Manaus, Amazon state; 3 – Venezuela; 4 – Colombia; 5 – Caxiuan□, Pará state; 6 – River Jamari, Rondônia state; 7 – Aripuan□, and 8 – Vila Rica, Mato Grosso state; 9 – Serra da Mesa (including the localities: a – 55 km N Niquelândia, b – 20 km NW Colinas do Sul, c – 40 km SW Minaçú, and d – 40 km NE Uruaçú), Goiás state; 10 – Brasília, Distrito Federal; 11 – Ipameri, Caldas Novas and Corumbaíba, Goiás state; 12 – Casa Grande, S□o Paulo state; 13 – Monte Verde, Espírito Santo state; 14 – Lagoa Santa, Minas Gerais state; 15 – Fazenda Unacau, Bahia state; 16 – Serra dos Cavalos, Pernambuco state. Circles: *Rhipidomys nitela*; squares: *R. leucodactylus* cytotypes; lozenges: *R. mastacalis* cytotypes. Numbers 1, 5, 9 and 11 – this paper; 2, 7 and 8 – Silva and Yonenaga-Yassuda (1999); 3 – Aguilera *et al*. (1994); 4 – Gardner and Patton (1976); 6, 13–16 – Zanchin *et al*. (1992); 10 and 12 – Svartman and Almeida (1993).

Table 1. Number of specimens (*n*), localities and biomes analysed in this paper. Colection points correspond to those in Fig. 1.

Species	*n*	Collection points	Biomes
Rhipidomys nitela	2	1	Amazon
R. mastacalis cytotype 1	2	9	Cerrado
R. mastacalis cytotype 2	12	9	Cerrado
R. leucodactylus	5	9, 11	Cerrado
R. leucodactylus cytotype 1	6	5, 9	Cerrado/Amazon

Table 2. Species, collection points (numbers as in Fig. 1), diploid (2n) and autosomal arm numbers (FN) and places of the signal of hybridization reported in this study and in the literature. p – short arm, q – long arm.

Species	Collection points	2n	FN	$(T_2AG_3)_n$ hybridized on:	References
			2n = 48–50		
Rhipidomys nitela	1	48	68	ends of p and q	this paper
R. nitela (sp. B)	2	50	71,72	ends of p and q	Silva and Yonenaga-Yassuda 1999
			2n = 44 / high FN cytotypes		
R. mastacalis cytotype 1	9	44	80	ends of p and q	this paper
R. mastacalis cytotype 2	9	44	76	ends of p and q	this paper
R. mastacalis	14,15	44	74	–	Zanchin *et al*. 1992
R. cearanus	16	44	high	–	Zanchin *et al*. 1992
			2n = 44 / low FN cytotypes		
R. latimanus	4	44	48	–	Gardner and Patton 1976
R. sclateri	3	44	48	–	Aguilera *et al*. 1994
R. leucodactylus	9,11	44	48	ends of p and q	this paper
R. leucodactylus	6	44	48	–	Zanchin *et al*. 1992
Rhipidomys sp.	10	44	48	–	Svartman and Almeida 1993
Rhipidomys sp.	10,12	44	49	–	Svartman and Almeida 1993
Rhipidomys sp.	13	44	50	–	Zanchin *et al*. 1992
R. leucodactylus cytotype 1	5,9	44	52	ends of p and q	this paper
R. cf. *mastacalis*	7,8	44	52	ends of p and q	Silva and Yonenaga-Yassuda 1999

number (FN), allowing us to separate them in two groups. One group included species with high FNs and the other species with low FNs. The two taxa of *R. mastacalis* (Lund, 1840) (*R. m.* cytotype 1, FN = 80, and *R. m.* cytotype 2, FN = 76) belonged to the first group. They were trapped in the same locality and displayed, respectively, 19 and 17 biarmed autosomes (Fig. 2b and c, respectively). Both taxa of *R. leucodactylus* (Tschudi, 1844) studied pertain to the species group with low FNs. In the 2 localities where it was trapped, *R. leucodactylus* showed the same FN = 48 karyotype (Fig. 2d), almost entirely consisting of acrocentrics (18 pairs). *R. leucodactylus* cytotype 1 (Fig. 2e), also in two localities, similarly to *R. leucodactylus*, has a karyotype with a majority of acrocentrics (16 pairs, FN = 52).

Rhipidomys nitela displayed C-bands in the centromeres of most autosomes and in the centromere and short arm of the X chromosome (Fig. 3a). *R. mastacalis* cytotype 1, *R. m.* cytotype 2 and *R. leucodactylus* showed similar patterns with centromeric bands in the X chromosome and in 1, 2, and 4 pairs of acrocentrics, respectively (Fig. 3b). In *R. leucodactylus* cytotype 1 the C-bands occurred in the

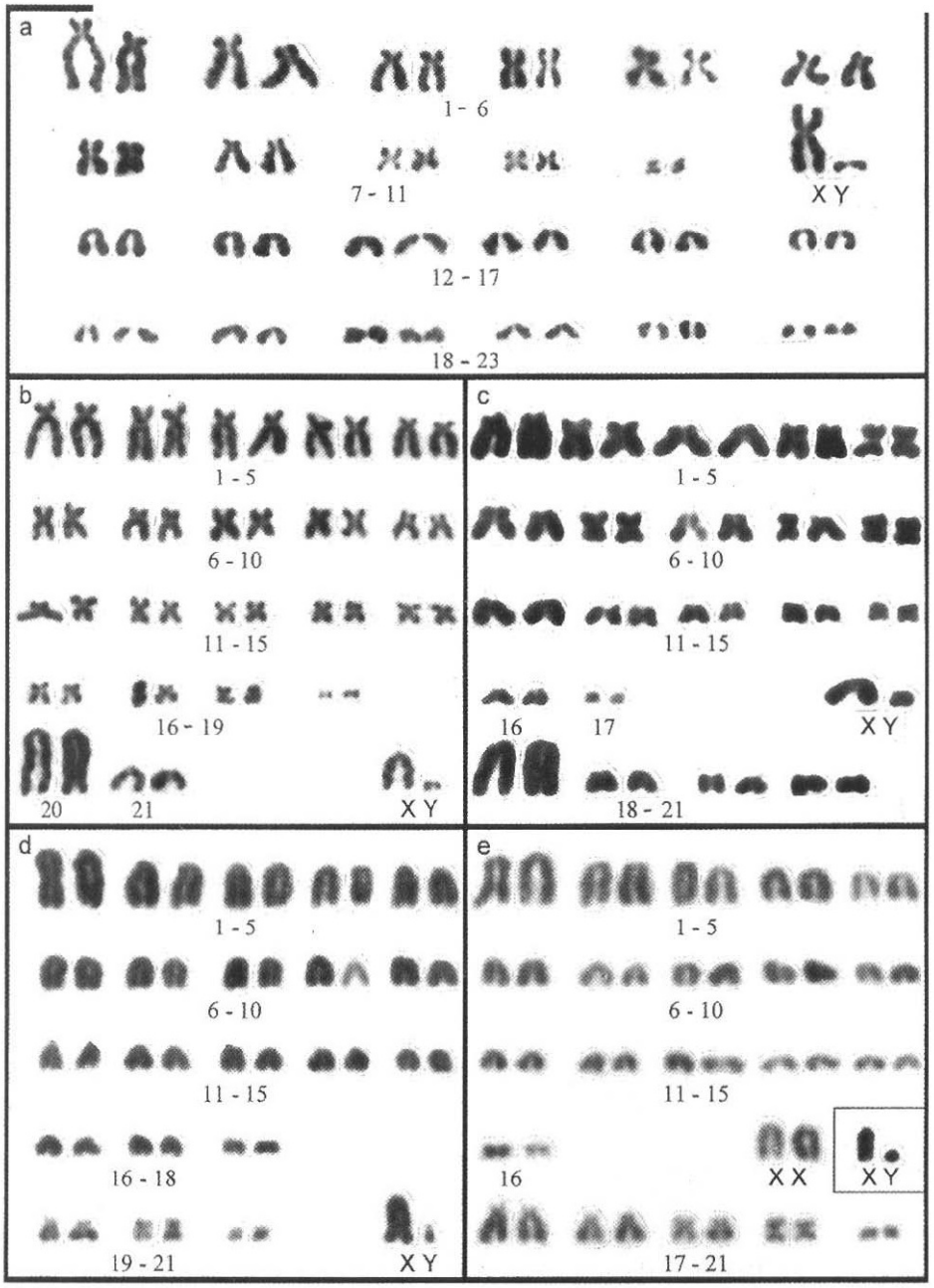

Fig. 2. Karyotypes in conventional staining of (a) *Rhipidomys nitela* (2n = 48, FN = 68), (b) *R. mastacalis* cytotype 1 (2n = 44, FN = 80), (c) *R. mastacalis* cytotype 2 (2n = 44, FN = 76), (d) *R. leucodactylus* (2n = 44, FN = 48), and (e) *R. leucodactylus* cytotype 1 (2n = 44, FN = 52), female (in the square the sex pair of a male).

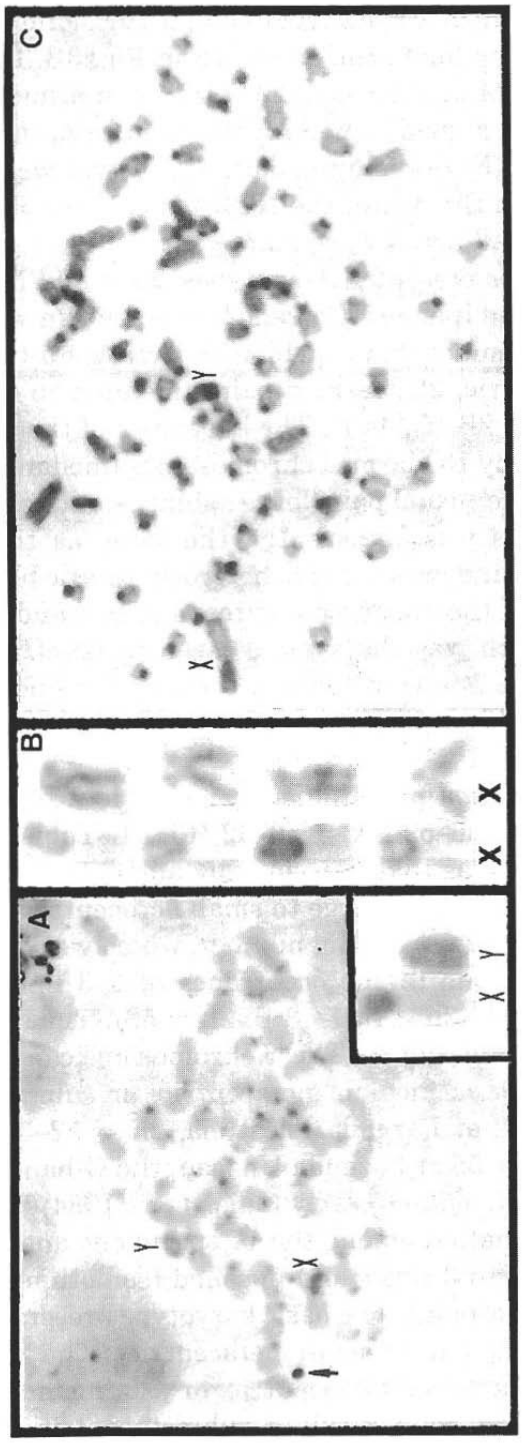

Fig. 3. Metaphase plates showing the C-band patterns observed in (a) *Rhipidomys nitela*, (b) *R. mastacalis* cytotype 1, and (c) *R. leucodactylus* cytotype 1. Sex chromosomes (X, Y) are marked.

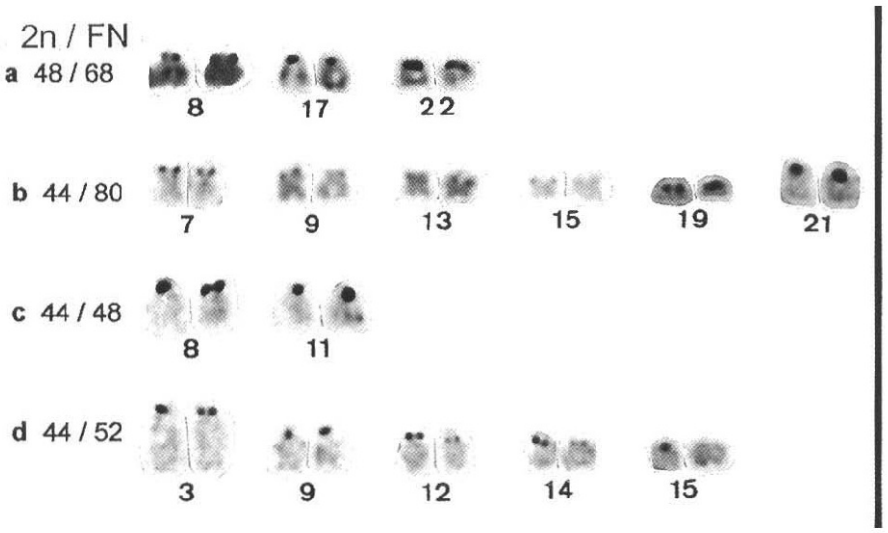

Fig. 4. The NOR bearing pairs, Ag-staining of a – *Rhipidomys nitela*, b – *R. mastacalis* cytotype 2, c – *R. leucodactylus*, and d – *R. leucodactylus* cytotype 1.

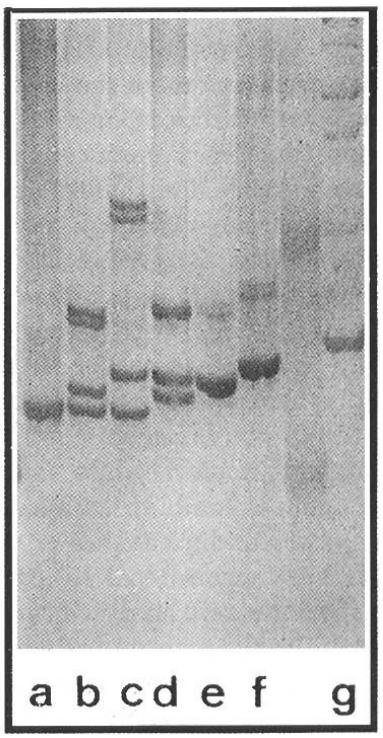

Fig. 5. Polyacrylamid-gel electrophoresis of the microsatellite "alleles" from the *Rhipidomys* species amplified with R47 and R65 primers. Lanes: a – 88–88bp; b – 88–91bp, and 101–103bp heteroduplex; c – 88–94bp, and 138–140bp heteroduplex; d – 91–94bp, and 105–106 heteroduplex; e – 94–94bp; (f) 97–97bp; g – molecular weight 100bp marker (plus pBR 322 digested with MspI).

centromeric region of most of the chromosomes (including the five biarmed pairs) and of the X chromosome (Fig. 3c). In all 5 taxa the Y chromosome was entirely heterochromatic. Three nucleolar organizer regions were observed in *R. nitela*, located in the short arms of pairs 8, 17, and 22 (Fig. 4a). In both cytotypes of *R. mastacalis*, 5 to 6 pairs (7, 9, 13, 15, 19, and 21) displayed NOR-bands, all in the short arms (Fig. 4b). In *R. leucodactylus* only 2 pairs (8 and 11) showed nucleolar organizers (Fig. 4c) and in *R. leucodactylus* cytotype 1 (Fig. 4d) this number rises to 5 pairs (3, 9, 12, 14, and 15).

The telomere $(T_2AG_3)_n$ probe hybridized both to short and long arms of all chromosomes of *R. nitela*, *R. mastacalis* cytotypes 1 and 2, *R. leucodactylus*, and *R. l.* cytotype 1 (Table 2). Of the 11 heterologous microsatellite DNA primers tested, only two presented amplification products in *Rhipidomys*, both originally designed for the *Rattus* species (R47 and R65, Fig. 5). R47 generated 4 "alleles" of 88bp, 91bp, 94bp, and 97bp size respectively, both in homozygous or heterozygous status. "Alleles" 88bp and 91bp pertained exclusively to *R. leucodactylus* (FN = 48, localities 9 and 11), the other 2 bands being found in the all taxa analysed. Two "alleles" were originated by primer R65, 1 of 172bp seeing in the 5 species investigated and the other (of 186bp) occurring in *R. leucodactylus* cytotype 1 only.

Discussion

Rhipidomys nitela is distributed throughout the Guianas, south of Venezuela to the north and center of Brazil, and its type locality is described as occurring in Guyana (Musser and Carleton 1993). We captured *R. nitela* in Surumú located in the northern region of the Brazilian Amazon (state of Roraima). This site is within the reported distribution area of the species. In specimens of this species collected in Amazon, Silva and Yonenaga-Yassuda (1999) found 2n = 50 and a large submetacentric X chromosome equal, apparently, to that we observed in Surumú. The karyotypes with 2n = 48–50, however, are unique since all other karyotyped species of *Rhipidomys* (see Table 2) showed diploid numbers of 44.

According to the number of pericentric inversions they carry (Zanchin *et al.* 1992, this paper), species with 2n = 44 may be joined into 2 groups, 1 with high FNs (74, 76, 80), and the other with low FNs (48, 49, 50, 52). The former group would include the *mastacalis* macrospecies described by Lund, 1840, whose type locality is Rio das Velhas, Lagoa Santa, state of Minas Gerais, Brazil. It is distributed throughout eastern and central Brazil, possibly in the Amazonian regions of Venezuela, Colombia, Ecuador, and Peru (Musser and Carleton 1993). The specimens reported by Zanchin *et al.* (1992), from the type locality (local 14, Table 2) and from Unacau (local 15), state of Bahia, presented FN = 74 in both localities. The specimens we analysed came from 4 localities (Fig. 1: collection points 9a–d) of central Brazil, a territory which is also located inside the distribution area of *mastacalis*. Because they have different numbers of biarmed elements (FN = 76, 80 vs 74) and are separated geographically, these cytotypes may be considered as

subspecies of *mastacalis*. These 3 taxa exhibit the same morphology of the sex chromosomes. Due to high FN, it is probable that *R. cearanus*, analysed by Zanchin *et al*. (1992) in Pernambuco (ie, inside the distribution area of *R. mastacalis*) also belongs to this group. Musser and Carleton (1993) classify *cearanus* as synonym of *R. mastacalis*.

The group of species of *Rhipidomys* which showed low FNs is more chromosomally polymorphic than the group with high FN. It includes numerous taxa which are subject to a great divergence in its classification and correspond to the distinct cytotypes with FN = 48, 49, 50, and 52. Detailed comparisons of these cytotypes indicated that all of them have the same basic karyotype, with observed differences due to the numbers of biarmed elements they bear. These fundamental numbers could correspond to taxonomic categories of species or subspecies grouped under a large cytotaxonomic entity represented by the macrospecies *R. leucodactylus* (Tschudi, 1844). This species has its type locality in eastern Peru, and occupies the Guianas, southern Venezuela, northern Brazil, Ecuador, and Peru (Musser and Carleton 1993). The cytotype representative of this macrospecies has FN = 48 and inhabits the Jamari River, Amazon (Zanchin *et al*. 1992). The animals we studied were collected at two localities (40 km SW Minaçú and Ipameri) of the Cerrado biome.

Several other *Rhipidomys* taxa with karyotypes with low FNs (from 48 to 52) were reported. *R. latimanus*, trapped by Gardner and Patton (1976) in Colombia and *R. sclateri* from Venezuela (Aguilera *et al*. 1994), presented FN = 48. Musser and Carleton (1993) relate that Thomas (1887) remarked that *sclateri*, named from British Guiana, was the eastern counterpart of Peruvian *R. leucodactylus*. Svartman and Almeida (1993) described specimens called *Rhipidomys* sp. with FN = 48 and 49 collected in S□o Paulo and in Brasilia with FN = 49, exclusively. Also in *Rhipidomys* sp., Zanchin *et al*. (1992) report an animal trapped on the Brazilian Atlantic coast (Monte Verde, see Fig. 1: collection point 13) presenting FN = 50. As *R. leucodactylus* cytotype 1, we analysed specimens with FN = 52 from the Cerrado biome (20 km NW Colinas do Sul) and from the Amazon biome (Caxiuan□). In two localities of the Amazon, Silva and Yonenaga-Yassuda (1999) found this same fundamental number (52).

In summary, the low FN species-group comprises the following taxa: *R. leucodactylus* of Brazil (Amazon and Cerrado), *R. latimanus* of Colombia, and *R. sclateri* of Venezuela, all with FN = 48; *Rhipidomys* sp. of S□o Paulo presenting FN = 48 and 49, and in Brasilia showing FN = 49; the FN = 50 cytotype of Monte Verde; and the FN = 52 taxon seen at Cerrado and at 3 localities of the Amazon. This species-group occupies a large part of the territory of South America, therefore extending the limits of *R. leucodactylus* from northern South America (Venezuela) to 25° South (state of S□o Paulo, Fig. 1).

Although the small sizes of some samples hinder definitive conclusions, microsatellite DNA data contributed in clarifying the relationships among some taxa. The primer R65 amplified only in the species of *Rhipidomys* out of 11 species of

thomasomyine and oryzomyine we previously investigated (Lima-Rosa *et al*. 2000). In this case it can be considered as a marker of the genus. The species-group of *Rhipidomys* with low FNs is unique because the bands of 88bp and 91bp (generated by the R47 primer) and that of 186bp (R65 primer) were displayed exclusively in it.

In conclusion, we found that the genus *Rhipidomys* accepts three larger species-groups. These are joined according to their diploid numbers (*R. nitela* with 2n = 48, 50 and the other species with 2n = 44), or by the numbers of their autosomal arms (*R. mastacalis* and related taxa with high FN versus *R. leucodactylus* and related taxa with low FN). The status of these species-groups is reinforced, partly, by the existence of exclusive "alleles" of microsatellite DNA.

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Appendix. Collection numbers and localities of capturing of specimens studied.

Voucher specimens: *Rhipidomys nitela*: AN817, AN908 (Surumú, Roraima state, 60°47'W, 04°11'N). *R. mastacalis* cytotype 1: MN36247 (20 km NW Colinas do Sul, Goiás state, 14°09'S, 48°04'W), MN37350 (40 km NE Uruaçú, Goiás state, 14°31'S, 49°08'W). *R. mastacalis* cytotype 2: MN36058, MN36196 (55 km N Niquelândia, Goiás state, 14°28'S, 48°27'W), MN36337*, MN36341, MN36358, MN36425 (20 km NW Colinas do Sul, Goiás state, 14°09'S, 48°04'W), MN36681, MN36833 (40 km SW Minaçú, Goiás state, 13°31'S, 48°13'W), MN37280*, MN37425, MN37438*, MN37439 (40 km NE Uruaçú, Goiás state, 14°31'S, 49°08'W). *R. leucodactylus*: OT4709, OT5070, OT6926, OT7657 (Ipameri, Caldas Nova and Corumbaíba, Goiás state, between 17°41'–17°56'S and 48°28'–48°32'W), MN36781* (40 km SW Minaçú, Goiás state, 13°31'S, 48°13'W). *R. leucodactylus* cytotype 1: AP111–115 (Caxiuan□, Pará state, 01°44'S, 51°23'W), MN36449 (20 km NW Colinas do Sul, Goiás state, 14°09'S, 48°04'W). *Specimens not karyotyped.