



CHROMOSOME CHARACTERIZATION OF BRAZILIAN SPECIES OF *CALOMYS* WATERHOUSE, 1837 FROM AMAZON, CERRADO AND PAMPAS DOMAINS (RODENTIA, SIGMODONTINAE)¹

(With 2 figures)

MARGARETE S. MATTEVI^{2, 3, 4}

TAIANA HAAG^{3, 4}

LUIZ FLAMARION B. OLIVEIRA^{4, 5}

ALFREDO R. LANGGUTH^{4, 6}

ABSTRACT: The karyotypes of 31 specimens of six taxa of the genus *Calomys* (Rodentia, Sigmodontinae) trapped in an extensive area of Brazil (between 11°-32°S and between 46°-61°W) are reported. In the Cerrado domain, *C. tener* showed 2n=66 and FN_a=66 karyotype with 32 pairs of autosomes, 31 of them being decreasing-sized acrocentric pairs, and one medium-to-small biarmed pair; *C. expulsus* showed a 2n=66 and FN_a=68 karyotype, with 30 pairs of acrocentric autosomes and two biarmed elements, a submetacentric pair 1 and the medium-to-small biarmed pair also seen in the karyotype of *C. tener*; in Ipamerí locality (Caldas Novas, Goiás) a female with 2n=64, FN_a=66 and a derivative karyotype of *C. expulsus* type was also observed. In the Pampas region a *C. laucha* female with 2n=64, FN_a=68 was trapped. In addition to the two biarmed pairs seen in *C. expulsus*, this individual also possessed a third large biarmed submetacentric element corresponding to the largest pair of the karyotype. In the Amazon region three *Calomys* specimens were analyzed. Two of them depicted a cytotype similar to that of *C. tener* (showing nevertheless 2n=64, FN_a=64 instead of 2n=66, FN_a=66), with an acrocentric pair 1 and the medium-to-small sized biarmed pair, but lacking one unidentified autosomal pair. At the same locality (Pimenta Bueno, Rondônia) *C. callidus* presented 2n=48, FN_a=66.

Key words: *Calomys*, Amazon, Pampas, Cerrado, karyotypes, Rodentia, Sigmodontinae.

RESUMO: Caracterização cromossômica de espécies brasileiras de *Calomys* Waterhouse, 1837 dos domínios Amazônico, do Cerrado e dos Pampas (Rodentia, Sigmodontinae).

São descritos os cariótipos de 31 exemplares de seis taxa do gênero *Calomys* (Rodentia, Sigmodontinae) provenientes de uma extensa área do Brasil (entre 11°-32°S e 46°-61°W). Na região do Cerrado foram observados *C. tener* que mostrou 2n=66 e FN_a=66, com um cariótipo constituído por 32 pares de autossomos, 31 deles sendo acrocêntricos de tamanho decrescente e um par metacêntrico de tamanho pequeno a médio; e *C. expulsus*, com 2n=66 e FN_a=68 e um cariótipo com 30 pares de autossomos acrocêntricos e mais dois elementos com dois braços, o par 1 submetacêntrico e o metacêntrico de pequeno a médio também visto no cariótipo de *C. tener*. Na localidade de Ipamerí (Caldas Novas, Goiás) foi também observada uma fêmea com 2n=64, FN_a=66 e com cariótipo do tipo *C. expulsus*. Na região dos Pampas foi coletada uma fêmea de *C. laucha* com 2n=64, FN_a=68. Além dos dois pares com dois braços vistos em *C. expulsus*, este indivíduo também apresentou um terceiro elemento com dois braços, um submetacêntrico grande que se constitui no maior par do cariótipo. No Amazonas foram analisados três espécimes de *Calomys*. Dois deles apresentaram um citotipo similar ao de *C. tener* (mostrando entretanto 2n=64, FN_a=64 em vez de 2n=66, FN_a=66), com o par 1 acrocêntrico, e o metacêntrico de pequeno a médio, mas faltando um par não identificado de autossomos. Na mesma localidade (Pimenta Bueno, Rondônia) *C. callidus* apresentou 2n=48, FN_a=66.

Palavras-chave: *Calomys*, Amazonas, Pampas, Cerrado, cariótipos, Rodentia, Sigmodontinae.

¹ Submitted on June 18, 2004. Accepted on January 21, 2005.

² Universidade Luterana do Brasil, Programa de Pós-Graduação em Diagnóstico Genético-Molecular. Av. Farroupilha, 8001, Canoas, 92420-280, RS, Brasil. E-mail: mattevi@terra.com.br

³ Universidade Federal do Rio Grande do Sul, Programa de Pós-Graduação em Genética e Biologia Molecular. Caixa Postal 15053, Porto Alegre, 91501-970, RS, Brasil. E-mail: taiahaag@yahoo.com.br

⁴ Fellow of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

⁵ Museu Nacional/UFRRJ, Departamento de Vertebrados. Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil. E-mail: melfo@terra.com.br

⁶ Universidade Federal da Paraíba, Departamento de Sistemática e Ecologia. 58059-900, João Pessoa, PB, Brasil. E-mail: alfredo@dse.ufpb.br

INTRODUCTION

Calomys Waterhouse, 1837 is a genus of South American rodents that belongs to the tribe Phyllotini of the subfamily Sigmodontinae. Its phylogenetic position is unclear, but it is generally considered a primitive branch of the tribe (HERSHKOVITZ 1962, PEARSON & PATTON 1976, STEPPAN 1995, STEPPAN & SULLIVAN 2000).

HERSHKOVITZ (1962) reduced the previously 10-15 species recognized in the genus (ELLERMAN 1941, CABRERA 1961) to only four, two of which, *C. laucha* Fischer, 1814, and *C. callosus* Rengger, 1830, later proved to be species complexes (PEARSON & PATTON 1976, WILLIAMS & MARES 1978, REIG 1986, CORTI, MERANI & VILLAFANE 1987). MUSSER & CARLETON (1993) and NOWAK (1999) listed nine and eight species respectively, but called attention to the fact that both the distributions and also the names mentioned in their synonymies should be observed with caution, considering that the genus was in need of a new revision. MUSSER & CARLETON (1993) listed the following species: *C. boliviae* Thomas, 1901 (= *fecundus* Thomas, 1926), *C. callidus* Thomas 1916, *C. hummelincki* Husson, 1960, *C. lepidus* Thomas, 1884, *C. musculinus* Thomas, 1913, *C. sorellus* Thomas, 1900, *C. callosus* (= *expulsus* Lund, 1841), *C. laucha*, and *C. tener* Winge, 1887, which was not recognized by NOWAK (1999). Later, a new *Calomys* species, *C. tocantinsi* Bonvicino, Lima & Almeida 2003, was described, increasing to 11 the number of species of the genus.

These species occur in a variety of habitats in Argentina, Bolivia, Brazil, Paraguay, Peru, Uruguay, Venezuela, Colombia, and Chile (MUSSER & CARLETON 1993) and some of them have been listed as etiological agents of numerous diseases, including hemorrhagic fever (GARCIA *et al.* 2000, SALAZAR-BRAVO *et al.* 2002).

The karyotypes of several species of *Calomys* have been previously reported, revealing a high chromosomal variation within the genus, with diploid numbers ranging from 36 to 66 (YONENAGA 1975, PEARSON & PATTON 1976, BRUM-ZORRILLA *et al.* 1990, VITULLO, ESPINOSA & MERANI 1990, SVARTMAN & ALMEIDA 1992, LISANTI *et al.* 1996, ESPINOSA *et al.* 1997, BONVICINO & ALMEIDA 2000, FAGUNDES *et al.* 2000, LIMA & KASAHARA 2001, BONVICINO, LIMA & ALMEIDA 2003). Here we describe the chromosomal complements of six putative taxa sampled in an extensive area ranged between 11°-

32°S and 46°-61°W, including localities of the Amazon, Cerrado, and Pampas domains in Brazil.

MATERIAL AND METHODS

The sample consists of 31 specimens referable to six putative units of the genus: *C. tener*, *C. expulsus*, *C. laucha*, *C. callidus*, *C. aff. expulsus*, and *Calomys* sp. which were trapped in five Brazilian localities (Fig.1, Appendix). Skins and skulls of the animals studied are deposited in the Mammal Collection of the Museu Nacional (MN), Rio de Janeiro and in the Mammal Collection of the Universidade Federal da Paraíba (UFPB), João Pessoa (voucher specimen numbers are listed in the Appendix).

Metaphase plates were obtained in the field from direct bone marrow preparations according to BAKER *et al.* (1982). Slides were stained with 5% Giemsa in a phosphate buffer, pH 6.8.

RESULTS

Three taxa were collected in localities of Cerrado domain (Tab.1). The two females of *C. tener* showed $2n=66$ and $FN_a=66$ with the karyotype constituted by 32 pairs of autosomes, 31 of them being decreasing-sized acrocentric pairs, and one medium-to-small biarmed pair (Fig.2a). The X chromosome is a large submetacentric chromosome, with size between those pairs numbers 1 and 2. *Calomys expulsus* occurred in three localities, and in Minaçu was trapped together with *C. tener*. All 24 specimens presented $2n=66$ and $FN_a=68$, with 30 pairs of acrocentric autosomes and two biarmed pairs: the submetacentric pair 1 and a medium-to-small pair also seen in the karyotype of *C. tener* (Fig.2b). The X chromosome, apparently with the same morphology of *C. tener*, is a large submetacentric and the Y chromosome is a small acrocentric. In Ipamerí (Goiás), a female with $2n=64$, $FN_a=66$, a karyotype similar to that of *C. expulsus* (both with two biarmed autosome pairs but the former without an acrocentric pair) was obtained (Fig.2c). The X chromosome is a large submetacentric, with size between those of pairs numbers 1 and 2.

In the Pampas (Tab.1), a female of *C. laucha* with $2n=64$ and $FN_a=68$ was trapped, showing, besides the two biarmed pairs seen in *C. expulsus*, a third biarmed pair, a large submetacentric which is the largest of the karyotype. This karyotype is the same presented in figure 2 of BRUM-ZORRILLA *et al.* (1990).



Fig. 1- Localities of collection: (1) Pimenta Bueno, Rondônia (Amazon); (2) Fazenda Regalito, Mambai, Goiás (Cerrado); (3) Minaçú, Goiás (Cerrado); (4) Ipameri, Goiás (Cerrado); (5) Taim, Rio Grande do Sul (Pampas).

From Pimenta Bueno, a site located at Amazon-Cerrado boundary (locality 1, Fig.1), three *Calomys* specimens were analyzed. Two of them depicted a cytotype similar to that of *C. tener* (showing $2n=64$, $FN_a=64$ instead of $2n=66$, $FN_a=66$), with an acrocentric pair 1 and the medium-to-small sized biarmed pair, but lacking one unidentified autosomal pair (Fig.2d). The X chromosome was distinct also, being more submetacentric than those seen in the other cytotypes. The third *Calomys* individual (a female) investigated in locality 1, presented $2n=48$, $FN_a=66$ showing the same karyotype described by VITULLO, ESPINOSA & MERANI (1990:101, Fig.1A) for *C. callidus* from Argentina.

DISCUSSION

Although *Calomys* is a genus found predominantly in southern South America, some of its species, namely *C. expulsus* (= *callosus*), *C. tener*, *C. laucha*,

and *C. tocantinsi*, inhabit regions of the Brazilian territory. *Calomys expulsus*, whose type locality is Lagoa Santa, Minas Gerais, Brazil, was considered by MUSSER & CARLETON (1993) as a synonym of *C. callosus* (type locality Neembucu, Paraguay). Based on karyological and morphological analyses, BONVICINO & ALMEIDA (2000), however, distinguished both species proposing a species status to *C. expulsus*. The individuals of *C. expulsus* studied by these authors were trapped in the Cerrado domain, in the same region where we captured the specimens analyzed in this study. All individuals of *C. expulsus*, both those we studied as well as those investigated by BONVICINO & ALMEIDA (2000), showed a $2n=66$, $FN_a=68$ karyotype, which is very different from the karyotype ($2n=36$, $FN_a=48$) described by PEARSON & PATTON (1976) for specimens of *C. callosus* from Paraguay. These findings corroborate, from a chromosomal stand point, the different identities of the two distinct taxonomic entities (species).

Table 1. Species, collections sites, specimen numbers (N), diploid (2n) and autosomal arm numbers (FN_a), autosomes, and X- and Y- chromosome morphologies of *Calomys* individuals analyzed in this study and in literature.

SPECIES	LOCALITY*	N	2n	FN _a	AUTOSOMES		X	Y	THIS STUDY	OTHERS
					A	Bi				
CERRADO DOMAIN										
<i>C. tener</i>	3	2	66	66	31	1	SM	**	Fig.2a	(1,2, 3)
	3	9	66	68	30	2	SM	A	Fig.2b	(2, 4)
<i>C. expulsus</i>	4	5								
	2	10								
<i>C. aff. expulsus</i>	4	1	64	66	29	2	SM	**	Fig.2c	
PAMPAS DOMAIN										
<i>C. laucha</i>	5	1	64	68	28	3	SM	**		(5)
AMAZON DOMAIN										
<i>Calomys</i> sp.	1	2	64	64	30	1	SM	A	Fig.2d	
<i>C. callidus</i>	1	1	48	66	10	13	SM	**		(6)

(*) Numbers correspond to those of figure 1.; (SM) submetacentric; (A) acrocentric; (Bi) biarmed; (SM) submetacentric; (**) female; (1) YONENAGA 1975; (2) BONVICINO & ALMEIDA 2000; (3) FAGUNDES *et al.* 2000; (4) SVARTMAN & ALMEIDA 1992; (5) BRUM-ZORRILLA *et al.* 1990; (6) VITULLO *et al.* 1990.

Calomys tener, whose type locality is Lagoa Santa, is found in Central Brazil (Cerrado) and is often considered a subspecies of *C. laucha* (MUSSE & CARLETON 1993, EISENBERG & REDFORD 1999). In Ipameri (locality 4) we trapped *C. tener* together with *C. expulsus*, but all the specimens of *C. tener* (2n=66, FN_a=66) analyzed, either from this site or from the other localities, differed from those of *C. expulsus* by having an acrocentric pair 1, apparently due to a pericentric inversion (this work, BONVICINO & ALMEIDA 2000). According to these authors, morphologic measures also differentiate *C. tener* from *C. expulsus*, the former being smaller. *Calomys expulsus* occurs in the Brazilian states of Pernambuco, Bahia, Goiás, and Minas Gerais, and *C. tener* occurs in the states of São Paulo, Minas Gerais, and Goiás, the two forms being sympatric in Minas Gerais and Goiás.

Calomys laucha also showed a high diploid number (2n= 64). Its type locality is near to Asunción, Paraguay, and has been obtained in northern Argentina and Uruguay, southwestern Bolivia, western Paraguay, and central western Brazil (MUSSE & CARLETON 1993). We trapped one individual of *C. laucha* in the south extreme of Brazil (Uruguayan boundary, parallel 32°S)

which, apparently, showed the same karyotype described by BRUM-ZORRILLA *et al.* (1990) for specimens from the neighbor locality of Laguna Negra, Uruguay.

In the Amazonian region (Pimenta Bueno, Rondônia, Fig. 1), in a savanna enclave, we collected a specimen with 2n=48, FN_a=66, a karyotype which was attributed by VITULLO *et al.* (1984) and VITULLO, ESPINOSA & MERANI (1990) to *C. callidus*. This is a large species with sharp interorbital edges which, together with *C. venustus*, had been synonymized (HERSHKOVITZ, 1962) with *C. callosus* (2n=36) but due to its distinctive karyotype it was considered as a full species by VITULLO, ESPINOSA & MERANI (1990). The 2n=48, FN_a=66 karyotype of this study is quite similar to the 2n=46, FN_a=66 reported by BONVICINO, LIMA & ALMEIDA (2003) in *C. tocantinsi* (also a large *Calomys* species), the difference being a biarmed pair, apparently.

Due to the wide morphologic uniformity presented by species of *Calomys*, phylogenetic hypotheses based on these characters have not been very informative and even the monophyly of the genus has been questioned (STEPPAN 1995). However,

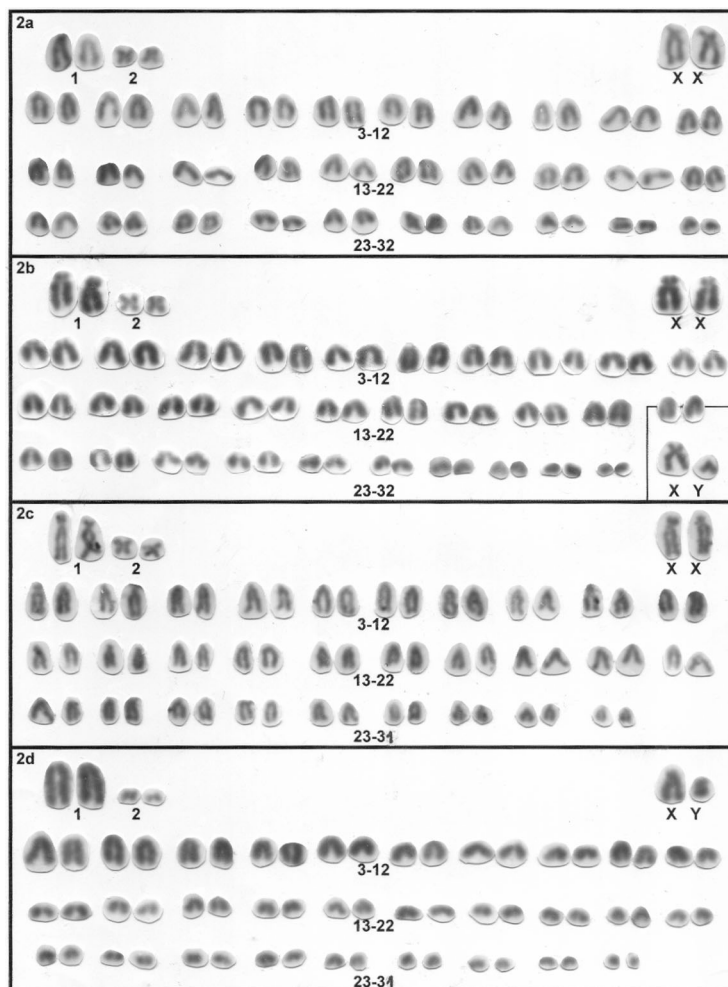


Fig.2- Karyotypes in conventional staining of a) *Calomys tener* ($2n=66$; $FN_a=66$), ♀ . b) *C. expulsus* ($2n=66$; $FN_a=68$), ♀ ; in the square the sex pair of a male. c) *C. aff. expulsus* ($2n=64$; $FN_a=66$), ♀ . d) *Calomys* sp. ($2n=64$; $FN_a=64$), ♂ .

the wide chromosomal variation which characterizes *Calomys* ($2n=36$ to 66) allowed VITULLO, ESPINOSA & MERANI (1990) and ESPINOSA *et al.* (1997) to cluster their species into three karyological groups which are the result of a progressive chromosomal number reduction due to centric fusion rearrangements: the *lauchahummenlincki* group ($2n=60-64$) to which the species with $2n=66$ (*tener* and, after, *expulsus*) can be allocated; the *callidus-venustus* group ($2n=46-56$) with intermediate diploid numbers; and the *callosus-lepidus* group ($2n=36-44$), the more divergent group in chromosomal morphology. The chromosomal analysis that we performed indicates that an extensive area (from 11° to $32^\circ S$) of Brazilian territory is occupied by species belonging to the high chromosomal number group (*C.*

expulsus, *C. tener*, and *C. laucha*). The species that inhabits the Amazonian locality (Pimenta Bueno) represents a karyotypically more derived group that includes the Argentinean specimens of *C. callidus* (reported by VITULLO, ESPINOSA & MERANI 1990) and *C. tocantinsi*, a taxon with similar karyotype described in the State of Tocantins. If confirmed, this clade also occupies a vast area of South American lowlands and deserves to be better investigated.

The phylogeny based on mitochondrial DNA analysis (SALAZAR-BRAVO *et al.* 2001, HAAG *et al.*, submitted) agrees in part with the chromosomal phylogenetic proposal. Two major clades are found, one of them clustering *C. lepidus* + *C. musculus* + *O. sorellus* and the other including six species (*Calomys* sp., *C. fecundus*,

C. callosus, *C. venustus*, *C. laucha*, and *C. tener*); *C. hummelincki* would occupy an intermediate position between both. It was also proposed that the former clade would be mostly associated with mountain habitats, with subsequent invasions of lowlands habitats, and the other group would include species restricted to the lowland habitats located at north and south of the Amazon basin. The Brazilian species we analyzed derived from the two major clades of the lowland clade of *Calomys*. This lowland clade is divided in two groups, one of them including the species with higher diploid numbers (in which the species that occur in Brazil would be located) and a more recent and chromosomally more derived, in which the species *C. callidus* that we studied in Amazon is included.

Another important characteristic of the genus *Calomys* is the great chromosomal differentiation it presents, making the number of described karyotypes greater than the number of nominal forms. This is also the case of our study, in which we found six different karyotypes among four species, two of them being evident variation of karyotypes already described for nominal species.

Although the chromosomal differences observed among the species of *Calomys* are eventually small (due to a single rearrangement as a centric fusion or a pericentric inversion apparently), they are, however, capable to differentiate the several taxa of the genus. This is the case, for instance, of *C. tener* with $2n=66$, $NF_a=66$, of *C. expulsus* with $2n=66$, $NF_a=68$, *C. aff. expulsus* with $2n=64$, $NF_a=66$, and *C. laucha* with $2n=64$, $NF_a=68$. Considering the small morphological differentiation seen among them, it is important to confer a higher weight to the karyotypical attribute in the diagnosis and recognition of the species status to the taxa of this genus.

ACKNOWLEDGMENTS

To A.P.Nunes (Museu Goeldi), J.L.P.Cordeiro (UFRGS), and J.A.Miranda (ULBRA), for field work help; and to L.S.Silva (UFRGS), and B.A.Carvalho (UFRGS), for technical support. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Financiadora de Estudos e Projetos (FINEP), Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul (FAPERGS), and Organization of the American States (OAS) have supported this study.

LITERATURE CITED

- BAKER, R.J.; HAIDUK, M.W.; ROBBINS, L.W.; CANDENA, A. & KOOP, B.F., 1982. Chromosomal studies of American bats and their systematic implications. In: MARES, M.A. & GENOWAYS, H.H. (Eds.) **Mammalian Biology in South America**. Pittsburg: Special Publications Pymatuning Laboratory of Ecology, University of Pittsburg. p.303-327.
- BONVICINO, C.R. & ALMEIDA, F.C., 2000. Karyotype, morphology and taxonomic status of *Calomys expulsus* (Rodentia, Sigmodontinae). **Mammalia**, Paris, **64**(3):339-351.
- BONVICINO, C.R.; LIMA, J.F.S. & ALMEIDA, F.C., 2003. A new species of *Calomys* Waterhouse (Rodentia, Sigmodontinae) from the Cerrado of Central Brazil. **Revista Brasileira de Zoologia**, Curitiba, **20**(2):301-307.
- BRUM-ZORRILLA, N.; DE CATALFO, G.H.; DEGIOVANANGELO, C.; WAINBERG, R.L. & FRONZA, G., 1990. *Calomys laucha* chromosome (Rodentia, Cricetidae) from Uruguay and Argentina. **Caryologia**, Florence, **43**(1):65-77.
- CABRERA, A., 1961. Catalogo de los mamíferos de América del Sur. **Revista del Museo Argentino Ciencias Naturales "Bernardino Rivadavia"**, Buenos Aires, **4**(2):309-732.
- CORTI, M.; MERANI, M. & SAND-VILLAFANE, G., 1987. Multivariate morphometrics of vesper mice (*Calomys*): preliminary assessment of species, population, and strain divergence. **Zeitschrift für Säugetierkunde**, Jena, **52**(2):236-242.
- EISENBERG, J.F. & REDFORD, K.H., 1999. **Mammals of the Neotropics: The Central Neotropics: Ecuador, Peru, Bolivia, Brazil**. Chicago: University of Chicago Press. 609p.
- ELLERMAN, J.R., 1941. **The families and genera of living rodents: Family Muridae**. London: British Museum (Natural History). 2v., 690p.
- ESPINOSA, M.B.; LASSERE, A.; PIANANIDA, M. & VITULLO, A.D., 1997. Cytogenetics of vesper mice, *Calomys* (Sigmodontinae): a new karyotype from the Puna region and its implication on chromosomal phylogeny. **Cellular and Molecular Life Sciences**, Basel, **53**(7):583-586.
- FAGUNDES, V.; SATO, Y.; SILVA, M.J.J.; RODRIGUES, F. & YONENAGA-YASSUDA, Y., 2000. A new species of *Calomys* (Rodentia, Sigmodontinae) from Central Brazil identified by its karyotype. **Hereditas**, Lund, **133**(2):195-200.
- GARCIA, J.B.; MORZUNOV, S.P.; LEVIS, S.; ROWE, J.; CALDERÓN, G.; ENRIA, D.; SABATINI, M.; BUCHMEIER, M.J.; BOWEN, M.D. & JEOR, S.C.S., 2000. Genetic diversity of the Junin virus in Argentina: geographic and temporal patterns. **Virology**, Oxford, **272**(1):127-136.
- HERSHKOVITZ, P., 1962. Evolution of Neotropical cricetine rodents (Muridae) with special reference to

- the phyllotine group. **Fieldiana: Zoology (New Series)**, Chicago, **46**:1-524.
- LIMA, J.F.S. & KASAHARA, S., 2001. A new karyotype of *Calomys* (Rodentia, Sigmodontinae). **Iheringia, Série Zoologia**, Porto Alegre, **91**(2):133-136.
- LISANTI, J.; DE BARALE, G.D.; SENN, E.P. & BELLA, J.L., 1996. Chromosomal characterization of *Calomys musculus* (Rodentia, Cricetidae). **Caryologia**, Florence, **49**(3-4):327-334.
- MUSSER, G.G. & CARLETON, M.D., 1993. Family Muridae. In: WILSON, D.E. & REEDER, D.M. (Eds.) **Mammals Species of the World - A Taxonomic and Geographic Reference**. Washington: Smithsonian Institution Press. p.501-756.
- NOWAK, R.M., 1999. **Walker's Mammals of the World**. 6.ed. Baltimore: Johns Hopkins University Press. 836p.
- PEARSON, O.P. & PATTON, J.L., 1976. Relationships among South American phyllotine rodents based on chromosome analysis. **Journal of Mammalogy**, Provo, **57**(2):339-350.
- REIG, O.A., 1986. Diversity patterns and differentiation of high Andean rodents. In: VUILLEUMIER, F. & MONASTERIO, M. (Eds.) **High Altitude Tropical Biogeography**. New York: Oxford University Press. p.404-440.
- SALAZAR-BRAVO, J.; DRAGOO, J.W.; TINNIN, D.S. & YATES, T.L., 2001. Phylogeny and evolution of the neotropical rodent genus *Calomys*: inferences from mitochondrial DNA sequence data. **Molecular Phylogenetics and Evolution**, San Diego, **20**(2):173-184.
- SALAZAR-BRAVO, J.; DRAGOO, J.W.; BOWEN, M.D.; PETERS, C.J.; KSIAZEK, T.J. & YATES, T.L., 2002. Natural nidality in Bolivian hemorrhagic fever and the systematics of the reservoir species. **Infections, Genetics and Evolution**, Montpellier, **1**(3):191-199.
- STEPPAN, S.J., 1995. Revision of the leaf-eared mice Phyllotini (Rodentia: Sigmodontinae) with a phylogenetic hypothesis for the Sigmodontinae. **Fieldiana: Zoology (New Series)**, Chicago, **80**:1-112.
- STEPPAN, S.J. & SULLIVAN, J., 2000. The emerging statistical perspective in systematics: a comment on Mares and Braun. **Journal of Mammalogy**, Provo, **81**(1):260-270.
- SVARTMAN, M. & ALMEIDA, J.C., 1992. Comparative karyotypic analysis of two *Calomys* species (Rodentia, Cricetidae) from Central Brazil. **Caryologia**, Florence, **45**(1):35-42.
- VITULLO, A.D.; ESPINOSA, M.B. & MERANI, M.S., 1990. Cytogenetics of vesper mice, *Calomys* (Rodentia, Cricetidae): robertsonian variation between *Calomys callidus* and *Calomys venustus*. **Zeitschrift für Säugetierkunde**, Jena, **55**(1):99-105.
- VITULLO, A.D.; KAJON, A.E.; PERCICH, R.; ZULETA, G.E. & MERANI, M.S., 1984. Caracterización citogenética de tres especies de roedores (Rodentia: Cricetidae) de la Republica Argentina. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"**, Buenos Aires, **13**(2):491-498.
- WILLIAMS, D.F. & MARES, M.A., 1978. A new genus and species of phyllotine rodent (Mammalia: Muridae) from northwestern Argentina. **Annals of the Carnegie Museum**, Pittsburgh, **47**:193-221.
- YONENAGA, Y., 1975. Karyotypes and chromosome polymorphisms in Brazilian rodents. **Caryologia**, Florence, **28**(2):202-210.

APPENDIX

Voucher specimens – BRAZIL - GOIÁS: 40km SW Minaçu, 13°31'S; 48°13'W: *C. tener* (MN36276, MN36473); *C. expulsus* (MN36230, MN36255, MN36270, MN36275, MN36289, MN36360, MN36447, MN36508, MN37281); Ipameri, Caldas Novas, and Corumbáiba, between 17°41'-17°56'S and 48°28'-48°32'W: *C. expulsus* (OT3686, OT3688, OT5180, OT5186, OT5763); *C. aff. expulsus* (OT5185); Fazenda Regalito, Mambai, 14°29'S; 46°06'W: *C. expulsus* (UFPB3053, UFPB3054, UFPB3055, UFPB3057, UFPB3059, UFPB3062, UFPB3063, UFPB3066, UFPB3067, UFPB3068); RIO GRANDE DO SUL, Taim Ecological Station, Rio Grande, (32°32'S; 52°32'W): *Calomys laucha* (LF952); RONDÔNIA: Pimenta Bueno, 11°43'S; 60°55'W: *Calomys* sp. (LF4974, LF5020); *C. callidus* (LF5067)