ISSN 0365-4508

ARQUIVOS DO MUSEU NACIONAL

Nunquam aliud natura, aliud sapienta dicit
Juvenal, 14, 321
In silvis academi quoerere rerum,
Quamquam Socraticis madet sermonibus
Ladisl. Netto, *ex Hor*

VOL.LXIII

N.1

RIO DE JANEIRO
Janeiro/Março
2005

Arquivos do Museu Nacional

ARQUIVOS
DO
MUSEU NACIONAL

VOLUME 63

NÚMERO 1

JANEIRO/MARÇO
2005

RIO DE JANEIRO

Arq. Mus. Nac.	Rio de Janeiro	v.63	n.1	p.1-204	jan./mar.2005

ISSN 0365-4508

Arquivos do Museu Nacional, mais antigo periódico científico do Brasil (1876), é uma publicação trimestral (março, junho, setembro e dezembro), com tiragem de 1000 exemplares, editada pelo Museu Nacional/Universidade Federal do Rio de Janeiro. Tem por finalidade publicar artigos científicos inéditos nas áreas de Antropologia, Arqueologia, Botânica, Geologia, Paleontologia e Zoologia. Está indexado nas seguintes bases de dados bibliográficos: Biological Abstracts, ISI – Thomson Scientific, Ulrich's International Periodicals Directory, Zoological Record, NISC Colorado e Periodica.

As normas para preparação dos manuscritos encontram-se disponíveis em cada número dos *Arquivos* e em htttp://acd.ufrj.br/~museuhp/publ.htm. Os artigos são avaliados por, pelo menos, dois especialistas na área envolvida e que, eventualmente, pertencem ao Conselho Editorial. O conteúdo dos artigos é de responsabilidade exclusiva do(s) respectivo(s) autor(es).

Os manuscritos deverão ser encaminhados para Museu Nacional/UFRJ, Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil.

Arquivos do Museu Nacional, the oldest Brazilian scientific publication (1876), is issued every three months (March, June, September and December). It is edited by Museu Nacional/Universidade Federal do Rio de Janeiro, with a circulation of 1000 copies. Its purpose is the edition of unpublished scientific articles in the areas of Anthropology, Archaeology, Botany, Geology, Paleontology and Zoology. It is indexed in the following bases of bibliographical data: Biological Abstracts, ISI – Thomson Scientific, Ulrich's International Periodicals Directory, Zoological Record, NISC Colorado and Periodica.

Instructions for the preparation of the manuscripts are available in each edition of the publication and at http://acd.ufrj.br/~museuhp/publ.htm. The articles are reviewed, at least, by two specialists in the area that may, eventually, belong to the Editorial Board. The authors are totally responsible for the content of the texts.

The manuscripts should be sent to Museu Nacional/UFRJ, Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil.

Financiamento

CNPq
Conselho Nacional de Desenvolvimento Científico e Tecnológico

Arquivos do Museu Nacional – vol.1 (1876) –
Rio de Janeiro: Museu Nacional.

Trimestral
Até o v.59, 2001, periodicidade irregular

ISSN 0365-4508

1. Ciências Naturais – Periódicos. I. Museu Nacional (Brasil).

CDD 500.1

APRESENTAÇÃO

O presente número dos Arquivos do Museu Nacional constitui uma homenagem póstuma ao Dr. João Moojen de Oliveira, que teria completado 100 anos no dia 1° de dezembro de 2004. O Dr. João Moojen foi o responsável pelo Setor de Mamíferos do Museu Nacional entre 1939 e 1969, ano em que se aposentou, tendo retornado a esta instituição como professor visitante entre 1979 e 1985, ano de seu falecimento.

João Moojen foi o responsável pelo desenvolvimento da Mastozoologia no Museu Nacional, reunindo grande parte do imenso acervo que hoje se encontra disponível aos pesquisadores. Além disso, contribuiu com diversos estudos originais em taxonomia e sistemática de mamíferos, em especial roedores, seu grupo de maior interesse.

A Mastozoologia no Brasil encontra-se atualmente em fase de expansão. A coleção de mamíferos do Museu Nacional tem desempenhado papel de extrema importância nesse contexto, uma vez que constitui a base de grande número de teses, dissertações e trabalhos científicos desenvolvidos nos últimos anos. Apesar disso, poucos mastozoólogos têm conhecimento da origem desse acervo e do seu principal mentor. Acreditamos que, mais que uma homenagem há muito devida, esta publicação vai informar as gerações mais novas a respeito da história recente do Museu Nacional, especialmente no que diz respeito às coletas que resultaram no copioso material hoje disponível na coleção de mamíferos. Neste sentido, esta homenagem ao Dr. Moojen também se estende a seus colaboradores, que tanto contribuíram com a boa documentação nos trabalhos de campo e com a preparação exemplar de espécimes-testemunho de pesquisas na área de Saúde Pública, base de nossa coleção.

Gostaríamos de agradecer aos colegas que submeteram manuscritos originais a este número-homenagem, que, da mesma forma que todos trabalhos submetidos às publicações do Museu Nacional, foram sujeitos à revisão por especialistas externos e por editores de área da Comissão de Publicações.

FOREWORD

This issue of the *Arquivos do Museu Nacional* is a posthumous *festschrift* in memory of Dr. João Moojen de Oliveira, who would have celebrated his 100th birthday on December 1st, 2004. Dr. Moojen was in charge of the Mammals Sector at the Museu Nacional, Rio de Janeiro, from 1939 until his retirement in 1969, and he subsequently returned to this institution as visiting professor from 1979 until 1985, the year of his death.

João Moojen was responsible for the development of mammalogy at the Museu Nacional. It was he who amassed a large part of the vast collection that researchers can now examine, and he also published several original works on mammalian taxonomy and systematics, especially on rodents, his major field of interest.

Today, mammalogy is a rapidly expanding field in Brazil. The Museu Nacional's mammal collection has played a vital role in this development, having formed the basis for a great many theses, dissertations and scientific papers produced in recent years. Even so, few mammalogists are aware of the origins of this collection and the inspiration behind it. We trust that this publication will not merely serve as a long-overdue tribute to Dr. Moojen, but also inform new generations about the Museu Nacional's recent history, particularly with regard to the collection programs that have resulted in the copious material now available in the mammalogy collection. In that sense, our tribute extends to Dr. Moojen's collaborators who collected mammal specimens for public health research programs: their thorough record-keeping and exemplary preparation of voucher specimens greatly enhance the value of our collection.

We wish to thank those colleagues who submitted original manuscripts for this *festschrift* volume. As occurs with all manuscripts submitted to Museu Nacional publications, their contributions were reviewed by independent expert peer reviewers and by subject editors on the Publications Board.

João Alves de Oliveira
Ulisses Caramaschi
Editores

CONSULTORES CIENTÍFICOS
COLABORADORES DESTE NÚMERO

Cleber J. R. Alho
Universidade de Brasília - DF

Fernando D. de Avila-Pires
Fundação Oswaldo Cruz - RJ

Jaime L. Benchimol
Fundação Oswaldo Cruz - RJ

Helena G. Bergallo
Universidade Estadual do Rio de Janeiro

Cibele R. Bonvicino
Instituto Nacional de Câncer, Rio de Janeiro

Leonora P. Costa
Universidade Federal do Espírito Santo

Valéria Fagundes
Universidade Federal do Espírito Santo

Pablo R. Gonçalves
Universidade Federal do Rio de Janeiro

Renato Gregorin
Universidade Federal de Lavras - MG

Carlos Eduardo de V. Grelle
Universidade Federal do Rio de Janeiro - RJ

Ines Horovitz
University of California - EUA

Sanae Kasahara
Universidade Estadual Paulista - SP

Thomas Lacher
Texas A & M. University - EUA

Yuri Leite
Universidade Federal do Espírito Santo - ES

Margarete Mattevi
Universidade Luterana do Brasil - RS

Leandro Monteiro
Universidade Estadual do Norte Fluminense - RJ

Luiz Flamarion B. de Oliveira
Universidade Federal do Rio de Janeiro - RJ

James L. Patton
Museum of Vertebrate Zoology - EUA

Bruce D. Patterson
Field Museum of Natural History - EUA

Leila M. Pessoa
Universidade Federal do Rio de Janeiro

Ulyses F. J. Pardiñas
Centro Nacional Patagonico - Argentina

Adriano L. Peracchi
Universidade Federal Rural do Rio de Janeiro

Alexandre Percequillo
Universidade Federal da Paraíba

Sérgio F. dos Reis
Universidade Estadual de Campinas - SP

Alfred L. Rosenberger
The City University of New York - EUA

Magali R. Sá
Fundação Oswaldo Cruz - RJ

Dante M. Teixeira
Universidade Federal do Rio de Janeiro

Christopher J. Tribe
University Museum of Zoology - Inglaterra

Diego Verzi
Universidad Nacional de La Plata - Argentina

Robert S. Voss
American Museum of Natural History - EUA

Marcelo Weksler
American Museum of Natural History - EUA

Yatiyo Yonenaga-Yassuda
Universidade de São Paulo

DEPOIMENTO: JOÃO MOOJEN DE OLIVEIRA
PIONEIRO DA MASTOZOOLOGIA BRASILEIRA

Em dezembro de 2004 comemorou-se o centenário de nascimento do zoólogo João Moojen de Oliveira, ex-naturalista e pesquisador do Museu Nacional, ex-professor da Universidade Federal do Rio de Janeiro, da Universidade Federal de Viçosa, do Colégio Pedro II, e um dos fundadores da Universidade de Brasília.

Conheci Moojen quando ele lecionou no primeiro Curso de Especialização em Peste, na Primeira Circunscrição Nordeste do Serviço Nacional da Peste (SNP), realizado no Recife em 1943. Ali, no laboratório do SNP, Moojen analisa fichas de ratos encontrados mortos no campo; a variedade de roedores silvestres o surpreende. Vai conhecer "de visu" a área aonde foram encontrados preás, bicos-de-lacre, punarés. À chefia do SNP apresenta projeto-piloto de estudo da fauna do agreste.

Moojen retorna ao Recife em 1945 com a finalidade de participar do segundo Curso de Especialização em Peste. Avalia os resultados do projeto-piloto realizado no município de Caruaru. Elabora, então, um amplo projeto objetivando o levantamento da fauna de roedores silvestres no Nordeste do Brasil. O plano contempla o estudo da sistemática de roedores e sua distribuição geográfica, variação numérica da população nas estações de chuva e de seca, variação na coloração da pelagem, da forma e medidas craniométricas dos cricetídeos.

Moojen debate com o diretor do SNP e assessores de epidemiologia, sendo o projeto incorporado às atividades daquele órgão; então, foram alocados recursos orçamentários específicos para sua execução ano a ano.

Na qualidade de diretor da 1ª Circunscrição Nordeste do SNP, contemporâneo do Prof. Moojen, transcrevo tópicos do que na época deixei registrado no "Diário do Médico", em cartas e publicações sobre o grande inquérito rodentológico:

"Em excursão ao agreste de Caruaru, o Prof. Moojen vislumbra a possibilidade de levantar a fauna de roedores do Nordeste, aproveitando a estrutura do SNP, sua rede de laboratórios na região, disponibilidade de guardas sanitários" [1].

Interessava ao zoólogo o estudo da sistemática e ecologia da fauna de cricetídeos de toda a região semi-árida do Nordeste; e ao Serviço de Peste o completo conhecimento das espécies, sua distribuição geográfica, ecótopos, prevalência sazonal, ectoparasitos, afim de ser estudada a participação dos roedores silvestres na circulação do micróbio da peste na área endêmica.

"O projeto indica locais preferenciais de captura: roçadas de milho, mandioca, feijão; capinzais, canaviais, algodoais, palmeirais; cercas de varas, pedra, avelós, macambira; qual a distância dos pontos de captura às habitações; tipo de habitação; cursos de água e coleções de água ("barreiros") existentes no local; tipo de armadilha e isca a usar (inclusive "arataca"); latas e sacos para conduzir animais silvestres ao laboratório sem perda de ectoparasitos" [2].

"A captura de roedores silvestres deve ser realizada em sítios quiescentes de peste, por equipes de três capturadores, munidos cada um de cem ratoeiras, para amostragem em ecótopos das diversas espécies. Na ficha de cada animal capturado são registrados o local da captura, data, flora da área, cultivos agrícolas, nome popular do animal capturado, coloração da pelagem, medidas anatômicas externas (pata traseira, orelha, cauda), sexo, idade (jovem, adulto), número de fetos, tipo de alimento encontrado no estômago; também são incluídos dados relativos ao meio ambiente: época de chuva, tipo de solo, clima, temperatura média, etc. Os animais taxidermizados, numerados, com seus crânios e mandíbulas limpos, secos, protegidos com verniz impermeabilizante, "DUCO", são enviados ao Prof. Moojen, no Museu Nacional, para estudo de sistemática. As pulgas e outros ectoparasitos, colocados em tubos identificados com o mesmo número do animal hospedeiro, são encaminhados ao Prof. Lindolfo Guimarães, no Museu de Zoologia da Universidade de São Paulo".

"Para que a quantidade e qualidade do trabalho realizado nesse inquérito rodontológico assumisse marcas insuperáveis, foi necessário o acompanhamento diuturno de todas as etapas de trabalho, pelos médicos chefes de distrito, estimulados pela presença do Prof. Moojen em amiudadas viagens" [3].

---

[1] ARCOVERDE DE FREITAS, C. Diário do médico do SNP. Arquivo da Casa de Oswaldo Cruz – FIOCRUZ.
[2] ARCOVERDE DE FREITAS, C., 1998. **Saúde no Brasil – nomes e fatos**. Recife: Edições Bagaço Ltda, 209p.
[3] ARCOVERDE DE FREITAS, C., 1988. **Histórias da peste e de outras endemias**, Rio de Janeiro: ENSP/FIOCRUZ, 214p.

O levantamento da fauna de roedores do Nordeste, concluído em 1955, exigiu o trabalho contínuo durante dez anos, sendo que a coleta sistemática se realizou entre 1945 e 1955.

"Somente a Primeira Circunscrição Nordeste do Serviço Nacional da Peste enviou para o Museu Nacional 44.214 espécimes de roedores e outros pequenos mamíferos" [4].

A enorme amostra de roedores e pulgas obtida nesse inquérito, a grande extensão da área de captura, o cuidado na preparação e registro desse riquíssimo material zoológico, bem expressam o rigor com que se trabalhou naquela época. Do material do Nordeste o Prof. Moojen descreveu uma nova espécie, *Zygodontomys pixuna*, e diversas outras têm-se revelado à luz das pesquisas realizadas desde então [5].

O detalhamento técnico-operacional é o mais eloqüente indicativo da importância do trabalho realizado pelo Prof. Moojen, que assim legou ao Museu Nacional valiosíssimo acervo, base dos estudos em desenvolvimento pelas novas gerações, que exaltam a sua memória. Honra ao Mérito.

Rio de Janeiro, janeiro de 2005

Celso Arcoverde de Freitas
Médico Sanitarista

João Moojen, Almir de Castro (Diretor do SNP) e Celso A. de Freitas (Chefe da 1ª. Circunscrição do SNP) em campo, agreste de Caruaru, 1945, durante o 2° Curso Preparatório de Peste. Fotografia cedida pelo Dr. Celso Arcoverde de Freitas ao Arquivo do Museu Nacional.

---

[4] ARCOVERDE DE FREITAS, C., 1957. Notícia sobre a peste no nordeste. In: **Revista Brasileira de Malariologia e Doenças Tropicais**, v.IX, n°1, 214p., Rio de Janeiro.

[5] OLIVEIRA, J.A.; GONÇALVES, P.R. & BONVICINO, C.R., 2003. Mamíferos da Caatinga. In: LEAL, I.R.; TABARELLI, M & SILVA, J.M.C. (Orgs.) **Ecologia e Conservação da Caatinga**. Recife, p.275-334.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.7-12, jan./mar.2005
ISSN 0365-4508

JOÃO MOOJEN (1904-1985) [1]

(Com 2 figuras)

FERNANDO DIAS DE AVILA-PIRES [2]

João Moojen, que não usava o sobrenome "de Oliveira" e dispensava o título de "Professor Doutor", foi figura marcante na Zoologia brasileira do século XX. Com sua simplicidade e profunda sabedoria, certa vez explicou que quando se alcança o reconhecimento dispensa-se o título: ninguém se refere a Aristóteles, Cícero, Robespierre ou Einstein como professor ou doutor. A marca que deixou nas instituições em que trabalhou e naquelas que ajudou a criar é indelével. Trinta anos depois que deixou Viçosa e que lá cheguei por sua indicação, falava-se ainda de suas lições de zoologia e de vida. Tornou-se legendário na Escola de Agronomia e Veterinária, hoje Universidade Federal de Viçosa, assim como seu ex-aluno que mais se destacou, José Cândido de Melo Carvalho, zoólogo de renome e campeão olímpico cuja marca de lançamento de dardo resistiu décadas antes de ser superada.

Uma biografia resumida de João Moojen foi publicada por NOMURA (1991).

João Moojen nasceu em Leopoldina, Minas Gerais, em 1 de dezembro de 1904. Cursou o Colégio Pedro II, no Rio de Janeiro, de 1918 a 1921, matriculando-se na Faculdade de Farmácia da atual Universidade Federal do Rio de Janeiro no ano seguinte. Cursou duas cadeiras na Faculdade de Medicina em 1924 e concluiu o curso nesse mesmo ano, recebendo seu diploma em 2 de junho de 1928. Em 1938 cursou as cadeiras de Anatomia Humana, Embriologia e Histologia na Faculdade de Medicina, mas não prosseguiu no curso.

Regressando a Minas Gerais como farmacêutico recém-formado, exerceu o magistério e a vice-direção do Ginásio Além Paraíba. De 1925 a 1932, lecionou História Natural, Ciências Naturais, Física, Química, Francês, Inglês, Geometria, História do Brasil e História das Civilizações, além de exercer a profissão de farmacêutico.

Em Além Paraíba, casou-se com D. Emília Costa Cruz Figueira.

Em 1933, recebeu convite do diretor J. Bello Lisboa para lecionar Zoologia e Biologia Geral na Escola Superior de Agricultura e Veterinária do Estado de Minas Gerais, a qual daria origem à atual Universidade Federal de Viçosa. Foi também Professor Substituto de Parasitologia e Entomologia. Chefiou o Departamento de Biologia de agosto de 1933 a dezembro de 1937, ano em que deixou Viçosa. Durante sua estada na ESAV, Moojen dedicou-se principalmente ao estudo de aves e deixou importante coleção zoológica no departamento, a qual constituiu embrião do atual Museu de Zoologia "João Moojen de Oliveira".

João Moojen na ocasião de sua formatura (1928). Arquivo da família Moojen.

[1] Submetido em 18 de junho de 2004. Aceito em 17 de janeiro de 2005.
[2] Instituto Oswaldo Cruz, Departamento de Medicina Tropical. Rio de Janeiro (aposentado).
E-mail: favila@matrix.com.br.

Moojen transferiu-se para o Rio de Janeiro em 1938, requisitado pelo Ministério da Educação e Saúde, para trabalhar no Museu Nacional. Naquele ano, assumiu o posto de professor de História Natural no Colégio Universitário da Universidade do Brasil, onde lecionou durante três meses.

Em 1938, Moojen foi contratado como professor comissionado e chefe do Departamento de Biologia Geral e Zoologia da Escola de Ciências da Universidade do Distrito Federal (UDF), cargo que ocupou até o ano seguinte. Essa universidade, de curta história, foi criada após longo debate sobre a identidade da universidade brasileira, que culminou em uma proposta que se opunha à filosofia da Reforma Francisco Campos e à legislação vigente, privilegiando a pesquisa. Criada por Decreto Municipal em 4 de abril de 1935, a UDF era constituída por cinco escolas: Ciências, Educação, Economia e Direito, Filosofia e Instituto de Artes. O grande arquiteto da nova universidade foi Anísio Teixeira, de quem Moojen foi amigo e colaborador por muitos anos, vindo a ser membro do Conselho da Fundação Universidade de Brasília de 1961 a 1962. O conservadorismo finalmente venceria e a UDF deixou de existir em meados de 1939, sendo seus cursos transferidos para a Faculdade Nacional de Filosofia (SCHWARTZMAN, 1982).

No dia 3 de janeiro de 1939, João Moojen ingressou na Divisão de Zoologia do Museu Nacional, tendo prestado concurso de títulos e provas para o cargo de naturalista do Ministério da Educação e Saúde, em 4 de julho do mesmo ano, com a monografia "As Espécies Brasileiras dos Gêneros *Echimys, Phyllomys* e *Cercomys*." A partir daí, dedicou-se ao estudo dos mamíferos. Chefiou as divisões de Invertebrados e Vertebrados entre 11 de julho de 1939 e 19 de janeiro de 1941 e a Divisão de Zoologia entre 20 de junho de 1941 e 23 de março de 1945, cargo para o qual seria reconduzido em 19 de maio de 1948, tendo desempenhado papel de destaque na revisão dos estatutos do Museu Nacional promovida na década de 1950. Com a transferência do Museu Nacional para a Universidade do Brasil, atual Universidade Federal do Rio de Janeiro (UFRJ), foi enquadrado como Pesquisador-Zoólogo e, mais tarde, como Professor Adjunto, permanecendo na ativa até 1969. Em 1979, tornou-se professor titular visitante da UFRJ.

Moojen obteve o PhD na Universidade de Kansas, centro tradicional em pesquisas e formação de mastozoólogos então dirigido por E. Raymond Hall, onde permaneceu de 1945 a 1948. Passou pela Universidade da Califórnia, recebendo forte influência do pensamento de Joseph Grinnell, realizando pesquisas paleontológicas no Arizona e Colorado durante quatro meses. Mais tarde, colaboraria intimamente com os trabalhos de Carlos de Paula Couto, no Museu Nacional, realizando coletas em Lagoa Santa, Minas Gerais, para poder identificar os fósseis descritos por Peter W. Lund no século XIX. Convidado a lecionar Mastozoologia Sul-americana na Universidade de Kansas, foi obrigado a recusar o convite por ter sido chamado de volta ao Museu Nacional. Do Field Museum, em Chicago, Moojen trouxe para o Museu Nacional um precioso arquivo da bibliografia de mamíferos neotropicais organizado por Wilfred Osgood. Nessa oportunidade, Moojen fotografou pessoalmente centenas de fichas catalogadas por espécie.Em 1950, doutorou-se em História Natural pela Faculdade Nacional de Filosofia da Universidade do Brasil. Professor por vocação, Moojen receberia convites para lecionar em diversas universidades. Foi convidado a ministrar cursos de pós-graduação em Viçosa em 1969 e na Universidade de Brasília em 1978.

De 1951 a 1974 foi professor adjunto do Colégio Pedro II, nomeado após aprovação em concurso de títulos. Como docente, Moojen foi examinador no concurso de habilitação para a Faculdade Federal de Odontologia (1938) e para a Cátedra de Zoologia da Faculdade de Agronomia da Universidade do Brasil.

Caçador emérito, integrou, como zoólogo, o Conselho Nacional de Caça e Pesca entre 1940 e 1943, quando foram estabelecidas as leis básicas de caça e pesca no país. Datam desse período os artigos publicados na "Caça e Pesca", que se definia como "uma revista para os adeptos do tiro e do anzol". De tiragem mensal, esse periódico vinha à luz sob os auspícios da Divisão de Caça e Pesca do Ministério da Agricultura. Algumas contribuições literárias de João Moojen foram ali publicadas sob o pseudônimo de João do Brejo. Não tive oportunidade de consultar toda a coleção, podendo haver outras contribuições que não constaram deste levantamento.

Desde seu ingresso no Museu Nacional, Moojen colaborou com o Departamento Nacional de Saúde, embrião do Ministério da Saúde,

realizando pesquisas de campo e cursos sobre peste bubônica. Sob sua orientação, foram estabelecidos laboratórios espalhados em toda a área de endemismo dessa doença. Técnicos bem treinados realizavam coletas rotineiras de roedores e seus ectoparasitos, o que levaria o Brasil a tornar-se o único país a possuir dados ininterruptos sobre a ocorrência de peste bubônica durante mais de 35 anos. Os mapas de campo preparados pelo pessoal do Serviço Nacional da Peste permitiam localizar cada fazenda, sítio ou residência nas diferentes circunscrições em que atuava.

Durante as campanhas da Fundação Rockefeller para estudar as zoonoses brasileiras, Moojen foi responsável pelos trabalhos de zoologia realizados entre 1943 e 1945 (SOPER *et al.*, 1943; SOPER, 1977).

Dessas colaborações resultou uma coleção mastozoológica riquíssima, com mais de oitenta mil exemplares, incorporados ao acervo do Museu Nacional. Ectoparasitos foram igualmente preservados e estudados, com a dupla finalidade de proceder inventários faunísticos e de compreender a epidemiologia de zoonoses como a peste bubônica e a febre amarela.

Foi zoólogo do Jardim Zoológico do Rio de Janeiro entre 1950 e 1952, iniciando uma colaboração profícua que permaneceu por muitos anos, com proveitos mútuos.

No Museu Nacional, estabeleceu as linhas mestras para as exposições de Anatomia Comparada e de Mamíferos durante a primeira gestão de José Cândido de Melo Carvalho.

Em 1959, Moojen foi convidado por Israel Pinheiro para planejar e instalar o Parque Zoobotânico de Brasília, de cujo conselho científico fez parte. No Distrito Federal, Moojen dirigiu o Departamento de Proteção à Natureza entre 1959 e 1961, tornando-se Superintendente Geral de Agricultura do Distrito Federal, de 1961 a 1962, por indicação dos técnicos de Agronomia e Veterinária.

Moojen integrou a comissão do Museu Nacional constituída para reformular o antigo Código de Caça, a qual propôs o Projeto de Lei de Proteção à Fauna (Lei nº 5197 de 3 de janeiro de 1967) que serviria de modelo para as legislações posteriormente adotadas pela Colômbia, Peru e Equador. Foi sua a idéia de transformar a legislação de caça e pesca em um código de proteção à natureza, sendo de sua autoria as definições fundamentais constantes nos primeiros artigos.

Em 1975, no Rio de Janeiro, Moojen foi convidado a chefiar o Serviço de Roedores da Fundação Estadual do Meio Ambiente (FEEMA), realizando importantes estudos sobre as populações de roedores urbanos em alguns bairros da cidade.

Sua atração pelos trabalhos de campo levou-o a realizar excursões científicas por todo o país. Constam oficialmente designações para realizar coletas nas seguintes regiões: Serra da Grama (Minas Gerais), de 14 a 21 de abril de 1935; Distrito de São Miguel (Minas Gerais), de 1 a 3 de novembro de 1935; Rio Matipó (Minas Gerais), de 2 a 16 de julho de 1936; Lagoa Feia (Rio de Janeiro), em agosto de 1941; Foz do Iguaçu (Paraná) e Santa Catarina, de 17 de novembro a 31 de dezembro de 1941; Ilha Seca, São Paulo e Salobra (Mato Grosso) em fevereiro de 1942; nos rios São Francisco e Grande (Minas Gerais e Bahia), de 7 de fevereiro a 4 de maio de 1942; Ilhéus (Bahia) de 2 a 24 de agosto e de 12 a 22 de outubro de 1944; nos rios Xingu, Culuene e em Aragarças e Xavantina (Mato Grosso), de 15 de junho a 6 de julho de 1948; Belo Horizonte (Minas Gerais), de 1 a 6 de julho de 1949; norte do Estado do Rio de Janeiro e sul do Espírito Santo, de 7 a 31 de julho de 1949; Amapá, de 15 de dezembro a 6 de janeiro e 1950. Em Brasília, Moojen realizou coletas extensas e descreveu um novo gênero e espécie de roedor e coletou uma nova espécie de jararaca.

Cândido de Mello Leitão dedicou-lhe o gênero *Moojenia* de opiliões gonileptídeos (MELLO-LEITÃO, 1935) e uma espécie de escorpiões botriurídeos, *Bothriurus moojeni* (MELLO-LEITÃO, 1945). Deferências semelhantes seriam prestadas por SCHUBART (1944), com o gênero *Moojenodesmus* de diplópodos vanhoefenídeos, e por Paulo de Miranda Ribeiro com o gênero *Moojenichthys* de peixes caracídeos (MIRANDA-RIBEIRO, 1956). AVILA-PIRES (1959) nomeou novo roedor cricetídeo como *Oryzomys ratticeps moojeni*, e HOGE (1966) descreveu *Bothrops moojeni*, cujo holótipo fora coletado em Brasília. PESSÔA, OLIVEIRA & REIS (1992) prestariam nova homenagem com uma nova espécie do grupo de roedores no qual Moojen foi o maior especialista, os ratos-espinho do gênero *Proechimys*. No presente volume uma nova espécie de *Oligoryzomys* é nomeada em sua homenagem (WEKSLER & BONVICINO, 2005).

Mais do que descrever novos gêneros e espécies,

João Moojen e Ralph M. Wetzel no Setor de Mamíferos do Museu Nacional em 1979. (Arquivo da família Moojen)

Moojen encontrava maior satisfação em redescobrir espécies descritas no século XIX e no início do século XX, das quais se conhecia apenas o holótipo.

Moojen tinha interesses variados que iam da música clássica à literatura e à cinofilia, tendo sido filiado ao Kennel Clube do Brasil. Formulou uma ração famosa, "Karnol", para cães e outra para aves. Dedicou-se ao estudo da nutrição animal, tendo prestado serviços como Assessor Técnico da Companhia Luz Stearica (Moinho da Luz, Rio de Janeiro) em 1962 e entre 1969 e 1971, como assessor técnico-científico da Socil Pró-Pecuária (São Paulo) entre 1965 e 1968, como consultor técnico da Anderson Clayton S.A., São Paulo, entre 1968 e 1969, e como Consultor Técnico da Industrial Irecê S.A., (Bahia) entre 1972 e 1975.

Moojen foi membro da famosa Society of the Sigma XI for the Protection of Research in Science (1947) e de várias associações profissionais, tais como Cooper Ornithological Society (1947), Phi Sigma Biological Society (1948), American Ornithologists Union (1947), American Society of Mammalogists (1945) e Sociedade Brasileira de Geografia (1952). Moojen tornou-se "fellow" da John Simon Guggenheim Memorial Foundation e teve papel relevante na formação de novos pesquisadores ao indicá-los para essa Fundação. Também foi membro da Sociedade Brasileira de Biologia, do Comitê Internacional de Proteção às Aves e Titular da Academia Brasileira de Ciências.

Desde sua criação, Moojen foi Bolsista do Conselho Nacional de Pesquisas (atual Conselho Nacional de Desenvolvimento Científico e Tecnológico, CNPq).

Não foi freqüentador de congressos, mas representou o Brasil no Simpósio Internacional de Estudos de Roedores e Ectoparasitos (Genebra, 1968), participando ainda do Congresso Internacional de Alimentação Animal (Madri, 1968) e do Simpósio sobre a Ação da Temperatura sobre os Animais Domésticos (Viçosa, 1969).

João Moojen faleceu no Rio de Janeiro no dia 1 de abril de 1985, deixando quatro filhos, doze netos e dois bisnetos.

REFERÊNCIAS BIBLIOGRÁFICAS

AVILA-PIRES, F.D., 1959. Nota prévia sobre nova espécie de *Oryzomys* do Brasil. **Atas da Sociedade de Biologia do Rio de Janeiro**, Rio de Janeiro, **3**(4):2.

HOGE, A., 1966. Preliminary account on Neotropical Crotalinae (Serpentes, Viperidae). **Memórias do Instituto Butantan**, São Paulo, **32**:109-184.

MELLO-LEITÃO, C., 1935. A propósito de alguns opiliões novos. **Memórias do Instituto Butantan**, São Paulo, **9**:367-411.

MELLO-LEITÃO, C., 1945. Escorpiões sul-americanos. **Arquivos do Museu Nacional**, Rio de Janeiro, **40**:6-468, 185 figs.

MIRANDA-RIBEIRO, P., 1956. On a new genus and a new species of South American fish. In: INTERNATIONAL CONGRESS OF ZOOLOGY (1953), 14., Copenhague, **Proceedings...**, Copenhague, p.546-547.

NOMURA, H., 1991. João Moojen de Oliveira. In: **Vultos da Zoologia Brasileira (II)**. Mossoró: Fundação Vingt-Um Rosado, Coleção Mossoroense, C, DCLXII,151-154 ang.

PESSÔA, L.M.; OLIVEIRA, J.A., DOS REIS, S.F., 1992. A new species of spiny-rat genus *Proechimys*, subgenus *Trinomys* (Rodentia, Echimyidae). **Zeitschrift für Saügetierkunde**, Jena, **57**:39-46.

SCHUBART, O., 1944. Os diplópodos de Pirassununga. **Acta Zoologica Lilloana**, Tucumán, **2**:321-440.

SOPER, F.L., 1977. **Ventures in World Health**. Washington: Pan American Health Organization, 137p.

SOPER, F.L.; WILSON, D.B.; LIMA, S. & ANTUNES, W.S., 1943. **The organization of permanent nation wide anti-*Aedes aegypti* measures in Brazil**. Nova Iorque: The Rockefeller Foundation, 365p.

SCHWARTZMAN, S., 1982. **Universidades e instituições científicas no Rio de Janeiro**. Brasília: Conselho Nacional de Desenvolvimento Científico e Tecnológico, 243p.

WEKSLER, M. & BONVICINO, C.R., 2005. Taxonomy of pigmy rice rats genus *Oligoryzomys* (Rodentia, Sigmodontinae) of the Brazilian Cerrado, with the description of two new species. **Arquivos do Museu Nacional**, Rio de Janeiro, **63**:113-130.

BIBLIOGRAFIA DE JOÃO MOOJEN

MOOJEN, J., [1933-1937], **Zoologia**. Polígrafo mimeografado para uso dos alunos da Universidade de Viçosa. 97p.

MOOJEN, J.; KUHLMANN, J.G. & DRUMMOND, O., 1935. **Relatório da excursão à Serra do Gramma, realizada de 14 a 21 de abril de 1935 pelos professores João Moojen de Oliveira, João Geraldo Kuhlmann e Octavio Drummond**. Escola Superior de Agricultura e Veterinária do Estado de Minas Gerais. Viçosa, 29p.

MOOJEN, J., 1935. O pardal e o problema do povoamento ornitológico das cidades. **Minas Gerais**, Belo Horizonte, (29 de setembro de 1935):p.9.

MOOJEN, J., 1935. Aves e pragas domésticas. **Folha Rural**, Viçosa, (novembro de 1935):p.3.

MOOJEN, J., 1936. O siriri; *Tyranus melancholicus* (Vieillot) e o bentevi *Pitangus maximiliani* (Cab. & Heine), amigos do apicultor. **O Campo**, Rio de Janeiro, **7**(81):13.

MOOJEN, J., 1937. Quinze dias no Matipó. **O Campo**, Rio de Janeiro, **8**(86):53-56.

MOOJEN, J., 1938. Valor econômico de *Molothrus bonariensis* (Gmel) chopim, gaudério, vira-bosta ou pássaro preto. **O Campo**, Rio de Janeiro, **9**(100):17.

MOOJEN, J., 1939. Sanguivorismo de *Diphylla ecaudata* Spix em *Gallus gallus domesticus* (L.). **O Campo**, Rio de Janeiro, **10**(114):70,.

MOOJEN, J., 1940. Aspectos ecológicos do Alto São Francisco. **O Campo**, Rio de Janeiro, **11**(124):22-24.

MOOJEN, J., 1940. Aspectos ecológicos do Alto São Francisco II. **O Campo**, Rio de Janeiro, **11**(127):22-25.

MOOJEN, J., 1940. Aspectos ecológicos do Alto São Francisco III. **O Campo**, Rio de Janeiro, **11**(129):57, 58 e 63.

MOOJEN, J., 1941. Aves coligidas em Ilha Seca (São Paulo) e Salôbra (Mato Grosso) pelo Museu Nacional em colaboração com a Comissão Científica do Instituto Oswaldo Cruz, entre 17/02 e 10/03/1940. In: Relatório de terceira excursão a zona da Estrada de Ferro Noroeste do Brasil realizada em fevereiro e março de 1940. **Memórias do Instituto Oswaldo Cruz**, Rio de Janeiro, **35**(3):660-668.

MOOJEN, J.; CARVALHO, J.C. & SOUZA-LOPES, H., 1941. Observações sobre o conteúdo gástrico de aves brasileiras. **Memórias do Instituto Oswaldo Cruz**, Rio de Janeiro, **36**(3):405-444.

MOOJEN, J., 1942. Sobre os "ciurídeos" das coleções do Museu Nacional, do Departamento de Zoologia de São Paulo e do Museu Paraense Emílio Goeldi. **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (1):1-55.

MOOJEN, J., 1942. Fazer o bem sem olhar a quem. **Caça e Pesca**, Rio de Janeiro, **1**:36-40. [conto, sob o pseudônimo de João do Brejo].

MOOJEN, J., 1942. O ratão d'agua. **Caça e Pesca**, Rio de Janeiro, **1**:26. [sob o pseudônimo de João do Brejo].

MOOJEN, J., 1942. O caçador perdido. **Caça e Pesca**, Rio de Janeiro, **1**:20. [sob o pseudônimo de João do Brejo].

MOOJEN, J., 1942. Caxinguelês e coatipurus. **Fauna**, Rio de Janeiro, **1**:3-4.

MOOJEN, J. & SILVA JR., M.S., 1942. Roedores domésticos e silvestres: sua relação com a peste e normas gerais da respectiva caracterização especifica. **Arquivos de Higiene**, Rio de Janeiro, **12**:145-167.

MOOJEN, J., 1942. Aspecto venatório do município de Campos: A fauna e sua proteção. **Caça e Pesca**, Rio de Janeiro, **17**:8-13.

MOOJEN, J., 1942. Aspecto venatório do município de Campos (cont.). **Caça e Pesca**, Rio de Janeiro, **18**:8-13.

MOOJEN, J., 1942. Aspecto venatório do município de Campos (cont.). **Caça e Pesca**, Rio de Janeiro, **19**:8-13.

MOOJEN, J., 1942. Ecogenização e domesticidade. **Boletim do Museu Nacional**, Rio de Janeiro, **14-17**(1938-1941):83-114, figs.1-13.

MOOJEN, J., 1942. Tecelagem doméstica. **Boletim do Museu Nacional**, Rio de Janeiro, **14-17**(1938-1941):381-386, figs.1-13.

MOOJEN, J., 1942. Observações sobre a alimentação do anu preto (*Crotophaga ani* Linnaeus, Cuculidae). **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (4):121-125.

MOOJEN, J., 1943. **As espécies brasileiras dos gêneros *Echimys, Phyllomys* e *Cercomys***. Rio de Janeiro. 102p., il. Monografia apresentada em concurso para o cargo de naturalista do Ministério de Educação e Saúde, Museu Nacional.

MOOJEN, J., 1943. Quem a vida passou. **Caça e Pesca**, Rio de Janeiro, **2**:19. [poesia, sob o pseudônimo de João do Brejo].

MOOJEN, J., 1943. Alguns mamíferos colecionados no nordeste do Brasil, com a descrição de duas espécies novas e notas de campo. **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (5):1-14.

MOOJEN, J., 1943. Fauna de Minas Gerais, aves. **Ceres**, Viçosa, **5**(26):115-120.

MOOJEN, J., 1943. **Captura e preparação de pequenos mamíferos para coleções de estudos**. Rio de Janeiro: Imprensa Nacional. 98p., il.

MOOJEN, J., 1944. Capivaras. **Revista do Museu Nacional**, Rio de Janeiro, **1**(1):16.

MOOJEN, J., 1945. O corrupião. **Revista do Museu Nacional**, Rio de Janeiro, **1**(3):20.

MOOJEN, J., 1945. Captura e preparação de pequenos mamíferos para coleção de estudos. **Fauna**, Rio de Janeiro, **2**:12-15.

MOOJEN, J., 1945. Prefácio. In: SANTOS, E. **Entre o Gambá e o Macaco (vida e costumes dos mamíferos do Brasil)**. Rio de Janeiro: F.Briquiet & Cia, p.5-6.

MOOJEN, J., 1947-1951. Plano para proteção dos Recursos Naturais do Estado do Rio de Janeiro para o governador Macedo Soares.

MOOJEN, J., 1948. Speciation in the brazilian spiny rats (genus *Proechimys*, family Echimyidae). **University of Kansas Publications Museum of Natural History**, Lawrence, **1**(19):301-406, figs.1-140.

MOOJEN, J., 1950. *Echimys (Phyllomys) Kerri* n.sp. (Echimyidae, Rodentia). **Revista. Brasileira de Biologia**, Rio de Janeiro, **10**(4):489-492.

MOOJEN, J., 1950. Sobre *Callithrix aurita* (E.Geoffroy, 1812) (Callithricidae, Primates). **Revista. Brasileira de Biologia**, Rio de Janeiro, **10**(4):501-502.

MOOJEN, J., 1950. **Chamber's Encyclopedia**. Verbetes sobre mamíferos sul-americanos. 50.ed., Londres: George Newnes Ltd, 15v.

MOOJEN, J., 1951. O Pointer Inglês. **Seleções Agrícolas**, Rio de Janeiro, **66**:13-19.

MOOJEN, J., 1951. O Pointer Inglês. **Seleções Agrícolas**, Rio de Janeiro, **67**:27-34.

MOOJEN, J., 1951. O Pointer Inglês. **Seleções Agrícolas**, Rio de Janeiro, **68**:33-36.

MOOJEN, J., 1952. A new *Clyomys* from Paraguay (Rodentia, Echimyidae). **Journal of the Washington Academy of Sciences**, Washington, **42**(3):102.

MOOJEN, J., 1952. **Os Roedores do Brasil**. Rio de Janeiro: Instituto Nacional do Livro, Biblioteca Científica Brasileira, 214p., il.

MOOJEN, J., 1954. **Descourlitz, Aves do Brasil**. Comentários sobre a sistemática e biologia das descrições. Rio de Janeiro: Kosmos. 120p., 2v., il.

MOOJEN, J., 1956. **Descourlitz, Pageantry of Tropical Birds**. Legendas de 48 pranchas coloridas Rio de Janeiro: Kosmos.

MOOJEN, J., 1958. Alexandre Rodrigues Ferreira e a Zoologia. In: CONSELHO NACIONAL DE PESQUISAS (Ed.) **Alexandre Rodrigues Ferreira na visão de quatro naturalistas do Museu Nacional**. Rio de Janeiro: Instituto Nacional de Pesquisas da Amazônia, publicação número 3, série Viagem Filosófica, p.15-18.

MOOJEN, J., 1958. *Sciurus cabrerai, n. novum* (Sciuridae, Rodentia). **Sessões da Academia Brasileira de Ciências**, Rio de Janeiro, **30**(4):50-51.

MOOJEN, J. 1965. Novo gênero de Cricetidae do Brasil central (Glires, Mammalia). **Revista Brasileira de Biologia**, Rio de Janeiro, **25**(3):281-285.

MOOJEN, J. & AVILA-PIRES, F.D., 1966. Mamíferos endêmicos do cerrado. In: AVILA-PIRES, F.D. Observações gerais sobre a mastozoologia do cerrado. **Anais da Academia Brasileira de Ciências**, Rio de Janeiro, **38**(Suplemento):337-338.

MOOJEN, J., 1972. Tradução e revisão técnica. In: MARTINS, L. (Ed.) 1972, *Os animais*. v.2-3. Rio de Janeiro: Bloch Editores.

MOOJEN, J., 1974. Cada ave no seu ninho. **Revista Geográfica Universal**, Rio de Janeiro, **1**:36-41.

MOOJEN, J., 1974. As reservas naturais do Quênia. **Revista Geográfica Universal**, Rio de Janeiro, **3**:348-359.

MOOJEN, J., 1975. Galápagos – o arquipélago encantado. **Revista Geográfica Universal**, Rio de Janeiro, **4**:404-415.

MOOJEN, J., 1975. Tubarões, o terror de milhões de anos. **Revista Geográfica Universal**, Rio de Janeiro, **6**:157-163.

MOOJEN, J., 1975. Sempre flamingos. **Revista Geográfica Universal**, Rio de Janeiro, **8**:404-411.

MOOJEN, J., 1975. Quando voam as cegonhas. **Revista Geográfica Universal**, Rio de Janeiro, **11**:26-35.

MOOJEN, J., 1979. Os roedores domésticos como fator sanitário e econômico nas áreas urbanas. FEEMA, **Relatório Técnico**, Rio de Janeiro, p.25-30.

MOOJEN, J.; REIS, S.F. & DELLAPE, M.V., 1988. Quantitative variation in *Thrichomys apereoides* (Lund, 1841) (Rodentia, Echimyidae) I. Non-geographic variation. **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (316):1-15.

MOOJEN, J., 1995. Lei da espécie. In: AVILA-PIRES, F.D. Lei da espécie. **Revista Brasileira de Zoologia**, Curitiba, **12**(4):1015-1023.

MOOJEN, J.; LOCKS, M. & LANGGUTH, A., 1997. A new species of *Kerodon* Cuvier, 1825 from the State of Goiás, Brazil (Mammalia, Rodentia, Caviidae). **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (377):1-10 [póstumo].

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.13-20, jan./mar.2005
ISSN 0365-4508

A COLEÇÃO DE MAMÍFEROS DO SERVIÇO NACIONAL DE PESTE NO MUSEU NACIONAL, RIO DE JANEIRO, BRASIL [1]

JOÃO ALVES DE OLIVEIRA [2, 3, 4]
STELLA MARIS FRANCO [2]

RESUMO: São reunidas informações sobre a coleção de mamíferos do Serviço Nacional de Peste (SNP), incluindo a abrangência geográfica das amostras, os protocolos empregados para captura, manipulação e transporte dos animais vivos, os métodos de preparação dos exemplares, o protocolo de registro de informações no campo, e o processamento dos espécimes no Museu Nacional, a partir de documentos originais.

Palavras-chave: Serviço Nacional de Peste, peste, mamíferos, inventário, roedores, Museu Nacional.

ABSTRACT: The collection of mammals of the National Plague Service in the Museu Nacional, Rio de Janeiro, Brazil. Information on the collection of mammals of the Serviço Nacional de Peste (SNP) ("National Plague Service") is summarized from original documents, including the geographic range of samples, capture protocols, handling and transportation of live specimens, specimen preparation, field record protocols, and specimens processing at the Museu Nacional.

Key words: Serviço Nacional de Peste, plague, mammals, mammal inventory, rodents, Museu Nacional.

INTRODUÇÃO

A coleção do Setor de Mastozoologia (Departamento de Vertebrados, Museu Nacional – UFRJ) abriga o maior acervo mastozoológico do Brasil e situa-se entre as 11 maiores coleções de mamíferos no ocidente (HAFNER *et al.*, 1997), com estimados 90 mil espécimes. Uma fração considerável desse acervo foi obtida através de projetos realizados nas décadas de 1930, 40 e 50 em convênios com órgãos da saúde pública, notadamente o Serviço de Estudos e Pesquisas sobre a Febre Amarela (SEPSFA) e o Serviço Nacional de Peste (SNP), ambos vinculados ao Ministério da Educação e Saúde. Estas coleções, coligidas e organizadas sob a orientação de João Moojen de Oliveira, constituem até hoje a base material mais significativa dos inventários mastozoológicos do leste do Brasil.

A coleção do SNP, com 55291 exemplares, corresponde ainda hoje, passados quase 50 anos do término das atividades de remessa de material daquela repartição, à maior parte da coleção de mamíferos do Museu Nacional. A importância desse acervo, constituído quase exclusivamente de pequenos mamíferos não-voadores, e majoritariamente de roedores, reside nas numerosas séries que foram obtidas nas diversas localidades amostradas. Situadas nas bases das serras que dividem o semi-árido nordestino, essas localidades distribuem-se em um eixo longitudinal que se estende do norte do Ceará até o centro-sul da Bahia. As séries obtidas para diversas espécies, coletadas simultaneamente em diferentes localidades ao longo de quatro anos, possibilitam a abordagem de questões que incluem desde a variação morfológica e a taxonomia até estudos sobre a biologia do desenvolvimento e análises da variação em caracteres bionômicos associada à sazonalidade da região. Entretanto, apesar da excelente documentação original relacionada ao SNP, diversas informações sobre a estruturação deste inventário, que poderiam ser úteis no delineamento de novas investigações com base no copioso material disponível, encontram-se dispersas em documentos diversos, disseminadas nos milhares de fichas individuais referentes ao projeto e em relatórios. O objetivo deste trabalho é resgatar e resumir uma parte dessas informações sobre a coleção de mamíferos do SNP, incluindo a abrangência geográfica das amostras, os protocolos empregados para captura, manipulação e transporte dos animais, os métodos de preparação dos espécimes, o protocolo de registro de informações no campo, e o processamento dos exemplares no Museu Nacional.

[1] Submetido em 18 de junho de 2004. Aceito em 13 de janeiro de 2005.
[2] Museu Nacional/UFRJ, Departamento de Vertebrados. Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil.
[3] E-mail: jaoliv@mn.ufrj.br.
[4] Bolsista do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

MÉTODOS

Este trabalho foi realizado através da consulta aos acervos referentes ao Serviço Nacional de Peste existentes no Setor de Mastozoologia do Museu Nacional, incluindo arquivos de fichas, etiquetas dos espécimes e mapas disponíveis. Também foram utilizados documentos depositados no Setor de Arquivos do Museu Nacional, além de documentos originais disponibilizados pelo Dr. Celso Arcoverde de Freitas, de seu arquivo pessoal, hoje cedido à Casa de Oswaldo Cruz (Fundação Instituto Oswaldo Cruz – Fiocruz, Rio de Janeiro).

RESULTADOS E DISCUSSÃO

Um histórico resumido da Peste Bubônica no Brasil e das atividades do Serviço Nacional de Peste, incluindo os métodos profiláticos empregados, podem ser encontrados em FREITAS (1957; 1989, 1998). Aqui apenas são relacionados os aspectos da estrutura organizacional daquela repartição, relevantes ao estudo dos mamíferos colecionados. O Serviço Nacional de Peste existiu de 1941 a 1956 e era estruturado em Circunscrições, Setores e Distritos. Havia quatro circunscrições, sendo que a "1ª. Circunscrição" abrangia os Estados de Pernambuco, Alagoas, Ceará e Paraíba e a "2ª. Circunscrição" correspondia ao Estado da Bahia. As outras duas circunscrições eram Rio de Janeiro (3ª.) e São Paulo (4ª.), que tratavam essencialmente da prevenção de peste portuária e não realizavam coletas de roedores silvestres; assim, a quase totalidade do material do Museu Nacional oriundo do SNP refere-se às duas primeiras circunscrições.

João Moojen lecionou sobre roedores silvestres e sobre preparação de pequenos mamíferos em Recife (PE), em 1943 e 1945, no âmbito dos Cursos de Especialização em Peste para os médicos que depois se tornariam chefes de distritos do SNP. Foi em 1943 que, segundo FREITAS (1989), idealizou a realização de um grande levantamento de pequenos mamíferos aproveitando a estrutura do SNP. Tal levantamento possibilitaria aos pesquisadores do SNP abordarem a questão da manutenção da bactéria da peste entre as populações de roedores silvestres; portanto houve interesse científico mútuo no desenvolvimento do inventário.

A captura de roedores silvestres já era realizada eventualmente pelo SNP para estudo epidemiológico em focos ativos de peste doméstica (propagada por ratos comensais) na dispersa zona rural, onde ocorre interação dos ratos sinantrópicos com os roedores silvestres. A organização do projeto e a preparação da estrutura para as coletas sistemáticas de pequenos mamíferos silvestres cobrindo toda a área semi-árida do Nordeste teve por base a avaliação dos resultados de um projeto-piloto organizado por João Moojen no agreste do Município de Caruaru (PE) em 1943 (FREITAS, 1998). A captura sistemática foi precedida da seleção e treinamento dos guardas mais habilitados ao trato com os animais vivos e que se dispusessem a se ausentar da sede distrital para as coletas em áreas mais remotas, e do pessoal de laboratório nas sedes dos distritos na taxidermia dos espécimes. Além disso, ajustes foram feitos na definição de protocolos para a coleta, registro de informações, manipulação e preparo dos espécimes e remessa de material ao Museu Nacional (mamíferos) e ao Museu de Zoologia da Universidade de São Paulo (ectoparasitos). A preparação para a realização do inventário em toda a sua abrangência geográfica (Tab.1) teria tomado os anos seguintes, pois as primeiras remessas de pequenos mamíferos silvestres do SNP na coleção do Museu Nacional datam de 1951. É relevante lembrar que entre abril de 1945 e janeiro de 1948 João Moojen esteve nos Estados Unidos, onde obteve seu doutorado na Universidade do Kansas em dezembro de 1947.

Protocolo de Coleta: Guardas capturadores eram os responsáveis não só pela disposição e verificação das armadilhas nos sítios de coleta, mas também pelo transporte dos animais ao laboratório, registro das informações de coleta, manutenção dos espécimes vivos quando fosse o caso e pela taxidermia dos exemplares, depois dos mesmos terem sido despulinizados e autopsiados, geralmente por um laboratorista.

A escolha dos sítios para coletas era determinada pela ocorrência anterior de foco de peste doméstica, em geral uma propriedade rural. Em torno desse foco, em um raio de 6km, identificavam-se as propriedades vizinhas, que eram trabalhadas pelos guardas capturadores em equipes de dois, simultaneamente, cada um com 10 ou 20 armadilhas para a captura de roedores vivos. A recomendação era que a captura fosse feita em culturas ou revestimentos florísticos uniformes, um de cada vez. É relevante mencionar que as coletas foram efetuadas em áreas rurais, especificamente em mosaicos de áreas cultivadas e fragmentos remanescentes de vegetação nativa.

Algumas indicações de como foram ajustados os protocolos para as coletas sistemáticas do SNP

foram preservadas em uma carta, enviada por João Moojen ao diretor da 1ª. Circunscrição, Celso Arcoverde de Freitas e ao Chefe do Distrito Pesqueira (PE), Saul Tavares de Melo, em 07/05/1952, quando estavam se iniciando as coletas de roedores silvestres no norte do Ceará. Nesta carta, Moojen propõe ajustes no protocolo para a captura dos roedores e ectoparasitos, discutidos entre ele e Osvaldo de Oliveira (então Chefe da 2ª. Circunscrição do SNP). Constatava-se ali que se a captura fosse feita a grande distância das sedes de distrito o material só poderia ser transportado ao laboratório uma ou duas vezes por semana, dadas as dificuldades de locomoção de então. A manutenção dos animais por maior tempo acarretaria a perda dos ectoparasitos, além da morte dos indivíduos, especialmente os que poderiam resultar positivos para o bacilo. Para evitar isso, era recomendado que nos primeiros três ou quatro meses as coletas se fizessem exclusivamente a uma distância das sedes que permitisse o transporte diário dos ratos ao laboratório. Uma vez apanhados cerca de 30 exemplares no local, se consideraria a amostragem suficiente, especialmente se aqueles correspondessem a mais de duas espécies. Depois de um colecionamento de quatro meses próximo às sedes (ou quando se esgotassem os hábitats diferentes), poder-se-ia então colecionar em lugares mais distantes e assim avaliar se o transporte de animais mantidos vivos por dois ou três dias determinaria a perda de ectoparasitos. Moojen também recomendava que os dois capturadores de cada distrito se ocupassem da captura sistemática em cada hábitat identificado, ou seja, nas culturas (mandioca, palmatória, milho, arroz, feijão, etc.), na caatinga, carrascal, mata, etc. Um dos guardas armaria dez ratoeiras em uma roça enquanto outro armaria outras dez na cobertura florística adjacente. Assim seria possível avaliar se as espécies da cultura eram as mesmas do meio original ou se apenas parte delas.

Manipulação dos espécimes e registro de informações: Cada guarda levava para o campo uma quantidade de latas para transporte dos espécimes igual ao de armadilhas em uso. Estas latas eram previamente preparadas e rotuladas com uma numeração seqüencial própria de cada distrito. À medida que os animais capturados eram retirados das armadilhas, cada um era colocado separadamente em uma lata, cujo número era anotado em uma ficha individual. Estas fichas, de cartolina, conhecidas como "fichas mod. 155", constituíam a base para todos os registros. O guarda capturador levava consigo as fichas em número igual ao de latas, e iniciava seu preenchimento já no campo, anotando o número da lata e as informações relativas ao espécime vivo que nela estava sendo transportado. O georreferenciamento do SNP estava baseado na unidade geográfica mais restrita de então, a propriedade rural (sítio, fazenda, engenho) onde foi realizada a coleta, bem como a designação do município, distrito, setor e circunscrição, a data da coleta e as condições meteorológicas na noite da captura. Na maior parte das vezes os animais coletados eram levados à sede dos distritos diariamente, especialmente quando havia veículos disponíveis para o transporte dos guardas. Quando os sítios amostrados ficavam longe da sede do distrito, ou quando não havia meio para o transporte diário dos exemplares, os guardas-capturadores mantinham os espécimes vivos, alimentando-os nas latas de transporte por até uma semana ou mais, segundo o que se pode verificar pelas datas de captura e de chegada ao laboratório anotadas nas fichas mod. 155 do SNP.

No laboratório cada animal era morto dentro da própria lata, com clorofórmio ou éter. Os ectoparasitos eram recolhidos em um tubo com álcool a 70°GL, rotulado com o mesmo número da lata e da ficha, precedido de um código alfanumérico que se referia às iniciais do distrito no caso da 1ª Circunscrição e ao número da circunscrição e primeira inicial do distrito no caso das amostras da 2ª Circunscrição. Para cada mamífero era preenchida uma etiqueta padronizada do SNP, com as informações sobre o nome popular do animal, nome científico, procedência, coletor, data de coleta e observações. O restante das informações, incluindo os resultados da autópsia e da inoculação, quando esta era feita, era incluído na fichas mod. 155 durante o processamento do espécime no laboratório do distrito. Na ficha mod. 155 eram anotadas a data da chegada ao laboratório, data da autópsia, medidas (comprimentos do corpo, cauda, orelha e pé (em milímetros), massa (em gramas), sexo, dados reprodutivos (número de fetos), informações sobre a coloração da pelagem, e o número de ectoparasitos encontrados, além de informações relativas à inoculação de cobaias para *Yersinia pestis* com material do espécime em questão.

A taxidermia era feita segundo os protocolos descritos em MOOJEN (1943). Peles foram preparadas de modo incipiente desde 1943 e

sistematicamente entre os anos de 1951 a 1953. Nos anos seguintes, da maioria dos espécimes coletados apenas os crânios foram preservados. Também nos casos em que o espécime já chegava morto ao laboratório, nos casos em que a pele já se encontrava em decomposição, apenas o crânio era aproveitado, recebendo uma etiqueta com o número original e sendo mantido em álcool para posterior limpeza. Apesar das instruções originais de que os crânios fossem remetidos em latas, desidratados, para o Museu Nacional, ou limpos manualmente por maceração nos distritos, a preparação dos crânios foi muito variável, com séries remetidas em diferentes estágios de preparação, em alguns distritos tendo-se revestido os crânios frágeis com diferentes vernizes ou mesmo com cera, como em algumas séries de Pesqueira (PE), para protegê-los. De relevância para a curadoria desses espécimes, um dos tipos de verniz, utilizado em alguns distritos da 1ª Circunscrição, é solúvel em acetona, ao passo que outro tipo, utilizado nos distritos da Bahia, é solúvel em álcool. Em todos os casos, o número original do SNP era escrito a nanquim sobre o crânio ainda nos distritos, o que garantiu a preservação da informação para a maioria dos espécimes até o presente. Os espécimes eram identificados provisoriamente por comparação com uma coleção de referência montada para este fim nas sedes dos distritos. Essa identificação preliminar era anotada nas etiquetas dos espécimes taxidermizados e nas fichas mod. 155.

Remessa de material: Os crânios eram acondicionados de diferentes maneiras em cada distrito de origem, freqüentemente individualizados em envelopes de papel rotulados com o número original, mas às vezes colados com verniz em folhas de papel, ou mesmo apenas empacotados conjuntamente. As etiquetas de espécimes preservados apenas como crânios eram remetidas na mesma caixa, para serem incluídas aos crânios posteriormente. As remessas eram acompanhadas de relações de espécimes, preparadas em quatro vias, com cópias destinadas ao Distrito de origem, ao respectivo Setor e à Diretoria do SNP, sendo que uma última cópia era encaminhada no pacote com ectoparasitos enviado ao Museu de Zoologia da Universidade de São Paulo. No caso dos mamíferos, juntamente com os espécimes eram encaminhadas ainda as respectivas fichas mod. 155 datilografadas. Estas são as fichas que ainda hoje concentram as informações sobre os espécimes do SNP na coleção do Museu Nacional.

O material que chegava ao Museu Nacional tinha a identificação verificada por João Moojen. As listas com identificações eram remetidas em quatro vias, uma original ao diretor do SNP, Aristides Celso Limaverde, duas aos Diretores da 1ª e 2ª Circunscrições do SNP, respectivamente Celso Arcoverde de Freitas, em Recife, e Oswaldo Bahia de Oliveira, em Salvador (BA), mantendo-se uma última na Secretaria (Direção) do Museu Nacional. Essas relações não foram localizadas no Museu Nacional e provavelmente muitos espécimes não tiveram sua identificação verificada, a julgar pela grande quantidade de exemplares incorretamente identificados nas fichas e etiquetas. Esta restrição, associada à necessária atualização das identificações em função de revisões taxonômicas, determina a necessidade da identificação do espécime-testemunho antes da utilização das informações registradas nas fichas mod. 155.

Acondicionamento dos espécimes no Museu Nacional: Em 1948 a coleção de mamíferos havia sido favorecida com o recebimento de 70 armários, 20 dos quais foram na época emprestados à coleção de aves para suprir necessidade urgente (relatório de João Moojen referente ao ano de 1948, Setor de Arquivo do Museu Nacional). Com a chegada do material do SNP, rapidamente criou-se uma demanda por mais armários. Existe um expediente de 13/11/1952 de João Moojen ao diretor do Museu Nacional informando que o material enviado pelo SNP estava sendo acomodado em caixas provisórias, onde podia ser vistoriado continuamente, até que novos armários fossem confeccionados, e solicitando a compra de 20 mil tubos de vidro e 30 mil rolhas para acondicionamento dos crânios, uma vez que o estoque de tubos havia se esgotado.

Durante muitos anos, apenas as séries representadas por peles e crânios foram organizadas nas gavetas dos armários, em seqüência taxonômica juntamente com o restante da coleção de mamíferos. A maior parte dos espécimes preservados somente como crânios permaneceu guardada em caixas, algumas originais, fora dos armários da coleção. A incorporação desse material à coleção, reiniciada na década de 1980 e que continua ainda hoje, paralelamente ao trabalho de informatização do acervo e à incorporação das coletas oriundas de projetos recentes, com freqüência tem revelado espécies que não haviam sido registradas originalmente.

Período das coletas e abrangência geográfica do levantamento do SNP: A coleção do SNP que se encontra depositada no Museu Nacional foi iniciada em meados de 1951 em Pernambuco, com capturas

ocorrendo a partir do mês de junho daquele ano nos distritos de Caruaru, Pesqueira e Triunfo. De julho de 1951 datam os primeiros exemplares do distrito de Garanhuns e de setembro do mesmo ano os de Bodocó. Em 1952 foram iniciadas as coletas em Crato (CE, janeiro), Viçosa (AL, abril), Feira, Serrinha, Jequié e Vitória da Conquista (BA, maio) e Palmeiras (BA, julho). No norte do Ceará, as coletas sistemáticas iniciaram-se em Fortaleza e Ipu em agosto de 1952, de quando também datam os primeiros exemplares de Palmeiras dos Índios (AL). Baturité (CE) foi o último distrito a iniciar as coletas, em fevereiro de 1953 (Tab.1).

João Moojen se fez presente em diversas ocasiões durante o desenvolvimento do inventário. Existem registros das seguintes portarias de excursão: (1) Portaria 23, de 9/7/1952, de excursão ao interior do Estado do Ceará, acompanhado do naturalista José Francisco da Cruz, entre 11/8 e 15/9/1952; nesta ocasião, quando estavam sendo iniciados os trabalhos de coleta em Fortaleza e Ipu, os guardas daqueles distritos foram treinados em taxidermia

Tabela 1. Resumo das informações sobre as coletas de mamíferos do Serviço Nacional de Peste (SNP) depositadas no Museu Nacional, Rio de Janeiro.

Circunscrição	Setor	Distritos	Início	Término	Total de meses	Total de mamíferos
1ª.	Recife	Caruaru	21/6/1951	11/2/1955	44	7002
		Garanhuns	06/7/1951	25/1/1955	42	5170
		Pesqueira	20/6/1951	18/12/1954	42	3796
		Triunfo	19/6/1951	18/1/1955	43	4658
	Fortaleza	Fortaleza	18/8/1952	30/12/1953	16	600
		Baturité	26/2/1953	09/12/1954	22	500
		Ipu	28/8/1952	18/9/1954	25	1207
	Crato	Bodocó	07/9/1951	31/8/1955	47	2583
		Crato	03/1/1952	22/9/1955	45	3143
	Maceió	Palmeira dos Indios	07/8/1952	02/12/1955	39	7400
		Viçosa	01/4/1952	20/12/1955	44	7486
Subtotal 1ª. Circunscrição						43545
2ª.	Feira de Santana	Feira de Santana	09/5/1952	11/5/1956	48	2607
		Palmeiras - Seabra	08/7/1952	22/3/1955	32	1965
	Jequié	Jequié - Jaguaquara	21/5/1952	14/4/1955	35	3125
		Conquista	22/5/1952	13/10/1955	40	2738
	Salvador	Serrinha	15/5/1952	12/7/1956	50	1311
Subtotal 2ª. Circunscrição						11746
Total Geral						55291

pelo Sr. Cruz; (2) Portaria 2, de 02/02/1953, de excursão aos Estados da Bahia, Pernambuco, Ceará e Alagoas, no período de 02 a 25/02/1953; (3) Portaria 31, de 10/11/1953, de excursão ao sul da Bahia e norte do Estado do Rio de Janeiro, incluindo Minas Gerais e Espírito Santo, realizada entre 28/12/1953 e 05/02/1954; (4) Portaria 18, de 07/06/1954, de excursão ao nordeste brasileiro por 35 dias; (5) Portaria 29, de 15/12/1954, de excursão aos Estados da Bahia, Pernambuco e Alagoas, realizada entre 07/02 e 12/04/1955; nesta viagem, João Moojen visitou diversos distritos do SNP, saindo de automóvel do Rio de Janeiro: Vitória da Conquista (10/2), Feira de Santana (11/2), Palmeira dos Índios (12 a 18/02), Viçosa (19 a 23/02); Garanhuns (24/02), Pesqueira (25/02 a 08/03), Triunfo (09 a 20 /03), Crato (21 a 30/03), Bodocó (01/04), Salgueiro (03/04), Palmeira dos Índios (04/04), Serrinha (06 a 07/04) e Jequié (09/04).

As coletas de mamíferos ocorreram em todos os distritos mencionados até o ano de 1954. Apenas no distrito de Fortaleza as coletas terminaram no final de dezembro de 1953. De Ipu (CE), os últimos exemplares enviados datam de setembro de 1954 e os de Baturité (CE) e Pesqueira (PE) de dezembro do mesmo ano. Os trabalhos nos distritos restantes prolongaram-se até 1955 (Tab.1). Quando da criação do DNERu (Departamento Nacional de Endemias Rurais), que substituiu o SNP em março de 1956, as remessas já haviam se encerrado em todos os distritos. Uma relação das espécies capturadas na 1ª. Circunscrição do SNP, com as quantidades obtidas nos 13 distritos, foi publicada por FREITAS (1957).

Mesmo depois de terminadas as remessas do SNP, João Moojen mantinha contato estreito com os diversos responsáveis pelos laboratórios de peste. Em uma carta de 22/11/1956 ao Sr. Pedro Cezar Forain Claussen, do DNERu em Vitória da Conquista (BA), solicitava que o pessoal de campo insistisse ao máximo na obtenção de roedores do gênero *Cercomys* (= *Thrichomys*) para inoculação; recomendava aumentar o número de ratoeiras, "utilizando todas as de tela", para compensar a redução das capturas com a época de chuvas, informando ainda que esperava visitar o distrito antes do final daquele ano. Existe de fato uma portaria de excursão ao sul da Bahia e norte de Minas Gerais em seu nome, por 35 dias (Portaria 51 de 16/10/1956).

Datam desta época os primeiros resultados publicados do levantamento de mamíferos silvestres e ectoparasitos realizado pelo SNP. FREITAS (1957) resume as informações coligidas na 1ª. Circunscrição, ao passo que NEVES (1957) apresenta evidências de enzootia de roedores na Serra de Baturité, Municípios de Baturité e Pacoti (CE), em 1954, e propõe uma hipótese para a persistência da peste nas zonas endêmicas. Neste importante trabalho, de circulação restrita, está documentado um aumento considerável de ratos silvestres no mês de outubro daquele ano, em diversos sítios, também registrado nas fichas relativas às coletas deste mês em Baturité (CE). Entretanto, poucos indivíduos teriam sido aproveitados para a coleção enviada ao Museu Nacional, segundo o que se pode depreender da consulta à coleção e às fichas mod. 155. Em outros sítios deste e de outros municípios e estados amostrados no mesmo período, também estão registrados esses aumentos das populações de roedores silvestres. Uma análise aprofundada deste material e das observações registradas nas fichas poderá revelar importantes informações sobre a amplitude geográfica e a magnitude desses episódios de explosão demográfica das populações de roedores.

Com o objetivo de mapear os casos de peste, o SNP preparava mapas dos distritos, com os sítios-foco identificados, atualizados constantemente. Cópias de alguns desses mapas ainda se encontram no Setor de Mastozoologia do Museu Nacional. Algumas das propriedades rurais mencionadas nas fichas do SNP também estão mapeadas nas cartas do Instituto Brasileiro de Geografia e Estatística (IBGE). A localização relativa dos diferentes sítios e as distâncias geográficas entre eles, entretanto, podem apenas ser estimadas, para a maioria dos casos, com base nas informações relativas ao foco de peste mais próximo e em outras informações disponíveis na ficha mod. 155, como a data de coleta e o nome coletor. Informações como os tipos de vegetação amostrados, embora muito detalhadas em alguns casos, são de difícil comparação entre diferentes distritos, mas podem servir para separar amostras das áreas de "brejo", onde freqüentemente estavam os cursos de água permanentes e a vegetação mais densa, e o "agreste", onde os cursos de água eram temporários, com vegetação menos densa. Essa distinção é típica nos limites de influência das bases de serras no nordeste do Brasil. É importante destacar que as coletas do SNP concentraram-se principalmente em áreas classificáveis como pertencentes ao meio agrário, característico dessas paisagens já no início da década de 1950. Nessas regiões, então já bastante

impactadas pela agricultura e pela pecuária, as áreas de vegetação nativa encontravam-se restritas a ilhas reduzidas, muito provavelmente de natureza secundária. A composição da fauna de roedores nesse meio é via de regra um subconjunto daquela do meio silvestre original, e as populações de algumas dessas espécies estão sujeitas a aumentos abruptos determinados pela abundância de recursos nas épocas de colheita em anos de alta produtividade. Esse fato pode explicar a ausência de algumas espécies no levantamento do SNP, a despeito das grandes séries coligidas, espécies estas que seriam posteriormente obtidas em localidades vizinhas às amostradas durante aquele projeto, assim como a superioridade numérica notável de algumas espécies, consideradas pragas de lavouras, em alguns casos obtidas durante episódios de "ratadas".

Desde a criação do DNERu, as atividades de pesquisa foram concentradas no Centro de Pesquisas Aggeu Magalhães, em Recife (PE), que se constituiu no laboratório de referência para peste no Brasil a partir da década de 1960. Foram realizadas diversas tentativas para a reedição do programa de peste silvestre no nordeste do Brasil pelos diretores do DNERu na década de 1960, com o objetivo de esclarecer como se perpetuava a enzootia nos períodos interzoóticos (*e.g.*, DE LA BARRERA, 1960). Entre 1965 e 1970, sob os auspícios da Repartição Sanitária Pan-Americana e do Ministério da Saúde, foi realizado um projeto sobre peste bubônica silvestre, conduzido por pesquisadores do Instituto Pasteur e do Museu de Paris, em Exu (PE), que resultou em uma coleção de roedores do nordeste depositada nesta última instituição (BALTAZARD, 1970).

Nas décadas seguintes, coletas de roedores silvestres com objetivo de monitorar a peste silvestre em áreas-foco foram realizadas quase ininterruptamente em vários dos focos endêmicos, sendo que diversos laboratórios regionais de peste, constituídos à maneira dos antigos distritos do SNP, foram criados e mantidos pelos órgãos que se seguiram ao DNERu nas décadas seguintes, a saber o Instituto Nacional de Endemias Rurais (INERU), a Superintendência de Campanhas Contra a Malária (SUCAM), e a Fundação Nacional de Saúde (FNS, FUNASA). Entretanto, embora tivessem sido coletadas muitas informações sobre os roedores autopsiados nesses laboratórios, os espécimes de pequenos mamíferos capturados foram quase que em sua totalidade descartados durante os mais de 30 anos de coletas que se seguiram até o término de todas as atividades destes laboratórios em março de 2003, não se tendo constituído jamais uma coleção de mamíferos nos moldes daquela do SNP. Uma pequena exceção está representada pelo material proveniente dos últimos anos de coleta do foco de peste de Teresópolis - Nova Friburgo, no Estado do Rio de Janeiro, que foi destinado ao Museu Nacional por intermédio do Laboratório de Biologia e Controle da Esquistossomose (LBCE), da Fiocruz, entre 1998 e 2003.

Apesar dos diversos projetos desenvolvidos a partir do acervo do SNP deve-se destacar que o mesmo ainda não foi estudado em sua totalidade e que diversos aspectos da biologia das espécies em questão ainda estão por ser abordados com base em futuros tratamentos do material e das informações coligidas. Por exemplo, no que diz respeito ao estudo dos ectoparasitos, enviados para o Museu de Zoologia da Universidade de São Paulo com uma referência inequívoca aos espécimes de mamíferos hospedeiros representada pelo número original do SNP, pouco foi feito com base nas informações levantadas além da descrição da variação taxonômica amostrada (GUIMARÃES, 1972). Lamentavelmente, a identificação dos ectoparasitos de cada hospedeiro jamais foi incorporada às fichas mod. 155, que possuíam campos previstos para isso, nem mesmo para uma parte dos mamíferos coletados.

De fato, a maior restrição para o pleno aproveitamento das informações coligidas pelo SNP foi sempre relacionada à dificuldade do processamento da volumosa quantidade de informações antes do advento dos computadores, mas também à ausência de continuidade no processamento dos espécimes e informações relacionadas, determinada principalmente pela falta de condições adequadas à curadoria (espaço físico e materiais - armários, gavetas, recipientes) que garantissem a incorporação e perpetuação desse acervo em sua totalidade.

A coleção do SNP é um dos produtos de uma profícua interação entre pesquisadores de diferentes áreas, estabelecida sob preceitos de competência e de colaboração científica elevados e respaldada na estrutura administrativa exemplar daquela repartição. Na estruturação daquele inventário, João Moojen pôde aplicar a experiência obtida com sua participação no inventário do SEPSFA, bem como durante o seu doutorado, quando travou contato com os grandes mastozoólogos e evolucionistas de sua época.

A fundamentação teórica relacionada a este inventário, especificamente no que tange ao potencial analítico exploratório das informações coligidas, que

incluem o tratamento quantitativo da variabilidade morfológica e o particionamento dos componentes ambientais e (micro)geográficos da variação, constitui evidência adicional, paralela à sua contribuição nas diversas outras atividades que desempenhou, do quanto João Moojen encontrava-se sincronizado com respeito às mais avançadas questões teóricas da biologia evolutiva em seu tempo.

AGRADECIMENTOS

Ao Dr. Celso Arcoverde de Freitas (ENSP-FIOCRUZ, aposentado), pelas informações transmitidas em relatos verbais e escritos em diversas ocasiões nos últimos 15 anos, assim como pela disponibilização de documentos e fotografias de seu arquivo pessoal, que em muito orientaram a preparação deste trabalho; ao pessoal do Setor de Arquivos do Museu Nacional, em especial às Sras. Maria José V. da C. Santos e Silvia Ninita de M. Estevão, pela atenção às solicitações pela localização de documentos relativos ao Dr. João Moojen. Pela leitura crítica de uma versão preliminar deste manuscrito e pela revisão final, agradecemos aos Drs. Celso Arcoverde de Freitas, Fernando Dias de Avila Pires (FIOCRUZ, aposentado) e Magali Romero Sá (FIOCRUZ).

REFERÊNCIAS BIBLIOGRÁFICAS:

BALTAZARD, M., 1970. Viagem de estudo ao Brasil para a organização de um projeto de pesquisas sobre a peste. **Revista Brasileira de Malariologia e Doenças Tropicais**, Rio de Janeiro, **22**:335-389p.

DE LA BARRERA, J.M., 1960. **Relatório sobre a peste no Brasil**. (Manuscrito não publicado).

FREITAS, C.A., 1957. Notícia sobre a peste no Nordeste. **Revista Brasileira de Malariologia e Doenças Tropicais**, Rio de Janeiro, **9**:123-133.

FREITAS, C.A., 1989. **Histórias da peste e outras endemias**. Rio de Janeiro: Escola Nacional de Saúde Pública, 216p.

FREITAS, C.A., 1998. **Saúde no Brasil – Nomes e Fatos**. Recife: Editora Bagaço, 209p.

GUIMARÃES, L., 1972. Contribuição à epidemiologia da peste endêmica no Nordeste do Brasil e Estado da Bahia. Estudo das pulgas encontradas nesta região. **Revista Brasileira de Malariologia e Doenças Tropicais**, Rio de Janeiro, **24**:95-164.

HAFNER. M.W.; GANNON, L.; SALAZAR-BRAVO, J. & ALVAREZ-CASTAÑEDA, J.L., 1997. **Mammal collections in Western Hemisphere, a survey and directory of existing collections**. Lawrence: American Society of Mammalogists, 93p.

MOOJEN, J.,1943. **Captura e preparação de pequenos mamíferos para coleções de estudo**. Rio de Janeiro: Imprensa Nacional, 98p.

NEVES, A.G., 1957. O problema da peste dos roedores silvestres no nordeste brasileiro. **Publicações Avulsas do Ministério da Saúde**, Rio de Janeiro, **1**:1-20.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.21-28, jan./mar.2005
ISSN 0365-4508

MAMÍFEROS COLECIONADOS PELO SERVIÇO DE ESTUDOS E PESQUISAS SOBRE A FEBRE AMARELA NOS MUNICÍPIOS DE ILHÉUS E BUERAREMA, ESTADO DA BAHIA, BRASIL [1]

SERGIO MAIA VAZ [2]

RESUMO: Esse estudo é uma pequena revisão das atividades do antigo "Serviço de Estudos e Pesquisas sobre a Febre Amarela (SEPSFA)", desenvolvidas em cooperação com a Divisão de Saúde Internacional da Fundação Rockefeller, na área dos municípios de Ilhéus e Buerarema, Estado da Bahia, envolvendo pesquisas sobre mamíferos selvagens e a febre amarela silvestre, entre dezembro de 1943 e abril de 1945. Baseado na coleção do Museu Nacional - Rio de Janeiro (MN), são relacionados os mamíferos obtidos nas quatro estações de coleta: Fortuna, Pirataquissé, Almada e Urucutuca. A lista de mamíferos apresentada em 1946 é atualizada.

Palavras-chave: Mamíferos, febre amarela, Ilhéus, Buerarema, Bahia, Brasil.

ABSTRACT: Mammals collected by the Yellow Fever Research Service in the municipalities of Ilhéus and Buerarema, State of Bahia, Brazil.

This study is a small revision of the activities of the former "Serviço de Estudos e Pesquisas sobre a Febre Amarela (SEPSFA)" developed in cooperation with the International Health Division of Rockefeller Foundation in the area of the municipalities Ilhéus and Buerarema, State of Bahia, involving research on wild mammals and jungle yellow fever, between December 1943 and April 1945. Based in a collection deposited in the Museu Nacional - Rio de Janeiro (MNRJ), the mammals obtained in four collection stations, namely: Fortuna, Pirataquissé, Almada, and Urucutuca, are listed. A list of mammals originally presented in 1946 is updated.

Key words: Mammals, yellow fever, Ilheus, Buerarema, Bahia, Brazil.

INTRODUÇÃO

Com a descoberta da modalidade silvestre da febre amarela, no vale do Canaã, no Estado do Espírito Santo (1932), surgiu o interesse em se identificar os possíveis hospedeiros vertebrados que pudessem abrigar o vírus.

Entre 1935 e 1954, pesquisas envolvendo mamíferos selvagens foram desenvolvidas em quase todo o território brasileiro, exceto no Acre, Rondônia, Amapá, Piauí, Rio Grande do Norte, Paraíba, Alagoas e Sergipe. Baseado no número de campo dos espécimes conservados no Museu Nacional, acredita-se que a quantidade de indivíduos capturados tenha sido superior a 25.000. Em alguns locais, as capturas duraram poucos dias; em outros semanas e há aqueles em que estas se estenderam por meses e até por mais de um ano (p.ex., Anápolis – GO, Ilhéus/Buerarema – BA, Passos – MG).

MATERIAL E MÉTODOS

O presente estudo é baseado em literatura, em depoimentos de antigos moradores locais, investigações de campo do autor e, fundamentalmente, nos espécimes conservados na coleção de mamíferos do Museu Nacional, Universidade Federal do Rio de Janeiro (MN).

As investigações de campo foram realizadas na área das antigas estações instaladas pelo Serviço de Estudos e Pesquisas sobre a Febre Amarela (SEPSFA) em Ilhéus. Foram visitadas a fazenda Pirataquissé (29-30/I), a fazenda Almada (31/I) e a vila de Urucutuca (01/II/2001).

Na revisão da lista de mamíferos capturados, elaborada por LAEMMERT JR. *et al.* (1946), foram utilizados os estudos de MOOJEN (1948, 1952), HERSHKOVITZ (1944, 1977, 1990, 1997), VIEIRA (1955), CABRERA (1958, 1961), ÁVILA-PIRES (1969), WETZEL & MOLDOLFI (1979), WETZEL & ÁVILA-PIRES (1980), CARLETON & MUSSER

[1] Submetido em 16 de junho de 2004. Aceito em 18 de dezembro de 2005.
[2] Museu Nacional/UFRJ, Departamento de Vertebrados. Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil. E-mail: smvaz@mn.ufrj.br.

(1989), EMMONS & FEER (1990), GOMES (1991), MUSSER & CARLETON (1993), WOODS (1993), WOZENCRAFT (1993), TRIBE (1996), PATTON & DA SILVA (1997), PINTO & RYLANDS (1997), VOSS & ANGERMAN (1997), MUSSER *et al.* (1998), EMMONS & VUCETICH (1998), KOBAYASHI & LANGGUTH (1999), EMMONS *et al.* (2002).

RESULTADOS

As investigações eram da responsabilidade do Serviço de Estudos e Pesquisas sobre a Febre Amarela (Ministério da Educação e Saúde) e contavam com o apoio da Divisão de Saúde Internacional da Fundação Rockefeller (International Health Division of the Rockefeller Foundation).

Os trabalhos de investigação ficavam centralizados em um laboratório de campo que se localizava no Pontal (Ilhéus). Para lá convergia o material capturado em quatro estações de coleta (Fortuna, Pirataquissé, Almada e Urucutuca) (Fig.1) e em fazendas e outros locais situados nas proximidades de cada estação. A estação de Fortuna localizava-se no município de Buerarema e, as demais, em Ilhéus.

O serviço de campo era chefiado pelo Dr. Hugo W. Laemmert e o laboratório pelo Dr. Leoberto de Castro Ferreira (HAMILTON & AZEVEDO, 1999).

Os primeiros mamíferos coletados pelo SEPSFA na região são procedentes do local conhecido como "Repartimento" e foram obtidos em 24 de dezembro de 1943. As pesquisas estenderam-se por 16 meses, tendo sido capturados os últimos espécimes em Urucutuca, no dia 26 de abril de 1945.

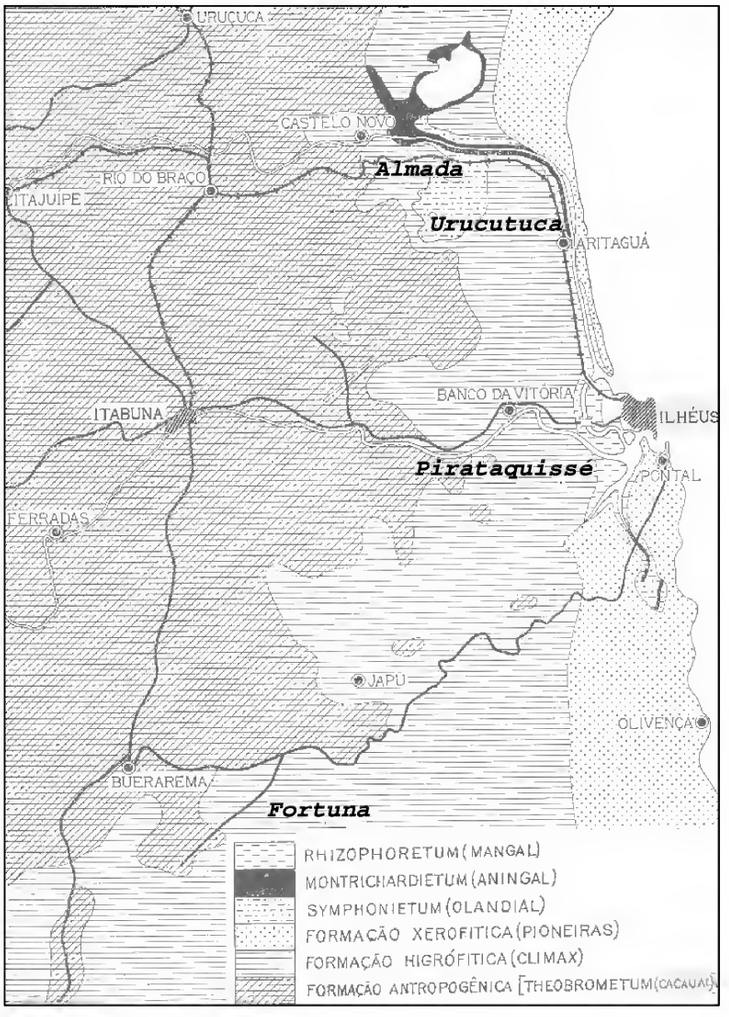

Fig.1- Mapa da região de Ilhéus/Buerarema contendo as estações de coleta do Serviço de Estudos e Pesquisas Sobre a Febre Amarela. (Modificado a partir de VELOSO, 1946 e HERSHKOVITZ, 1977)

A Estrada de Ferro de Ilhéus teve participação importante no transporte dos espécimes colecionados nas áreas das estações de Almada e Urucutuca. Os depoimentos de antigos moradores da região (senhores Wilson Santana, 66 anos e José Maria dos Santos, 75 anos) confirmam que animais "eram embarcados vivos" nas antigas estações/paradas ferroviárias de Lava-Pés, Almada e Urucutuca.

Vários técnicos, auxiliados por moradores locais, estiveram envolvidos na captura dos mamíferos. Entre esses profissionais destacaram-se os senhores Galdino J. Pereira e Pedro de Mello Britto, pela grande experiência de ambos nos trabalhos de campo.

Os espécimes coletados foram identificados pelo naturalista do Museu Nacional, Dr. João Moojen de Oliveira, que teve a oportunidade de visitar a região no ano de 1944, em três períodos distintos (fevereiro/março; agosto e outubro). Em 1948, ele descreveu uma subespécie (*Proechimys iheringi denigratus*) a partir de exemplar capturado na "Mata do Ribeirão da Fortuna" (MOOJEN, 1948). Posteriormente, MOOJEN (1952) publicou observações a respeito de particularidades de alguns roedores (abundância, época de reprodução, número de embriões, etc.) oriundos das estações de coleta.

As regiões onde ficavam as estações de Fortuna, Pirataquissé e Almada foram objeto de levantamento florístico, o qual foi realizado pelo botânico Henrique Pimenta Veloso, durante "13 meses consecutivos de observações de campo" (VELOSO, 1946).

Fortuna

Localização – Município de Buerarema (14°58'S, 39°14'W).

Cobertura vegetal predominante – Vegetação primária (ano 1944).

Localidades onde ocorreram as pesquisas – Fazenda Ribeirão da Fortuna (mata D, G, P, mata da lagoa, est. da mata do cacau); Repartimento; Santa Rita, Japu; rodovia Buerarema Km 5.

Espécies capturadas – *Didelphis aurita, Marmosa murina, Metachirus nudicaudatus, Micoureus demerarae, Diclidurus albus, Rhinophyla pumilio, Dasypus novemcinctus, Cerdocyon thous, Leontopithecus chrysomelas, Callithrix kuhlii, Sciurus aestuans, Rattus rattus, Blarinomys breviceps, Oryzomys laticeps, Oryzomys russatus, Rhipidomys maculipes, Thaptomys nigrita, Dasyprocta leporina, Phyllomys pattoni, Proechimys (Trinomys) denigratus.*

Pirataquisse

Localização – Município de Ilhéus, distrito de Banco da Vitória (14°48'S, 39°07'W).

Cobertura vegetal predominante – Vegetação primária (ano 1944).

Localidades onde ocorreram as pesquisas – Fazenda Pirataquissé (mata C, M, S, do Limoeiro); faz. Ibaiti; São Pedro; faz. Primavera; faz. Brejo Grande; faz. Saudades; faz. Santa Luzia; faz. Triunfo; faz. Promissão.

Espécies capturadas – *Didelphis aurita, Gracilinanus agilis, Marmosa murina, Marmosops incanus, Metachirus nudicaudatus, Micoureus demerarae, Monodelphis americana, Phyllostomus hastatus, Carollia perspicillata, Rhinophyla pumilio, Sturnira lilium, Bradypus torquatus, Dasypus novemcinctus, Tamandua tetradactyla, Cerdocyon thous, Gallictis vittata, Potos flavus, Procyon cancrivorus, Callithrix kuhlii, Sciurus aestuans, Rattus rattus, Akodon cursor, Nectomys squamipes, Oligoryzomys eliurus, Oryzomys laticeps, Oryzomys russatus, Thaptomys nigrita, Sphiggurus insidiosus, Chaetomys subspinosus, Phyllomys pattoni.*

Almada

Localização – Município de Ilhéus, distrito de Rio do Braço (14°39'S, 39°11'W).

Cobertura vegetal predominante – Vegetação secundária (ano 1944).

Localidades onde ocorreram as pesquisas – Fazenda Almada (capoeira do mico, capoeira do cacau); Barbosa; faz. Progresso; ilha do Bonfim; faz. do Bonfim; estrada do Retiro; estação Lava-Pés; Lava-Pés; Lava-Pés de Dentro; Mirante; faz. Santa Rita; Baleia; Ponto da Baleia: Ribeira das Pedras; faz. Quixadá; faz. Pedra Branca; faz. Santa Luzia; faz. Corumbá, faz. Tamburi, faz. São José; faz. São Luiz; faz. Provisão; faz. Ipiranga; distrito de Castelo Novo – faz. Novo Horizonte; faz. Viçosa; faz. Bonsucesso; faz. São Francisco.

Espécies capturadas – *Chironectes minimus, Didelphis aurita, Marmosa murina, Marmosops incanus, Metachirus nudicaudatus, Micoureus demerarae, Phyllostomus hastatus, Lonchophyla mordax, Anoura caudifera, Glossophaga soricina, Carollia perspicillata, Rhinophyla pumilio, Molossus molossus, Cerdocyon thous, Leontopithecus chrysomelas, Callithrix kuhlii, Sciurus aestuans, Rattus rattus, Akodon cursor, Nectomys squamipes, Oligoryzomys eliurus, Oecomys sp., Oryzomys laticeps, Oryzomys russatus, Rhipidomys maculipes, Thaptomys nigrita, Galea spixii, Phyllomys pattoni, Callistomys pictus.*

URUCUTUCA

Localização – Município de Ilhéus, distrito de Aritaguá (14°39'S, 39°07'W).

Cobertura vegetal predominante – Área pantanosa inundada durante os meses das chuvas, com predominância de vegetação baixa e aquática, apresentando "ilhas" com vegetação clímax (ano 1944).

Localidades onde ocorreram as pesquisas – Urucutuca; fazenda Retiro; Sambaituba; Cajucatinga.

Espécies capturadas – D*idelphis aurita, Marmosa murina, Marmosops incanus, Metachirus nudicaudatus, Micoreus demerarae, Bradypus torquatus, Dasypus novemcinctus, Callithrix kuhlii, Cebus xanthosternus, Akodon cursor, Nectomys squamipes, Oligoryzomys eliurus, Oryzomys laticeps, Oryzomys russatus, Rhipidomys maculipes, Thaptomys nigrita, Phyllomys pattoni.*

Além das áreas das estações citadas, houve também coletas na região do Pontal (fazendas São José, Itinga e Santo Antonio) e Olivença (faz. Areal), tendo sido coletados espécimes de *Callithrix kuhlii* (n=2), *Cuniculus paca* (n=2) e *Chaetomys subspinosus* (n=1).

Segundo LAEMMERT JR. *et al.* (1946) foram capturados 5.322 mamíferos durante as pesquisas. Atualmente sabe-se que esse número foi maior, pois na listagem então apresentada não constavam algumas espécies (*Cavia* sp.; *Cuniculus paca*) e há casos em que a quantidade de espécimes capturados foi superior ao informado (*Dasypus novemcinctus* – 12 ao invés de 6; *Dasyprocta leporina* – 8 ao invés de 7).

No tocante à relação dos mamíferos com a febre amarela silvestre, as investigações possibilitaram o isolamento do vírus em primatas doentes (*Callithrix kuhlii*) em quatro ocasiões distintas (proximidades da estação ferroviária de Lava-Pés - 07/VI/1944, fazenda Bonfim - 07/VIII/1944 e fazenda Almada - 10 e 13/VIII/1944) (LAEMMERT JR. & FERREIRA, 1945). Em LAEMMERT JR. (1946), LAEMMERT JR. *et al.* (1946) e WADDEL & TAYLOR (1946, 1948) encontram-se observações sobre a transmissão experimental em laboratório para testar a susceptibilidade de mamíferos procedentes da área de Ilhéus/Buerarema a diferentes linhagens de vírus da febre amarela.

Atualmente, 3.481 espécimes de mamíferos capturados durante as pesquisas do SEPSFA, em Ilhéus/Buerarema, acham-se depositados na coleção do Museu Nacional. Certamente, é a mais importante coleção mastozoológica já reunida naquela região.

Tabela 1. Relação de espécies capturadas em Ilhéus/Buerarema, Estado da Bahia, pelo Serviço de Estudos e Pesquisas sobre a Febre Amarela (dez/1943 - abr/1945).

TÁXONS	SEPSFA [1]	MN [2]
Ordem DIDELPHIMORPHIA		
Chironectes minimus (Zimmermann, 1780)	1	1
Didelphis aurita Wied, 1826	247	160
Gracilinanus agilis (Burmeister, 1854)	41	25
Marmosa murina (Linnaeus, 1758)	142	97
Marmosops incanus (Lund, 1840)	131	94
Metachirus nudicaudatus (E.Geoffroy, 1803)	282	244
Micoureus demerarae (Thomas, 1905)	178	101
Monodelphis americana (Muller, 1776)	17	9
Philander frenata (Olfers, 1818)	1	1
	(1.040)	(732)

continua...

... continuação

TÁXONS	SEPSFA [1]	MN [2]
Ordem XENARTHRA		
Bradypus torquatus Illiger, 1811	8	6
Dasypus novemcinctus Linnaeus, 1758	6	12
Tamandua tetradactyla (Linnaeus, 1758)	7	6
	(21)	(24)
Ordem CHIROPTERA		
Diclidurus albus Wied-Neuwied, 1820	-	2
Phyllostomus hastatus (Pallas, 1767)	-	4
Lonchophyla mordax Thomas, 1903	14	1
Anoura caudifera (E. Geoffroy, 1818)	5	1
Glossophaga soricina (Pallas, 1766)	19	1
Carollia perspicillata (Linnaeus, 1758)	10	8
Rhinophylla pumilio Peters, 1865	-	4
Artibeus sp.	2	1
Sturnira lilium (E. Geoffroy, 1810)	-	1
Molossus ater E. Geoffroy, 1805	12	-
Molossus molossus (Pallas, 1766)	1	1
Não identificados	18	9
	(81)	(33)
Ordem PRIMATES		
Callithrix kuhlii (Wied-Neuwied, 1826)	1829	957
Leontopithecus chrysomelas (Kuhl, 1820)	14	12
Alouatta guariba (Humboldt, 1812)	3	3
Callicebus melanochir Wied-Neuwied, 1820	2	2
Cebus xanthosternos Wied-Neuwied, 1826	3	1
	(1851)	(975)
Ordem CARNIVORA		
Cerdocyon thous (Linnaeus, 1766)	6	6
Eira barbara (Linnaeus, 1758)	1	1
Galictis vittata (Schreber, 1776)	3	3
Potos flavus (Schereber, 1774)	17	15
Procyon cancrivorus (Cuvier, 1798)	1	1
	(28)	(26)

continua...

TÁXONS	SEPSFA [1]	MN [2]
Ordem ARTIODACTYLA		
Pecari tajacu (Linnaeus, 1758)	1	1
Ordem RODENTIA		
Sciurus aestuans Linnaeus, 1766	16	14
Rattus rattus (Linnaeus, 1758)	11 [a]	6
Akodon cursor (Winge, 1887)	207	141
Blarinomys breviceps (Winge, 1887)	7	5
Nectomys squamipes (Brants, 1827)	318	192
Oligoryzomys eliurus (Wagner, 1845)	182	153
Oecomys sp.	29	15
Oryzomys laticeps (Lund, 1840)	878	671
Oryzomys russatus (Wagner, 1848)	266	159
Rhipidomys maculipes (Pictet & Pictet, 1844)	53	41
Thaptomys nigrita (Lichtenstein, 1829)	255	216
Sphiggurus insidiosus (Olfers, 1818)	6	6
Cavia sp.	-	2
Galea spixii (Wagler, 1831)	4	1
Dasyprocta leporina (Linnaeus, 1758)	7	8
Cuniculus paca (Linnaeus, 1766)	-	2
Chaetomys subspinosus (Olfers, 1818)	14	14
Phyllomys pattoni Emmons, Leite, Kock & Costa, 2002	10 [b]	9
Callistomys pictus (Pictet, 1843)	3	3
Trinomys denigratus Moojen, 1948	34	32
	(2.300)	(1.690)
TOTAL	5.322	3.481

(1) Segundo LAEMMERT *et al.* (1946); (2) material conservado no Museu Nacional, Universidade Federal do Rio de Janeiro; (a) onze espécimes foram identificadas como pertencentes ao gênero *Rattus*: 6 como *R. r. frugivorus* e 5 como *R. r. rattus;* (b) na lista original aparecem duas espécies de *Phyllomys*: *P. blainvillei* e *P. brasiliensis*.

AGRADECIMENTOS

À bióloga Antonia Marli V. da Encarnação (Centro de Pesquisas do Cacau - CEPLAC) e ao Sr. Washington Ferreira dos Santos (Ilhéus), pela ajuda para poder visitar a área das antigas estações de pesquisa do SEPSFA (Pirataquissé, Almada e Urucutuca); aos senhores Wilson Santana (Almada) e José Maria dos Santos (Urucutuca), pelas informações prestadas.

REFERÊNCIAS BIBLIOGRÁFICAS

ÁVILA-PIRES, F.D., 1969. Taxonomia e zoogeografia do gênero *Callithrix* Erxleben, 1777. **Revista Brasileira de Biologia**, Rio de Janeiro, **29**(1):49-64.

CABRERA, A., 1958. Catalogo de los mamiferos de America del Sur. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"**, Ciências Zoológicas, Buenos Aires, **4**(1):1-307.

CABRERA, A., 1961. Catalogo de los mamiferos de America del Sur. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"**, Ciências Zoológicas, Buenos Aires, **4**(2):309-732.

CARLETON, M.D. & MUSSER, G.G., 1989. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): A synopsis of *Microryzomys*. **Bulletin of the American Museum of Natural History**, New York, **191**:1-83.

EMMONS, L.H. & FEER, F., 1990. **Neotropical rainforest mammals: A field guide**. Chicago: The University of Chicago Press. xiv, 281p.

EMMONS, L.H. & VUCETICH, M.G., 1998. The identity of Winge's *Lasioromys villosus* and the description of a new genus of echimid rodent (Rodentia: Echimyidae). **American Museum Novitates**, New York, **3223**:1-11.

EMMONS, L.H.; LEITE, Y.L.R.; KOCK, D. & COSTA, L.P., 2002. A review of the named forms of *Phyllomys* (Rodentia: Echimyidae). **American Museum Novitates**, New York, **3380**:1-40.

GOMES, N.F., 1991. **Revisão sistemática do gênero *Monodelphis* (Didelphidae: Marsupialia)**. São Paulo. 180p. Dissertação (Mestrado em Zoologia), Instituto de Biociências da Universidade de São Paulo.

HAMILTON, W. & AZEVEDO, N., 1999. A febre amarela no Brasil: memórias de um médico da Fundação Rockeller. **História, Ciências, Saúde – Manguinhos**, Rio de Janeiro, **5**(3):733-754.

HERSHKOVITZ, P., 1944. A systematic review of the Neotropical water rats of the genus *Nectomys* (Cricetinae). **Miscellaneous Publications, Museum of Zoology, University of Michigan**, Michigan, **58**:1-88.

HERSHKOVITZ, P., 1977. **Living New World monkeys (Platyrrhini) with an introduction to Primates**, Vol. 1. Chicago: University Chicago Press. xiv, 1117p.

HERSHKOVITZ, P., 1990. Titis, New World monkeys of the genus *Callicebus* (Cebidae, Platyrrhini): a preliminary taxonomic review. **Fieldiana, Zoology, New Series**, Chicago, **55**:1-109.

HERSHKOVITZ, P., 1992. The South American gracile mouse opossums, genus *Gracilinarus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notes on general morphology and relationships. **Fieldiana, Zoology, New Series**, Chicago, **70**:1-56.

HERSHKOVITZ, P., 1997. Composition of the family Didelphidae Gray, 1821 (Didelphoidea: Marsupialia), with a review of the morphology and behavior of the included four-eyed pouched opossums of the genus *Philander* Tiedemann, 1808. **Fieldiana, Zoology, New Series**, Chicago, **86**:1-103.

KOBAYASHI, S. & LANGGUTH, A., 1999. A new species of titi monkey, *Callicebus* Thomas, from north-eastern Brazil (Primates, Cebidae). **Revista Brasileira de Zoologia**, Curitiba, **16**(2):531-551.

LAEMMERT JR., H.W., 1946. Studies on susceptibility of Marsupialia to different strains of yellow fever virus. **American Journal of Tropical Medicine**, Baltimore, **26**(1):33-46.

LAEMMERT JR., H.W. & FERREIRA, L.C., 1945. The isolation of yellow fever virus from wild-caught marmosets. **American Journal of Tropical Medicine**, Baltimore, **25**(3):231-232.

LAEMMERT JR., H.W.; FERREIRA, L.C. & TAYLOR, R.M., 1946. An epidemiological study of jungle yellow fever in an epidemic area in Brazil. II-Investigations of vertebrate hosts and arthropod vectors. **American Journal of Tropical Medicine**, Supplement, Baltimore, **26**(6):23-69.

MOOJEN, J., 1948. Speciation in the Brazilian spiny rats (genus *Proechimys*, family Echimyidae). **University of Kansas Publications of the Museum of Natural History**, Lawrence, **1**(19):301-406.

MOOJEN, J., 1952. **Os Roedores do Brasil**. Rio de Janeiro: Ministério da Educação e Saúde, Instituto Nacional do Livro. 214p.

MUSSER, G.G. & CARLETON, M.D., 1993. Family Muridae. In: WILSON, D.E. & REEDER, D.M. (Eds.) **Mammal Species of the World: A taxonomic and geographic reference**. Washington & London: Smithsonian Institution Press, 2.ed. p.501-755.

MUSSER, G.G.; CARLETON, M.D.; BROTHERS, E.M. & GARDNER, A.L., 1998. Systematic studies of oryzomyine rodents (Muridae, Sigmodontinae): diagnoses and distribution of species formerly assigned to *Oryzomys* "*capito*". **Bulletin of the American Museum of Natural History**, New York, **236**:1-376.

PATTON, J.L. & DA SILVA, M.N.F., 1997. Definition of species of pouched four-eyed opossuns (Didelphidae, *Philander*). **Journal of Mammalogy**, Provo, **78**:90-102.

PINTO, L.P.S. & RYLANDS, A.B., 1997. Geographic distribution of the golden-headed lion tamarin, *Leontopithecus chrysomelas*: implications for its management and conservation. **Folia Primatologica**, Basel, **68**:161-180.

TRIBE, C.J., 1996. The Neotropical rodent genus *Rhipidomys* (Cricetidae: Sigmodontinae) – a taxonomic revision. 316p. Thesis (Doctor of Philosophy), University College London.

VELOSO, H.P., 1946. A vegetação do município de Ilhéus, Estado da Bahia. I- Estudo sinecológico das áreas de pesquisas sobre a febre amarela silvestre realizadas pelo S.E.P.F.A.. **Memórias do Instituto Oswaldo Cruz**, Rio de Janeiro, **44**(1):13-103.

VIEIRA, C.O.O., 1955. Lista remissiva dos mamíferos do Brasil. **Arquivos de Zoologia do Estado de São Paulo**, São Paulo, **8**(1):341-474.

VOSS, R.S. & ANGERMANN, R., 1997. Revisionary notes on neotropical porcupines (Rodentia: Erethizontidae). 1. Type material described by Olfers (1818) and Kuhl (1820) in the Berlin Zoological Museum. **American Museum Novitates**, New York, **3214**:1-44.

WADDELL, M.B. & TAYLOR, R.M., 1946. Studies on cyclic passage of yellow fever virus in South American mammals and mosquitoes. II- Marmosets (*Callithrix penicillata* and *Leontocebus chrysomelas*) in combination with *Aedes aegypti*. **American Journal of Tropical Medicine**, Baltimore, **26**(4):455-463.

WADDELL, M.B. & TAYLOR, R.M., 1948. Studies on cyclic passage of yellow fever virus in South American mammals and mosquitoes. IV - Marsupials (*Metachirus nudicaudatus* and *Marmosa*) in combination with *Aedes aegypti* as vector. **American Journal of Tropical Medicine**, Baltimore, **28**(4):87-100.

WETZEL, R.M. & MONDOLFI, E., 1979. The subgenera and species of long-nosed armadillos, genus *Dasypus* L. In: EISENBERG, J.F. (Ed.) **Vertebrate Ecology in the Northern Neotropics**. Washington: Smithsonian Institution Press. p.43-63.

WETZEL, R.M. & ÁVILA-PIRES, F.D., 1980. Identification and distribution of the recent sloths of Brazil (Edentata). **Revista Brasileira de Biologia**, Rio de Janeiro, **40**(4):831-836.

WOODS, C.A., 1993. Suborder Hystricognathi. In: WILSON, D.E. & REEDER, D.M. (Eds.) **Mammal Species of the World: A taxonomic and geographic reference**. Washington & London: Smithsonian Institution Press, 2.ed. p.771-806.

WOZENCRAFT, W.C., 1993. Order Carnivora. In: WILSON, D.E. & REEDER, D.M. (Eds.) **Mammal Species of the World: A taxonomic and geographic reference**. Washington & London: Smithsonian Institution Press, 2.ed. p.279-348.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.29-39, jan./mar.2005
ISSN 0365-4508

FATORES AMBIENTAIS E A REPRODUÇÃO DE MARSUPIAIS E ROEDORES NO LESTE DO BRASIL [1]

(Com 7 figuras)

RUI CERQUEIRA [2]

RESUMO: Pequenos mamíferos (roedores e marsupiais) neotropicais do leste do Brasil foram estudados em relação aos fatores responsáveis pelo início da estação reprodutora. Os primeiros estudos utilizaram os dados de espécies depositados no Museu Nacional e, posteriormente, trabalhos de campo e de laboratório. Dois modos de reprodução foram concebidos. Constatou-se que os marsupiais têm o início da estação reprodutora determinado pela variação do fotoperíodo. Os roedores Sigmodontini no Nordeste do Brasil têm sua reprodução iniciada pela chegada da estação chuvosa. O modo de reprodução dos marsupiais é, portanto, marcadamente estacional e relativamente independente das condições ambientais com solstícios e equinócios funcionando como fatores próximos. O modo de reprodução dos Sigmodontini é determinado pela possibilidade das fêmeas acumularem reservas e está ligado diretamente aos fatores primários.

Palavras-chave: Marsupiais, roedores, fatores ambientais, reprodução, estação reprodutiva, ecologia da reprodução, chuva, duração do dia.

ABSTRACT: Environmental factors and the reproduction of eastern Brazilian marsupials and rodents.

Small neotropical mammals were studied in relation to factors determining the onset of the breeding season. The first studies were based on data from specimens housed at the Museu Nacional, Rio de Janeiro, and were followed by field and laboratory studies. Two modes of reproduction were first proposed. Later, it was found that marsupials have the onset of the breeding season determined by the variation of photoperiod. The Sigmodontini rodents in Northeastern Brazil have their reproduction set by the beginning of the rainy season. Therefore, the marsupial mode of reproduction is markedly climatically seasonal, being somewhat independent of environmental conditions, solstices and equinoxes functioning as proximal factors. The Sigmodontini mode of reproduction has the onset of the breeding season determined by the storage of reserves by the females being linked directly to primary factors.

Key words: Marsupials, rodents, environmental factors, reproduction, breeding season, reproductive ecology, rainfall, day lenght.

INTRODUÇÃO

João Moojen desempenhou papel importante na Mastozoologia brasileira pois seus trabalhos inauguraram os estudos de especiação no país (MOOJEN, 1948). Moojen participou ativamente, como mentor, da construção da nossa principal coleção, a do Museu Nacional. Na década de 1940 ele interagiu com o Serviço de Estudos de Pesquisas da Febre Amarela (SEPSFA), então financiado pela Fundação Rockfeller como parte do esforço de guerra. Desta maneira, as amostras de mamíferos coletados por zoólogos americanos daquele serviço ficaram, em parte, no Brasil. Mesmo material que havia já sido enviado retornou. Uma parte da coleção, no entanto, ficou no campus do Instituto Oswaldo Cruz e só foi localizada em 1970, quando então foi incorporada ao Museu Nacional.

Moojen tinha idéias claras de que era necessário dominar os métodos de estudo. O contacto com o SEPSFA levou-o a escrever um pequeno e seminal livro sobre a coleta e preparação de pequenos mamíferos (MOOJEN, 1943), estabelecendo o padrão brasileiro para esta atividade. O SEPSFA tinha um protocolo padrão de coleta e Moojen utilizou essa experiência para formular um protocolo para o Serviço Nacional de Peste (SNP) do então Ministério da Educação e Saúde. Com este serviço iniciou-se um trabalho de monitoramento da peste. Dezenas de milhares de exemplares foram coletados e enviados para o Museu Nacional até 1956, juntamente com as fichas de coleta, tornando esta coleção a maior da

[1] Submetido em 18 de junho de 2004. Aceito em 26 de janeiro de 2005.
[2] Universidade Federal do Rio de Janeiro, Departamento de Ecologia, Laboratório de Vertebrados, CP 68020, 21941-590, Rio de Janeiro, RJ, Brasil. Bolsista do Conselho Nacional do Desenvolvimento Científico e Tecnológico (CNPq).

América Latina e uma das melhores em termos de dados sobre os animais coletados.

Um aspecto importante dessas fichas são dados sobre o habitat, informações sobre a presença e número de embriões no útero e sobre a vascularização dos testículos, no caso dos machos, juntamente com os tamanhos corporais externos. Cada crânio e pele taxidermizada veio acompanhado de uma dessas fichas. Utilizando essas informações comecei a estudar a reprodução de marsupiais e roedores a partir da década de 1970, com vários colaboradores. Com esses dados pode-se não apenas caracterizar a reprodução de várias espécies, como também avançar no conhecimento da ecologia das estratégias bionômicas. Apresento esses estudos em ordem do desenvolvimento das idéias. Inicialmente revejo os conceitos básicos utilizados.

Fatores ambientais controladores da reprodução

Duas ordens de fatores são considerados na Ecologia da Reprodução: os fatores últimos, ou primários, e os fatores próximos (BAKER, 1938). Os fatores últimos seriam as condições ecológicas gerais, com efeitos maiores no fim do ciclo reprodutivo, quando os jovens mamíferos estão desmamando. A segunda ordem de fatores seriam os fatores próximos, fatores ambientais que funcionam como estímulos diretos ou indiretos à iniciação do ciclo reprodutivo. Como as condições quando do desmame não estão necessariamente presentes no início da estação reprodutiva, outros fatores ambientais, como a temperatura ou a duração do dia, podem funcionar como sinais para o início dessa estação (BAKER, 1938). Como veremos, os fatores próximos podem, em certos casos, constituir também fatores primários e, em outros casos, estar bem distantes da situação ambiental onde efetivamente ocorre a reprodução.

Estação reprodutiva é o período em que ocorrem os eventos reprodutivos ciclo oestral, fecundação, gravidez, amamentação e desmame. O início da estação reprodutiva será desencadeado por um fator próximo que pode ser percebido pelo organismo. A estação reprodutiva não tem necessariamente relação com as estações climáticas.

Procurei, a partir das primeiras análises, definir modelos de estações reprodutivas gerais e capazes de instruir as pesquisas seguintes (CERQUEIRA, 1988). Mais do que modelos no sentido estrito (LEVINS, 1966; LEWONTIN, 1963) foi proposta uma hipótese de que dois modos básicos de estação reprodutiva ocorreriam entre os pequenos mamíferos. Como será visto, a análise dos dados veio a mostrar a validade destes modelos.

A reprodução do Cassaco, *Didelphis albiventris* Lund 1841 e da Catita, *Monodelphis domestica* Wagner 1842 e as condições ambientais.

Dados de 662 espécimens de 16 localidades de coleta pelo SNP do cassaco, *Didelphis albiventris* foram reunidos. Cada exemplar foi classificado em uma de sete classes de idade dentária (CERQUEIRA-SILVA, 1980). Os dados reprodutivos são de dois tipos nas fichas do SNP: para as fêmeas, se existiam embriões no útero e para os machos se os testículos estariam ou não vascularizados. Neste último caso constatei que o dado era por demais variável para ter valia. Na verdade, desde o estudo de BIGGERS (1966) ficava claro que apenas a constatação da presença de espermatozóides à luz dos túbulos é indicação de possibilidade reprodutiva nos machos. Já a presença de embriões nas fêmeas é dado insofismável.

O trabalho consistiu em discutir os padrões de crescimento de machos e fêmeas e tamanhos mínimos de fêmeas grávidas, indexadas por classes de idade dentárias. As fêmeas podiam engravidar ainda muito pequenas (tamanho mínimo de 207g), ainda na classe de idade 5, em que o último molar ainda não está funcional. O estudo mostrava também um crescimento craniano e corporal grande entre as classes 5 e 6-7. Estas duas últimas classes não apresentaram diferenças significativas quanto ao tamanho (CERQUEIRA-SILVA, 1980).

O número de embriões observado foi considerado como sendo o tamanho de ninhada. Justifica-se este dado porque as condições dos laboratórios de campo dificilmente permitiriam ao pessoal do SNP detectar embriões no início da gestação. Presumindo-se que a mortalidade no útero no final da gravidez fosse negligenciável, pode-se então obter diretamente dos dados depositados no Museu Nacional este importante parâmetro bionômico. Os dados não indicaram haver influência da paridade no tamanho de ninhada. A média do tamanho de ninhada foi 4,5 filhotes (CERQUEIRA, 1984).

Foram anotadas as datas de coleta em que havia fêmeas grávidas juntando-se os dados de todos os anos e locando-os em gráficos, juntamente com a curva normal de chuva. A interpretação era de que os machos não teriam quiescência reprodutiva e que a gravidez das fêmeas dependeria do período chuvoso. Este estudo foi inicialmente apresentado como parte de minha tese de doutoramento (CERQUEIRA-SILVA, 1980) e posteriormente teve

nova versão publicada (CERQUEIRA, 1984).

Uma outra análise foi feita com os dados da espécie *Monodelphis domestica* com material do SNP em colaboração com Helena Bergallo. Inicialmente foi analisada a relação entre a chuva ocorrida no período de coleta e a freqüência de fêmeas grávidas, não se revelando correlação significativa (Fig.1). H. Bergallo resolveu testar a correlação entre a normal de chuva e a reprodução, encontrando uma correlação significativa (r=0,355; $p<0.05$; g.l.=46) (Fig.5). Como tal média é a expressão de estações climáticas determinadas pelo movimento da Terra em torno do Sol, suspeitou-se que o fator desencadeante do início da estação reprodutiva fosse a variação do fotoperíodo, que, testado, também foi significativo. Cabe notar que a reprodução não tinha correlação com a chuva efetivamente ocorrida no período (r=0,173; $p>0.05$; g.l.=46; Fig.1). O fator próximo seria o solstício de verão (Fig.2).

Estudos com marsupiais australianos revelaram que pontos notáveis da curva da variação do fotoperíodo estavam relacionados com o início da reprodução. A glândula pineal é a responsável pelo controle interno do desencadear da reprodução. O fator próximo é a duração do dia. Desta maneira as estações reprodutivas são coincidentes com as estações climáticas, mas não com os fenômenos meteorológicos (TYNDALE-BISCOE *et al.*, 1974; RENFREE, 1981).

Este estudo foi mais completo do que o feito com *Didelphis albiventris*. Novamente notou-se que as fêmeas na idade 5, isto é, aquelas ainda sem o ultimo molar funcional, eram as primeiras a apresentarem-se grávidas, o mesmo padrão dos cassacos. Um peso mínimo também era necessário. O padrão de crescimento era também diferente dos cassacos, pois os machos cresciam todo tempo numa taxa maior do que as fêmeas, com exceção do final do crescimento. Também não se observaram diferenças significativas entre os tamanhos das classes finais de idade. Este trabalho constituiu a monografia de graduação de H.BERGALLO (1985) e foi posteriormente publicado como dois artigos (CERQUEIRA & BERGALLO, 1993; BERGALLO & CERQUEIRA, 1995).

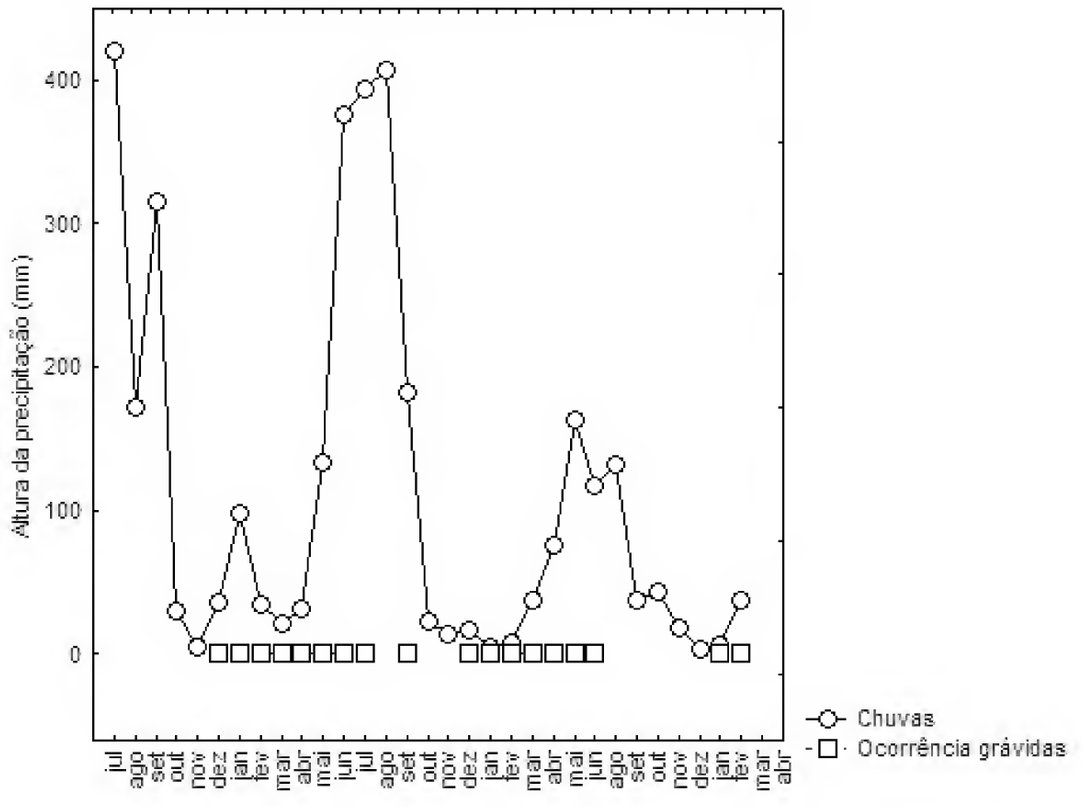

Fig.1- Ocorrência de fêmeas grávidas e chuvas no período de observação – (○) total da chuva mensal em Garanhuns (Dados do Instituto Nacional de Meteorologia), (□) ocorrência de fêmeas com embriões no útero (Dados das fichas de coleta do Serviço Nacional de Peste).

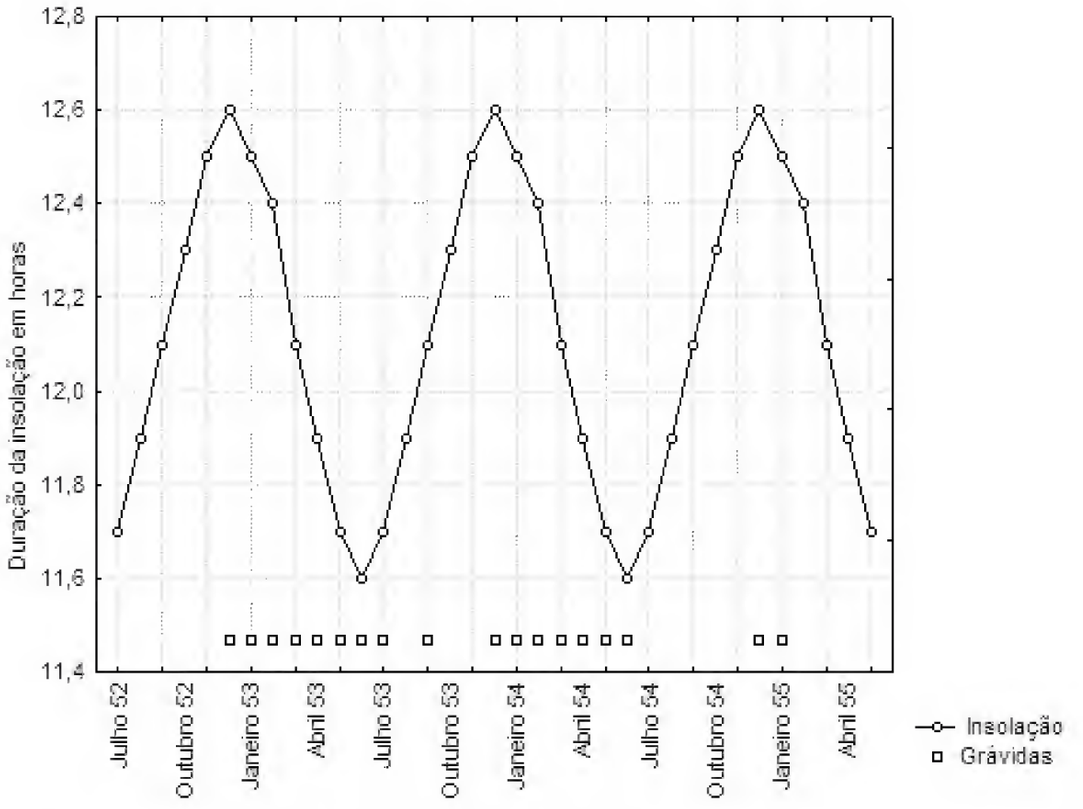

Fig.2- Ocorrência de fêmeas grávidas e a insolação máxima mensal – (O) insolação máxima mensal calculada a partir de tabelas de RAMOS *et al* (1989), (□) Ocorrência de fêmeas grávidas no período de observação (Dados das fichas de coleta do Serviço Nacional de Peste).

Outros estudos com marsupiais da floresta atlântica do Rio de Janeiro

A descoberta feita com o material do Serviço Nacional de Peste levou ao estudo do fenômeno em outras regiões. Dados coletados na restinga de Barra de Maricá, Estado do Rio de Janeiro, mostraram relação entre a duração máxima do fotoperíodo e a ocorrência de fêmeas com filhotes na bolsa (Fig.3). Os dados mostravam que fêmeas apareciam lactantes a partir de julho, havendo atividade reprodutiva até março. Dado que a gravidez dura em torno de 12 dias (HINGST *et al.*,1998), pode-se supor que o início da estação reprodutiva seja ligado ao solstício de inverno. Outros estudos no Estado do Rio de Janeiro mostraram padrão semelhante. Em Sumidouro, *Didelphis aurita* Wied 1826 inicia sua reprodução em julho com atividade reprodutiva até março (GENTILE *et al.*, 2000) e *Philander frenata* Olfers, 1818 apresentou o mesmo padrão de início da reprodução, terminando eventualmente os últimos desmames em abril (GENTILE *et al.*, 2000). Padrão similar foi observado na Serra dos Orgãos (GENTILE *et al.*, 2004).

Este padrão reprodutivo confirmava a hipótese de que se pode trabalhar com um modelo que foi denominado estacional (CERQUEIRA, 1988), onde o início e o fim da estação reprodutiva são desencadeados pela mudança da estação climática determinada pela inclinação relativa da Terra em relação ao Sol (Fig.4). Na média, as condições favoráveis tanto à lactação quanto ao desmame ocorrem quando a situação é favorável (Fig.5). Tanto os dados de campo obtidos diretamente quanto os de coleção confirmaram a existência de um modo particular de atividade reprodutiva para os marsupiais.

Se o modelo estacional de reprodução para explicar a estacionalidade reprodutiva dos marsupiais que estudamos é correto, então ele deveria aplicar-se numa escala maior. Para isto, eu e Vitor Rademaker levantamos os dados reprodutivos relativos ao gênero *Didelphis* Linnaeus, 1758 em toda a sua área de distribuição para testar de o modelo aplicar-se-ia

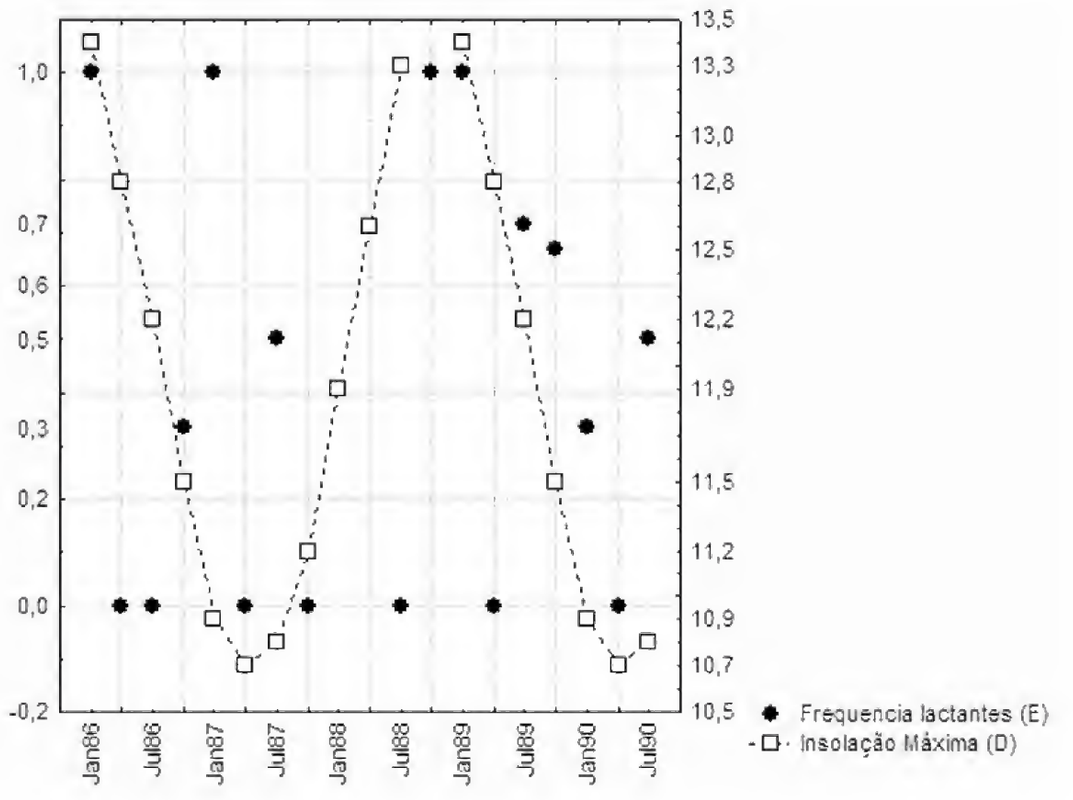

Fig.3- Relação entre a freqüência de fêmeas de *Philander frenata* lactantes e a duração máxima do dia.

a todo o gênero. O resultado que encontramos mostrou que as estações reprodutivas variam com a latitude, sendo que em torno do equador a reprodução é contínua. Quando as populações afastam-se do equador a duração do período reprodutivo diminui, com um início sempre marcado pela mudança das estações. No hemisfério Norte começa em dezembro próximo ao equador e em maiores latitudes em março. A duração do dia correlaciona-se com o início da estação reprodutiva (R=-0.81, R^2=0.65 N=34, *P*<0.001) e a duração desta com a latitude (R= -0.61, R^2=0.35, N=36, *P*<0.001) (GENTILE *et al.*, 2004; RADEMAKER, 2001). Desta maneira, diminui o número de ninhadas pois o tempo de lactação é curto e a reprodução é pós-desmame (D'ANDREA, 1992). Quando o período reprodutivo fica curto, aumenta o tamanho de ninhada, havendo correlação significativa entre latitude e tamanho de ninhada (R=0.73, R^2=0.53, N=41, *P*<0.001).

Desta forma vê-se que o estudo iniciado com o material reunido por João Moojen permitiu um avanço significativo da nossa compreensão sobre o modo de reprodução dos marsupiais neotropicais.

A REPRODUÇÃO DOS SIGMODONTÍNEOS NO NORDESTE DO BRASIL E O DESENCADEAR DA ESTAÇÃO REPRODUTIVA

Os dados de 96 exemplares de *Rhipidomys cearanus* Thomas, 1910 (=*Rhipidomys macrurus* (Gervais, 1855), TRIBE, 1996) foram analisados de forma similar a *Didelphis albiventris*,: considerando-se seis classes de idade (seguindo CERQUEIRA & KLACZKO, 1975) e utilizando-se as medidas corporais e a presença de embriões. Neste caso foi utilizado também o registro sobre vegetação e solo para determinar que macrohabitat era utilizado pela espécie (Fig.6). O trabalho foi feito em colaboração (CERQUEIRA, VIEIRA & SALLES, 1989) com base nos dados das fichas de coleta e os exemplares coletados em São Benedito, na Serra do Ibiapaba, Ceará.

Os resultados mostraram que apenas depois de terem todos os dentes molares funcionais as fêmeas se reproduziam, desde que tivessem um peso mínimo. Os dados relativos à presença de embriões foram analisados cumulativamente e, como no estudo de *D. albiventris*, apenas a presença de fêmeas grávidas, assim como das várias classe de idade, foi comparada graficamente com a chuva efetivamente caída no período de observação na

região (Fig.7). O dado analisado desta forma permite que os fatores próximos e primários possam ser deduzidos. Neste caso, a chuva seria, como suposto no estudo anterior, a responsável pelo início da estação reprodutiva. Como se pode notar na figura 7, o início da estação reprodutiva se dá com um mês do início da chuva. Desta maneira a chuva seria o aparente fator próximo a desencadear a reprodução. Os machos mostraram taxas muito mais elevadas de crescimento. Também neste estudo pôde-se estimar o tamanho médio de ninhada (4,17 filhotes).

Um outro estudo feito à mesma época, mas publicado posteriormente (CERQUEIRA & LARA, 1991), reuniu as informações das fichas do SNP de quatro regiões diferentes, duas em brejos do sertão (Pacoti, Ceará e Triunfo, Pernambuco), uma no agreste (Anadia, Alagoas) e uma na transição entre a Mata Atlântica e o agreste (Feira de Santana, Bahia). Neste caso, os dados de todos os sigmodontinos de cada região foram agrupados e contrastados com a presença de embriões. Considerou-se a freqüência de fêmeas grávidas (*i.e.*, o número de fêmeas grávidas dividido pelo número total de fêmeas coletadas) e a quantidade de chuva que ocorreu à época da coleta. Com exceção de Feira de Santana, todas as amostras tiveram correlações significativas entre a freqüência de fêmeas grávidas e a chuva com um mês de defasagem. O estudo confirmava o que já havia sido observado em São Benedito, com a chuva atuando como um fator próximo para o início da estação reprodutiva.

Ainda outro estudo em curso com *Calomys expulsus* Lund, 1841 coletados em Vitória da Conquista, na Bahia, também utilizando as coleções de exemplares e fichas do SNP, tem revelado resultados similares. Esta pesquisa ainda está em curso.

A chuva ao umedecer o solo desencadeia a germinação de sementes. Estratégias variadas ocorrem em plantas de deserto para evitar que a primeira chuva não leve a todas as sementes a germinarem, pois se não houver subsequentemente mais chuvas a espécie extinguir-se-ia localmente (MACARTHUR, 1972). Os dados que analisamos indicam que chuvas esparsas não iniciam a estação reprodutiva, sendo necessário que a curva de chuva esteja crescendo por um mês para que se registrem fêmeas grávidas. Os dados que analisamos sobre o tamanho e idade mínima das fêmeas registradas

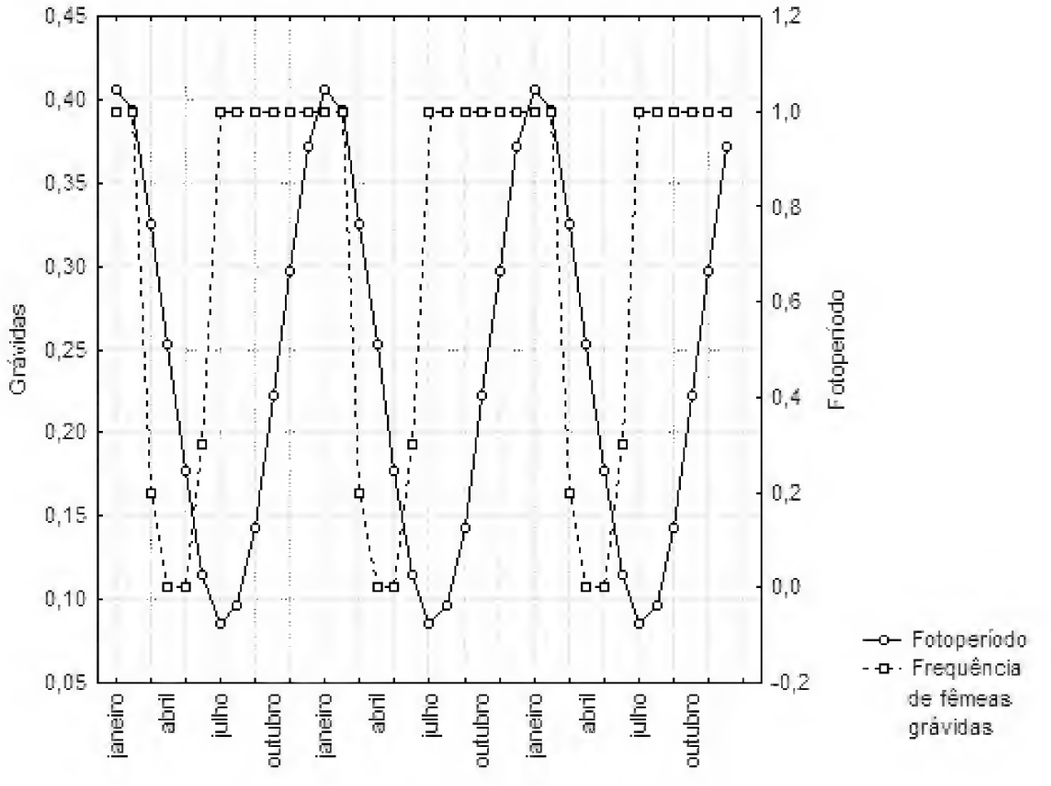

Fig.4- Representação gráfica do modelo estacional determinístico.

como grávidas sugerem que a estrutura demográfica (dependente da estação reprodutiva anterior) e o grau de desenvolvimento e tamanho estariam também ligados a reprodução. Sabe-se que existe nos mamíferos a necessidade de um acumulo líquido de gordura nas fêmeas (FRISCH, 1988). Nossos estudos posteriores com base em sigmodontinos criados em cativeiro (ARARIPE, 2000; D'ANDREA *et al.*, 1996; DEL CONTO, 2002; HINGST, 1995) mostraram que as fêmeas com alimentação *ad libitum* reproduzem-se muito antes de completar o crescimento, assim que o conjunto dos molares está completamente funcional, o que ocorre entre 40 e 50 dias de nascidas. Este achado experimental confirmou a hipótese levantada anteriormente a partir dos dados das fichas do SNP (CERQUEIRA *et al.*, 1989). Da mesma forma, as fêmeas reproduzem-se continuamente desde a primeira parição se mantida a alimentação *ad libitum*. O ciclo de gestação é, na maioria das espécies estudadas, em torno de 20 dias com estro pós-parto o que significa que se a fêmea encontra condições ambientais capazes de permitir que engorde, em 70 dias seus filhotes podem começar a se reproduzir. Nossos estudos mostraram também que o crescimento completa-se a partir do centésimo dia. Sendo animais de ciclos de vida não muito longos (cerca de dois anos em cativeiro), eles podem aproveitar as condições favoráveis de imediato. As chuvas no semi-árido levam ao aumento da produtividade vegetal que permite um aumento das reservas energéticas no corpo dos cricetídeos. O sinal para a reprodução é um certo nível de gordura acumulada (FRISCH, 1988, REID & VAN VUGT, 1987). Assim podemos dizer que, para esses roedores, não há um fator próximo distinto dos primários: quando estes últimos estão no nível adequado, ocorre a reprodução.

Os roedores são a maior parte da coleção do Serviço Nacional de Peste no Museu Nacional. No entanto apenas dois estudos foram até o momento completados.

Modos de reprodução

Os estudos iniciais sugeriram dois modos de reprodução nos mamíferos que poderiam ser compreendidos, de forma simplificada, como modelos (CERQUEIRA, 1988). Um modelo seria o estacional, em que o modo de reprodução estaria caracterizado pelo início e o fim da estação reprodutiva sendo desencadeados pela mudança

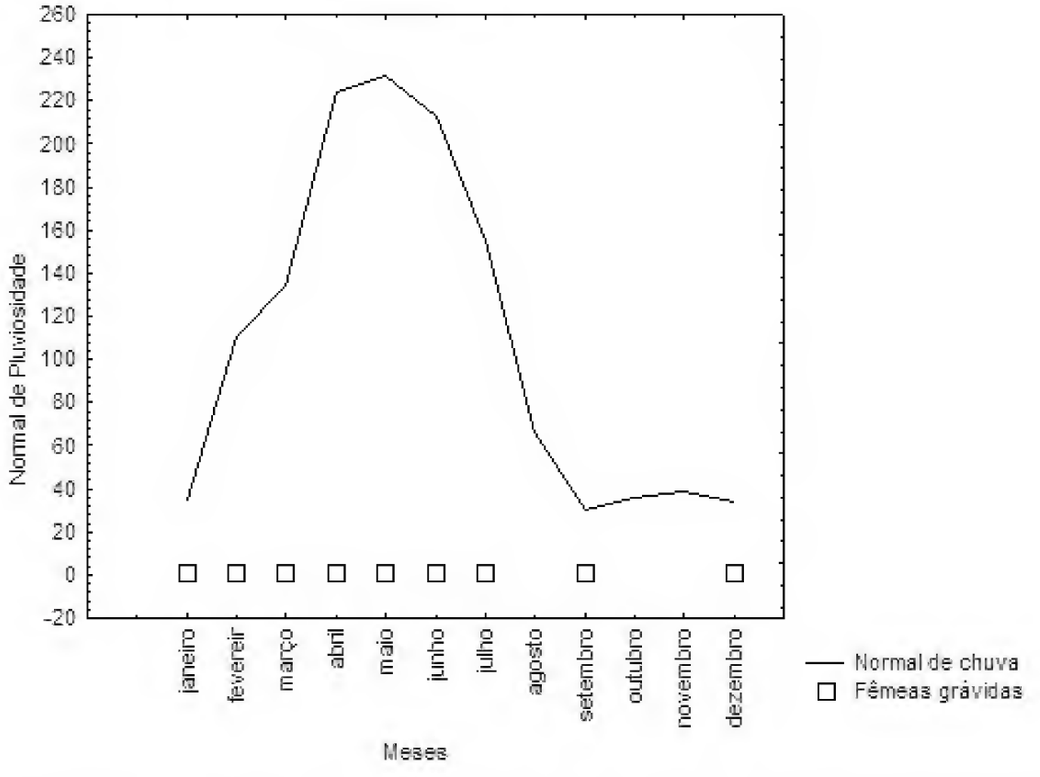

Fig.5- Curva normal da chuva e ocorrência de grávidas (□). Dados como da figura 1. Baseado em BERGALLO & CERQUEIRA, 1994.

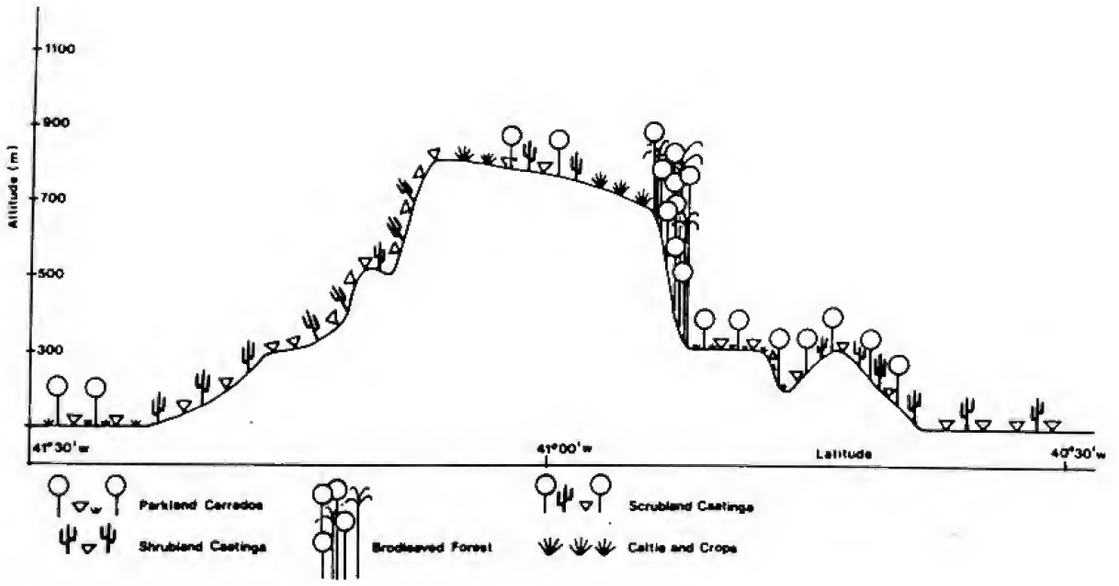

Fig.6- Perfil da vegetação da Serra do Ibiapaba, Ceará. Os dados das fichas de coleta permitiram mostrar que o animal foi coletado apenas na Floresta Ombrófila (*Broadleaved Forest*) e nas caatingas arbustiva (*Shrubland*) e arbórea (*Scrubland*). De CERQUEIRA *et al.*, 1989.

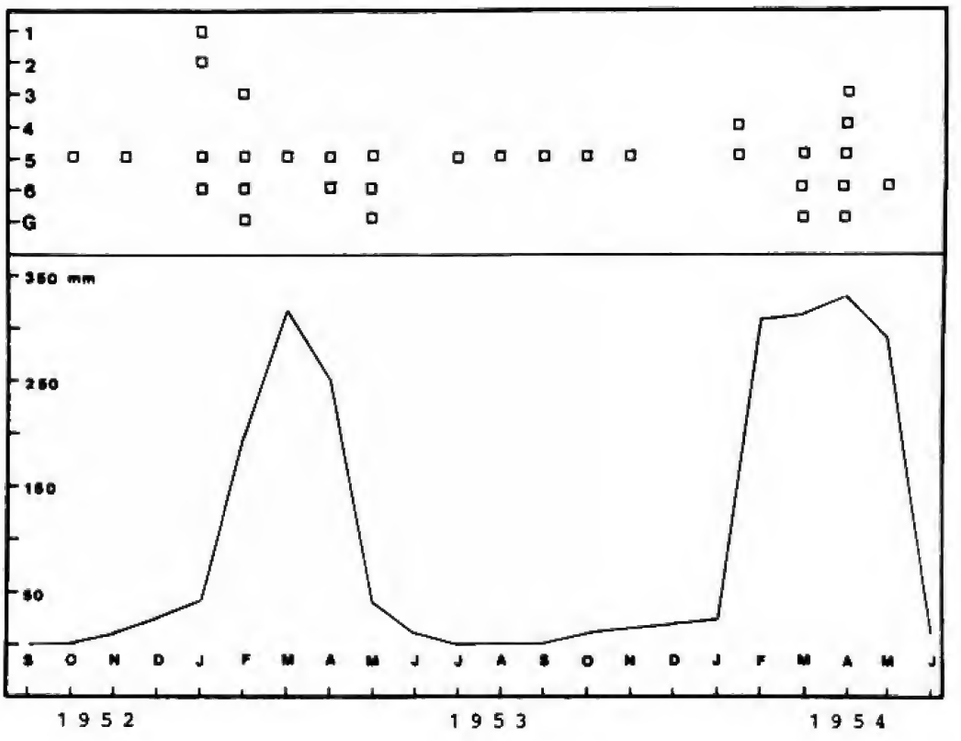

Fig.7- Chuva e reprodução de *Rhipidomys* na Serra de Ibiapaba, Ceará – (abscissa) meses de coleta, (ordenada) na parte de cima da figura: (□) ocorrência no período das várias classes de idade (números) e presença de fêmeas grávidas (G). Parte de baixo da figura: Chuva no período. De CERQUEIRA *et al.*, 1989.

da estação astronômica. O provável sinal seria a variação na duração do dia. O outro modelo seria aquele em que o tamanho da população (*N*) seguiria diretamente o nível de recursos (*K*). Neste caso, as fêmeas engravidariam quando houvesse recursos num certo nível.

Tais modelos são simplificações pois no primeiro modo a capacidade da fêmea emprenhar também depende de sua condição física, como visto em *Monodelphis domestica* (BERGALLO & CERQUEIRA, 1994) e de outros fatores fisiológicos como estro pós-desmame (D'ANDREA *et al.*, 1994) e as condições ambientais diretas estariam claramente influenciando a reprodução como no outro modelo. A diferença seria no quê desencadearia a estação reprodutiva.

Há várias conseqüências destes modos de reprodução. Por exemplo, se a reprodução ocorre desencadeada pelos ciclos astronômicos (o modelo estacional) e o animal tiver capacidade de viver em condições xéricas, mesmo com um ciclo de vida curto ele poderá persistir no semi-árido. *Monodelphis domestica* tem boa capacidade de concentração urinária (FONSECA & CERQUEIRA, 1991) e por isto podemos supor que isto explique sua persistência na caatinga (BERGALLO & CERQUEIRA, 1994).

Animais de ciclo de vida curto que iniciem a estação reprodutiva apenas quando as condições são favoráveis, sofrerão extinções locais sempre que as condições forem desfavoráveis. Aparentemente, os sigmodontinos do Nordeste do Brasil não apresentam adaptações às condições xéricas e por isto necessitam de chuvas suficientes para que a matriz potencial do solo permita a produção vegetal. Como há probabilidade de seca por todo o ano, a cada cinco anos a combinação do modo de reprodução com a ecofisiologia destes animais poderia ser responsável pela persistência deles apenas em regiões mais umidas ou mésicas chamadas localmente de brejos (CERQUEIRA, 1988; BERGALLO & CERQUEIRA, 1994).

No início do estudo foram propostos estes dois modelos para os modos de reprodução. A pesquisa subseqüente mostrou que eles tinham aplicabilidade.

CONCLUSÃO E PERSPECTIVAS

Os estudos iniciados com os dados da coleção do Museu Nacional se mostraram extremamente frutíferos. As idéias iniciais de que dois modos de reprodução existiriam confirmaram-se. Outras análises um pouco mais amplas das estratégias bionômicas (das quais a reprodução é parte) permitem que o estudo de populações vá além da descrição fenomenológica da variação populacional. Por exemplo, estudos demográficos passam a ser possíveis (por exemplo, KAJIN, 2004).

Novos estudos são necessários para detalhar estes modos de reprodução e para a possível construção de modelos mais complexos. Por exemplo, seria interessante maior detalhamento da reprodução de *Didelphis*, mapeando a variação latitudinal, assim como verificar se todos os Didelphimorphia seguem o mesmo modelo. Os sigmodontinos, por sua vez, vão apresentar padrões populacionais mais variados, pois estações reprodutoras marcadas puderam ser verificadas onde as estações climáticas são muito diferenciadas, enquanto em regiões mais úmidas o fenômeno seria mais sutil.

Teria sido muito difícil o avanço que se conseguiu nestes anos tanto nos estudos de reprodução como nos de populações em geral, se João Moojen não tivesse promovido uma coleta em larga escala com a aquisição simultânea de dados reprodutivos e de habitat. A lição que fica, e que precisa ser aplicada, é de que a coleta de exemplares para estudos taxonômicos pode servir de base para o desenvolvimento de toda a Mastozoologia se seguir o padrão que Moojen estabeleceu.

AGRADECIMENTOS

Gostaria de agradecer às várias gerações de estudantes e colaboradores do Laboratório de Vertebrados, particularmente os citados no texto, que permitiram o desenvolvimento dos estudos sobre reprodução aqui revistos. Agradeço a João Alves de Oliveira e a dois revisores anônimos pelas sugestões para melhorar o manuscrito. Os trabalhos foram financiados por auxílios de várias fontes: CNPq, FUJB, FAPERJ, PROBIO/MMA/GEF, PRONEX.

REFERÊNCIAS

ARARIPE, L.O., 2000. **Reprodução, crescimento e desenvolvimento em duas espécies do gênero *Calomys* (Rodentia: Sigmodontinae)**. 129p. Dissertação (Mestrado em Genética), Programa de Pós-graduação em Ciências Biológicas (Genética) Departamento de Genética, Universidade Federal do Rio De Janeiro.

BAKER, J.R., 1938. The evolution of breeding seasons. In: DE BEER, G.R. (Ed.) **Evolution, Essays Presented to E. S. Goodrich**. Oxford, Oxford University Press.

BERGALLO, H.G. & CERQUEIRA, R., 1994. Reproduction and growth of the opossum *Monodelphis domestica* (Mammalia: Didelphidae) in Northeastern Brazil. **Journal of Zoology**, Londres, **232**:551-563.

BERGALLO, H.G., 1985. **Reprodução e crescimento da catita *Monodelphis domestica* (Marsupialia, Polyprotodontia), em alguns municípios do Estado de Pernambuco**. 88p. Monografia (Bacharelado em Ciências Biológicas), Instituto de Biologia, Universidade do Estado do Rio de Janeiro.

BIGGERS, J.D., 1966. Reproduction in male marsupials. **Symposia of the Zoological Society of London**, Londres, **15**:251-280.

CERQUEIRA-SILVA, R., 1980. **A study of neotropical *Didelphis* (Mammalia, Polyprotodontia, Didelphidae)**. 414p PhD Thesis, University College London.

CERQUEIRA, R. & BERGALLO, H.G., 1993. A possible case of photoperiod controlling the reproduction of a South American marsupial. **Ciência e Cultura**, Rio de Janeiro, **45**:140-141.

CERQUEIRA, R. & KLACZKO, L.B., 1975. Biometric studies on *Holochilus brasiliensis* (Rodentia, Cricetidae) I. Ontogenetic variation of a population at Crato, Notheastern Brazil. **Revista Brasileira de Biologia**, Rio de Janeiro, **35**:35-38.

CERQUEIRA, R. & LARA, M., 1991. Rainfall and reproduction of cricetid rodents in Northeastern Brazil. In: BOBCEK, B.; PERZANOVSKI, K.K. & REGELIN, W.L. (Eds.) **Global Trends in Wildlife Management**. Cracóvia: Swiat Press. v.1., p.545-549.

CERQUEIRA, R., 1984. Reproduction de *Didelphis albiventris* dans le nord-est du Brésil (Polyprotodontia, Didelphidae). **Mammalia**, Paris, **48**:95-104.

CERQUEIRA, R., 1988. Modelos de estações reprodutivas em mamíferos. In: ENCONTRO INTERDISCIPLINAR DE ECOLOGIA MATEMÁTICA, Rio de Janeiro, **Atas...**, Rio de Janeiro: Laboratório Nacional de Computação Científica.

CERQUEIRA, R., 2000. Ecologia funcional de mamíferos numa restinga do Estado do Rio de Janeiro In: ESTEVES, F.A. & LACERDA, L.D. (Orgs.) **Ecologia de Restingas e Lagoas Costeiras**. Rio de Janeiro: NUPEM/UFRJ.

CERQUEIRA, R.; SALLES, L.O. & VIEIRA, M.V., 1989. Habitats and reproduction of *Rhipidomys cearanus* (Rodentia, Cricetidae). **Ciência e Cultura**, Rio de Janeiro, **42**:1009-1013.

D'ANDREA, P.S., 1992. **Biologia reprodutiva e critérios para estimativa de idade de *Philander opossum* (Didelphimorphia, Didelphidae)**. 123p. Dissertação (Mestrado), Programa de Pós-graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro.

D'ANDREA, P.S.; CERQUEIRA, R. & HINGST, E.D., 1994. Age estimation of the Gray Four Eyed Opossum, *Philander opossum* (Didelphimorphia, Didelphidae). **Mammalia**, Paris, **58**:283-291.

D'ANDREA, P.S.; HORTA, C.; CERQUEIRA, R. & REY, L., 1996. Breeding of water rat *Nectomys squamipes* in the laboratory. **Laboratory Animals**, Londres, **30**:369-376.

DEL CONTO, V., 2002. **Genética quantitativa e variação microgeográfica de *Akodon cursor* (Rodentia: Sigmodontinae) em fragmentos florestais no Estado do Rio de Janeiro**. 100p. Dissertação (Mestrado), Programa de Pós-graduação em Ciências Biológicas (Genética), Departamento de Genética, Universidade Federal do Rio de Janeiro.

FONSECA, C.R.S.D. & CERQUEIRA, R., 1991. Water and salt balance in a South American marsupial, the four eyed opossum, *Philander opossum*. **Mammalia**, Paris, **55**:421-432.

FRISCH, R.E., 1988. Fatness and fertility. **Scientific American**, New York, **258**:88-95.

GENTILE, R.; D'ANDREA, P.S.; CERQUEIRA, R. & MAROJA, L.S., 2000. Population dynamics and reproduction of marsupials and rodents in a Brazilian rural area: a five-year study. **Studies in Neotropical. Fauna and Environment**, Lisse, **35**:1-9.

GENTILE, R.; FINOTTI, R.; RADEMAKER, V. & CERQUEIRA, R., 2004. Population dynamics of four marsupials and its relation to resource production in the Atlantic Forest in southeastern Brazil. **Mammalia**, Paris, **68**:5-15.

HINGST, E.D., 1995. **Reprodução, crescimento e desenvolvimento em *Bolomys lasiurus* (Rodentia, Sigmodontinae)**. 130p. Dissertação (Mestrado), Programa de Pós-graduação em Ciências Biológicas (Ecologia) Departamento de Ecologia, Universidade Federal do Rio de Janeiro.

HINGST, E.D.; D'ANDREA, P.S. & CERQUEIRA, R., 1998. Breeding of *Philander frenata* (Didelphimorphia, Didelphidae) in captivity. **Laboratory Animals**, Londres, **32**:434-438.

KAJIN, M., 2004. **Populações de *Didelphis aurita* (Didelphimorphia, Didelphidae) na Floresta Atlântica de encosta em Guapimirim, Estado do Rio de Janeiro. Comparação de métodos de estimativa populacional e tabelas de vida**. 75p. Dissertação (Mestrado), Programa de Pós-graduação em Ciências Biológicas (Ecologia), Departamento de Ecologia, Universidade Federal do Rio de Janeiro.

LEVINS, R., 1966. The strategy of model building in population biology. **American Scientist**, New York, **54**:421-431.

LEWONTIN, R., 1962. Models, mathematics and metaphors. **Synthese**, Dordrecht, **15**:222-244.

MOOJEN, J., 1943. **Captura e Preparação de Pequenos Mamíferos para Coleções de Estudo**. Rio de Janeiro: Imprensa Nacional.

Mac ARTHUR, R.M., 1972. **Geographical Ecology**. New York: Harper and Row. 269p.

MOTTA, M.F.D., 1988. **Estudo do desenvolvimento extra uterino de *Didelphis aurita* Wied, 1826, em cativeiro – Investigação de critérios para estimativa de idade**. 116p Dissertação (Mestrado), Programa de Pós-graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro..

RADEMAKER, V., 2001. **Ecologia de populações e reprodução de *Didelphis*, com particular ênfase em *D. aurita* em uma área perturbada de Mata Atlântica na Serra dos Orgãos, Guapimirim, RJ**. 44p. Dissertação (Mestrado) Curso de Pós Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Universidade Federal de Minas Gerais.

RAMOS, F.; OCCHIPINTI, A.G.; VILANOVA, N.A.; REICHARDT, K.; MAGALHÃES, P.C. & CLEARY, R.W., 1989. **Engenharia Hidrológica**. Rio de Janeiro: ABRH/UFRJ, 404p.

REID, R.L. & VAN VUGT, D.A., 1987. Weight-related changes in reproductive functions. **Fertility & Sterility**, Los Angeles, **18**:905-913.

RENFREE, M.B., 1981. Marsupials: alternative mammals. **Nature**, London, **239**:100-101.

TRIBE, C.J., 1996. **The Neotropical genus *Rhipidomys* (Cricetidae: Sigmodontinae) - a taxonomic revision**. 316p PhD Thesis, University College London.

TYNDALE-BISCOE, C.H.; HEARN, J.P. & RENFREE, M.B., 1974. Control of reproduction in macropodid marsupials. **Jounal of Endocrinology**, Bristol, **63**:589-614.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.41-48, jan./mar.2005
ISSN 0365-4508

INTERGRADATION OF HABITATS OF NON-VOLANT SMALL MAMMALS IN THE PATCHY CERRADO LANDSCAPE [1]

CLEBER J. R. ALHO [2]

ABSTRACT: The relevant literature on the community composition, population densities, habitat preference, and interspecific relations of small mammals in the Cerrado biome of central Brazil is surveyed, and their community structure in different habitats of the open savanna as well as in forested habitats, especially gallery forests, is analyzed. Small mammal communities differ along a gradient of natural habitats in the Cerrado landscape. There are habitat generalists occurring in more than three types of habitat (pan-habitat species) and habitat specialists, showing a high degree of fidelity to habitat. Most species are of the latter kind, displaying high habitat specificity. Habitat structure is the major factor determining small mammal communities within the Cerrado landscape. Community differences appear to be a function of local mosaic factors as well as differences among river basins, between high plateau forested habitats and lowland valley forests, or between moister open areas with soft soil and abundant grass versus very dry and rocky microhabitats.

Key words: Cerrado, conservation, habitats, marsupials, rodents, small mammals.

RESUMO: Intergradação de hábitats de pequenos mamíferos não-voadores na paisagem retalhada do bioma Cerrado.

Contribuições consistentes para o conhecimento dos pequenos mamíferos do bioma Cerrado do Brasil central são examinadas, especificamente sobre composição de comunidades, densidade de populações e preferência de hábitat. A estrutura de comunidade de pequenos mamíferos é analisada em hábitats diferentes do Cerrado aberto bem como em hábitats florestados das matas de galeria. As comunidades de pequenos mamíferos diferem num gradiente de hábitats da paisagem do Cerrado. Há espécies hábitat-generalistas que ocorrem em mais de três tipos de hábitats (espécies pan-habitativas) e espécies hábitat-especialistas, restritas a um tipo de hábitat, que compreendem a maioria das formas, indicando alta especificidade. Estrutura de hábitat é o fator mais importante para determinar a comunidade de pequenos mamíferos no Cerrado. Essas diferenças parecem ser função das características locais dos mosaicos, como também diferenças entre bacias hidrográficas, ou ainda, diferenças entre hábitats florestados localizados nos platôs altos comparados com matas de vales em depressão, ou diferenças detectadas em porções de solos úmidos de Cerrado com abundância de gramíneas, comparados com microhábitats de solos secos e pedregosos.

Palavras-chave: Cerrado, conservação, hábitats, marsupiais, pequenos mamíferos, roedores.

INTRODUCTION

The Cerrado biome of central Brazil comprises savanna-like vegetation, ranging from open grassland to closed-canopy forested savanna and even true forest along rivers. It originally covered nearly two million km^2, and is the second largest Brazilian biome after Amazonia (EITEN, 1972; 1993; RIBEIRO & WALTER, 1998, 2001).

The region is not homogeneous in geology, soils, and vegetation cover, which varies from site to site (FELFILI *et al.*, 1994; FURLEY, 1996). It is very easy to cross markedly different kinds of habitats within a distance of only 100-200 meters, from dense gallery forest, through open wet bog and mesic grassland, to arboreal savanna. The patterns of habitat intergradation are even more complex in ecotone zones of broad contact between biomes (Cerrado-Amazonia to the north; Cerrado-Caatinga to the northeast; Cerrado-Atlantic Forest to the east, and Cerrado-Pantanal to the west). These contact zones vary from moist to semi-arid regions.

The intensive human occupation of the Cerrado biome started in 1960, after the inauguration of Brasília, the Nation's new capital. Cattle ranching and, more recently, soybean plantations are the major land use activities (ALHO & MARTINS, 1995; ALHO, *in press*).

This highly mosaic biome is home to endemic plant species and patchily distributed animals. For

[1] Submitted on May 19, 2004. Accepted on January 31, 2005.

[2] Universidade para o Desenvolvimento do Estado e para a Região do Pantanal (UNIDERP), Programa de Pós-Graduação em Meio Ambiente e Desenvolvimento Regional. Rua Ceará, 333; Campo Grande, 79003-010, MS, Brasil. E-mail: alho@unb.br.

example, it is common to find small mammal species with a preference for forest habitats or for open habitats within the same study area. In the gallery forest, surrounded by open savanna habitats, forest-dwelling arboreal genera such as *Oecomys*, *Oryzomys*, *Oligoryzomys*, and *Rhipidomys* occur within a few meters of open-habitat dwellers such as *Bolomys* and *Oxymycterus*. The genus *Oligoryzomys* also occur in both open and forested habitats. Despite many significant contributions to our knowledge of Cerrado ecology, small mammal distribution and habitat use over the last two decades, the community dynamics and use of space by species within this mosaic landscape are still incompletely understood.

The objective of this review is to document the distribution of small mammals in different kinds of habitats within the Cerrado landscape, to evaluate the relative contribution of the biome to faunal knowledge, to relate the distribution of these species to the mosaic of habitats, and to highlight conservation challenges.

MATERIAL AND METHODS

The savanna vegetation known as Cerrado *sensu lato* (spelled herein with upper-case initial) comprises a variety of different habitats (EITEN, 1972, 1993; RIBEIRO & WALTER, 1998, 2001). Open savannas are termed "campo", ranging from campo limpo (literally "clean field": grassland without shrubs or trees), through campo sujo ("dirty field", with scattered small shrubs), to campo cerrado (savanna with a scattered cover of gnarled trees); wet campo occurs on permanently moist soils. Open-canopy wooded savanna with a grassy understory is known as cerrado *sensu stricto* (lower-case initial), whereas tall, dense, forested savanna with a closed or semi-closed canopy is cerradão. True forest penetrates deep into the Cerrado landscape in narrow bands along rivers and creeks (gallery forests, riverine forests); semi-deciduous mesophytic forest may also be found on well-drained upland slopes. The floristic composition of cerrado, cerradão, mesophytic forest, and gallery forest differs from that of the wet forests with palm trees, locally known as veredas, that are located in waterlogged valley bottoms within the Cerrado (RATTER, 1986; EITEN, 1972, 1993).

This review of small mammal ecology in the Cerrado is based on information presented in published works and graduate dissertations, most of which have been produced during the last twenty years.

RESULTS AND DISCUSSION

Small mammal species show a high degree of habitat fidelity in their distribution within the Cerrado landscape (ALHO, 1981, 1993; ALHO *et al.*, 1986; OLIVEIRA, 1993; REIS, 1993; TALAMONI, 1996; GASTAL, 1997; LACHER & ALHO, 2001; PALMA, 2002). Habitat is an important factor in community structure: species occurring in forested habitats (gallery forests, riverine forests, mesophytic forests, and cerradão) show considerable habitat differences, as do those occupying open savanna habitats (cerrado, campo, wet campo, campo sujo, campo cerrado). The same pattern is also observed when taxonomic groups such as marsupials, murids or echimyids are analyzed (LACHER & ALHO, 2001; PALMA, 2002). Most field work carried out by researchers in the Cerrado is based on trapping along transects through sampling habitats or in grids of capture stations for capture-mark-release-recapture programs. Generally there are substantial differences in the success rates of trap lines along transects or in grids, depending on the kind of habitats (forested habitats have lower rates) and the season (the dry season peak of seeding grasses results in more individual recruitment of open habitat dwellers). Thus, capture success is not homogeneous within the habitats, ranging from 2% to 8% of total trap-nights, 5% being a good success rate. Additionally, different methods may suggest different population sizes: for instance, pit fall traps differ from Sherman traps, and some species, such as *Cavia aperea*, tend to avoid traps altogether. Intensive capture-recapture routines indicated that small mammals were caught in close proportion to their occurrence in a given sample habitat (ALHO, 1981, 1993; ALHO *et al.*, 1986; OLIVEIRA, 1993; REIS, 1993; TALAMONI, 1996; GASTAL, 1997; LACHER & ALHO, 2001; PALMA, 2002).

The distribution of small mammal species among available habitats, based on transitions of vegetation types, reveals that there are habitat generalists and habitat specialists (Tab.1). Three marsupials (*Monodelphis domestica*, *Monodelphis americana*, and *Didelphis albiventris*) are categorized as habitat generalists since they are usually captured in more than three types of habitats. The common opossum *Didelphis albiventris* is caught in gallery forest, cerrado, campo cerrado, and cerradão, and also is commonly seen alive or killed by cars in Brasília and other cities.

Table 1. Species list of small mammals by habitat according to intensive capture-mark-recapture field work surveying the Cerrado landscape.

SPECIES	HABITATS	SOURCES
RODENTS – HABITAT GENERALISTS		
Bolomys lasiurus	Cerrado (s.s.); campo; wet campo; campo-cerrado	Alho *et al.*, 1986; Lacher & Alho, 2001; Palma, 2002
Oryzomys subflavus	Ecotones of Cerrado and Atlantic Forest and of Cerrado and Caatinga - cerrado (s.s.); wet campo; campo-cerrado; gallery forest	Langguth & Bonvicino, 2002; Bonvicino, 2003; Alho *et al.*, 1986; Lacher & Alho, 2001; Palma, 2002.
Oryzomys scotti	Cerrado (s.s.); campo; wet campo; campo-cerrado.	Langguth & Bonvicino, 2002; Bonvicino, 2003.
Oryzomys maracajuensis	Cerrado (s.s.); campo; wet campo; campo-cerrado.	Langguth & Bonvicino, 2002; Bonvicino, 2003.
Oryzomys marinhus	Cerrado (s.s.); campo; wet campo; campo-cerrado.	Langguth & Bonvicino, 2002; Bonvicino, 2003.
MARSUPIALS – HABITAT GENERALISTS		
Monodelphis domestica	Cerrado (s.s.); campo; campo cerrado; wet campo; gallery forest	Alho *et al.*, 1986; Lacher & Alho, 2001; Palma, 2002
Didelphis albiventris	Cerrado (s.s.); campo; campo-cerrado; gallery forest; mesophytic forest	Alho *et al.*, 1986; Lacher & Alho, 2001; Palma, 2002
Monodelphis americana	Cerrado (s.s.); campo; campo-cerrado; gallery forest	Alho *et al.*, 1986; Lacher & Alho, 2001; Palma, 2002
RODENTS – HABITAT SPECIALISTS		
Akodon lindberghi (listed as *Plectomys paludicola*)	Gallery forest	Alho *et al.*, 1986
Akodon cursor	Gallery forest; mesophytic forest; cerradão	Alho *et al.*, 1986; Mares & Ernest, 1995; Gastal, 1997; Palma, 2002
Akodon montensis	Campo; cerradão; gallery forest.	Oliveira, 1993; Talamoni, 1996
Calomys expulsus	Campo; cerrado (s.s.).	Bonvicino & Almeida, 2000; Bonvicino *et al.*, 2003; Oliveira, 1993; Palma, 2002.
Calomys tener	Campo; cerrado (s.s.).	Bonvicino & Almeida, 2000; Bonvicino *et al.*, 2003; Oliveira, 1993; Palma, 2002.
Calomys tocantinsi	Cerrado (s.s.); campo.	Bonvicino & Almeida, 2000; Bonvicino *et al.*, 2003.
Nectomys squamipes	Gallery forest	Gastal, 1997; Palma, 2002
Oecomys bicolor	Gallery forest; cerradão	Gastal, 1997; Palma, 2002
Oecomys cleberi	Gallery forest	Locks, 1981
Oecomys concolor	Gallery forest	Gastal, 1997; Palma, 2002
Oligoryzomys microtis	Gallery forest with influence of Amazonia (= vereda); wet campo	Lacher & Alho, 2001.
Oligoryzomys stramineus	Gallery forest	Talamoni, 1996; Gastal, 1997; Palma, 2002

continued...

... conclusion

SPECIES	HABITATS	SOURCES
RODENTS – HABITAT SPECIALISTS		
Oligoryzomys fornesi	Gallery forest; cerrado (*s.s.*) and cerradão.	Myers *et al.*, 1995.
Oligoryzomys nigripes (= *O. eliurus*)	Gallery forest; cerrado (*s.s.*) and cerradão.	Myers & Carleton, 1981; Talamoni, 1996; Gastal, 1997; Lacher & Alho, 2001; Palma, 2002
Oryzomys megacephalus (= *O. capito*)	Gallery forest	Talamoni, 1996; Gastal, 1997; Palma, 2002
Oxymycterus delator	Gallery forest	Palma 2002
Oxymycterus roberti	Wet campo	Gastal, 1997; Lacher & Alho, 2001
Pseudoryzomys simplex	Campo-cerrado	Talamoni, 1996
Proechimys longicaudatus	Gallery forest (valley forest)	Gastal, 1997; Lacher & Alho, 2001; Palma, 2002
Clyomys laticeps	Cerrado (*s.s.*)	Palma, 2002
Trichomys apereoides	Cerrado (*s.s.* – rocks)	Lacher & Alho, 2001; Palma, 2002
Cavia aperea	Campo-cerrado; wet campo	Alho et al., 1986; Talamoni, 1996; Gastal, 1997
Rhipidomys mastacalis	Gallery forest (valley forest); cerradão.	Tribe, 1996; Gastal, 1997; Lacher & Alho, 2001; Palma, 2002
Rhipidomys macrurus	Gallery forest (valley forest); cerradão.	Tribe, 1996.
Euryzygomatomys spinosus (= *E. guiara*)	Cerrado (*s.s.*); campo-cerrado	Woods, 1993; Lacher & Alho, 2001
Thalpomys lasiotis	Cerrado (*s.s.*)	Alho *et al.*, 1986
Thalpomys cerradensis	Cerrado (*s.s.*)	Palma, 2002
Neacomys spinosus	Gallery forest	Lacher & Alho, 2001
Wiedomys pyrrhorhinos	Cerrado (*s.s.*)	Reis, 1993
MARSUPIALS – HABITAT SPECIALISTS		
Caluromys lanatus	Mesophytic forest	Talamoni, 1996
Caluromys philander	Gallery forest	Lacher & Alho, 2001; Palma, 2002
Gracilinanus agilis	Cerradão; gallery forest (valley forest)	Gastal, 1997; Lacher & Alho, 2001; Palma, 2002
Micoureus demerarae	Gallery forest (valley forest)	Lacher & Alho, 2001; Palma, 2002
Philander opossum	Gallery forest	Alho *et al.*, 1986; Palma, 2002
Marmosops noctivagus	Gallery forest (valley forest)	Lacher & Alho, 2001
Marmosa murina	Gallery forest (wet forest)	Lacher & Alho, 2001
Chironectes minimus	Gallery forest	Alho *et al.*, 1986; Mares & Ernest, 1995
Thylamys velutinus	Cerrado (*s.s.*)	Vieira & Palma, 1996
Thylamys karimii	Cerrado (*s.s.*)	Reis, 1993

Generalist rodents (*Bolomys lasiurus* and *Oryzomys subflavus*), are caught in more than three different open habitats. Taxonomic studies have shown that this so-called *Oryzomys subflavus* is in reality a group of species: while *O. subflavus* is found in the ecotones of the Cerrado with the Atlantic Forest and the Caatinga, *O. scotti* is found in the Cerrado of central Brazil, where *O. maracajuensis* and *O. marinhus* also occur (LANGGUTH & BONVICINO 2002; BONVICINO, 2003). *Bolomys lasiurus* is one of the most common terrestrial small mammal species of the cerrado *s.s.* Its species density is around 11 individuals per hectare and home range sizes vary from 200 to 2,500m^2, most of the adult animals occupying an area of around 800m^2; the areas occupied by adult males overlap with those of adult females more than with other groups of the same species, such as juveniles (ALHO & SOUZA, 1982). The average greatest displacement recorded for species, considering four or more recaptures, varies from 9m for *Akodon cursor* to 54m for *Gracilinanus agilis*, but the greatest movements of most species are between 20 and 40 m within their home range areas (GASTAL, 1997). Some recently described rodent species such as *Akodon lindberghi*, *Thalpomys cerradensis*, and *Microakodontomys transitorius* appear to be very restricted to their habitats and are rarely listed in field works. This may be due to the patchy nature of the Cerrado landscape, which probably led to the loss of the habitat of *Juscelinomys candango*, described by Moojen in 1965.

Among the species that occur in all forested habitats (Tab.1), habitat preference varies among different types of gallery forests, riverine forests (mata ciliar), mesophytic forest, and forested savanna (cerradão). Surveys in cerradão are scarce, and data on community composition for this habitat is, therefore, still incomplete. Small mammals occurring in open habitats, including arboreal savanna (cerrado) and all kinds of grasslands (campos) are either generalists (with a wide range of habitat use) or specialists (with habitat specificity).

Sex ratios of small mammals do not differ significantly from 1:1. Species show a rapid turnover in the study areas, with few animals persisting for one year (ALHO & SOUZA, 1982; MARES & ERNEST, 1995; GASTAL, 1997). Persistence of marked individuals in different study areas varies from 2 to 12 months from the first to the last capture. Mean persistence varies from 2 to 4 months. GASTAL (1997) reports a *Cavia aperea* recorded for 14 months in Brasília.

Reproductive activities and young individuals recorded in the surveys indicate, in general, reproduction throughout the year, but with peaks during the dry and/or wet seasons, depending on the species. *Bolomys lasiurus* has a peak in May-June. *Rhipidomys* displays three peaks: June-July (dry period), November-December (wet period), and August-September (dry period), whereas females of *Proechimys* are more sexually active in September-October (end of the dry season), according to GASTAL (1997). Small mammal biomass is greatest during the dry season (peaking in October, the end of dry period) both for forest dwellers and open habitat dwellers (GASTAL, 1997).

Detailed analysis using different methods has shown a high degree of habitat specificity for small mammals in open and forested habitats of the Cerrado landscape (NITIKMAN & MARES, 1987; LACHER & ALHO, 1989; LACHER *et al.*, 1989; HENRIQUES & ALHO, 1991; ALHO, 1993; MARES & ERNEST, 1995; TALAMONI, 1996; GASTAL, 1997; LACHER & ALHO, 2001; PALMA, 2002). Some studies have shown quantitative habitat variables which correlate with species richness and abundance of Cerrado small mammal species, including microhabitat components (ALHO, 1981; ALHO *et al.* 1986; LACHER *et al.* 1989; HENRIQUES & ALHO, 1991; LACHER & ALHO, 2001). A clear association between small mammal density and kind of habitats has been shown (GASTAL, 1997; TALAMONI, 1996; LACHER & ALHO, 2001; PALMA, 2002). Community compositions differ between two grassland habitats: drier habitat has fewer species, with 38% of the overall population density of the more mesic formation. *Oxymycterus roberti*, for example, prefers a narrow range of habitat within the Cerrado, being restricted to the moister portion of the grassland that has soft soil and abundant grass *Tristachia leostachya* (LACHER *et al.*, 1989).

Population parameters of gallery forest dwellers (*Didelphis albiventris*, *Gracilinanus agilis*, *Philander opossum*, *Akodon cursor*, *Nectomys squamipes*, *Oligoryzomys nigripes*, *Oecomys bicolor*, *Oryzomys capito*, *Rhipidomys mastacalis*, and *Proechimys roberti*), such as species richness, diversity, and biomass, are correlated with forest basal area, whereas the evenness of the total small mammal fauna is correlated with vegetation cover (GASTAL, 1997). In addition, species richness and diversity are correlated to gallery forest complexity, expressed by vertical habitat diversity.

When two sympatric rodent species are examined (*Bolomys lasiurus* and *Oxymycterus roberti)* for eight simultaneous microhabitat variables, patterns of habitat utilization and species relationships are distinct. The two species differ markedly in three microhabitat variables: plant species richness, forb ground cover, and distance to the nearest tree or shrub. While *Bolomys* is more a generalist, *Oxymycterus* is more a specialist associated with less diverse lower forbs, shrub, tree cover and higher ground cover (HENRIQUES & ALHO, 1991).

Small mammals have the ability to explore the vertical strata of the habitat. Some genera are essentially arboreal, such as *Oecomys* and *Rhipidomys*. Experimental work carried out in a laboratory setting to test the scansorial and particularly the climbing ability of *Oligoryzomys nigripes* (formerly *O. eliurus*) and *Oryzomys subflavus* (*Oryzomys subflavus* species group) has demonstrated these species' ability to explore the arboreal stratum. They ascend trees using their tails as balancing aids: the animal keeps its tail stretched parallel to the branch when climbing. *Oligoryzomys nigripes* exhibits better arboreal performance than *Oryzomys subflavus* (ALHO & VILLELA, 1984).

The combination of vegetation type and substrate structured the community of 19 terrestrial species studied in the Cerrado of Mato Grosso into several smaller communities with little faunal overlap (LACHER & ALHO, 2001). This study showed that most species were captured in only one or two of the qualitative habitat types. There were open-habitat species that were completely absent from forest, and forest species that were captured only in forest habitats. Additional cluster analysis of those 19 species confirmed the separation made by qualitative classification of habitats based on plant species composition and other habitat characteristics. The results for habitat associations of small mammal species determined by cluster analysis of soil and vegetation structural characteristics (independently of plant species composition) generated five fairly distinct clusters. The gallery forest cluster grouped the same set of species that had previously been assigned to gallery forest (*Neacomys spinosus*, *Oryzomys megacephalus*, *Nectomys squamipes*, *Oecomys bicolor*, *Proechimys longicaudatus*, and *Caluromys philander*), confirming the earlier analysis. The cluster analysis also grouped the six species that had previously been associated with wet campo (*Oligoryzomys microtis* — occurring at the Cerrado-Amazonia contact zone, *Oligoryzomys nigripes* (= *eliurus*), *Oryzomys subflavus* species group, *Bolomys lasiurus*, *Monodelphis domestica*, and *Marmosa murina)*. The grouping of species was essentially the same whether it was done qualitatively by habitat type or by a quantitative analysis of structural aspects of the vegetation and substrate of the habitat (LACHER & ALHO, 2001).

Small mammals of the Cerrado show a distinct population fluctuation as a function of marked seasonality (dry and wet seasons). *Bolomys lasiurus*, for example, shows a recruitment of young into populations when there is abundance of Cerrado grass seeds (at the end of the wet season and beginning of the dry season), and five species of gallery forest dwellers (*Oecomys bicolor*, *Oecomys concolor*, *Oligoryzomys nigripes*, *Rhipidomys mastacalis*, and *Gracilinanus agilis*) display peaks during the wet season and population decline during the dry season, although this pattern is not clear for all species (ALHO *et al.*, 1986; MARES & ERNEST, 1995). While *Oecomys bicolor* densities peak at the end of the dry season, *Oecomys concolor* presents greater density in the middle of the dry season (GASTAL, 1997). Both species are arboreal but *O. bicolor* uses the upper stratum (more than 80% of captures occur in trees) while *O. concolor* uses the stratum closer to the ground. In surveys comparing disturbed and undisturbed canopies in gallery forests, *Oecomys bicolor* proves to be sensitive to habitat modification by occurring at lower densities (PALMA, 2002). When the same analysis is carried out for disturbance of the forest understory, all species are affected.

Nectomys squamipes is only captured in the interior of the gallery forest, in habitat associated with water. Peaks of species abundance, biomass and richness occur at the beginning of the dry season, when *Bolomys lasiurus* in the open habitats and *Proechimys roberti* in the gallery forest are the dominant species (GASTAL, 1997). The species of *Oligoryzomys* are associated with the gallery forest but *O. microtis* is found at the forest edge in the Cerrado-Amazonia contact zone (LACHER & ALHO, 2001).

In large-scale analyses, such as comparisons among different river basins, small mammal communities differ in composition and abundance (LACHER & ALHO, 2001; PALMA, 2002). The latter author concluded that the small mammal communities of the Tocantins river basin are different from those of the Paraná/São Francisco river basins; the differences are more notable between basins rather than within basins. While the Paraná/São Francisco

communities are composed of essentially the same species, the Tocantins community has a greater number of species, particularly marsupials. Differences were also detected between small mammal communities of plateaus (above 900m) and lowland depressions (PALMA, 2002). In addition, the larger and the more pristine the forested habitats, the greater is the number of small mammal species in the community.

The small mammal community stays intact until a drastic habitat disturbance affects habitat integrity, for example inundation due to the formation of a reservoir for a hydroelectric plant (ALHO *et al.*, 2003).

All these findings appear to be consistent with the mosaic aspect of different niches present within the Cerrado biome. It is still too early to pursue a unifying conclusion on the Cerrado small mammal community assemblage, although current knowledge has opened the door to discussions of community organization. Large-scale habitat disturbances, such as the use of fire and the conversion of natural vegetation into pasture or soybean plantations, have the potential to alter population parameters, community structure, use of space and other ecological requirements of the Cerrado small mammal assemblages. Patches of cerradão, for example, are rapidly disappearing as natural vegetation is converted into agricultural land or pastures for cattle ranching, since the soils in these areas are generally richer in nutrients. Such environmental alterations can damage habitat specialists and benefit pan-habitat species, changing community composition associated with pristine habitat gradients in the Cerrado landscape. *Bolomys lasiurus*, for example, has adopted peri-urban habits and is found in areas of human occupation inhabiting natural habitats recently converted into crop fields, and recently it has been incriminated in the spread of hantavirus. In the outskirts of Brasília in 2004, the Health Service of the Federal District confirmed 37 cases of the disease in humans with 16 deaths.

ACKNOWLEDGEMENTS

I am grateful to the Museu Nacional editors of this special volume in honor of João Moojen, especially João Oliveira, for the kind assistance throughout the preparation of this manuscript; two anonymous reviewers improved a previous version of this manuscript, and Christopher J. Tribe provided additional valuable and substantiated comments and suggestions on the final version.

LITERATURE CITED

ALHO, C.J.R., 1981. Small mammal populations of Brazilian Cerrado: the dependence of abundance and diversity on habitat complexity. **Revista Brasileira de Biologia,** Rio de Janeiro, **41**(1):223-230.

ALHO, C.J.R., 1993. Distribuição da fauna num gradiente de recursos em mosaico. In: PINTO, M.N. (Ed.) **Cerrado: Caracterização, ocupação e perspectivas**. Brasília: Editora Universidade de Brasília, p.213-264

ALHO, C.J.R.; STRÜSSMANN, C.; VOLPE, M.; SONODA, F.; MARQUES, A.A.B.; SCHNEIDER. M.; SANTOS JR., T.S.S. & MARQUES, S.R., 2003. **Conservação da Biodiversidade da Bacia do Alto Paraguai. Monitoramento da fauna sob impacto ambiental**. Campo Grande: Editora UNIDERP, 466p.

ALHO, C.J.R. (in press). Desafios para a conservação do Cerrado face às atuais tendências de uso e ocupação. In: SCARIOT, A. (Org.) **Simpósio sobre biodiversidade e conservação do Cerrado**. Brasília: IBAMA-MMA.

ALHO, C.J.R. & MARTINS, E.S., 1995. **De grão em grão o Cerrado perde espaço. Cerrado – Impacto do Processo de Ocupação**. Brasília: WWF-Brasil, 66p.

ALHO, C.J.R.; PEREIRA, L.A. & PÁDUA, A.C., 1986. Patterns of habitat utilization by small mammal populations in the Cerrado biome of Central Brazil. **Mammalia**, Paris, **50**(4):447-460.

ALHO, C.J.R. & SOUZA, M.J., 1982. Home range and use of space in *Zygodontomys lasiurus* (Cricetidae, Rodentia) in the Cerrado of Central Brazil. **Annals of Carnegie Museum**, Pittsburgh, **51**:127-132.

ALHO, C.J.R. & VILLELA, O.M.M., 1984. Scansorial ability in *Oryzomys eliurus* and *O. subflavus* (Rodentia: Cricetidae) from the Cerrado. **Revista Brasileira de Biologia,** Rio de Janeiro, **44**(4):403-408.

BONVICINO, C.R. & ALMEIDA, F.C., 2000. Karyotype, morphology and taxonomic status of *Calomys expulsus* (Rodentia: Sigmodontinae). **Mammalia**, Paris, **64**:339-351.

BONVICINO, C.R., 2003. A new species of *Oryzomys* (Rodentia, Sigmodontinae) of the *subflavus* group from the Cerrado of central Brazil. **Zeitschrift für Saügertierkunde**, Jena, **68**:78-90.

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**, Rio de Janeiro, **20**:301-307.

EITEN, G., 1972. The Cerrado vegetation of Brazil. **Botanical Review**, New York, **38**:201-341.

EITEN, G., 1993. Vegetação do Cerrado. In: PINTO, M.N (Ed.) **Cerrado: caracterização, ocupação e perspectivas**. Brasília: Editora Universidade de Brasília, p.17-73.

FELFILI, J.M.; HARIDASAN, M.; MENDONÇA, R.C.; FILGUEIRAS, T.S.; SILVA JR., M.C. & RESENDE, A.V., 1994. Projeto biogeografia do bioma cerrado: vegetação e solos. **Cadernos de Geociências**, Brasília, **12**:75-166

FURLEY, P.A., 1996. The influence of slope on the nature and distribution of soils and plant communities in the central Brazilian Cerrado. In: ANDERSON, M.G. & BROOKS, S.M. (Eds.) **Advances in hillslope processes**, Chichester: J.Wiley. p.327-346

GASTAL, M.L.A., 1997. **Ecologia de comunidades de pequenos mamíferos em matas de galeria de Brasília**. Brasília. 124p. Doctoral Thesis, Departamento de Ecologia, Universidade de Brasília.

HENRIQUES, R.P.B. & ALHO, C.J.R., 1991. Microhabitat selection by two rodent species in the Cerrado Central Brazil. **Mammalia**, Paris, **55**(1):50-56.

LACHER, T.E., Jr. & ALHO, C.J.R., 1989. Microhabitat use among small mammals in the Brazilian Pantanal. **Journal of Mammalogy**, Provo, **70**(2):396-401.

LACHER, T.E., Jr. & ALHO, C.J.R., 2001. Terrestrial small mammal richness and habitat associations in an Amazon forest-Cerrado contact zone. **Biotropica**, Storrs, **33**(1):171-181.

LACHER, T.E., Jr.; MARES, M.A. & ALHO, C.J.R., 1989. The structure of the small mammal community in a Central Brazilian savanna. In: REDFORD, K.H. & EISENBERG, J.F. (Eds.) **Advances in Neotropical Mammalogy**. Gainesville: Sandhill Crane Press, p.137-162.

LANGGUTH, A. & BONVICINO, C.R., 2002. The *Oryzomys subflavus* species group, with description of two new species (Rodentia, Muridae, Sigmodontinae). **Arquivos do Museu Nacional**, Rio de Janeiro, **60**:285-294.

LOCKS, M., 1981. Nova espécie de *Oecomys* de Brasília-DF (Cricetidae, Rodentia). **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (300):1-5.

MARES, M.A. & ERNEST, K.A., 1995. Population and community ecology of small mammals in a gallery forest of Central Brazil. **Journal of Mammalogy**, Provo, **76**(3):750-768.

MYERS, P.; LUDRIGAN, B. & TUCKER, P.K., 1995. Molecular phylogenetics of oryzomyine rodents: the genus *Oligoryzomys*. **Molecular Phylogenetics and Evolution**, New York, **4**:372-382.

MYERS, P. & CARLETON, M.D., 1981. The species of *Oryzomys (Oligoryzomys)* in Paraguay and the identity of Azara's "Rat sixième ou Rat à Tarse Noir". **Miscellaneous Publications of the Museum of Zoology, University of Michigan**, Ann Arbor, **161**:1-41.

NITIKMAN, L.Z. & MARES, M.A., 1987. Ecology of small mammals in a gallery forest of Central Brazil. **Annals of Carnegie Museum**, Pittsburgh, **56**:75-95.

OLIVEIRA, P.S., 1993. **Estudo de duas comunidades de pequenos mamíferos do Cerrado, na Reserva Ecológica do IBGE (RECOR) Brasília, DF**. Brasília. 101p. Master's Dissertation. Programa de Pós-Graduação em Ecologia, Departamento de Ecologia, Universidade de Brasília.

PALMA, A.R.T., 2002. **Estrutura de comunidades de pequenos mamíferos no Cerrado.** Brasília. 126p. Doctoral Thesis. Programa de Pós-graduação em Ecologia, Departamento de Ecologia, Universidade de Brasília.

RATTER, J.A., 1986. **Notas sobre a vegetação da Fazenda Água Limpa (Brasília-DF)**. Brasília: Editora Universidade de Brasília, 136p.

REIS, M.L., 1993. **Estudo das comunidades de pequenos mamíferos não-voadores em duas áreas de Cerrado (*sensu stricto*) de diferentes tamanhos, inseridas dentro de uma grande floresta plantada na Fazenda Jatobá (Correntina, BA)**. Brasília. 91p. Master's Dissertation. Programa de Pós-graduação em Ecologia, Departamento de Ecologia, Universidade de Brasília.

RIBEIRO, J.F. & WALTER, B.M.T., 1998. Fitofisionomias do bioma Cerrado. In: SANO, S.M. & ALMEIDA, S.P. (Eds.) **Cerrado: ambiente e flora**. Planaltina: Embrapa Cerrados, p.89-166.

RIBEIRO, J.F. & WALTER, B.M.T., 2001. As matas de galeria no contexto do bioma Cerrado. In: RIBEIRO, J.F.; FONSECA, C.E.L. & SOUSA-SILVA, J.C. (Eds.). **Cerrado: caracterização e recuperação de matas de galeria**. Planaltina: Embrapa Cerrados, p.29-47.

TALAMONI, S.A., 1996. **Ecologia de uma comunidade de pequenos mamíferos da Estação Ecológica de Jataí, município de Luís Antonio-SP**. São Carlos. 179p. Doctoral Thesis. Programa de Pós-Graduação em Ecologia e Recursos Naturais, Universidade Federal de São Carlos.

TRIBE, C.J., 1996. **The neotropical rodent genus *Rhipidomys* (Cricetidae: Sigmodontinae). A taxonomic revision**. London. 316p. Doctoral Thesis. University College London.

VIEIRA, E.M. & PALMA, A.R.T., 1996. Natural history of *Thylamys velutinus* (Marsupialia, Didelphidae) in Central Brazil. **Mammalia**, Paris, **60**(3):481-484.

WOODS, C.A., 1993. Suborder Hystricognathi. In: WILSON, D.E. & REEDER, D.M. (Eds.) **Mammal Species of the World. A taxonomic and geographic reference**, 2nd ed. Washington: Smithsonian Institution Press, p.771-806.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.49-62, jan./mar.2005
ISSN 0365-4508

MODELS OF THE DISTRIBUTION OF *ZYGODONTOMYS BREVICAUDA* (ALLEN & CHAPMAN, 1893) (MAMMALIA: MURIDAE) IN THE SAVANNAS OF RORAIMA, NORTHERN BRAZIL [1]

(With 7 figures)

JOSÉ LUIS PASSOS CORDEIRO [2]
LUIZ FLAMARION B. OLIVEIRA [3, 4, *]

ABSTRACT: The present study describes the distribution of *Zygodontomys brevicauda* (Rodentia, Sigmodontinae) relating the presence/absence of the species to a digital database on the vegetation of savannas of the northeastern State of Roraima , Brazil. The study area is situated in the Surumu River region, between 03°58'-04°27'N and 60°13'-61°16'W, and is composed mainly of savanna formations. In a total effort of 9479 trap days, the trap success for *Z. brevicauda* was 0.57%. The probability of capture of the species was calculated for each trap station through logistic regression, using structural characteristics of each habitat. The association of capture probabilities with different habitat classes using a LANDSAT-TM satellite image allowed a spatial view of the potential distribution of the species considering the habitat mosaic of the region. The species is at least partially dependent on the savanna-forest boundary. The models show a high frequency of apparently unsuitable areas, especially of open and closed savannas, which might suggest that habitat occupancy is far from saturated. *Zygodontomys brevicauda* appears to be a colonizing species, and was shown to be associated particularly with the edges of the gallery forests. This habitat type may act as source habitats for open savannas.

Key words: *Zygodontomys brevicauda*, Sigmodontinae, Lavrado, savanna, Roraima, GIS.

RESUMO: Modelos de distribuição de *Zygodontomys brevicauda* (Allen & Chapman, 1893) (Mammalia: Muridae) nas savanas de Roraima, norte do Brasil.

O presente estudo avalia a distribuição potencial de *Zygodontomys brevicauda* (Rodentia, Sigmodontinae) relacionando a presença/ausência da espécie através de uma base digital de dados sobre a vegetação das savanas do nordeste do Estado de Roraima, Brasil. A área de estudo situa-se na região do Alto e Médio Rio Surumu (3°58'-4°27'N; 60°13'-61°16'W) e é composta por várias formações, sendo mais extensas as de savana. Foram empregadas 9.479 armadilhas-dia e o sucesso de captura de *Z. brevicauda* foi de 0.57%. As probabilidades de captura da espécie foram calculadas para cada estação de captura através de regressões logísticas utilizando variáveis estruturais dos hábitats. As associações das probabilidades de captura com as diferentes classes de hábitats, reconhecidas via imagem de satélite LANDSAT-TM, permitiram avaliar a distribuição potencial da espécie no mosaico de hábitats da região. A espécie está parcialmente associada às áreas de contato savana-floresta. O modelo evidenciou alta freqüência de áreas potencialmente vagas, especialmente nas savanas arbóreas abertas e graminosas, sugerindo forte insaturação dos hábitats. *Zygodontomys brevicauda* é potencialmente uma espécie colonizadora dessas classes de hábitats, com as áreas de borda das matas de galeria atuando como hábitats-fonte para as savanas abertas.

Palavras-chave: *Zygodontomys brevicauda*, Sigmodontinae, Lavrado, savanas, Roraima, SIG.

INTRODUCTION

The relationships of organisms with habitat deals with structures that vary in size from a very small scale like topographic features to a very large scale, such as barriers that inhibit movements of the megafauna (McCOY & BELL, 1991). Changes in physical attributes at several scales, as from microhabitat to landscape, may have direct and significant effects upon the spatial distribution of organisms. Knowledge of the pattern of habitat used by a species is useful to understand the adaptations and the viability of populations. Habitats are commonly described in terms of vegetation types

[1] Submitted on June 14, 2004. Accepted on January 26, 2005.
[2] Universidade Federal do Rio Grande do Sul, Centro de Ecologia, Laboratório de Geoprocessamento, 91501-970, Porto Alegre, RS, Brasil.
[3] Museu Nacional/UFRJ, Departamento de Vertebrados. Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil. E-mail: melfo@terra.com.br.
[4] Fellow of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).
[*] Corresponding author.

but may also include many other features such as soil type, topography, microclimate, and shelters.

Savanna describes a range of vegetation characterized by its physiognomy as well as by its floristics (EITEN, 1982). The term includes several intermediate formations between evergreen forest and desert found in tropical and subtropical regions featuring a xeromorphic landscape or landscapes which vary from pure grassland to open woodland (STOTT, 1991). In tropical savannas the climate is warm, there is a long dry season, and the plants often are drought-tolerant.

The biogeographic history of Amazonia and the relationships between the Amazonian savannas and other regions of South America have been discussed extensively by several authors (COLINVAUX, 1987; HAFFER, 1987; MARROIG & CERQUEIRA, 1997; MÜLLER, 1973; SILVA, 1995; VOSS, 1991; WHITMORE & PRANCE, 1987). Nevertheless, information regarding the composition of the nonforest mammal fauna of northern Amazonia and its relationship with habitat and landscape features is either scarce or entirely absent. VOSS (1991) presented data on the distribution of several nonforest mammals in the northern Neotropics, including northern Brazil.

The relatively small patches of Amazonian savannas currently are disjunct in relation to other open landscapes (Llanos, Gran-Sabana, and Cerrado) of tropical South America (HUECK & SEIBERT, 1981). The largest continuous area occurs in the State of Roraima, although little is known of its floristic composition (MIRANDA & ABSY, 1997). The area has a long history of economic activity with cattle breeding and herding dating back to 1787 (RADAMBRASIL, 1975). This kind of activity may have influenced today's forest-savanna limit, particularly as a result of the annual burning of the savannas to favor cattle grazing. On the other hand, these limits varied greatly during the Holocene due to climatic fluctuations (DESJARDINS *et al.*, 1996).

The Amazonian savannas are similar in structure to the cerrados of central Brazil, but are classified differently due to the absence of some plant species which are characteristic of the Cerrado, and to differences in soil and climate (EITEN, 1978). Given the strong seasonality of the region, the organisms that inhabit these areas are subject to the effects of extensive environmental fluctuation, especially small mammals.

The recent increase in human population and in agricultural and pastoral activities have caused devastation of large areas, both in central Brazil and the Amazon. Open formations are particularly impacted by agricultural expansion (NEPSTADT *et al.*, 1997; RATTER *et al.*, 1997). Consequently, an understanding of the relationship between habitat features and distribution of the fauna is important in conservationist decision-making. The identification of the relationship between species and classes of habitat serves as reference source for the evaluation of the effects of environmental damage. Furthermore, savanna formations are subject to extreme variations in rainfall and usually by seasonal fires enhanced by the human habit of pasture burning (HAMMOND & STEEGE, 1998; NEPSTADT *et al.*, 1997). These pressures may influence species diversity and composition as well as population viability.

This research employs concepts used in *GAP Analysis* (SCOTT *et al.*, 1993), including the use of recent vegetation and land use maps and the interpretation of LANDSAT-TM satellite images as indirect indicators of species distribution. However, *GAP Analysis* is not refined enough to identify high quality areas (MUNGER *et al.*, 1998). This information may be refined through the interpretation of species/habitat association via logistic regression and evaluation of landscape features.

Zygodontomys rodents occur in savannas, in xeromorphic formations, and grasslands of northwestern Central and South America. The species inhabits lowland and montane rainforest on a continental shelf island off northwestern North South America. Two species are recognized (*Z. brevicauda* (Allen & Chapmanm, 1893) and *Z. brunneus* Thomas, 1898) and several populations show disjunct distribution in isolated savannas north of the Amazon River, where they are considered an important element of open formations (VOSS, 1991). The species feed on seeds, fruit pulp, grass, and insects (VOSS, 1991; NOWAK, 1999).

The present study describes a logistic regression analysis relating the presence/absence of *Zygodontomys brevicauda* to a digital database of the savanna vegetation of northeastern Roraima, Brazil. The structural environmental variables examined were those considered potentially important for predicting the spatial distribution of small mammals in the region.

Such variables include the potential availability of shelters and variables related to the gradient between dense forest vegetation and the adjacent open savannas. Some variables express the habitat physiognomy of savannas in northeastern Roraima.

METHODS

Study area

This study was conducted in the region of the Surumu River in the State of Roraima, northern Amazonia, Brazil (Fig.1) (60°47'W and 4°11'N). The climate is mainly type Aw of the Köppen system, with mean temperatures varying from 26° to 29°C throughout the year. The dry season usually lasts from December through March and the rainfall in this season is on average 36.2mm/month. Rainfall in the period from March to July usually surpasses 50% of the total volume of the annual rainfall (BARBOSA, 1997). The abundance of grass pollen shown by palynological records (Miocene-Pliocene) suggests a vast dominion of open savannas in northern Amazonia and Roraima (SCHAEFER & JÚNIOR, 1997). Formations in Roraima currently range from dense humid forests to open savanna formations. This span of physiognomies does not reflect the richness of savanna tree species (SILVA, 1997). The most plausible hypothesis used to explain the origin and present distribution of this mosaic is related to the paleoclimatic changes, although little information is available for Roraima (DESJARDINS, *et al.*, 1997). SANAIOTTI (1997) emphasized that only three species (*Byrsonima crassifolia, B. coccolobifolia* – Malpighiaceae, and *Curatella americana* - Dilleniaceae) together represent more than 80% of the relative dominance of trees in the savanna. The collective dominance of these species was independent of soil structure and nutrient content.

The inventory of savannas in Roraima is not complete. Therefore, the classification shown by the project RADAMBRASIL (1975) is usually used in research done on the region (*e.g.*, SILVA, 1997). Open landscapes, locally known as "Lavrados", cover approximately 16% of the state (37,800km²). Within the study area, the Radambrasil project recognized two phytoecological regions: Steppe Savanna and Savanna.

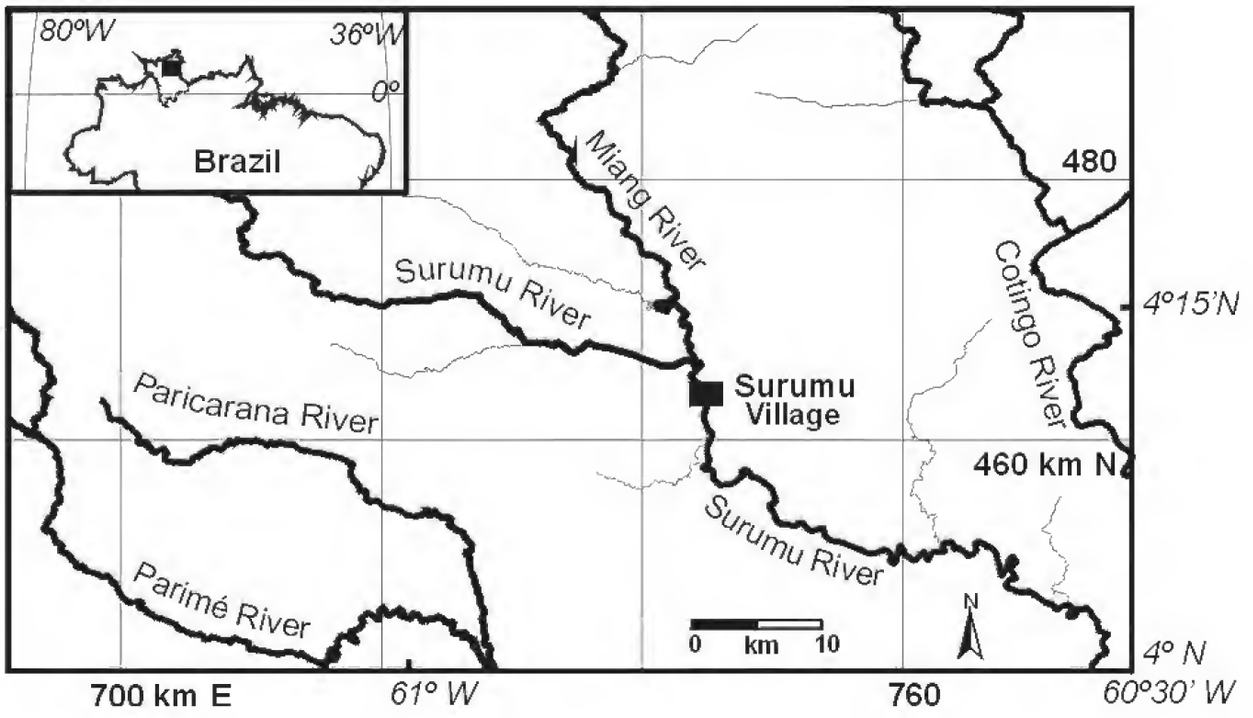

Fig.1- General position of the study area, showing the main village and major rivers of the Upper and Middle Surumu River region, Roraima, Brazil. Grid shows UTM coordinates.

Steppe Savanna ("Região da Savana Estépica") occurs in a sub-region of the dissected surface of the high Surumu River, on flat or hilly and uneven terrain. Steppe Savanna is further subdivided into four categories. (i) Dense Tree Steppe Savanna ("Savana Estépica Arbórea Densa") features a little known floristic composition with elements from the Amazonian forest adapted to a dry season (SILVA, 1997). The formation is deciduous and the tree species (*Aspioderma, Tabebuia, Schinopsis, Cassia, Acacia, Mimosa, Piptadenia, Spondia*, etc.) are xeromorphic and differ from the homologous genera from the Boreal Chaco and the Caatinga. The region also contains components of the Amazon Forest (*Mora, Centrolobium, Brosimum*). (ii) Open Tree Steppe Savanna ("Savana Estépica Arbórea Aberta") has an arboreal stratum composed by shorter, thinner, and more scattered trees than in Dense Tree Steppe Savanna, and the grass cover is more developed. (iii) Steppe Park Savanna ("Savana Estépica Parque") is similar to Open Tree Steppe Savanna except that it has a less continuous tree canopy. Cyperaceae and short grasses (Gramineae) are more evident in the herbaceous stratus. (iv) Grassy Steppe Savanna ("Savana Estépica Graminosa") is typical of flat areas in open valleys, on top of flat sandy areas, and also along small watercourses. Savanna grasses (*Andropogon* and *Trachypogon*) prevail in the ground layer.

The Savanna ("Região da Savana") features either hilly or flat areas and sediments of the Surumu Formation. It is associated with the dissected surfaces of the middle Surumu River, and consists of three subdivisions. (i) Open Tree Savanna ("Savana Arbórea Aberta") has a low and sparse cover of trees between 5 and 7m in height. Grass cover is relatively discontinuous with a prevalence of *Trachypogon* spp. and *Andropogon* spp. (ii) Park Savanna ("Savana Parque") features a grassland physiognomy but isolated trees may also be present. Some stands are composed by *Curatella americana*. (ii) Grassy Savanna ("Savana Graminosa") includes temporary ponds and is dominated by dense grass cover, particularly *Trachypogon plumosus* and *Andropogon angustatus*.

Habitat description

Trap stations where animals were captured (n=54) and a sample of the stations without captures (n=72) were used to estimate capture probabilities of *Z. brevicauda* at the trap sites and to evaluate the potential distribution of the species in the landscape mosaic. Several structural variables (Tab.1), described for the same set of captures by NUNES (2001), were used to describe each trap station. The structural variables and the landscape features were used to describe each physiognomic group in the LANDSAT-TM image. Trap sites and probabilities were then associated with the habitat classes recognized in a thematic map of vegetation and compared to the information available from the phytoecological map of the Radambrasil Project (RADAMBRASIL, 1975).

GIS analysis

GIS analysis was conducted with the help of Geographical Information System (GIS) IDRISI 2 for Windows (EASTMAN, 1997) and CartaLinx (HAGAN, 1998). The latter was used to elaborate vector format maps on a digitizing tablet, using map sheets NB.20-Z-D-V MI14 (Pereira Village) and NB.20-Z-D-IV/I MI-13/3 (Ereu River) on a scale of 1:100,000 (IBGE, 1980). These cartographic maps along with road and hydrologic maps were used to produce digital images. The phytoecological map from the project Radambrasil (map sheet NA./NB. 20 - Boa Vista / Roraima; scale 1:1,000,000), was digitized and later rasterized using the POLYRAS module in the IDRISI software.

Classification was done using LANDSAT (TM) image (orbit 232 – 057, of March 5th, 1996 in 30m resolution). A false color composition, with bands 3, 4, and 5 (COMPOSIT module), was used as a reference, followed by georeferencing (RESAMPLE module) into the UTM (Universal Transverse Mercator) reference system. An unsupervised classification (ISOCLUSTER module) with bands 3, 4, and 5 - LANDSAT (TM) and the false color composition were utilized to identify classes of vegetation. Vector files of points (500 points were recorded for several classes of habitat in the field, via GPS receptor - Global Positioning System Garmin II-Plus) were then used in EDIT module and integrated to a data bank containing information related to the descriptive variables of the landscape. These points were after used in the reclassification process (RECLASS module) to produce classes of vegetation cover. The phytoecological classification by the project RADAMBRASIL (1975) for the State of Roraima was used as reference.

Delimitations of the class Gallery Forest (GF) and of

the contact areas between Gallery Forest and Open Tree Savanna (EOTSGF) and also between Gallery Forest and Open Tree Savanna on Hydromorphic Soil (EOTSHGF) were drawn based on the previously classified image. Any forest formation inside a buffer measuring 100m from each side of any course of water was considered Gallery Forest by the BUFFER module of the software IDRISI. This same module helped to define contact areas between Gallery Forest and both Open Tree Savannas (OTS and OTSH). Contact was considered as a 60m wide strip, a distance required to double the resolution of the LANDSAT (TM) image.

Sampling

Field studies of *Z. brevicauda* were conducted from 20th September to 10th October 1998. Trap lines were placed to maximally sample habitat heterogeneity in the region, including several types of savanna, gallery forest, and ecotones. Trap stations were placed 15m apart and consisted of only one trap, either a wire mesh cage trap (9x9x22cm or 11x12x29.6cm), a Sherman trap (7.5x9.4x30cm), or a snap–trap (Victor® Mouse Trap). The traps were baited with fresh cassava slices and a mixture of peanut butter, industrialized fishmeal, and oatmeal. Also, 36 sets of pitfall traps were arranged throughout the sampled habitats. Each pitfall set was composed of four buckets buried in the ground, one in the center and connected to the other three by a plastic sheet, forming a barrier to prevent small mammals from passing through the set (HANDLEY & KALKO, 1993). Traps were checked every morning for a total of 9,479 trap days. Some habitats outside the areas were sampled to complement the information, but

Table 1. Definition of thirteen structural variables measured at each trap site to compare *Zygodontomys brevicauda* presence/absence.

Variable	Description of variable quantified at each trap site
FHD100	Foliage height density from 20cm to 100cm. Based on ROSENZWEIG & WINAKUR (1969) and modified by OLIVEIRA (1990).
LIT	Relative importance of litter. Calculated by multiplying litter cover versus height where cover was measured by a tube measuring 2.1cm in diameter and placed vertically to soil (OLIVEIRA, 1990).
RIHERB	Relative importance of herb layer. Calculated by multiplying herb cover height and cover. Cover was measured similarly to LIT (OLIVEIRA, 1990).
HSHRUB	Mean height of shrubs around the trap site (NUNES, 2001).
CANHT	Canopy height. Estimated through the use of a clinometer.
CANCV	Canopy cover. Estimated through the use of a spherical densiometer (NUNES, 2001).
ROCK	Percentage of rock cover. Measurement refers to rock cover on soil in two transects which were centered on the capture station. Cover measurements obtained in a manner similar to that used in LIT (OLIVEIRA, 1990).
NUMTREE	Total number of trees in a circle centered on the trap site.
TREEDIS	Mean distance between trees in a 10m radius circle on the trap site.
GALFDIS	Distance from the capture station to the nearest Gallery Forest.
WATDIS	Distance from the capture station to the nearest body of water.
RIROCK	Relative importance of rocks. Results were obtained by using the presence of rocks in classes 1, 2, 3, and 4 (arbitrary scale) considering squares centered in the capture station (NUNES, 2001). The result represents the average number of classes in the squares.

not included in the analysis. Five species of small mammals were trapped besides the *Z. brevicauda* captured (Didelphidade: *Monodelphis brevicaudata* (Erxleben, 1777); Muridae: *Oligoryzomys* sp., *Sigmodon alstoni* (Thomas, 1881), *Rhipidomys nitela* Thomas, 1901; Echimyidae: *Proechimys* cf. *guyannensis*). Karyotype data of the studied population and comparisons with those reported for Venezuela and Costa Rica, and with other regions of northern Amazonia are provided by MATTEVI *et al.* (2002). Voucher specimens are deposited in the Mammal Collection of the Museu Nacional, Rio de Janeiro, Brazil.

Statistical analysis

The information collected in the surveys was used to derive a statistical habitat association model for *Z. brevicauda* based on logistic regression. The environmental structural variables were standardized to unit variance (Z transformed) (STATISTICA, 1999). To estimate capture probability, trap sites were coded for the presence (=1) and absence (=0) of species. Occurrence probabilities were estimated by use of the Logistic Regression equation.

$$P_i = 1 / (1 + e^{-Z})$$

where

$$Z = b_0 + b_1X_1 + b_2X_2 + ... + b_nX_n$$

and X_n the habitat structural variables, b_n the regression coefficients and b_0 the coefficient estimated from the data (intersections). Estimated probabilities were then associated with the identified habitats in the LANDSAT (TM) image classification used as basis for the identification of potential species distribution in the study region.

Four models were built in order to evaluate the potential distribution of *Z. brevicauda*:

Model I - all variables and all trapping sites, which are related to all classes of habitat (Savannas and Gallery Forest), were included in the analysis;

Model II - all variables are included, while all trapping sites, which were in Dense Tree Savanna (DTS), were excluded from the analysis;

Model III - all variables and all trapping sites in Dense Tree Savanna and Gallery Forest (DTS and GF) were excluded from the analysis;

Model IV - all variables and all trapping sites in Dense Tree Savanna (DTS), Gallery Forest (GF), Edge of Open Tree Savanna and Gallery Forest (EOTSGF) and Edge of Open Tree Savanna on Hydromorphic Soil and Gallery Forest (EOTSHGF) were excluded from the analysis.

The goodness of fit of each model was evaluated by the χ^2 test. The acceptance of significance suggests that the model produced adequately models the data and that regression parameters are statistically significant (STATISTICA, 1999).

To estimate the concordance and discordance percentages between the captures and the predicted occurrence, probabilities associated to each station that had rates over 0.5 (50% probability) were considered positive (1) and when less than 0.5, were considered negative (0). Occurrence probabilities for *Z. brevicauda* were represented by the median capture probability in capture stations in each class of habitat. Whenever the median probability for a given class of habitat was more than 0.5 (capture expected by the model), a distribution map along with classes which showed the same pattern was generated. Furthermore, a high capture probability zone (occurrence probability median of more than 75%), this time with a higher requirement in order to include classes of habitat, was established for probabilities higher than 0.75.

RESULTS

Classes of vegetation identified by unsupervised classification of the satellite image are described on table 2. Based on the distribution patterns of the observed classes and the phytoecological regions taken from the Radambrasil Project (RADAMBRASIL, 1975), the Steppe Savanna Region included 16.78% of forest cover and a rougher relief compared to the Savanna phytoecologic region, which showed 3.37% of forest cover. The Savanna region is recognized by the prevalence of open formations where landscape is composed largely of Grassy Savannas on Hydromorphic Soil (61.45%). Herbaceous savannas correspond to the regions most affected by human activity, which is almost entirely represented by extensive cattle breeding areas.

Small-mammal capture success was 1%, of which 57% were *Z. brevicauda*, the most abundant species. Percentages of concordance and discordance of each model built via logistic regression are shown on table 3. All models of capture probability of *Z. brevicauda* (PiZYG) were significant ($P<0.05$), showing concordance among the results between 72.2 and 75.4%. In models I and II ($\chi^2=21.264$; d.f.=12; $P=0.0047$ and $\chi^2=24.240$; d.f.=12; $P=0.019$, respectively), which correspond to the potential distribution of *Z. brevicauda* (PiZYG), habitat distribution showed similar results

when the median probability was considered. The Edge of Open Tree Savanna on Hydromorphic Soil and Gallery Forest (EOTSHGF) was the only habitat to show medians higher than 0.5 (Fig.2). This class showed a higher median in Model II, going from 0.53 to 0.7 (Fig.3). When Dense Tree Savanna (DTS) and Gallery Forest (GF) habitats were excluded from the analysis (Model III; χ^2=25.615; d.f.=12; P=0.012), the importance of transition zone between Open Tree Savanna on Hydromorphic Soil and Gallery Forest (EOTSHGF) was emphasized. The edge zone between Open Tree Savanna and Gallery Forest was also shown to be important. Both edge zones appear to be the most suitable areas of occurrence of this species (Fig.4).

The layout of these probabilities among the classes of habitat remained the same in Model IV (χ^2=20.071; d.f.=12; P=0.066). However, none of the habitat classes showed median probability over 0.5 for *Z. brevicauda* (Fig.5). Although *Z. brevicauda* is a known nonforest species (VOSS, 1991), it rarely occurred in open areas distant from forests. Patches of microhabitat (not shown on this scale) found within classes of tree and herbaceous savannas could be important elements for population viability. In contrast to what was expected, considering that *Z. brevicauda* normally prefers open areas, the probability map drawn from potential distribution maps emphasize edge habitats (EOTSGF and EOTSHGF) as areas of high occurrence. These classes, when gathered into one potential distribution map with criteria above 50% of probability (Fig.6), show high probability zones for the species, where EOTSHGF (Fig.7) is related to a high occurrence probability (median higher than 0.75). These zones feature patches or linear forms dispersed throughout the landscape and are associated with transition areas between open and closed formations, sometimes adjacent to seasonal water courses that drain the hills. Cover by edge zones (EOTSGF and EOTSHGF) constitute a very small proportion (4.93%) in comparison to that of savanna in the region.

Table 2. Classes of vegetation and their areas in the upper and middle Surumu River region, identified via classification of a LANDSAT-TM image (Thematic Map of Actual Vegetation).

CLASSES	DESCRIPTION	AREA (km²)
Woodland	Occurring along the Phytoecologic region in Dense Tropical Forest, as well as covering the main mountain ranges of the Savanna region (Serra do Mel, Marari, Banco, Alemanha, etc.).	554.33
Woodland 1	Open Forest without Palm trees (RADAMBRASIL, 1975).	252.61
GF	Gallery Forest. Forest formations under the influence of a 100m wide border.	244.73
EOTSGF	Edge of Open Tree Savanna and Gallery Forest.	96.09
EOTSHGF	Edge of Open Tree Savanna on Hydromorphic Soil and Gallery Forest. Like EOASGF, EOTSHFG distributes linearly throughout the landscape (Figs. 6 and 7).	84.68
DTS	Dense Tree Savanna. A well-developed tree layer, sparse or lacking herb and shrub layer. Rock outcrops (granite) in its interior.	459.76
OTS	Open Tree Savanna. Discontinuous tree layers where shrubs are either lacking or very sparse. Herb layer present although discontinuous. Usually presenting rocky ground.	609.51
OTSH	Open Tree Savanna on Hydromorphic Soil. Discontinuous tree layers where shrubs are either lacking or very sparse. Herb layer is well-developed. Deeper, more humid soil when compared to OAS.	252.56
GSH	Grassy Savanna on Hydromorphic Soil. Tree and shrub layers are absent. Herbaceous layer where short grasses prevail.	1,650.603.00
GSPE	Grassy Savanna on Partially Exposed Soil. Herb layer sparse and discontinuous.	108.60
TEMPL 1	Temporary Lakes with dense vegetation on its banks.	91.35
TEMPL 2	Temporary Lakes with less water and less dense vegetation.	4.01
RPLANT	Rice Plantation.	5.27
TESOIL	Totally Exposed Soil.	43.18
EROCK	Exposed Rocks.	17.01
CLOUD	Cloud cover at the time of data collection by satellite.	39.76

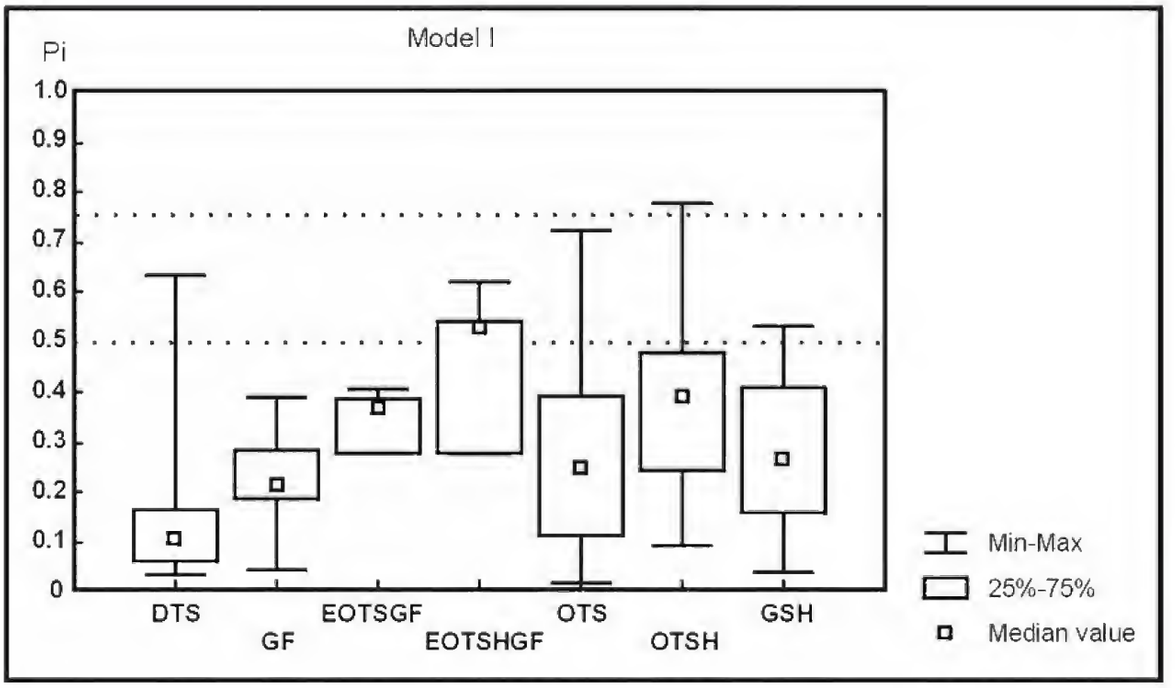

Fig.2- Distribution of the probabilities of occurrence (PiZYG) of *Zygodontomys brevicauda* in classes of habitats (Model I). Abbreviation of the classes of habitat according to table 2.

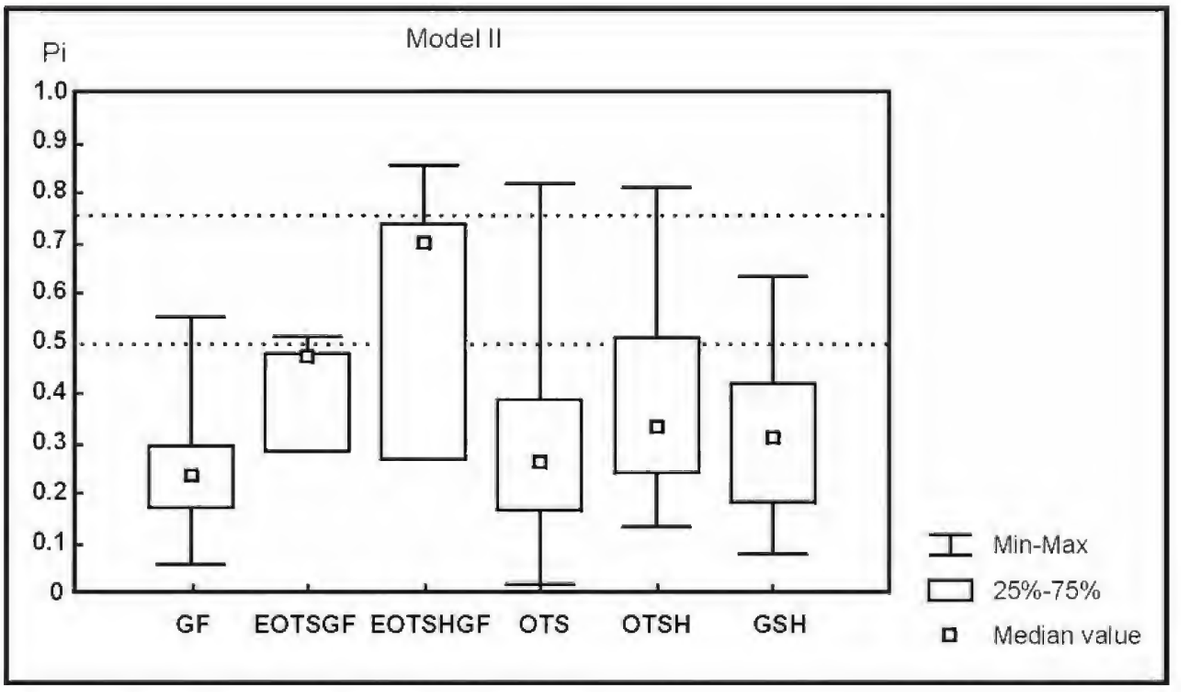

Fig.3- Distribution of the probabilities of occurrence (PiZYG) of *Zygodontomys brevicauda* in classes of habitats (Model II). Abbreviation of the classes of habitat according to table 2.

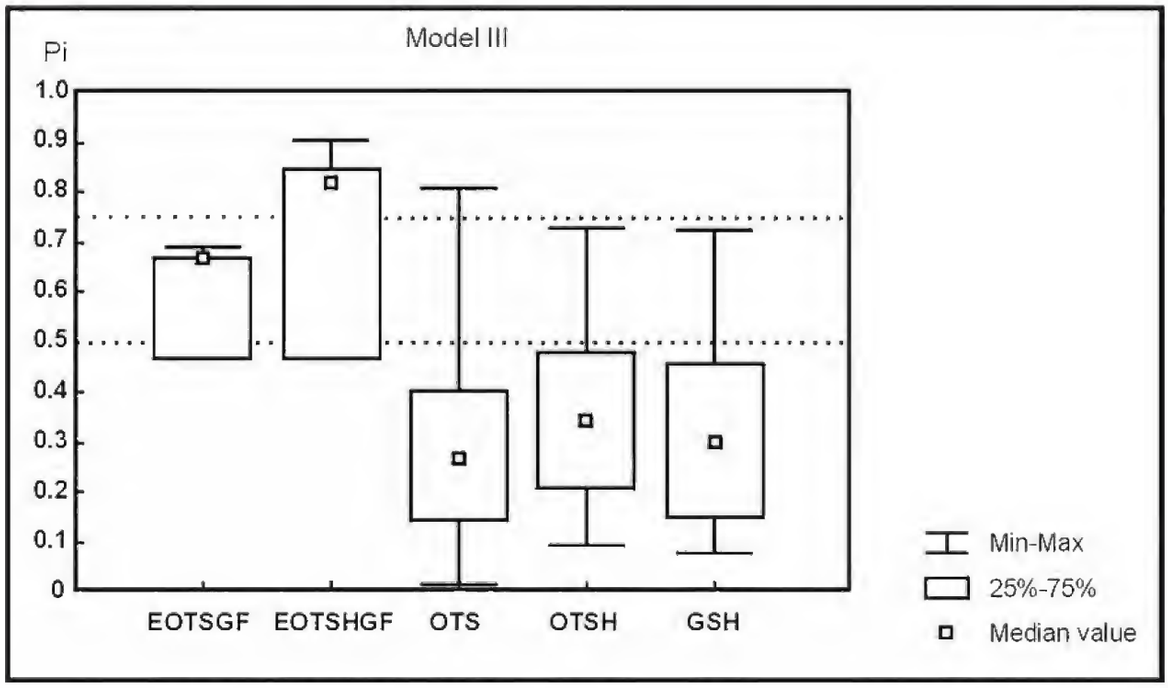

Fig.4- Distribution of the probabilities of occurrence (PiZYG) of *Zygodontomys brevicauda* in classes of habitats (Model III). Abbreviation of the classes of habitat according to table 2.

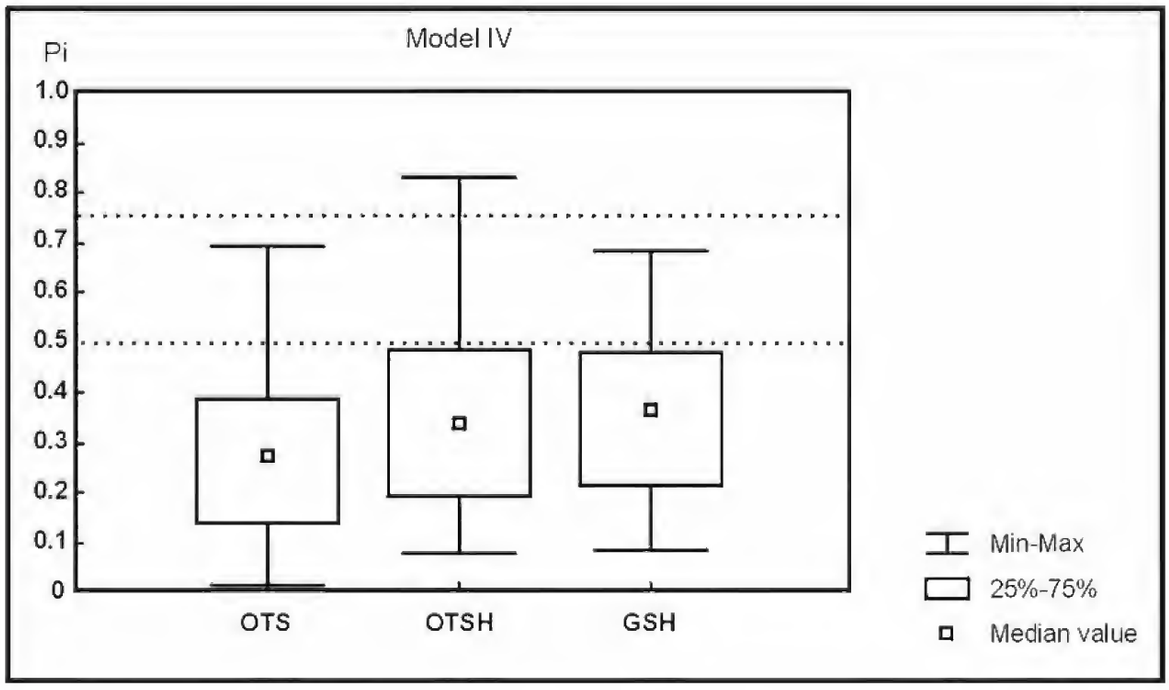

Fig.5- Distribution of the probabilities of occurrence (PiZYG) of *Zygodontomys brevicauda* in classes of habitats (Model IV). Abbreviation of the classes of habitat according to table 2.

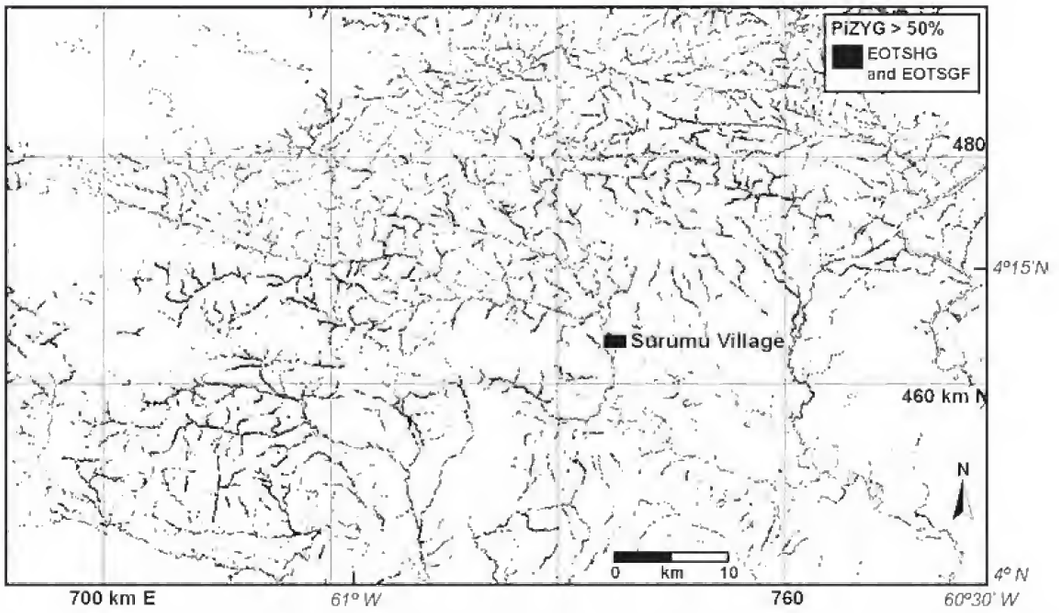

Fig.6- Occurrence-probability map for *Zygodontomys brevicauda* in the Upper and Middle Surumu River region, Roraima, Brazil. EOTSGF (Edge of Open Tree Savanna and Gallery Forest) and EOTSHGF (Edge of Open Tree Savanna on Hydromorphic Soils and Gallery Forest) correspond to an occurrence probability zone of over 50% (PiZIG>0.50). Grid shows UTM coordinates.

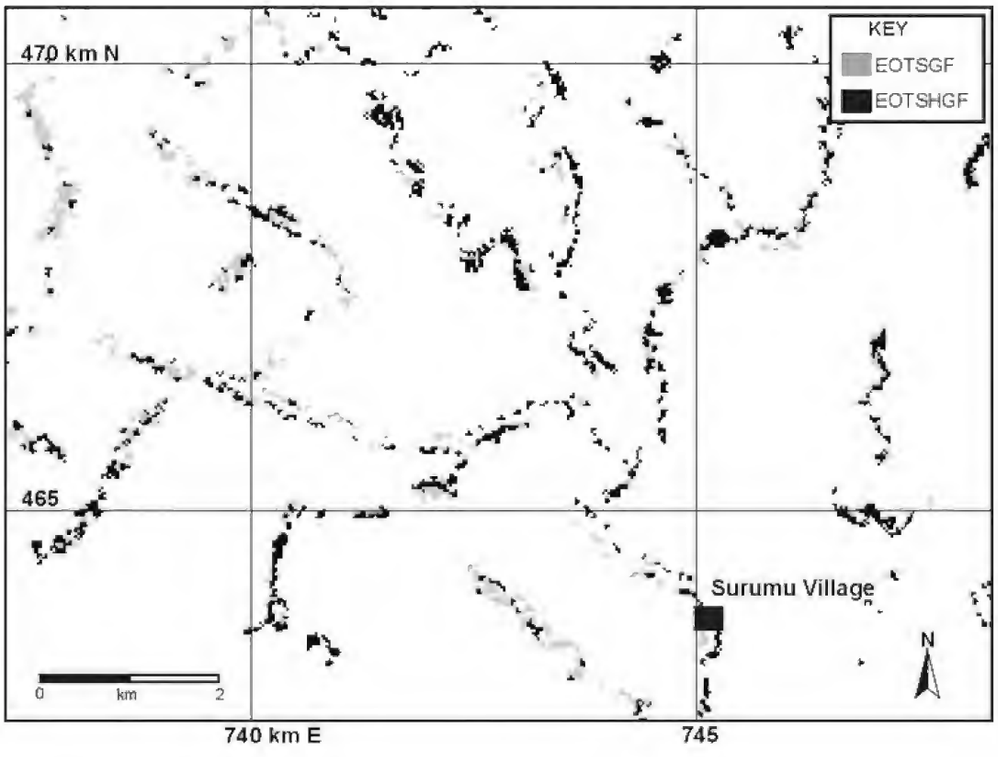

Fig.7- Detail of figure 6: occurrence probability map for *Zygodontomys brevicauda* in the Upper and Middle Surumu River region, Roraima, Brazil – around the Surumu Village. EOTSGF (Edge of Open Tree Savanna and Gallery Forest) corresponds to an occurrence probability zone of 50% (0.75>PiZIG>0.50) and EOTSHGF (Edge of Open Tree Savanna on Hydromorphic Soils and Gallery Forest) to a high probability zone, for occurrence probabilities of over 75% (PiZIG>0.75). Grid featuring UTM coordinates.

Table 3. Regression coefficients (Logistic Regression) of variables and their contribution to prediction of the occurrence of *Zygodontomys brevicauda*.

	χ^2 (df=12) P [a]	β_0 [b]	Structural Variables of Habitats [c]											Concordance Discordance (%) [d]
			FHD100	LIT	RIHERB	HSHRUB	CANHT	CANCV	ROCK	TREEDIS	NUMTREE	GALFDIS	WATDIS	RIROCK	
Model I	21.26	-1.038	0.194	-0.074	-0.058	0.564	0.046	0.237	0.269	0.214	-0.253	-0.321	0.901	-0.871	72.2
	0.005**		0.35	0.77	0.80	0.03**	0.88	0.41	0.25	0.33	0.30	0.28	0.01**	0.00**	27.8
Model II	24.24	-0.814	0.266	-0.099	-0.132	0.671	0.358	0.360	0.250	0.169	-0.415	-0.734	1.5220	-0.522	73.9
	0.019**		0.22	0.68	0.58	0.01**	0.26	0.23	0.42	0.45	0.12	0.06*	0.00**	0.09*	26.1
Model III	25.61	-0.575	0.200	-0.079	-0.244	0.724	0.171	0.267	0.113	0.069	-0.465	-1.142	1.178	-0.542	73.0
	0.012**		0.37	0.76	0.33	0.01**	0.63	0.38	0.66	0.77	0.09*	0.01**	0.01**	0.09*	27.0
Model IV	20.07	-1.344	0.282	-0.560	-0.265	0.659	-0.724	0.573	0.123	0.170	-0.443	-0.751	1.652	-0.595	75.4
	0.066*		0.24	0.26	0.30	0.02**	0.26	0.10*	0.64	0.47	0.13	0.17	0.02**	0.07*	24.6

(') $0.10 \geq P > 0.05$; (**) $P < 0.05$; [a] Chi-Square (χ^2), degree of freedom (df) and significant value (P) for each Model; [b] intersection; [c] regression coefficient of the variables and significant value. Abbreviation of the structural variables shown on table 1; [d] concordance was considered either when estimated capture probabilities, via regression, were over to 0.5 and captures were positive, or when probability was below 0.5 and captures did not occur.

DISCUSSION

Low rates of capture success are common for tropical small mammal communities in savanna areas (O'CONNELL, 1982; AUGUST, 1983; FONSECA & REDFORD, 1984). Poor conditions are usually reflected in low capture success in spite of serious trapping efforts (O'CONNELL, 1982). BARNETT & CUNHA (1998) had a capture success of 1.82% and ascribe it to environmental and zoogeographic features. Density, especially for *Zygodontomys*, could be higher in the beginning of the dry season, decreasing towards its end in consequence of heavy flooding in seasonal habitats. However, population fluctuations are not regular and show strong differences as regards dry seasons of previous years, but density is always higher than that in the wet season (O'CONNELL, 1982). The role of forest-savanna boundaries either in mammal assemblage features or in species distribution in the Neotropics is poorly understood. The dependence of mammal species on forest-savanna boundaries considering the vegetation types, its degree of vagility, and its type of interaction with plants and its size category were studied by MEDELLIN & REDFORD (1992). Restricted distribution along gallery forests, and the importance of contact zones with other habitat types has been stressed for small mammal on savannas of central Brazil (LACHER *et al.,* 2001; MARES *et al.,* 1986; MARES *et al.,* 1989; NITIKMAN & MARES, 1987). A low proportion of species, where observed, associated solely with savannas. We found that *Z. brevicauda*, which is associated with open areas, showed high probability of occurrence in transition areas between both types of Open Tree Savannas and Gallery Forest. This suggests that these areas present mesic conditions when compared to adjoining habitats that may present resource limitation and other local factors related to vegetation cover, setting a lower limit on local density. Such habitats may serve as buffer from environmental fluctuations as drought, high solar incidence, fire and eventually flooding. As density increases, individuals should occupy alternative habitats toward open savannas but these habitat types may be more extreme. Savannas in Roraima feature a dry period (December-March) as well as high solar incidence (BARBOSA, 1997). This may seriously affect small mammal fauna inhabiting open areas, especially in those subject to livestock ranching and seasonal fires. On the other hand, vast areas of savannas are not homogeneous in featuring adequate microhabitats; their availability and spatial

arrangement must determine population viability of small mammals. The terrestrial small mammal captures in the region were mainly related to herbaceous and bushy formations associated with more humid soil. Nevertheless, ecotones make adequate habitats by offering mesic conditions and the viability of the population is at least partially dependent on the savanna-forest boundary. The models show a high frequency of potentially vacant areas, especially in open treeless savannas.

Distribution patterns of species in the region, particularly for *Z. brevicauda*, must be controlled by access to discrete suitable patches in the identified classes. The species may be a colonist of these habitat types where the edges of the Gallery Forest act as source habitats for open savannas. Patches of microhabitat, not shown on the studied scale, and found within classes of tree and herbaceous savannas could be important elements for population viability. Vacant habitats and microhabitats, either those of ephemeral or temporally unstable conditions, may be a feature of the region and extensive temporary empty areas may be a special characteristic of grasslands of northern Amazon. This can be an important aspect in the seasonal dynamics of small mammal fauna of northern Brazil. Additionally, forest-savanna complexes are being altered by cattle grazing and agriculture, and may qualitatively and quantitatively set new levels for the viability of components of the fauna in this poorly known region.

ACKNOWLEDGEMENTS

We thank Reinaldo I. Barbosa (Instituto Nacional de Pesquisas da Amazônia - INPA, Boa Vista, RR), for the logistic support and for assistance in accessing the study region. We thank the Geoprocessing Laboratory, Department of Ecology, Universidade Federal do Rio Grande do Sul, Brazil, in particular Prof. Heinrich Hasenack. To Andrea P. Nunes (Museu Goeldi), for measuring the habitat-structure variables, and to Tânia Sanaiotti (INPA, Manaus, AM), for the suggestions regarding the identification of the classes of vegetation. We are grateful to all the participants in the field survey, especially to Fernanda Trierveiler (Porto Alegre, RS), Carlos A. Caetano (Museu Nacional, Rio de Janeiro – MN), and Sérgio M. Vaz (MN), who provided assistance in collection of specimens. We thank Ulisses Caramaschi, Helianne de Niemeyer, and Décio F. de Moraes Jr. (MN), for their collaboration in field work. We thank Danielle Crawshaw (Porto Alegre, RS) and Maria Elaine A. de Oliveira (Universidade Federal Fluminense), for helpful comments on the manuscript. We are indebted to C.E.R.Schaefer (Universidade Federal de Viçosa) and J.Agostinho (Boa Vista, RR) for valuable information about the study region. Finally, we would like to express our deepest thanks to Margarete Mattevi (Universidade Federal do Rio Grande do Sul), for her continuing kindness and enthusiasm on the survey of small mammal faunas. This research was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (Grants number 400641/97-6, and 302663/2003-7).

LITERATURE CITED

AUGUST, P., 1983. The role of habitat complexity and heterogeneity in structuring tropical mammal communities. **Ecology**, Washington, **64**:1494-1507.

BARBOSA, R.I., 1997. Distribuição das chuvas em Roraima. In: BARBOSA, R.I.; FERREIRA, E.J.G. & CASTELLÓN, E.G. (Eds.) **Homem, Ambiente e Ecologia no Estado de Roraima**. Manaus: INPA. p.325-335.

BARNETT, A.A. & CUNHA, C.A., 1998. Small mammals of Ilha de Maracá. In: MILLIKEN, W. & RATTER, J. (Eds.) **Maracá: The Biodiversity and Enviroment of an Amazonian Rainforest**. Chichester: John Wiley & Sons Ltd. p.189-210.

COLINVAUX, P.A., 1987. Environmental history of the Amazon Basin. **Quaternary of South America and Antarctic Peninsula**, Rotterdam, **5**:223-237.

DESJARDINS, T.; CARNEIRO FILHO, A.C.; MARIOTTI, A.; CHAUVEL, A. & GIRARDIN, C., 1996. Changes of the forest-savanna boundary in Brazilian Amazonia during the Holocene revealed by stable isotope ratios of soil organic carbon. **Oecologia**, Heidelberg, **108**:749-756.

DESJARDINS, T.; CARNEIRO FILHO, A. & CHAUVEL, A., 1997. Flutuação do limite floresta-cerrado durante o holoceno em Roraima. In: BARBOSA, R.I.; FERREIRA, E.J.G, & CASTELLÓN, E.G. (Eds.) **Homem, Ambiente e Ecologia no Estado de Roraima**. Manaus, INPA. p.307-323.

EASTMAN, J.R., 1997. IDRISI for Windows v.2.0 user's guide. Worcester: Clark University.

EITEN, G., 1978. Delimitatons of the cerrado concept. **Vegetatio**, Den Haag, **36**:169-178.

EITEN, G., 1982. Brazilian "Savanas". In: HUNTLEY, B.J. & WALKERS, B.H. (Eds.) **Ecology of Tropical Savannas**. New York: Springer Verlag. p.25-47.

FONSECA, H. & REDFORD, K.W., 1984. The mammals of IBGE's Ecological Reserve, Brasilia, and an analysis of the role of gallery forest in increasing diversity. **Revista Brasileira de Biologia**, Rio de Janeiro, **44**:517-523.

HAFFER, J., 1987. Biogeography of Neotropical birds. In: WHITMORE, T.C. & PRANCE, G.T. (Eds.) **Biogeography and Quaternary History in Tropical America**. Oxford: Clarendon Press. p.105-150.

HAGAN, J.E., 1998. **Cartalinks: the Spatial Data Builder user's guide**. Worcester: Clark University.

HAMMOND, D.S. & STEEGE, H.T., 1998. Propensity for fire in Guianan Rainforest. **Conservation Biology**, Malden, **12**(5):951-953.

HANDLEY, C.O., JR. & KALKO, E.K.V., 1993. A short history of small mammal pitfall trapping. **Virginia Journal of Science**, Richmond, **44**:19-26.

HUECK, K. & SEIBERT, P., 1981. **Vegetationskarte von Südamerika**. Stuttgart: Gustav Fischer Verlag. 90p.

IBGE, 1980. Folhas NB.20-Z-D-V MI14 (Vila Pereira) e NB.20_Z-D-IV/I MI-13/3 (Rio Ereu) em escala 1:100.000. Cobertura aérea de 1980 da Secretaria de Planejamento da Presidência da República. Instituto Brasileiro de Geografia e Estatística.

LACHER, T.E., JR. & ALHO, C.J.R., 2001. Terrestrial small mammal richness and habitat associations in an Amazonian-Cerrado contact zone. **Biotropica**, Lawrence, **33**:171-181.

MARES, M.A.; BRAUN, J.K. & GETTINGER, D.D., 1989. Observations on the distribution and ecology of the mammals of Cerrado grasslands of central Brazil. **Annals of Carnegie Museum**, Pittsburgh, **58**:1-60.

MARES, M.A.; ERNEST, K.A. & GETTINGER, D.D., 1986. Small mammal community structure and composition in the Cerrado Province of central Brazil. **Journal of Tropical Ecology**, New York, **2**:289-300.

MARROIG, G. & CERQUEIRA, R., 1997. Plio-Pleistocene South American history and the Amazon lagoon hypothesis: a piece in the puzzle of amazonian diversification. **Journal of Comparative Biology**, Ribeirão Preto, **2**(2):103-119.

MATTEVI, M.S.; HAAG, A.P.; NUNES, A.P.; OLIVEIRA, L.F.B.; CORDEIRO, J.L.P. & ANDRADES-MIRANDA, J., 2002. Karyotypes of Brazilian representatives of genus *Zygodontomys* (Rodentia, Sigmodontinae). **Mastozoología Neotropical**, Tucumán, **9**(1):33-38.

McCOY, E.D. & BELL, S.S., 1991. Habitat structure: the evolution and diversification of a complex topic. In: BELL, S.S.; McCOY, E.D. & MUSHINSKY, H.R. (Eds.) **Habitat Structure. The Physical Arrangement of Objects in Space**, London: Chapman and Hall. p.3-27.

MEDELLIN, R.A. & REDFORD, K.H., 1992. The role of mammals in neotropical forest-savanna boundaries. In: FURLEY, P.A.; PROCTOR, J. & RATTER, J.A. (Eds.) **Nature and Dynamics of Forest-Savanna Boundaries**. London: Chapman & Hall. p.519-548.

MIRANDA, I.S. & ABSY, M.L., 1997. A flora fanerogâmica das savanas de Roraima. In: BARBOSA, R.I.; FERREIRA, E.J.G. & CASTELLÓN, E.G. (Eds.) **Homem, Ambiente e Ecologia no Estado de Roraima**. Manaus: INPA. p.445-454.

MÜLLER, P., 1973. **The Dispersal Centers of Terrestrial Vertebrates in the Neotropical Realm. A Study in the Evolution of the Neotropical Biota and its Native Landscapes**. The Hague: Dr. W. Junk B.V. Publishers. 244p.

MUNGER, J.C.; GERBER, M.; MADRID, K.; CARROLL, M-A.; PETERSEN, W. & HEBERGER, L., 1998. U. S. National Wetland Inventory Classications as predictors of the occurrence of Columbia spotted frogs (*Rana luteiventris*) and Pacific treefrogs (*Hyla regilla*). **Conservation Biology**, Malden, **12**(2):320-330.

NEPSTADT, D.C.; KLINK, C.A.; UHL, C.; VIEIRA, I.C.; LEFEBVRE, P.; PEDLOWSKI, M.; MATRICARDI, E.; NEGREIROS, G.; BROWN, I.F.; AMARAL, E.; HOMMA, A. & WALKER, R., 1997. Land-use in Amazonia and Cerrado of Brazil. **Ciência e Cultura,** Rio de Janeiro, **49**(1/2):73-86.

NITIKMAN, L.Z. & MARES, M.A., 1987. Ecology of small mammals in a gallery forest of central Brazil. **Annals of Carnegie Museum**, Pittsburgh, **56**:75-95.

NOWAK, R.M., 1999. **Walker's Mammals of the World** – 6th ed. Vol. II. Baltimore: The Johns Hopkins University Press. 1936p.

NUNES, A., 2001. **Gradientes estruturais dos hábitats em savanas amazônicas: implicações sobre a distribuição e ocorrência das espécies de pequenos mamíferos terrestres (Rodentia, Didelphimorphia)**. Rio de Janeiro. 224p. Tese (Doutorado em Ciências Biológicas), Programa de Pós-Graduação em Zoologia, Museu Nacional, Universidade Federal do Rio de Janeiro.

O'CONNELL, M.A., 1982. Population biology of North and South American grassland rodents: a comparative review. In: MARES M.A. & GENOWAYS, H.H. (Eds.) **Mammalian Biology in South America**. Pittsburgh: Special Publications Series, Pymatuning Laboratory, University of Pittsburgh. p.167-185.

OLIVEIRA, L.F.B., 1990. **The tole of habitat structural gradients on the distribution of small rodents in the South Brazilian restinga (Mammalia, Rodentia, Cricetidae)**. Saarbrücken, Germany. 213p. Thesis (Ph.D. Biogeography), Universität des Saarlandes.

RADAMBRASIL, 1975. Projeto Radambrasil - Levantamento dos Recursos Naturais; Vol.8. Folha NA.20 Boa Vista, e parte das Folhas NA.21, NB.20 e NB.21. Ministério das Minas e Energia, Rio de Janeiro.

RATTER, J.A.; RIBEIRO, J.F. & BRIDGEWATER, S., 1997. The Brazilian Cerrado vegetation and threats to its biodiversity. **Annals of Botany,** London, **80**:223-230.

ROSENZWEIG, M.L. & WINAKUR, J., 1969. Population ecology of desert rodent communities: habitat and environmental complexity. **Ecology**, Washington, **50**(4):558-572.

SANAIOTTI, T.M., 1997. Comparação fitossociológica de quatro savanas de Roraima. In: BARBOSA, R.I.; FERREIRA, E.J.G. & CASTELLÓN, E.G. (Eds.) **Homem, Ambiente e Ecologia no Estado de Roraima**. Manaus: INPA, p.481-488.

SCHAEFER, C.E.R. & JÚNIOR, J.F.V., 1997. Mudanças climáticas e evolução da paisagem em Roraima: uma resenha do Cretáceo ao Recente. In: BARBOSA, R.I.; FERREIRA, E.J.G. & CASTELLÓN, E.G. (Eds.) **Homem, Ambiente e Ecologia no Estado de Roraima**. Manaus: INPA. p.231-265.

SCOTT, J.M.; DAVIS, F.; CSUTI, B.; NOSS, R.; BUTTERFIELD, B.; GROVES, C.; ANDERSON, H.; CAICCO, S.; D'ERCHIA, F.; EDWARDS, T.C., Jr.; ULLIMAN, J. & WRIGHT, R.G., 1993. GAP analysis: a geographic approach to protection of biological diversity. **Wildlife Monographs**, Bethesda, **123**:1-41.

SILVA, J.M.C., 1995. Biogeographic analysis of the South American Cerrado avifauna. **Steenstrupia**, Copenhagen, **21**:49-67.

SILVA, E.L.S., 1997. A vegetação de Roraima. In: BARBOSA, R.I.; FERREIRA, E.J.G. & CASTELLÓN, E.G. (Eds.) **Homem, Ambiente e Ecologia no Estado de Roraima**. Manaus: INPA. p.401-415.

STATISTICA, 1999. Statistica for Windows 5.5. Statsoft, Tulsa, Oklahoma.

STOTT, P., 1991. Recent trends in the ecology and management of the world's savanna formations. **Progress in Physical Geography**, London, **15**:18-28.

VOSS, R.S., 1991. An introduction to the Neotropical muroid rodent genus *Zygodontomys*. **Bulletin of the American Museum of Natural History**, New York, **230**:1-113.

WHITMORE, T.C. & PRANCE, G.T., 1987. **Biogeography and Quaternary History in Tropical America**. Oxford: Clarendon Press. 214p.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.63-74, jan./mar.2005
ISSN 0365-4508

MORPHOMETRIC DIFFERENTIATION AND DISTRIBUTIONAL NOTES OF THREE SPECIES OF *AKODON* (MURIDAE, SIGMODONTINAE, AKODONTINI) IN THE ATLANTIC COASTAL AREA OF BRAZIL [1]

(With 3 figures)

LENA GEISE [2, 3]
DIEGO ASTÚA DE MORAES [2]
HARLEY SEBASTIÃO DA SILVA [4, 5]

ABSTRACT: Twenty cranial measurements and three body variables were compared among samples of three species of the genus *Akodon* previously identified by karyotype, using univariate (ANOVAs) and multivariate (Discriminant analyses) methods. A geographic analysis for *A. montensis* and *A. cursor* from localities in the State of Rio de Janeiro and adjacent areas was also performed. *Akodon montensis* presented smaller values for most cranial measurements, whereas *A.* aff. *cursor* showed larger values, with *A. cursor* showing intermediate cranial size. The discriminant analysis revealed a clear separation of *A.* aff. *cursor* from *A. cursor*, while all other pair of species presented partial overlap. All *A.* aff. *cursor* and most *A. cursor* were correctly classified, but classification of the *A. montensis* sample was less successful, probably due to the greater size or to the size-related variation in cranial shape of some older specimens. In the studied area, *A. montensis* was exclusively collected in altitudes higher than 800m above sea level, whereas *A. cursor* was found from sea level to altitudes above 1000m. ANOVAs showed one significantly different climatic variable, suggesting some segregation between these two species. Correct classification based solely on the discriminant function extracted on the basis of the present samples could not be fully achieved, although our results suggest that larger samples of kariotypically identified specimens will allow more conclusive patterns on the morphometric differentiation of these taxa.

Key words: Rodentia, biogeography, Atlantic Forest, morphometrics, distribution.

RESUMO: Diferenciação morfométrica e notas sobre a distribuição de três espécies de *Akodon* (Muridae, Sigmodontinae, Akodontini) na área costeira atlântica do Brasil.

Vinte medidas cranianas e três variáveis corpóreas foram comparadas entre amostras de três espécies do gênero *Akodon* previamente identificadas por cariótipo, através de análises de variância e análise discriminante. Uma análise geográfica para *A. montensis* e *A. cursor* foi conduzida para amostras de localidades do Estado do Rio de Janeiro e adjacências. *Akodon montensis* apresentou valores menores para a maioria das medidas cranianas e *A.* aff. *cursor* as maiores medidas, com *A. cursor* apresentando um tamanho craniano intermediário. A análise discriminante mostrou uma separação clara de *A.* aff. *cursor* e *A. cursor*, enquanto que os demais pares de espécies se sobrepuseram parcialmente. Todos os exemplares de *A.* aff. *cursor* e a maioria dos de *A. cursor* foram corretamente classificados, mas a classificação da amostra de *A. montensis* apresentou resultados menos satisfatórios, possivelmente relacionados ao tamanho maior ou à variação na forma craniana relacionada ao tamanho em alguns espécimens mais velhos. Na área estudada, *A. montensis* foi coletado exclusivamente em altitudes superiores a 800m acima do nível do mar, ao passo que *A. cursor* foi encontrado do nível do mar até altitudes acima de 1000m. As ANOVAs evidenciaram uma variável climática significativamente diferente, sugerindo alguma segregação entre estas duas espécies. Uma classificação correta baseada somente na função discriminante revelada pelas amostras analisadas aqui não pôde ser obtida, mas as tendências na estruturação da variação morfométrica entre as amostras de espécimens sugerem que com amostras maiores será possível obter padrões mais conclusivos sobre a diferenciação morfométrica destes táxons.

Palavras-chave: Rodentia, biogeografia, Floresta Atlântica, morfometria, distribuição.

[1] Submitted on June 14, 2004. Accepted on January 31, 2005.
[2] Universidade do Estado do Rio de Janeiro, Instituto de Biologia, Departamento de Zoologia, Laboratório de Zoologia de Vertebrados - Mastozoologia. Rua São Francisco Xavier, 524, Maracanã, 20550-900, Rio de Janeiro, RJ, Brasil.
[3] Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico - CNPq. E-mail: geise@uerj.br.
[4] Museu Nacional/UFRJ, Programa de Pós-graduação em Ciências Biológicas (Zoologia). Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil.
Fellow of Coordenação de Aperfeiçoamento Pessoal de Ensino Superior (CAPES).
[5] Universidade Federal do Rio de Janeiro, Instituto de Biologia, Departamento de Ecologia, Laboratório de Vertebrados. Av. Brigadeiro Trompovsky, s/nº, 21941-590, Ilha do Fundão, Rio de Janeiro, RJ, Brasil.

INTRODUCTION

Among the highly diverse sigmodontine rodents, some genera in the Atlantic Forest include cryptic species, whose correct identification can only be assessed with the use of genetic techniques. For example, specimens of *Brucepattersonius* Hershkovitz, 1998 (a recently described akodont genus including several cryptic species) with similar morphological and karyological features could only be differentiated through the analysis of mitochondrial DNA (SMITH & PATTON, 1993). Similarly, the genus *Akodon* Meyen, 1833, also does not present well defined species boundaries as determined by classical morphological characters, although it represents one of the most speciose genera within the Akodontini tribe (SMITH & PATTON, 1993), with 45 recognized species (MUSSER & CARLETON, 1993). Such morphological similarity between two or more congeneric species reduce the usefulness of previously collected specimens that did not happen to be identified by genetic tools.

Among species of the genus *Akodon* usually trapped in the Atlantic coastal area of Brazil, three of them, *Akodon montensis* (Thomas, 1913), *A. cursor* (Winge, 1888), and *A.* aff. *cursor* are morphologically so similar that a precise diagnosis based solely on morphometric characters is not always possible (GEISE, WEKSLER & BONVICINO, 2004). The two former species were grouped together in the so-called *cursor* complex (LIASCOVICH & REIG, 1989), in which GEISE, SMITH & PATTON (2001) also include *A.* aff. *cursor* and another yet undescribed species studied by SILVA & YONENAGA-YASSUDA (1998). Maximum parsimony and neighbor joining analyses of mtDNA sequences with bootstrap values of 62% and 79% respectively showed that *A.* aff. *cursor* form a distinct monophyletic clade (GEISE, SMITH & PATTON, 2001).

The specific status of these species is well defined on a genetic basis, based both on karyological (GEISE, CANAVEZ & SEUÁNEZ, 1998; CHRISTOFF, 1997) and molecular (mitochondrial DNA) data (D´ÉLIA, GONZÁLEZ & PARDIÑAS, 2003; GEISE, SMITH & PATTON, 2001). An analysis of the occurrence of the gall bladder performed among 15 Akodontini species allowed a complete discrimination of two of those species, *A. cursor* and *A. montensis* (GEISE, WEKSLER & BONVICINO, 2004).

The species studied here range from Argentina (D´ÉLIA, GONZÁLEZ & PARDIÑAS, 2003) to the Northeastern coastal area of Brazil (MAIA & LANGGUTH, 1981). Empirical collecting data using only specimens identified through complementary techniques shows differentiation in the geographic range and preference of habitats, with *A. cursor* occurring between 15°17'S to 25°28'S and 39°00'W to 48°49'W, and *A. montensis* from 19°38'S to 30°14'S and 42°08'W to 59°18'W (SILVA, 2001). Some altitudinal differentiation was suggested in part of their geographic distribution (Rio de Janeiro State), where *A. cursor* was observed from sea level to localities upon *ca.* 800m. In altitudes greater than that only *A. montensis* was collected, together with other species, such as *A. reigi* González, Langguth & Oliveira, 1998 and *A. serrensis* Thomas, 1902 (GEISE, 1995; GEISE, WEKSLER & BONVICINO, 2004).

In this paper we analyze the morphometric differentiation between the cryptic species *Akodon montensis*, *A. cursor* and *A.* aff. *cursor*, using individuals captured in a wide range of their known distribution. The purpose of this analysis was to determine if these three cryptic species could be diagnosed on morphometric grounds, using only specimens which had their identification confirmed by karyotypic data. Since some altitudinal differentiation among *A. montensis* and *A. cursor* was formerly observed by GEISE (1995), a detailed analysis of collecting localities was also performed in order to elucidate how these species segregate according to climatological and altitudinal data. Our study is aimed to clarify the identities and altitudinal distributions of these three species.

MATERIAL AND METHODS

Specimens were collected with live-traps. Chromosomes were obtained directly from bone marrow as described by FORD & HAMERTON (1956) or obtained from bone marrow cultures with cells cultured in MEM Dulbecco's medium. Skins and skulls for all specimens were prepared following standard procedures (*e.g.* WILSON *et al.*, 1996). The data set was complemented with specimens deposited in museums only when karyological information was available (Appendix).

Twenty cranial measurements were obtained with a digital caliper: condylo-incisive length (CIL), breadth between occipital condyles (BOC), length of diastema (LDI), length of palatal bridge (LPB), length (LIF) and breadth of incisive foramina (BIF), length of maxillary molar row (LMR), breadth of upper first molar (BFM), breadth

across molars (BAM), length of bulla (LBU), height of skull, measured posteriorly to the border of third molar and orthogonal to skull length (HSK), length of the rostrum, measured from the internal border of the anterorbital bridge of maxillary to the nasal tip (LRO), rostrum width (ROW), least interorbital width (LIW), orbital internal length, measured between the internal borders of the anterorbital bridge of maxillary and of the squamosal process of zygomatic arch (OIL), zygomatic breadth (ZIB), breadth of braincase (BBR), breadth of zygomatic plate (BZP), height of mandible, measured across the angular and condyloid processes (HMA), length of mandible, measured from the incisive basis to the condyloid process (LMA) (Fig.1). Age classes were determined according to molar teeth wear (CERQUEIRA *et al.*, 1989), and only adult specimens were considered for statistical analyses. Additionally, body length (BL), tail length (TL) and body weight (W) were also compared between taxa.

Sexual dimorphism within each species was assessed through t-tests for each measurement, using Bonferroni corrected p-values (á = 0.05/20 = 0.0025). In order to evaluate whether specific traits could be used as morphometric diagnostic characters, all measurements were compared among the three species through Analyses of Variance (ANOVAs), using the same Bonferroni corrected p-values as above, and followed by Tukey post-hoc comparisons tests. Finally, a Discriminant Analysis was conducted to determine the amount of multivariate differentiation among the three species.

Collecting localities for *A. montensis* and *A. cursor* in the State of Rio de Janeiro and in adjacent regions in the states of São Paulo and Minas Gerais were analyzed with respect to altitude and nine climatic variables: annual mean temperature (AMT), annual minimum mean temperature (MMT), annual maximum mean temperature (MXT), annual minimum absolute temperature (MBT), annual maximum absolute temperature (MAT), annual total precipitation (PRC), annual total cloudiness (CLD), annual relative humidity (HUM), and annual rainy days (RAI), to investigate the existence of patterns of altitudinal and climatic segregation in the distribution of these taxa. Climatic variables among collecting localities were compared with Analyses of Variance (ANOVAs) for each variable, using Bonferroni corrected p-values (á = 0.05/9 = 0.006).

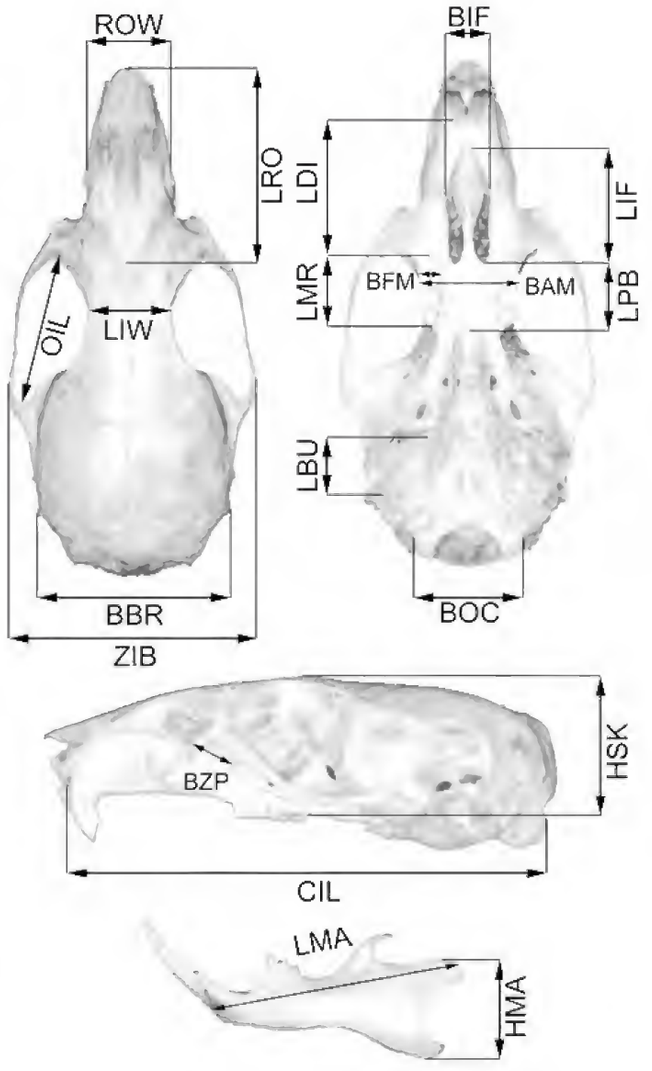

Fig.1- Cranial measurements used in this study. Refer to text for measurement definitions and acronyms.

RESULTS

The total sample sizes for each species and sex, along with their respective means and standard deviations are presented in table 1.

Sexual dimorphism was found in 14 out of 20 measurements for both *A. cursor* and *A. montensis* (Tab.1), with males larger than females for all skull traits, while no sexual dimorphism could be detected for *A.* aff. *cursor*. The interaction between sex and species was evaluated in a Multivariate Analysis of Variance with all measurements, testing for sex, species, and sex*species effects. Since no significant sex*species effect was detected (*i.e.*, the direction of the dimorphism is the same in all species and

measurements), the effect of sex differences was removed by adding the mean difference for each measurement to the females values. Sexes were then pooled for all subsequent analyses, which were carried out on these transformed values.

The ANOVAs revealed significant differences among species in all of the 20 cranial and mandibular measurements (Tab.2), as well as in body measurements and weight. In all cases *A. montensis* was significantly smaller than either *A. cursor* or

Table 1. Descriptive statistics – mean ± standard deviation (sample size) – of the 20 cranial measurement for each species and sex separately.

	A. aff. *cursor*		*A. cursor*		*A. montensis*	
	♂	♀	♂	♀	♂	♀
CCBA	28.57±0.93 (5)	27.66±1.43 (15)	28.20±1.20 (114)*	27.18±1.17 (94)	27.15±1.06 (52) *	25.71±1.21 (39)
LCON	6.90±0.16 (5)	6.69±0.31 (15)	6.89±0.24 (118)	6.82±0.27 (94)	6.49±0.22 (50)	6.35±0.21 (39)
DIAS	8.40±0.51 (6)	8.07±0.54 (15)	8.26±0.52 (117) *	7.92±0.50 (95)	7.98±0.49 (52) *	7.52±0.53 (40)
PPAL	4.08±0.15 (6)	4.08±0.37 (15)	4.25±0.28 (117)	4.18±0.31 (95)	3.79±0.30 (52) *	3.61±0.24 (39)
CFIN	6.96±0.58 (6)	6.60±0.57 (15)	6.46±0.41 (117) *	6.27±0.39 (95)	6.42±0.43 (52)	6.13±0.51 (39)
LFIN	2.28±0.18 (6)	2.24±0.19 (15)	2.41±0.20 (118) *	2.28±0.17 (95)	2.30±0.18 (52) *	2.17±0.14 (40)
SMOS	4.66±0.20 (6)	4.64±0.13 (15)	4.46±0.16 (119)	4.45±0.18 (95)	4.25±0.16 (51)	4.21±0.20 (40)
LM01	1.31±0.06 (6)	1.33±0.06 (15)	1.30±0.08 (118)	1.29±0.07 (95)	1.23±0.07 (52)	1.20±0.06 (40)
M1M1	6.02±0.32 (6)	5.93±0.27 (15)	5.97±0.34 (118)	5.87±0.31 (95)	5.67±0.29 (52) *	5.42±0.27 (40)
CBUL	5.12±0.24 (6)	5.10±0.26 (15)	4.69±0.27 (114)	4.70±0.27 (90)	4.89±0.30 (52)	4.83±0.23 (40)
ACRA	8.61±0.36 (6)	8.41±0.32 (15)	8.68±0.26 (119) *	8.49±0.29 (95)	8.26±0.32 (52) *	7.99±0.26 (40)
CROS	12.45±0.57 (6)	11.72±0.88 (15)	11.55±0.56 (118) *	11.20±0.57 (93)	11.49±0.58 (52) *	10.99±0.67 (39)
LROS	5.56±0.17 (6)	5.26±0.27 (15)	5.61±0.38 (117) *	5.28±0.37 (93)	5.24±0.40 (52) *	4.87±0.31 (39)
LCIN	5.30±0.21 (6)	5.22±0.23 (15)	5.40±0.19 (119) *	5.30±0.19 (95)	5.08±0.24 (52)	4.95±0.19 (40)
CORB	9.78±0.62 (6)	9.53±0.49 (15)	9.79±0.43 (119) *	9.44±0.41 (94)	9.28±0.34 (52) *	8.86±0.31 (39)
LZIG	15.49±0.54 (5)	15.07±0.45 (11)	15.69±0.56 (108) *	15.11±0.64 (85)	14.48±0.66 (44) *	13.82±0.51 (32)
LCCR	12.29±0.46 (6)	11.93±0.33 (15)	12.30±0.45 (111) *	12.07±0.49 (92)	11.89±0.41 (51) *	11.48±0.39 (40)
LPZI	2.94±0.14 (6)	3.01±0.32 (15)	3.06±0.25 (119) *	2.92±0.28 (94)	2.72±0.26 (52) *	2.55±0.22 (40)
AMAN	6.97±0.34 (6)	6.62±0.43 (15)	6.73±0.39 (114) *	6.53±0.33 (89)	6.27±0.37 (52) *	5.97±0.40 (39)
CMAN	15.45±0.82 (6)	15.12±0.89 (14)	15.19±0.73 (116) *	14.73±0.66 (93)	14.38±0.71 (52) *	13.67±0.69 (39)
BL	122.83±6.05 (6)	117.80±11.77 (15)	121.60±9.29 (106)	117.33±9.04 (91)	115.21±8.13 (46)	108.83±11.10 (38)
TL	101.83±7.28 (6)	93.87±10.29 (15)	93.53±10.62 (99)	90.44±7.56 (82)	93.01±10.13 (48)	88.41±8.44 (35)
W	57.00±6.16 (6)	45.67±12.09 (15)	53.19±11.45 (105)	45.23±10.64 (84)	43.31±11.14 (48)	36.43±12.83 (35)

(*) significant differences between sexes from t-tests, at the Bonferroni-corrected p level of 0.0025. Refer to text for measurements acronyms. Cranial and body measurements in mm, weight in g.

A. aff. *cursor*, or than both. In those cases in which significant differences were found between *A. cursor* and *A.* aff *cursor*, the former presented larger values. Therefore, an overall size gradient exists between these three species, with *A.* aff. *cursor* being the largest (*A.* aff. *cursor* is larger than *A. cursor* in seven out of 20 cranial variables and tail length, and larger than *A. montensis* in 19 out of 20 cranial and all body variables), followed by *A. cursor* (which is larger than *A. montensis* in 17 out of 20 variables, and in body length and weight), and finally by *A. montensis* (Tabs.1 and 2).

The Discriminant Function was significant (Wilks' lambda = 0.1338, $p < 0.001$). Ordination of the specimens along the two Canonical Axes is shown in figure 2, and both the Standard and Jacknifed classification matrices are presented in tables 3-4. None of the two canonical axes provide complete separation between any of the three groups (Fig.2). However, there is no overlap between specimens of *A.* aff. *cursor* and *A. cursor* along a combination of the two functions, while the former overlap with the *A. montensis* sample along both axes. Samples of *A. cursor* and *A. montensis* overlap partially, indicating that there is some morphometric differentiation between these two species, as could be seen in the univariate analyses. Most of the overlap observed between the *A. montensis* and the two other samples is due to a few *A. montensis* specimens, most of them misclassified, which consisted of old specimens (age class 6).

Table 2. Results of the Analyses of Variance among the three species. All ANOVAs were found significant at the Bonferroni-corrected p level of 0.0025.

Measurement	Significant pairwise differences Tukey post-hoc tests		
CIL		afc-mon	cur-mon
BOC		afc-mon	cur-mon
LDI		afc-mon	cur-mon
LPB	afc-cur	afc-mon	cur-mon
LIF	afc-cur	afc-mon	
BIF	afc-cur		
LMR	afc-cur	afc-mon	cur-mon
BFM		afc-mon	cur-mon
BAM		afc-mon	cur-mon
LBU	afc-cur	afc-mon	cur-mon
HSK		afc-mon	cur-mon
LRO	afc-cur	afc-mon	
ROW		afc-mon	cur-mon
LIL		afc-mon	cur-mon
OIL		afc-mon	cur-mon
ZIB		afc-mon	cur-mon
BBR		afc-mon	cur-mon
BZP	afc-cur	afc-mon	cur-mon
HMA		afc-mon	cur-mon
LMA		afc-mon	cur-mon
BL		afc-mon	cur-mon
TL	afc-cur	afc-mon	
W		afc-mon	cur-mon

Significantly different pairs of species (as determined by the Tukey post-hoc tests) are indicated (afc) *Akodon* aff. *cursor*; (cur) *A. cursor*; (mon) *A. montensis*. Refer to text for measurements acronyms.

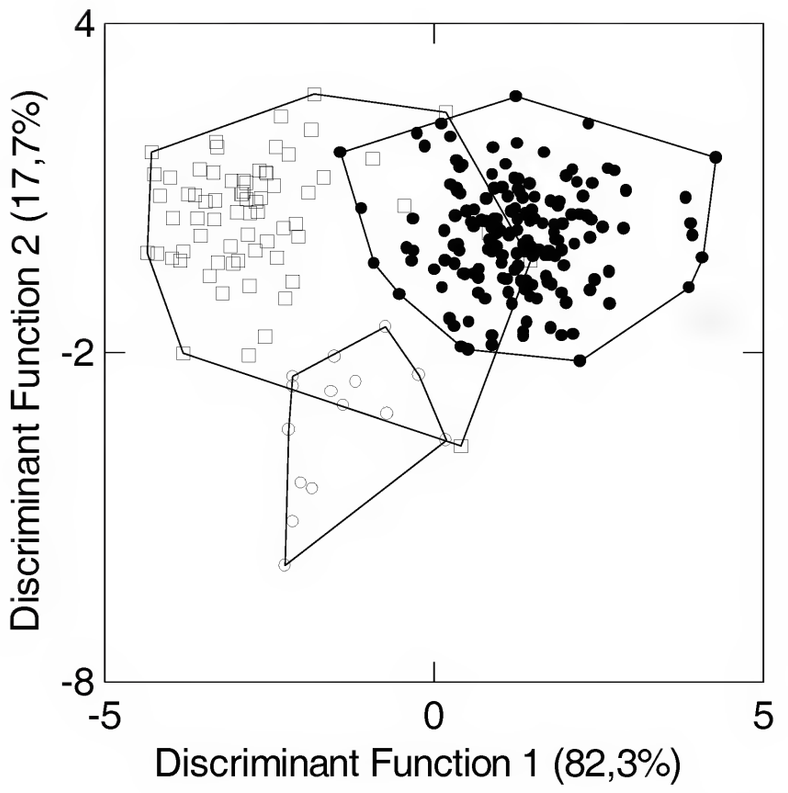

Fig.2- Plot of the Canonical scores extracted from the discriminant analyses, and percentages of total variance explained by the two functions. (○) *Akodon* aff. *cursor*, (●) *Akodon cursor*, (□) *Akodon montensis*.

Table 3. Classification matrix determined by the discriminant function.

Species	Predicted group membership			
	A. aff. *cursor*	*A. cursor*	*A. montensis*	% correct
A. aff. *cursor*	15	0	0	100
A. cursor	0	163	3	98
A. montensis	4	4	62	89
Total	19	167	65	96

The percentage of overall correctly classified specimens was 96%. The percentage of correctly classified specimens was better for both *A.* aff. *cursor* and *A. cursor*, with all specimens correctly classified for the former and 98% for the latter (Tab.3). *Akodon montensis* also presented an elevated amount of correctly classified individuals (89%), with a few specimens being erroneously classified. As expected, the amounts of correctly classified specimens are slightly lower in the jacknifed classification matrix (Tab.4), but these results are consistent with the standard matrix, suggesting that the discriminant function determined is good. The greater reduction observed in the percentage of correctly classified specimens for *A.* aff. *cursor* is mostly due to its reduced sample size.

In localities from Rio de Janeiro State and its vicinities (Fig.3) *A. montensis* was not found in altitudes below 800m above sea level and *A. cursor* was found from sea level to altitudes above 1000m. The ANOVAs showed that only one climatic variable is significantly different, namely annual mean temperature (p=0.004), suggesting some segregation between these two species (Tab.5).

Table 4. Jackknifed classification matrix determined by the discriminant function.

SPECIES	PREDICTED GROUP MEMBERSHIP			
	A. aff. *cursor*	*A. cursor*	*A. montensis*	% correct
A. aff. *cursor*	12	2	1	80
A. cursor	2	160	4	96
A. montensis	4	4	62	89
Total	18	166	67	93

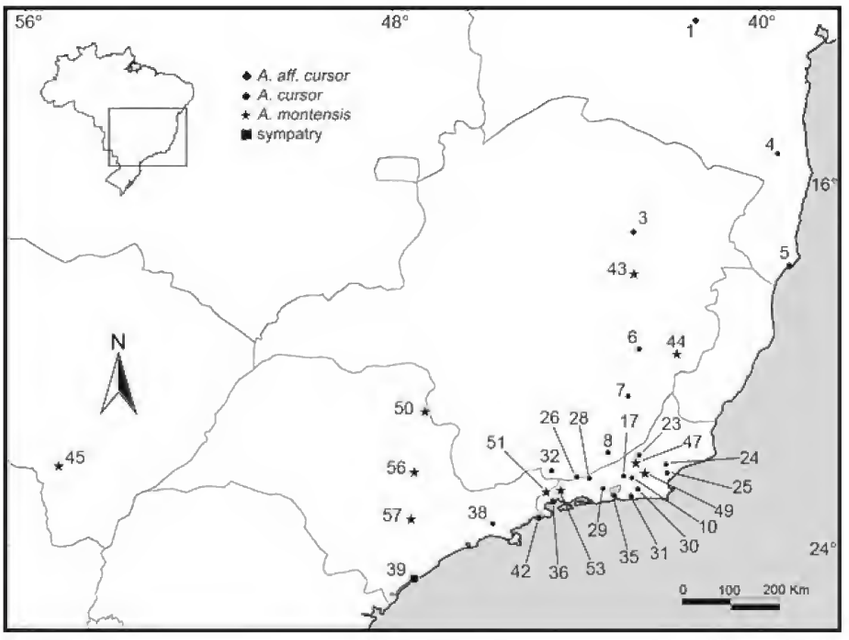

Fig.3- Map with collecting localities numbered according to the appendix. Some localities presented in the map refer to more than one locality listed in the appendix: 1 = 1, 2; 10 = 10 to 16; 17 = 17 to 22, 48; 25 = 25, 27; 32 = 32, 33; 36 = 36, 37; 45 = 45, 56; 53 = 40, 53, 54.

Table 5. ANOVA results for climatic variables between *A. cursor* and *A. montensis*.

VARIABLES	F	p
AMT	9.560	0.004*
MMT	3.510	0.701
MXT	0.192	0.664
MBT	0.637	0.430
MAT	1.393	0.246
PRC	3.788	0.060
CLD	7.764	0.008
HUM	1.357	0.252
RAI	1.067	0.309

Significant values are marked with *. Refer to text for acronyms.

DISCUSSION

The taxonomic status of both *A. cursor* and *A. montensis* is well defined. The first species presents diploid numbers equal to 14, 15 or 16 (CERQUEIRA, FERNANDEZ & QUINTELA, 1990; RIEGER, LANGGUTH & WAIMER, 1995). Specimens with diploid numbers of 24/25 have been referred to as *A. montensis*, in a taxonomic assignment that may need a reevaluation, as specimens with both diploid numbers have been collected in the type locality of *A. cursor* (Lagoa Santa, MG) (GEISE, SMITH & PATTON, 2001). This question could be addressed by including the type material of both species in a morphometric analysis, provided that reliable morphometric discrimination could be established beforehand on the basis of genetically identified samples.

Akodon montensis was originally described as a subspecies of *A. arviculoides* (Thomas, 1913), and latter related to *A. cursor* by XIMENEZ & LANGGUTH (1970). Although there are now abundant distributional, chromosomal, molecular, and morphological data supporting their species status (GEISE, 1995; RIEGER, LANGGUTH & WAIMER, 1995; SBALQUEIRO & NASCIMENTO, 1996; CHRISTOFF, 1997; GEISE, CANAVEZ & SEUÁNEZ, 1998; GEISE, SMITH & PATTON, 2001; GEISE, WEKSLER & BONVICINO, 2004), confusion remains, because these two taxonomic entities are difficult to distinguish by external or craniodental characters.

Descriptive statistics (Tab.1) and univariate analyses indicate that *A. montensis* is smaller than the two remaining species, as revealed by significant differences found in all measured traits between this species and either one or both the other species. The analyses also indicate that *A.* aff. *cursor* is significantly larger than the other two species. These opposite trends in skull size lead to a better separation between *A. montensis* and *A.* aff. *cursor* than between any of these and *A. cursor* (Tab.2). Nevertheless, the general smaller size in *A. montensis* also leads to significant differences in most measurements when compared to *A. cursor.*

The multivariate analysis yielded slightly different results, and did not provide a complete segregation between all of the three species (Fig.2). The greater differences found between *A.* aff. *cursor* and *A. montensis* in the univariate analyses are partially recovered in the discriminant analysis. Although there is some overlap between the two samples, most of this overlap is due to a single, aged *A. montensis* individual, highly divergent from the rest of the sample. However, while in the univariate analyses *A. cursor* was better distinguished from *A. montensis* than from *A.* aff. *cursor*, in the multivariate approach it showed no overlap with the latter, while partially overlapping with the former. These results are also recovered in the classification matrices (Tabs.3-4). Again, most of this overlap is related to a few aged *A. montensis* specimens, all of them misclassified in the analysis. These results also indicate that, while the univariate differentiation between *A. cursor* and *A.* aff. *cursor* was only observed in a few cranial measurements, the multivariate results represent additional evidence for the separation of these two taxa in separate species.

These results suggest that although some specific traits are clearly different between the analyzed groups, overall and precise differentiation between *A. cursor* and *A. montensis* cannot be achieved based on morphometric grounds solely. While 98% of all *A. cursor* specimens were correctly identified with the use of the discriminant function, some *A. montensis* were erroneously identified as either *A. cursor* or *A.* aff. *cursor* (about 10%). It is important to note that most of these specimens are particularly old. Since *A. montensis* appears to be the smallest of the three species analyzed here, it could be expected that larger and older specimens could resemble the other taxa more closely. In a previous analysis comparing only *A. cursor* and *A. montensis*, CHRISTOFF (1997) obtained similar results, although with slightly better classification for *A. montensis* and better discrimination of these two species. His results also indicate that most of the differentiation between these two taxa is allometric. While an evaluation of the allometric relationships among the studied taxa was not the primary goal of this study, this is consistent with our results, in as much as *A. montensis* shows partial multivariate segregation from *A. cursor*, coupled with significantly smaller values recorded for most measured characters. Thus, the lack of a complete segregation noted above in the multivariate analyses between these two taxa are more probably related to smaller specimens of *A. cursor* that end up erroneously classified as *A. montensis* or overlapped with these in figure 2, simultaneously to larger specimens of *A. montensis* being classified as *A. cursor.* This morphometric similarity may be related purely to size (since almost all variables were significantly different between the two taxa), or most probably to size-related (*i.e.* allometric) shape differences in the skull and mandible. CHRISTOFF (1997) also considers *A.* aff. *cursor* and *A. cursor* to be conspecific, but results presented here indicate a clear morphometric differentiation between these two groups, recovered both in the multivariate and in the univariate analyses. These results are in agreement with all previous genetic results (D´ÉLIA, GONZÁLEZ & PARDIÑAS, 2003; GEISE, SMITH & PATTON, 2001; GEISE, CANAVEZ & SEUÁNEZ, 1998; CHRISTOFF, 1997).

Nevertheless, the sample of *A.* aff. *cursor* used here is much smaller than the two others, and it cannot be determined whether its separation from the remaining two is an artifact of the variance estimates for this species, since discriminant function analyses depend on within-group variation as related to between-group variation to determine axes orientations, as well as within group

orientation, and both factors are influenced by sample size (PIMENTEL, 1992; MARCUS, 1990). Thus, further morphometric analyses surely need to be carried out when a larger number of karyotyped specimens becomes available. The resolution of the taxonomic issue related to the correct matching of the morphological form represented by the type of *A. cursor* from Lagoa Santa with the karyotypical forms of either 2n=14/15/16 or 2n=24/25 is therefore dependent on the availability of better classification functions obtained with greater sample sizes.

GEISE (1995), in a previous geographical analysis, showed that *A. cursor* and *A. montensis* presented completely separated altitudinal distributions, indicating that in the Rio de Janeiro State and surrounding localities they rarely occur in sympatry. In our samples, both species were recorded together only in two localities (Bananal and Iguape; localities #40 and 39). This finding corroborates other results which show that these two species have different geographic distribution patterns (SILVA, GRELLE & GEISE, in preparation).

Although in Rio de Janeiro State *A. montensis* is not found in altitudes below 800m above sea level, it does occur below this level at higher latitude localities. Climatic variables, such as temperature, can account for such altitudinal distribution of this species, forcing it to higher altitudes (with lower temperatures) in lower latitude localities. GEISE (1995) had showed an altitudinal segregation around 800m, with one species occurring above (*A. montensis*) and other occurring below (*A. cursor*) this altitude, in this same area. However, recently some *A. cursor* specimens were collected above this altitude (reaching 1,227m) in Bananal (Locality #40) and 850m in Serrinha do Alambari (Locality #32). We believe that these specific records of *A. cursor* in an altitude supposedly exclusive to *A. montensis* could be explained by habitat and microclimatic changes caused by deforestation. Both localities show high levels of habitat degradation and deforestation, the former consisting of modified grasslands (where forest was almost completely removed) and the second (Locality # 32) being an area with secondary forest. *Akodon cursor* can present a distinct physiology that allows it to invade open areas more easily, as in the present studied area it is usually found from sea level to the Rio Paraíba Basin in open and quite degraded areas. During the last 10 years, one of the authors (L.Geise) observed that *A. montensis* is more frequently trapped in better preserved vegetational formations, such as for example those present in Itatiaia (GEISE *et al.*, 2004; GEISE, SMITH & PATTON, 2001), Teresópolis, Nova Friburgo, and Bocaina (Localities # 48, 49 and 51). A study comparing microgeographical ecological differences among these two species, such as the one performed between two populations of *A. cursor* (CERQUEIRA *et al.*, 2003), could possibly lead us to a better understanding of such habitat different usages. The significant differences between species found in annual mean temperature can be an artifact of the low number of analyzed localities of *A. montensis* in the present study.

ACKNOWLEDGMENTS

We thank C.E.Grelle (UFRJ), E.D.Hingst-Zaher (MZUSP), G.M.Yazbeck (UFMG), H.G.Bergallo (UERJ), J.L.Patton (MVZ-Berkeley), M.Lara (Broad Institute of MIT and Harvard), R.T.Santori (FFP-UERJ), R.Cerqueira (UFRJ), for some collected specimens; H.Seuánez (INCA/UFRJ) and R.Cerqueira for laboratory facilities; G.Marroig (USP) provided precious advice on statistical procedures. Brazilian Institute of Environment and Natural Resources (IBAMA) granted us license for collecting specimens. Financial support was provided by grants from WWF, CNPq, FAPERJ, PROBIO and PRONEX. D.Astúa de Moraes was supported by a grant from FAPESP (Proc. 00/11444-7) and L.Geise from CNPq (302580/2002-6).

LITERATURE CITED

CERQUEIRA, R.; VIEIRA, M.V. & SALLES, L.O., 1989. Habitat and reproduction of *Rhipidomys cearanus* at São Benedito, Ceará (Rodentia, Cricetidae). **Ciência e Cultura**, Campinas, **41**(10):1009-1013.

CERQUEIRA, R.; FERNANDEZ F.A.S. & QUINTELA, M.F.S., 1990. Mamíferos da restinga de Barra de Maricá, Rio de Janeiro. **Papéis Avulsos de Zoologia**, São Paulo, **37**(9):141-157.

CERQUEIRA, R.; SANTORI, R.T.; GENTILE, R. & GUAPIASSU, S.M.S., 2003. Microgeographical ecological differences between two populations of *Akodon cursor* (Rodentia, Sigmodontinae) in a brazilian restinga. **Journal of Advance Zoology**, Gorakhpur, **24**(1&2):46-52.

CHRISTOFF, A.U., 1997. **Contribuição à sistemática das espécies do gênero *Akodon* (Rodentia: Sigmodontinae) do leste do Brasil: estudos anatômicos, citogenéticos e de distribuição geográfica**. DSc thesis, Universidade de São Paulo, 163p.

D´ÉLIA, G.; GONZÁLEZ, E.M. & PARDIÑAS, U.F.J., 2003. Phylogenetic analysis of Sigmodontinae rodents (Muroidea), with special reference to the akodont genus *Deltamys*. **Mammalian Biology**, Gena, **68**:351-364.

FORD, C.E. & HAMERTON, J.L., 1956. A colchicine hypotonic citrate squash sequence for mammalian choromosome. **Stain Technical**, Baltimore, **31**:247-251.

GEISE, L., 1995. **Os roedores Sigmodontinae do Estado do Rio de Janeiro (Rodentia, Muridae). Sistemática, citogenética, distribuição e variação geográfica**. D.Sc. Thesis, Universidade Federal do Rio de Janeiro, 389p.

GEISE, L.; CANAVEZ, F.C. & SEUÁNEZ, H.N., 1998. Comparative karyology in *Akodon* (Rodentia, Sigmodontinae) from Southeastern Brazil. **Journal of Heredity**, Cary, **89**:158-163.

GEISE, L.; SMITH, M.F. & PATTON, J.L., 2001. Diversification in the genus *Akodon* (Rodentia, Sigmodontinae) in Southeastern South America: mitochondrial DNA sequence analysis. **Journal of Mammalogy**, Lawrence, **82**(1):92-101.

GEISE, L.; WEKSLER, M. & BONVICINO, C.R., 2004. Presence or absence of gall bladder in some Akodontini rodents (Muridae, Sigmodontinae). **Mammalian Biology**, Gena, **69**(3):1-5.

GEISE, L.; PEREIRA, L.G.; BOSSI, D.E.P. & BERGALLO, H.G., 2004. Pattern of elevational distribution and richness of non volant mammals in Itatiaia National Park and its surrounding in Southern Brazil. **Brazilian Journal of Biology**, São Carlos, **64**(3B):599-612.

LIASCOVICH, R.C. & REIG, O.A., 1989. Low chromosomal number in *Akodon cursor montensis* Thomas, and karyologic confirmation of *Akodon serrensis* Thomas in Misiones, Argentina. **Journal of Mammalogy**, Lawrence, **70**(2):391-395.

MAIA, V. & LANGGUTH, A., 1981. New karyotypes of brazilian *Akodon* rodents with note on taxonomy. **Zeitschrit für Säugetierkunde**, Hamburg and Berlin, **46**(4):241-249.

MARCUS, L.F., 1990. Traditional morphometrics. In: ROHLF, F.J. & BOOKSTEIN, F.L. (Eds.) **Proceedings of the Michigan Morphometrics Workshop**. Michigan: University of Michigan Museum of Zoology. p.77-122.

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.

MYERS, P. & CARLETON, M.D., 1981. The species of *Oryzomys* (*Oligoryzomys*) in Paraguay and the identity of Azara's "Rat sixième ou Rat à Tarse Noir". **Miscellaneous Publications. Museum of Zoology, University of Michigan**, **161**: i-iii, 41p.

NEFF, N.A. & MARCUS, L.F., 1980. **A survey of multivariate methods for systematics**. New York: American Museum of Natural History. 221p.

PIMENTEL, R.A., 1992. An introduction to ordination, principal components analysis and discriminant analysis. In: SORENSEN, J.T. & FOOTTIT, R. (Eds.) **Ordination in the study of morphology, evolution and systematics of insects: Applications and quantitative genetics rationals**. Amsterdam: Elsevier. p.11-28.

RIEGER, T.T.; LANGGUTH, A. & WAIMER, T.A., 1995. Allozymic characterization and evolutionary relationships in the Brazilian *Akodon cursor* species group (Rodentia-Cricetidae). **Biochemical Genetics**, Austin, **33**(9/10):283-295.

SBALQUEIRO, I.F. & NASCIMENTO, A.P., 1996. Occurrence of *Akodon cursor* (Rodentia, Cricetidae) with 14, 15 and 16 chromosome cytotypes in the same geographic area in Southern Brazil. **Revista Brasileira de Genética**, São Bernardo do Campo, **19**(4):565-569.

SILVA, H.S., 2001. **Padrões de distribuição de três espécies de rodeores neotropicais do gênero *Akodon* (Rodentia, Sigmodontinae)**. Monografia de Bacharelado. Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 49p.

SILVA, M.J.J. & YONENAGA-YASSUDA, Y., 1998. Karyotype and chromosomal polymorphism of an undescribed *Akodon* from Central Brazil, a species with the lowest diploid chromosome number in rodents. **Cytogenetics and Cell Genetics**, Basel, **81**:46-50.

SMITH, M.F. & PATTON, J.L., 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. **Biological Journal of the Linnean Society**, London, **50**:149-177.

VOSS, R.S., 1988. Systematics and ecology of Ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. **Bulletin of the American Museum of Natural History**, New York, **188**(2):260-493.

WILSON, D.E.; COLE, F.R.; NICHOLS, J.D.; RUDRAN, R. & FOSTER, M., 1996. **Measuring and monitoring biodiversity. Standard methods for mammals**. Washington: Smithsonian Institution Press. 409p.

XIMENEZ, A. & LANGGUTH, A., 1970. *Akodon cursor montensis* en el Uruguay (Mammalia, Cricetidae). **Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo**, Montevidéu, **128**:1-7.

APPENDIX

Specimens examined: MN – Museu Nacional, Rio de Janeiro; MZUSP – Museu de Zoologia da Universidade de São Paulo; MVZ – Museum of Vertebrate Zoology, University of California, Berkeley. Other acronyms correspond to field number of collectors: EDH (E.Hingst-Zaher), HB, HGB-DB , HGB-REGUA and HGB-CFVC (H.G.Bergallo), JLP (J.L.Patton), RTS (R.T.Santori), LC and LPC (L.P.Costa); YL (Y.Leite), BRP (B.R.Portugal) and CEG (C.E.Grelle). MC, LS, PE, PB, FS, SU – field numbers of collecting localities, collection of the Laboratório de Vertebrados, Depto. Ecologia, Universidade Federal do Rio de Janeiro; EEB – field numbers of MZUSP. U = undetermined sex. Numbers between brackets are localities number in figure 3. To avoid repetition of locality names in the second reference only the number is given.

Akodon aff. *cursor* – BRAZIL - BAHIA: [1] Morro da TeleBahia, Lençóis (12°32'S, 41°24'W, 560m) (♂ : CD137, 157, 178; ♀ : CD141, 143, 242); [2] Remanso, Lençóis (12°36'S, 41°21'W, 464m) (♂ : CD30, 94, 164; ♀ : CD5, 27, 62, 66, 102-104, 110, 124). MINAS GERAIS: [3] Estação Ecológica Acauã, Turmalina (17°08'S, 42°46'W, 800 m) (♀ : LC74, YL71, 80).

Akodon cursor (Winge, 1887) – BRAZIL - BAHIA: [4] Fazenda Água Santa, Pau Brasil (15°27'S, 39°37'W, 90m) (♂ : LG196; ♀ : LG190, 200); [5] Helvécia, Nova Viçosa (17°53'S, 39°22'W, 52m) (♂ : MN47992). MINAS GERAIS: [6] Parque Estadual do Rio Doce, Marliéria (19°43'S, 42°39'W, 300m) (♂ : LC84, 98; ♀ : LC88, 90, YL87, 88, 96); [7] Mata do Paraíso, Viçosa (20°45'S, 42°53'W, 650m) (♂ : MN35936, 35937, 35939; ♀ : MN35934, 35935); [8] Sítio Maglândia, Simão Pereira (21°58'S, 43°19'W, 500m) (♂ : MN33688, 33691, 33693-95, 33697, 35918; ♀ : MN33690, 33692, 33696, BPR07). RIO DE JANEIRO: Cachoeiras de Macacu Municipality: [9] Reserva de Guapiaçu (no coordinates data) (♂ : HGB-REGUA2; ♂ : HGB-REGUA1, 17); [10] Sítio Rosimary (22°29'S, 42°51'W, 54m) (♂ : FS11-12, 25, 30, 40, 41, FS14-05, 39; ♀ : FS11-23, 47, 83, FS14-41); [11] Fazenda Pica Pau Amarelo (22°30'S, 42°45'W, 200m) (♂ : FS13-27, 32, 91, FS17-15, 20, 43; ♀ : FS17-16, 18, 21, 39, 40, 44-46); [12] Conjunto de Fazendas (ex. Sítio do Rio Doce) (22°31'S, 42°47'W, 100m) (♂ : FS16-24, 25, 40; ♀ : FS12-14, 15, 32, FS16-07, 33); [13] (22°31'S, 42°48'W) (♂ : FS6-9, 13, 30-32); [14] Bairro Quizanga (22°31'S, 42°51'W, 100m) (♂ : FS16-29, 37); [15] (22°34'S, 42°54'W, 150m) (♂ : FS15-41, 43, 58, 80, 81, 86, FS18-4-6; ♀ : FS15-40, 42, 44, 45, 57, FS18-12, 27, 34, 35); [16] (22°35'S, 42°54'W, 150m) (♂ : FS15-13, 50-52, FS18-22; ♀ : FS18-13); Guapimirim Municipality: [17] Garrafão (22°29'S, 43°00'W) (♀ : ORG 46); [18] Parque Nacional da Serra dos Órgãos, sede Guapimirim (22°29'S, 42°59'W, 470m) (♂ : PSS15); [19] Fazenda Iguaçú (22°31'S, 42°53'W) (♂ : FS5-57, 59, FS8-31, 58; ♀ : FS8-28, 77); [20] Fazendas Consorciadas (22°33'S, 42°53'W, 15m) (♂ : FS5-3, 58, 69, FS8-73, 79, 80, FS17-2, 3, 13, 35; ♀ : FS5-22, 36, 37, FS8-19, 76, FS13-28, FS17-1, 8, 14, 17); [21] Fazenda Chorona (22°33'S, 42°57'W, 140m) (U: FS4-71, ♂ : FS4-2, 3, 4, 6, 8, 9, 11, 37, 42, 43, 45, 46, 53-55, 58, 61, 81, FS7-8; ♀ : FS4-10, 14, 19, 33, 36, 41, 48, 56, 75, FS7-25); [22] Centro de Primatologia (22°38'S, 42°58'W, 100m) (♀ : HGB405); [23] Vale do Pamparrão, Sumidouro Municipality (22°02'S, 42°39'W, 300m) (♂ : MN43750, 43754, SU8, 9); [24] Glicério, Macaé Municipality (22°14'S; 42°03'W, 250m) (♂ : MN35928, 35931; ♀ : MN35929, 35930, 35932, 35933); [25] Reserva União, Casimiro de Abreu Municipality (22°25'S; 42°02'W, 50m) (♂ : MN59115; ♀ : MN35941); [26] Pinheiral, Piraí Municipality (22°30'S, 44°00'W, 345m) (♂ : CEG70, 75, 77; ♀ : CEG73, 74, 78); [27] Morro de São João, Casimiro de Abreu Municipality (22°32'S; 42°02'W, 260m) (♀ : MN35940); [28] Fazenda São José das Paineiras, Mendes Municipality (22°32'S, 43°44'W, 610m) (♂ : MN35913); [29] Tinguá, Nova Iguaçu Municipality (22°45'S, 43°26'W, 125m) (♂ : MN26810, 28810, ♀ : 28928); [30] Catimbau Grande, Rio Bonito Municipality (22°46'S; 42°40'W, 200m) (♂ : MN35915, 35917, ♀ : 35916); [31] Restinga de Barra de Maricá, Maricá Municipality (22°55'S; 42°49'W, 3m) (U: MN26839, 28948, 30140, ♂ : MN26791, 26791, 26815, 26844, 27825, 28813, 28833, 28843, 28946; ♀ : MN26853, 28543, MC229); [32] Serrinha do Alambari, Resende Municipality (22°22'S, 44°33'W, 850m) (♂ : MN47988, 47989, 47993, 47994; ♀ : MN47986, 47987, 47990, 47991); Itatiaia Municipality [33] Piscina Maromba, Parque Nacional de Itatiaia (22°26'S, 44°37'W, 620m) (♂ : HGB-DB22; ♀ : HGB-DB21), [34] Parque Nacional de Itatiaia (no coordinates data) (♀ : HGB-CFVC 1, 3, 6); [35] Rio de Janeiro Municipality (22°54'S, 43°12'W, 2m) (♀ : MZUSP24168); [36] Mambucaba, Angra dos Reis Municipality (23°01'S, 44°31'W, 100m) (♂ : MN42760, MAM5; ♀ : MN42762, 42766); [37] Tarituba, Paraty Municipality (23°02'S, 44°35'W, 105m) (♀ : MN62185, 62186).

SÃO PAULO: [38] Salesópolis (23°31'S, 45°50'W, 806m) (♂ : MZUSP27429); [39] Iguape (24°43'S, 47°33'W, 20m) (♂ : MZUSP24169); [40] Trilha das Pedras Vermelhas, Bananal (22°47'S, 44°21'W, 1227m) (♂ : EEB665); [41] Icapara (no coordinates data) (♂ : MZUSP27428), [42] Picinguaba, Ubatuba Municipality (23°22'S, 44°50'W) (♀ :MN98069);

Akodon montensis (Thomas, 1913) – BRAZIL - MINAS GERAIS: [43] Jambreiro, Nova Lima Municipality (18°04'S, 42°46'W, 913m) (♂ : LG207); [44] Fazenda Montes Claros, Estação Biológica de Caratinga, Caratinga Municipality (19°50'S, 41°50'W, 320m) (♂ : MN31450). MATO GROSSO DO SUL: Dourados Municipality [45] Fazenda Maringá, 54km W de Dourados (22°16'S, 55°18'W, 427m) (U: LPC612, 614-621, 663, 671, 673, 680-682; ♂ : LPC622, 633, 635, 640, 656, 661, 662, 676, 678; ♀ : LPC641, 654, 655, 657, 659, 672, 674, 677); [46] Balança Velha, 55km W de Dourados (22°20'S, 55°18'W, 518m) (U: LPC611, ♂ : JLP16989, 16996-98; ♀ : JLP16990-95). RIO DE JANEIRO: [47] Fazenda São José da Serra, Serra do Paqueque, Sumidouro Municipality (22°12'S; 42°44'W, 1033m) (♂ : MCL26, 36; ♀ : MCL28, 33); [48] Sede do Parque Nacional da Serra dos Órgãos, Teresópolis Municipality (22°24'S, 42°59'W, 871m) (U: FS10-45; ♂ : FS10-2, 3, 8, 14, 26, 31, 43, 44, 46, 52, 53, 61, 72, 84, 87, 89, 94, 97; ♀ : FS10-27, 28, 30, 33, 39, 65, 77, 96); [49] Sítio Xitaca, Debossan, Nova Friburgo Municipality (22°26'S; 42°32'W, 1100m) (♂ : MN35925). SÃO PAULO: [50] Clube Náutico de Araraquara, Araraquara Municipality (21°05'S, 47°19'W, 664m) (♂ : RTS13); [51] Parque Nacional da Bocaina, São José do Barreiro Municipality (22°50'S, 44°41'W, 1400m) (♀ : HGB-DB8); Estação Ecológica de Bananal, Bananal Municipality: [52] Trilha da Casa Velha (no coordinates data) (♂ : EEB713); [53] Trilha do Rio das Cobras (22°28'S, 44°22'W, 1164m) (♀ : EEB563, 676); [40] (♂ :EEB695; ♀ : EEB680); [54] Trilha das Sete Quedas (22°48'S, 44°22'W) (♂ : EEB703; ♀ : EEB651); [55] Trilha do Alemão (no coordinates data) (♀ : EEB678); [56] Fazenda São José, Rio Claro Municipality (22°24'S, 47°33'W, 850m) (♀ : SJ1, RTS8); [57] Floresta Nacional de Ipanema, Sorocaba (23°26'S, 47°37'W, 701m) (U: LPC793, ♂ : LPC810, 855, 856, 859, 863, 866-868, 870; ♀ : 799, 858, 860, 862, 869, 872); [39] (♂ : MZUSP24174, 24176, 24178; ♀ : MZUSP24175, 24177).

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.75-88, jan./mar.2005
ISSN 0365-4508

VARIAÇÃO GEOGRÁFICA EM CARACTERES CRANIANOS QUANTITATIVOS DE *KERODON RUPESTRIS* (WIED, 1820) (RODENTIA, CAVIIDAE) [1]

(Com 5 figuras)

GISELE LESSA [2, 3]
PABLO R. GONÇALVES [3]
LEILA MARIA PESSÔA [4, 5]

RESUMO: A variação geográfica em caracteres cranianos de nove amostras populacionais recentes e uma amostra sub-fóssil foi investigada através da amplitude de distribuição do roedor histricomorfo *Kerodon rupestris* (Wied, 1820), endêmico do semi-árido brasileiro. Análises univariadas e multivariadas foram baseadas em 22 caracteres medidos em 319 espécimens. Os resultados mostraram que a variação craniana apresentou um padrão clinal de aumento de tamanho do norte para o sul. A população localizada ao norte, proveniente de Itapajé (CE), possui o menor tamanho craniano quando comparada à do sul, proveniente de Botumirim (MG). Estas duas populações encontram-se completamente discriminadas no espaço multivariado de caracteres cranianos. As demais amostras situam-se em posição intermediária entre as populações do norte e do sul. Uma população de *Kerodon acrobata* inserida em uma segunda análise, ocupou um espaço inteiramente isolado em relação às demais populações de *K. rupestris*, revelando a distinção morfométrica entre as duas espécies do gênero. Padrões clinais na variação morfométrica não têm sido considerados para a delimitação de subspécies; no entanto, níveis diferenciados de variação infraespecífica estão ocorrendo entre as populações estudadas de *K. rupestris*. O padrão observado em *K. rupestris* sugere uma estrutura de variação que pode estar associada ao isolamento dos diferentes afloramentos rochosos habitados pela espécie. Estudos adicionais abordando limites geográficos de variação genética serão necessários para definir o nível preciso de diferenciação entre essas populações.

Palavras-chave: *Kerodon rupestris*, variação geográfica, morfometria craniana, nordeste, Brasil.

ABSTRACT: Geographic variation in quantitative cranial characters of *Kerodon rupestris* (Wied, 1820) (Rodentia, Caviidae).

Geographic variation in cranial characters in nine recent population samples and one sub-fossil sample was investigated throughout the range of distribution of the histricomorph rodent *Kerodon rupestris* (Wied, 1820), endemic of the semi-arid region in Brazil. Univariate and multivariate analyses based on 22 measurements taken from 319 specimens show that overall size variation follows a north-south clinal pattern of increasing size. The northern population from Itapajé (CE) showed the smaller cranial size when compared to the southern population from Botumirim (MG). The Itapajé and the Botumirim populations were completely discriminated in the multivariate space. The other populations occupied an intermediate position in relation to the northern and southern samples. A sample of *Kerodon acrobata*, included in a second analysis, occupied a completely distinct multivariate space in relation to *K. rupestris* samples. revealing the morphological distinction between the two species of the genus. A clinal pattern of variation has not been considered in the delimitation of subspecies. Nevertheless, different levels of variation are occurring among the populations of *K. rupestris*.The pattern observed in *K. rupestris* suggests a structure of variation that may be related to the isolation among rock outcrops inhabited by the species throughout its distributional range. Additional studies addressing the geographical limits of genetic variation will be necessary to show the precise level of differentiation among these populations.

Key words: *Kerodon rupestris*, geographic variation, cranial morphometrics, northeastern, Brazil.

---

[1] Submetido em 14 de junho de 2004. Aceito em 13 de janeiro de 2005.

[2] Museu de Zoologia João Moojen de Oliveira, Universidade Federal de Viçosa. Vila Giannette, n° 32, Campus Universitário, Viçosa, 36570-000, MG, Brasil. E-mail: gislessa@yahoo.com.br.

[3] Museu Nacional/UFRJ, Programa de Pós-Graduação em Ciências Biológicas (Zoologia). Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil.

[4] Universidade Federal do Rio de Janeiro, IB, Departamento de Zoologia. Ilha do Fundão, 21941-590, Rio de Janeiro, RJ, Brasil.

[5] Bolsista do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

INTRODUÇÃO

A subfamília Caviinae inclui os gêneros *Galea* Meyen, 1831, *Cavia* Pallas, 1766, *Kerodon* Cuvier, 1825, e *Microcavia* Gervais & Ameghino, 1880 (WOODS, 1993), distribuídos em uma extensa área da América do Sul (MARES & OJEDA, 1982). Dentre os poucos estudos morfométricos realizados com representantes da subfamília, inclui-se a análise da forma craniana em *Kerodon*, *Cavia* e *Galea* que empregou métodos multivariados (REIS *et al.*, 1988), revelando que as trajetórias ontogenéticas de *Galea* e *Kerodon* são mais semelhantes entre si do que com a de *Cavia*.

O gênero *Kerodon* atinge as maiores dimensões corporais dentre os Caviinae e tem sido considerado como um especialista, uma vez que desde o Pleistoceno se distribui pela região do semi-árido e pequena extensão do semi-úmido (categorias climáticas definidas por AB'SÁBER, 2003) do Brasil setentrional, onde encontra-se confinado a afloramentos rochosos (LACHER, 1981; ALHO, 1982; GUIDON *et al.*, 1993. Atualmente, duas espécies são registradas para o gênero: *Kerodon rupestris* (Wied, 1820), com distribuição conhecida do Piauí ao norte de Minas Gerais (LACHER, 1981; MARES & OJEDA, 1982; ALHO, 1982) e *K. acrobata* Moojen, Locks & Langguth, 1997, conhecida apenas da sua localidade tipo no rio São Mateus, Goiás (MOOJEN *et al.*, 1997). Estudos recentes mostram que *K. rupestris* é o roedor histricognato registrado em maior número de localidades na Caatinga (OLIVEIRA *et al.*, 2003), constituindo uma das poucas espécies de mamíferos endêmicas a este bioma. Apesar desta ampla distribuição geográfica, até o momento nenhum estudo foi realizado no sentido de avaliar a existência de variação entre as populações de *K. rupestris*.

A proposta deste estudo foi buscar padrões de variação geográfica em caracteres cranianos em amostras populacionais desta espécie, utilizando métodos morfométricos univariados e multivariados. Inferências sobre o nível de diferenciação de populações recentes e de amostras sub-fósseis foram feitas comparando a variação morfométrica destas populações e de uma população de *K. acrobata*, em uma análise posterior.

MATERIAL E MÉTODOS

Foram utilizados 319 indivíduos de *K. rupestris* provenientes de nove localidades ao longo da área de distribuição conhecida para a espécie, além de 16 exemplares sub-fósseis coletados em grutas calcárias nos municípios de Ourolândia, Morro do Chapéu e Campo Formoso, localizados na porção central do Estado da Bahia. Adicionalmente, uma amostra de quatro indivíduos de *K. acrobata*, provenientes da localidade tipo, Rio São Mateus (GO), foi incluída (Fig.1). Os exemplares estudados estão depositados no Setor de Mastozoologia do Museu Nacional, Universidade Federal do Rio de Janeiro (MN), no Museu de Zoologia, Universidade de São Paulo (MZUSP) e no Setor de Paleontologia do Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais (MCL) (Apêndice). Os exemplares depositados na coleção de mamíferos do Museu Nacional foram coletados em quase sua totalidade no período entre 1952 a 1955, durante o levantamento da fauna de roedores silvestres da região do Nordeste do Brasil realizado pelo Serviço Nacional de Peste (SNP), sob a coordenação do naturalista do Museu Nacional, Dr. João Moojen de Oliveira.

Os exemplares provenientes das grutas da Bahia foram coletados pela equipe de Paleontologia do Museu de Ciências Naturais da PUC/Minas no período de 1977 a 1986. O material estudado foi encontrado em locais distantes das respectivas aberturas naturais, em zona afótica, associado à megafauna pleistocênica herbívora extinta. As três grutas onde se realizaram as coletas estão situadas na porção norte da Chapada Diamantina, no Estado da Bahia, em calcários neoproterozóicos do Grupo Una (Formação Salitre) na borda nordeste da Bacia Sedimentar de Irecê (LESSA *et al.*, 1998; BERBERT-BORN & KARMANN, 2000). A origem destes restos de animais exógenos no interior das grutas deve-se provavelmente a fenômenos de carreamentos aqüíferos temporários ou mesmo anômalos durante o final do Pleistoceno e início do Holoceno (CARTELLE, 1992).

Todos os crânios foram observados sob lupa e as medidas cranianas foram tomadas com paquímetro eletrônico. Foram analisados 22 caracteres morfométricos cranianos para cada população de *K. rupestris* e de *K. acrobata*, definidos em VAN GELDER (1968), PATTON & ROGERS (1983), REIS *et al.* (1988) e OLIVEIRA (1992): (A_1A) comprimento occipito-nasal – dorsal: distância máxima entre a borda anterior do nasal e a borda posterior do supraoccipital; (A_1B) comprimento nasal (dorsal: distância entre as extremidades anteriores e posteriores dos nasais); (A_1C) comprimento rostral 1 – dorso-ventral: maior distância entre a linha de sutura ventral maxila-pré-maxila e a borda anterior do nasal; (SA_1) comprimento rostral 2 – dorso-lateral: distância entre a borda

anterior do nasal a linha dorsal da sutura fronto-lacrimal; (DD_1) largura rostral – dorsal: largura do rostro sobre a linha de sutura entre o maxilar e o pré-maxilar; (EE_1) largura da constrição interorbital – dorsal: menor largura interorbital; (BU) comprimento do frontal – dorsal: distância entre as suturas naso-frontal e fronto-parietal; (UV) comprimento do parietal – dorsal: distância entre as suturas fronto-parietal e parieto-occipital; (FF_1) diástema – ventral: distância entre a borda posterior do alvéolo do incisivo à borda anterior do alvéolo do primeiro molariforme superior; (F_1G) comprimento da série molar superior – ventral: maior distância entre a borda alveolar anterior do primeiro molar e a borda alveolar posterior do último molar; (FH) comprimento do palato – ventral: distância entre a borda posterior do alvéolo do primeiro incisivo à chanfradura da fossa mesopterigóide = chanfradura posterior do palatino; (HQ) comprimento pós-palatal – ventral: distância entre a chanfradura da fossa mesopterigóide e a borda anterior do forâmen magno; (GG_1) largura do maxilar – ventral: distância entre os bordos vestibulares dos alvéolos dos últimos molariformes superiores; (II_1) comprimento do forâmen incisivo – ventral: distância entre as bordas anterior e posterior do forâmen incisivo; (FP) comprimento basilar – ventral: distância entre a linha de sutura basiesfenóide-basioccipital e o plano da margem posterior do primeiro inciso superior; (TK) comprimento condilobasal – ventral: distância entre a borda posterior do côndilo occipital e a borda anterior da pré-maxila; (LL_1) comprimento bular – ventral: comprimento da porção timpânica da bula auditiva; (NN_1) largura zigomática – ventral: maior distância entre as bordas laterais dos arcos zigomáticos; (OO_1) largura entre os processos paraoccipitais – lateral: maior distância entre as bordas laterais dos processos paraoccipitais; (PP_1) altura craniana – lateral: entre a linha de sutura-basiesfenóide-basioccipital e a superfície dorsal do parietal; (CM) altura rostral – lateral: distância perpendicular ao longo do eixo do crânio entre a borda posterior do forâmen incisivo e a superfície dorsal dos nasais; (RR_1) comprimento mandibular – lateral: distância diagonal entre o côndilo mandibular e a borda posterior do alvéolo do primeiro incisivo (Fig.2).

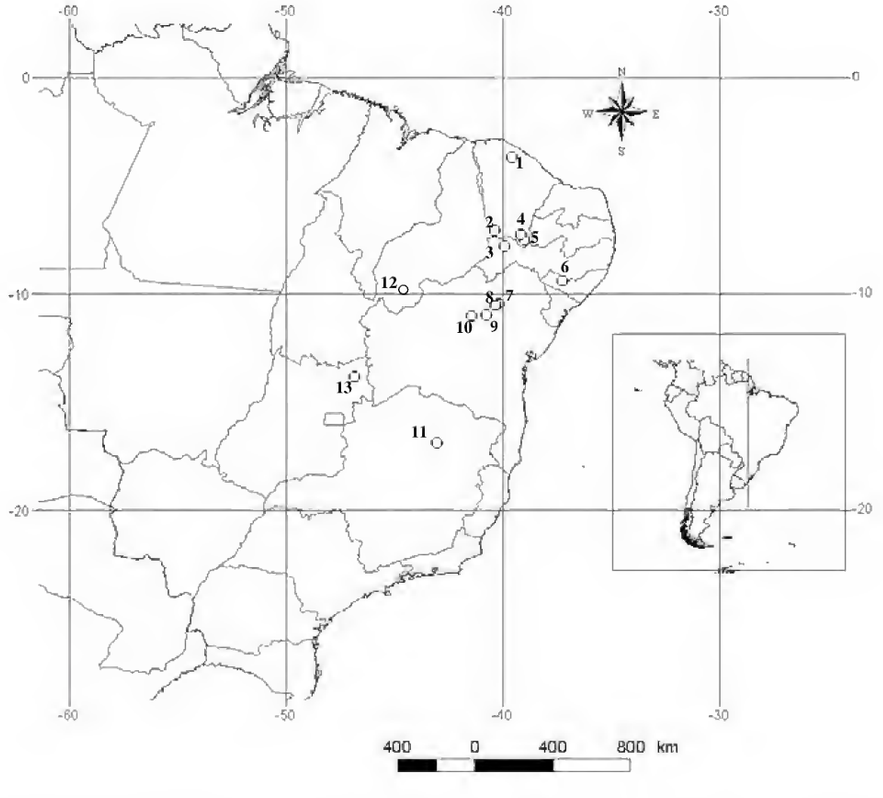

Fig. 1- Localidades onde foram coletadas as amostras populacionais de *Kerodon rupestris* e *K. acrobata*, utilizadas neste estudo: (1) Itapajé, (2) Campos Sales, (3) Exú-Bodocó, (4) Brejo Santo, (5) Missão Velha, (6) Santana do Ipanema, (7) Senhor do Bonfim, (8) Toca da Boa Vista, (9) Toca dos Ossos, (10) Gruta dos Brejões, (11) Botumirim, (12) Guaribas, (13) Rio São Mateus.

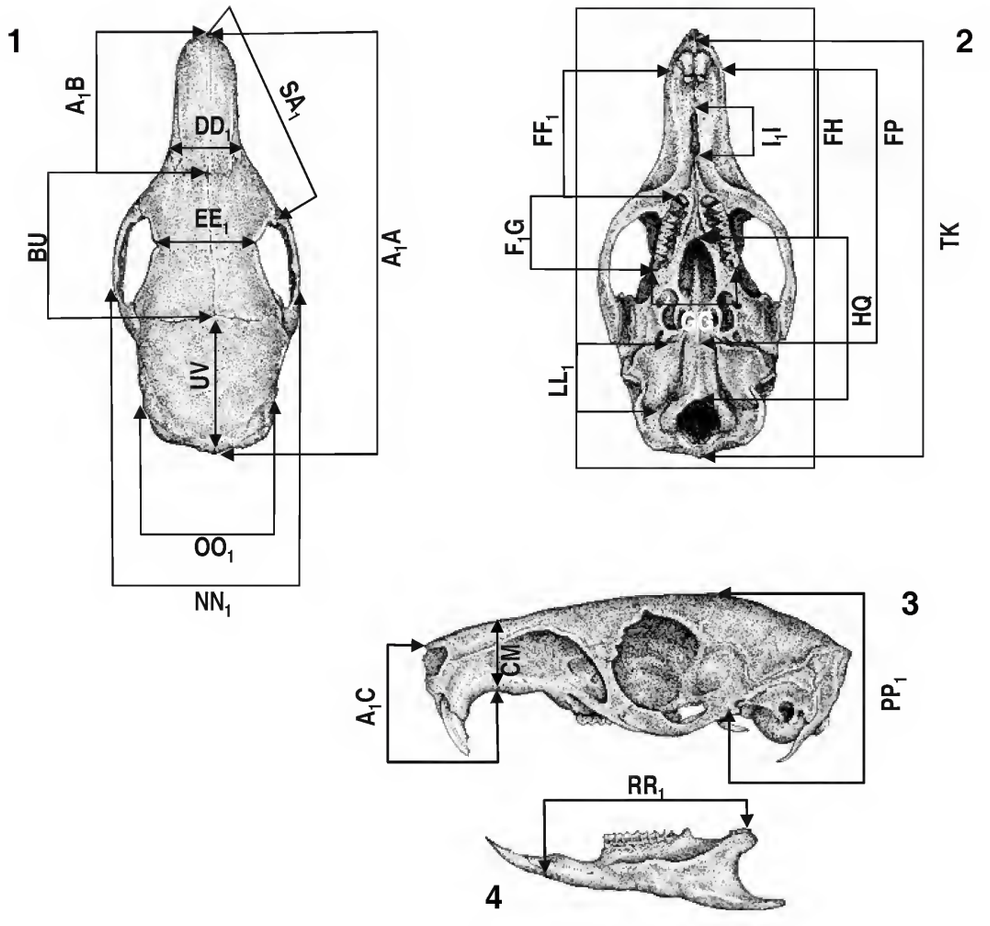

Fig.2- Crânio de um espécime adulto macho de *Kerodon rupestris* proveniente de Campos Sales, Ceará, indicando os pontos entre os quais foram feitas as mensurações citadas no texto: (1) vista dorsal, (2) vista ventral, (3) vista lateral, (4) vista lateral da mandíbula.

O dimorfismo sexual pouco acentuado em caracteres cranianos e a definição de cinco classes de idade foram úteis para a classificação etária de indivíduos de uma população de sub-fósseis provenientes de grutas calcárias na Bahia (LESSA, 2004). Tendo em vista a ausência significativa de dimorfismo sexual e a delimitação de classes de adultos, as análises geográficas foram efetuadas com os sexos combinados e incluíram diferentes classes de adultos, o que possibilitou o aumento dos números amostrais para cada população.

Para cada população ou grupo de populações foram feitos os cálculos da média e do desvio-padrão para todos os caracteres medidos. Para testar a hipótese nula de igualdade entre as médias das diferentes populações foi empregada a análise de variância ANOVA (SOKAL & ROHLF, 1981) utilizando o software MINITAB versão 13.

As análises multivariadas foram realizadas inicialmente para uma matriz com os dados originais das nove populações de *K. rupestris*. Entretanto, sendo a população de Campos Sales numericamente maior do que as demais, foi necessária uma seleção aleatória de seus indivíduos entre as diferentes classes de idade com posterior inclusão desses à matriz original, com o objetivo de homogeneizar as estimativas da variância.

Dentre os indivíduos sub-fósseis, algumas estruturas cranianas apresentaram-se fragmentadas, impossibilitando a mensuração de 11 caracteres em média. Os dados ausentes foram estimados para estes indivíduos através do método "Expectation-Maximization", que utiliza como critério a manutenção da estabilidade da matriz de covariância-variância (STRAUSS *et al.*, 2003).

Padrões de variação em tamanho e forma entre as diferentes localidades foram exploradas através da Análise de Componentes Principais (MANLY, 1994). Os valores de todas as variáveis foram transformados em logaritmos, objetivando a equalização das escalas de variação dos diferentes caracteres (NEFF & MARCUS, 1980). Devido às correlações positivas e significativas entre as variáveis morfométricas originais e o primeiro componente principal, esse eixo foi interpretado como uma estimativa de tamanho multivariado (STRAUSS, 1985). Os escores do componente principal para os dois primeiros eixos foram representados graficamente para revelar padrões de variação de tamanho e forma entre as populações de *K. rupestris*.

Uma Análise Canônica Discriminante Independente-do-Tamanho ("Size-Free Canonical Discriminant Analysis") foi realizada para testar a similaridade de tamanho e forma craniana entre as populações. Nesta metodologia a influência do tamanho intrapopulacional (crescimento) é removida, maximizando-se os componentes de variação interpopulacionais (REIS *et al.*, 1990).

Posteriormente, foram construídos dendrogramas através do método de UPGMA ("Unweighted Pair-Group Method using Arithmetic Averages") implementado sobre as distâncias de Mahalanobis estimadas a partir da matriz de resíduos em relação ao primeiro componente principal, e portanto corrigida para o efeito do tamanho. O método de UPGMA agrupa as distâncias entre amostras par a par, reunindo as duas populações com a menor distância de Mahalanobis que em seguida são conectados a outros grupamentos hierarquicamente, de acordo com as distâncias médias entre eles (MANLY, 1994). Apenas amostras maiores do que 10 indivíduos de *K. rupestris* foram utilizadas nestas análises.

As populações com pequeno número de indivíduos foram alocadas numa classificação probabilística às amostras grandes (maiores do que 10 indivíduos) com base nas distâncias de Mahalanobis, mais uma vez estimadas a partir da matriz corrigida para efeitos do tamanho intragrupal, em 1000 interações de "booststrap".

Estes procedimentos estatísticos foram implementados utilizando rotinas e funções escritas por R. E. Strauss em MATLAB 4.3 (MathWorks), disponíveis em http://www.biol.ttu.edu/Faculty/FacPages/Strauss/Matlab/matlab.htm.

RESULTADOS

Diferenças entre as amostras foram encontradas para todos os caracteres craniométricos mensurados (Tab.1). Os valores das médias indicaram que as populações de sub-fósseis (BA) e a de Botumirim (MG) possuem maiores dimensões cranianas quando comparadas às de Brejo Santo (CE), Exú-Bodocó (PE), Campos Sales (CE) e Santana do Ipanema (AL). A população de Itapajé (CE) mostrou os menores valores nas dimensões cranianas. A análise de variância univariada (ANOVA) detectou heterogeneidade entre as populações, estando os caracteres cranianos com diferenças altamente significativas entre estas populações ($P<0,0001$) (Tab.1).

A comparação das médias cranianas destas sete populações de *K. rupestris* com uma população de *K. acrobata* (GO) revelou 21 variáveis maiores na segunda espécie, sendo que apenas o comprimento do parietal foi significativamente maior na população de sub-fósseis de *K. rupestris* (Tab.1).

Quando a variação craniana presente nas amostras reunidas foi analisada de forma multivariada o primeiro componente principal (CP1) respondeu por 86,1% do total da variação enquanto o segundo componente principal (CP2) explicou 4,2%. Todos os 22 caracteres estudados apresentaram coeficientes de correlação positivos, o que possibilitou a interpretação do CP1 como um eixo de variação geral do tamanho (STRAUSS, 1985) (Tab.2). Assim, a maior parte da variabilidade morfométrica (86,1%) nas amostras das diferentes populações de *K. rupestris* pode ser atribuída ao fator geral de tamanho e a variabilidade restante, como expressão da forma (Fig.3).

Um padrão de variação das amostras em relação ao tamanho pode ser visualizado ao longo do CP1, apesar de se observar considerável área de sobreposição entre as amostras com distribuição geográfica mais central. O resultado encontrado corrobora os valores da estatística descritiva onde os indivíduos da amostra de Itapajé (CE) apresentaram menor tamanho ao passo que os exemplares das amostras de sub-fósseis (BA) e a de Botumirim (MG) apresentam as maiores dimensões cranianas. As demais amostras situam-se em posições intermediárias, preenchendo o intervalo entre as amostras citadas acima (Fig.3A).

Tabela 1. Estatística Descritiva (média e desvio-padrão) e Análise de Variância Univariada (ANOVA) dos indivíduos de *Kerodon rupestris* com sexos combinados de idade 4 provenientes de 7 diferentes amostras e uma amostra de *K. acrobata*.

Variáveis	Campos Sales (n= 18)		Bodocó-Exú, (n=12)		Santana do Ipanema (n=19)		Brejo Santo (n=5)		Itapajé (n=6)		Sub-Fósseis (n=14)		Botumirim (n=7)		*K. acrobata* (n=1)		
	Méd	DP	Med	DP	Méd	DP	Méd	DP	Méd	DP	Méd	DP	Méd	DP	Méd	DP	F
A1A Comp. occip-nasal	69.43	2.53	70,93	1.93	68.84	1.63	70.99	0.49	68.68	2.55	71.34	1.65	72.29	2.48	82.79	ϕ	8.56
A1B Comp. nasal	23.04	1.58	22.99	1.86	23.00	0.88	23.37	0.31	21.29	1.69	21.99	1.63	23.03	1.22	24.93	ϕ	3.39
A1C Comp. rostral 1	18.25	1.33	18.93	1.05	18.54	0.79	18.67	0.80	18.97	0.75	19.28	0.72	18.45	1.15	24.66	ϕ	10.25
SA1 Comp. rostral 2	32.58	1.89	33.36	1.61	32.49	1.09	32.84	0.49	32.80	1.29	33.50	1.90	34.36	1.06	41.62	ϕ	11.60
DD1 Larg. rostral	15.16	0.98	15.29	0.75	15.22	0.91	14.66	0.77	14.96	1.38	15.78	1.19	15.92	1.23	17.69	ϕ	2.12
EE1 Larg.const.interorb.	16.05	0.69	16.65	0.87	15.38	1.07	16.87	1.12	16.41	0.36	17.44	1.23	15.82	0.87	18.40	ϕ	7.99
BU Comp. frontal	25.69	1.17	26.78	1.24	24.98	1.23	25.20	0.55	27.17	1.29	28.13	2.61	27.83	1.48	34.40	ϕ	18.66
UV Comp. parietal	18.70	1.01	19.71	1.08	18.51	0.89	19.75	0.73	18.23	0.85	19.96	1.75	18.90	0.65	19.22	ϕ	3.67
FF1 Comp. diastema	19.70	1.26	20.38	1.00	19.95	0.59	20.46	0.60	20.22	1.34	20.74	1.62	19.95	0.93	25.71	ϕ	9.63
F1G Comp.série.molar.sup	14.15	0.71	15.03	0.44	14.09	0.46	14.51	0.39	14.00	1.02	15.68	1.19	15.91	0.83	18.01	ϕ	14.83
FH Comp. palato	28.05	1.63	29.00	1.52	27.97	1.04	28.70	1.71	28.32	1.77	30.56	2.32	29.05	1.17	35.58	ϕ	9.80
HQ Comp.pós-palatal	27.55	1.29	28.59	1.00	27.91	1.26	29.15	0.80	27.14	0.98	28.44	1.84	28.02	0.83	31.64	ϕ	5.83
GG1 Larg. maxilar	13.70	0.62	14.07	0.78	13.75	0.79	14.37	0.47	14.16	0.68	14.12	0.81	15.06	0.92	15.46	ϕ	6.48
II1 Comp. fora. incisivo	6.06	0.79	6.52	0.72	6.90	0.67	6.74	0.58	7.45	0.43	7.87	1.02	6.87	1.06	ϕ	ϕ	13.28
FP Comp. basilar	44.07	2.04	45.77	1.92	44.58	1.25	45.88	1.45	43.99	2.24	47.66	1.50	45.85	1.25	55.01	ϕ	12.66
TK Comp. condilobasal	68.07	2.37	69.51	2.05	67.50	1.00	69.62	0.99	67.73	2.35	70.86	0.95	70.47	1.59	80.93	ϕ	15.28
LL1 Comp. bular	11.61	0.52	12.38	0.65	11.33	0.65	11.73	0.49	11.30	0.99	11.91	1.25	11.62	0.45	14.66	ϕ	6.08
NN1 Larg.zigomática	33.02	1.37	33.67	1.21	33.60	0.76	33.99	0.76	34.34	1.52	36.50	2.10	34.91	1.00	39.09	ϕ	10.72
OO1 Larg.entre.proc.parao	21.93	0.77	22.64	0.97	21.48	0.98	22.71	0.95	21.13	0.59	23.00	0.62	22.08	0.77	23.96	ϕ	4.69
PP1 Alt. craniana	17.51	0.68	17.85	0.27	16.94	0.55	18.70	0.51	18.22	0.35	18.85	0.98	18.16	0.30	20.51	ϕ	10.81
CM Alt. rostral	12.33	0.74	12.71	0.39	12.18	0.67	12.52	0.81	12.15	0.48	12.70	0.97	12.10	0.65	13.52	ϕ	1.82
RR1 Comp. mandibular	39.90	1.91	40.75	1.31	39.47	1.66	40.79	1.20	38.83	1.68	ϕ	ϕ	41.09	1.10	46.66	ϕ	ϕ

(ϕ) dado faltante, (n) tamanho da amostra, valor (F) e probabilidade associada (P) à variância.

Tabela 2. Coeficientes do Componente Principal 1 e 2 (CP1 e CP2) e das Variáveis Canônicas Independente-do-Tamanho 1 e 2 (VCI 1 e VCI 2) derivados da análise de 21 caracteres de populações de *Kerodon rupestris* e de *K. acrobata*.

CARACTERES	CP1	CP2	VCI 1	VCI 2
A1A Comprimento occipito-nasal	0.985	0.083	0.236	0.435
A1B Comprimento do nasal	0.961	0.098	0.016	0.449
A1C Comprimento rostral 1	0.972	0.024	0.228	0.323
SA1 Comprimento rostral 2	0.988	0.046	0.220	0.447
DD1 Largura rostral	0.904	0.013	0.180	0.478
EE1 Largura da constrição interorbitária	0.824	-0.032	0.379	0.132
BU Comprimento do frontal	0.882	0.017	0.512	0.414
UV Comprimento do parietal	0.713	0.082	0.237	0.180
FF1 Comprimento do diastema	0.983	0.007	0.170	0.362
F1G Comprimento da série molar superior	0.940	0.054	0.304	0.523
FH Comprimento do palato	0.973	-0.006	0.259	0.394
HQ Comprimento pós-palatal	0.904	0.102	-0.003	0.352
GG1 Largura do maxilar	0.927	0.117	0.165	0.436
II1 Comprimento do forâmem incisivo	0.818	-0.572	0.382	0.418
FP Comprimento basilar	0.992	0.045	0.211	0.417
TK Comprimento condilobasal	0.986	0.086	0.226	0.420
LL1 Comprimento bular	0.770	0.155	0.237	0.221
NN1 Largura zigomática	0.837	0.069	0.293	0.390
OO1 Largura entre os processos paraoccipitais	0.758	0.186	0.116	0.314
PP1 Altura craniana	0.832	0.041	0.457	0.226
CM Altura rostral	0.927	0.135	0.055	0.331
RR1 Comprimento mandibular	0.966	0.110	0.161	0.455

Os eixos de maior variação das amostras diferem ao longo do segundo componente principal (PC2) e indicam a orientação diferenciada da amostra de Botumirim (MG), que divergiu das demais. Ocorreu sobreposição entre as outras populações; entretanto pode-se observar discriminação das amostras de Itapajé (CE) e de sub-fósseis (BA) (Fig.3B).

Na Análise Discriminante Canônica Independente-do-Tamanho, incluindo as populações de *K. rupestris* e a de *K. acrobata*, as duas primeiras variáveis canônicas explicam 38,2% e 21,1% respectivamente, da discriminação morfométrica craniana entre os grupos não relacionada ao fator intrapopulacional de tamanho (Fig.4).

As populações de *K. acrobata* e *K. rupestris* foram completamente discriminadas ao longo da primeira variável canônica (VC1; Fig.4A). O comprimento do nasal, a altura craniana, o comprimento do forâmen palatino e a largura da constrição interorbitária

foram os caracteres que mais contribuíram para a diferenciação destas duas amostras em relação às demais (Tab.2).

As populações de *K. rupestris* provenientes de Botumirim (MG) e de Itapajé (CE) representaram os extremos da variação ao longo do segundo eixo (VC2), enquanto as demais populações ocuparam um espaço multivariado intermediário entre estas duas populações (Fig.4).

Elipses de 95% de confiança foram obtidas para os centróides para facilitar a interpretação dos padrões discriminatórios dentro de *K. rupestris* e entre *K. acrobata* e *K. rupestris* (Fig.4B). Para *K. rupestris*, na primeira variável canônica três grupos foram discriminados no espaço morfométrico: 1) Itapajé (CE), 2) Campos Sales (CE) + Missão Velha (CE) + Santana do Ipanema (AL) + Exú-Bodocó (PE) + Brejo Santo (CE) 3) Botumirim (MG) e sub-fósseis (BA). Um quarto grupo foi discriminado referente a amostra de *K. acrobata* (GO).

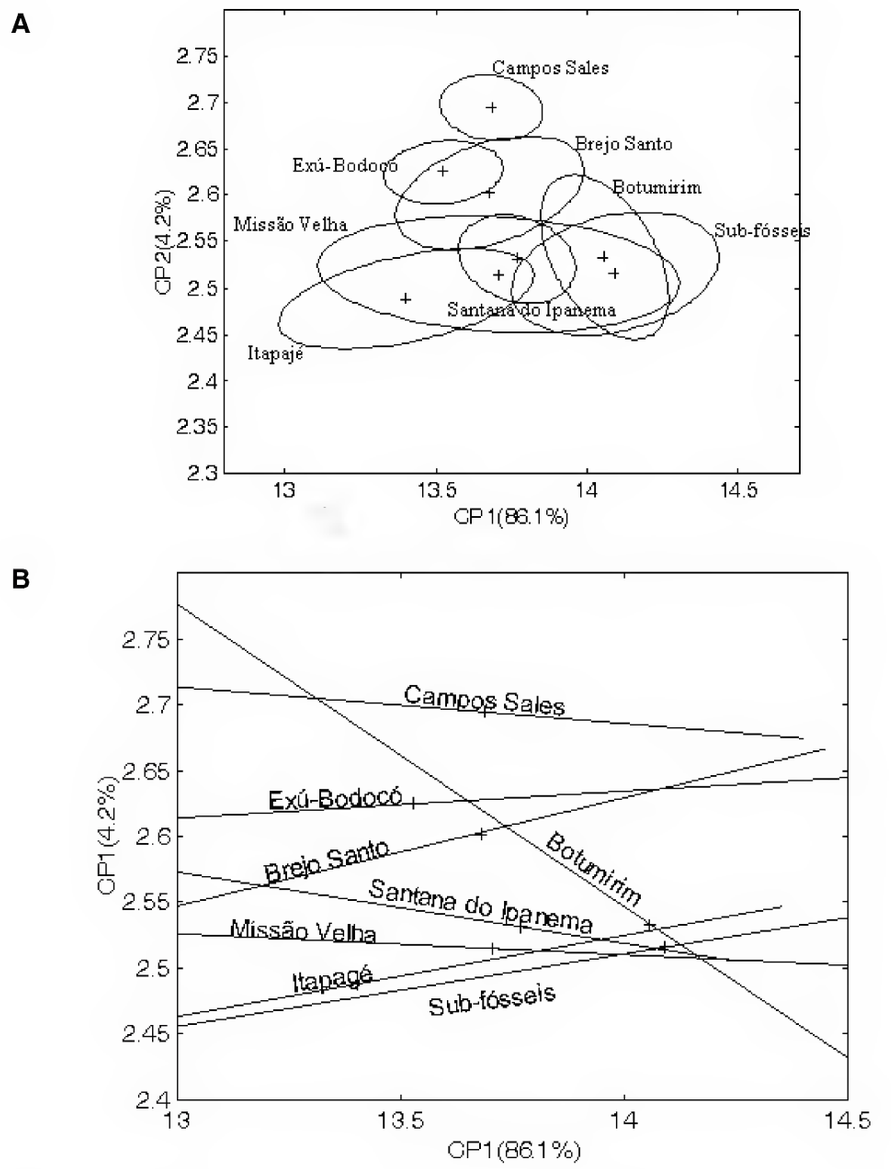

Fig.3- Análise de Componentes Principais (CP1 e CP2) realizada com amostras populacionais mais numerosas de *Kerodon rupestris*. (A) representação das elipses com 95% de confiança de oito populações de *K. rupestris* em relação ao primeiro (CP1) e ao segundo (CP2) componentes principais; (B) maiores eixos de variação das nove amostras populacionais. Os valores entre parênteses correspondem a porcentagens da variabilidade total contida em cada componente.

O padrão de agrupamento fornecido pelo método UPGMA demonstra que *K. acrobata* destaca-se claramente do contínuo formado pelas populações de *K. rupestris*, apresentando a maior distância de Mahalanobis em relação a todas as amostras. As amostras de *K. rupestris* dividem-se em três grupos principais: um formado pelas populações de Botumirim (MG) e a de sub-fósseis (BA), outro pela amostra de Itapajé e um grupo maior com dois subgrupos: o primeiro que inclui as amostras de Missão Velha (CE) e Santana do Ipanema (AL); e o segundo com as amostras de Exú-Bodocó (PE), Campos Sales (CE) unidas à amostra de Brejo Santo (CE) (Fig.5).

As duas amostras de *K. rupestris* de tamanho reduzido provenientes das localidades de Senhor do Bonfim (BA) e Guaribas (PI) foram probabilisticamente alocadas às demais amostras, incluindo *K. acrobata*. A população de Senhor do Bonfim (BA) associou-se fortemente à amostra de sub-fósseis (BA) (99%) enquanto a população de Guaribas (PI)

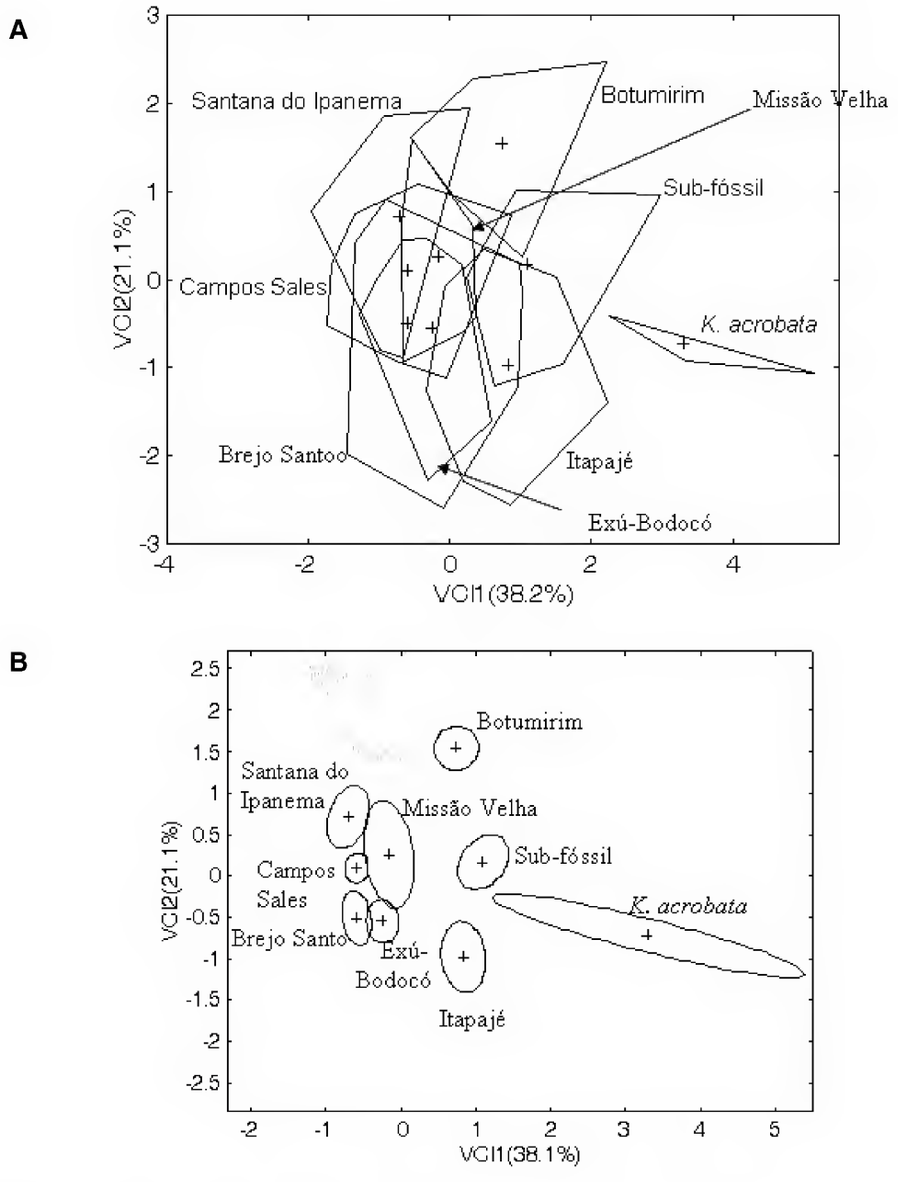

Fig.4- Análise Canônica Independente-do-Tamanho (VCI 1 e VCI 2). (A) Representação dos escores individuais de oito amostras numerosas de *Kerodon rupestris* e uma de *K. acrobata* em relação aos dois maiores eixos de discriminação independente-do-tamanho (VCI 1 e VCI 2). (B) Representação das elipses de 95% de confiança destas amostras em relação aos dois primeiros eixos de discriminação.

associou-se com as amostras de Itapajé (CE), *K. acrobata* (GO) e a de sub-fósseis (BA) respectivamente em 44,55%, 31,68% e 22,77% das interações de "bootstrap" (Tab.3).

Tabela 3. Alocações probabilísticas (%) das amostras numericamente pequenas de *Kerodon rupestris* (colunas) às amostras numericamente grandes (linhas) de acordo com os valores relativos da distância de Mahalanobis reiterados 1000 vezes.

	Senhor do Bonfim (BA)	Canto Verde (PI)
Campos Sales (CE)	0	0
Exú-Bodocó (PE)	0	0
Santana do Ipanema (AL)	0	0
Brejo Santo (CE)	0	0
Itapajé (CE)	0,01	0,45
Sub-fóssil (BA)	0,99	0,23
Botumirim (MG)	0	0
Missão Velha (CE)	0	0,01
K. acrobata (GO)	0	0,32

DISCUSSÃO

As análises quantitativas realizadas neste estudo mostraram a existência de variação geográfica significativa em caracteres cranianos morfométricos em populações de *K. rupestris*. A análise de componentes principais e a análise discriminante canônica independente-do-tamanho revelaram uma estrutura de variação das amostras em um cline de incremento de tamanho craniano no sentido geográfico norte-sul. A população de *K. acrobata* discrimina-se como uma unidade isolada no espaço multivariado e não se sobrepõe ao cline de dimensões cranianas encontrado para *K. rupestris*, o que confirma a distinção morfológica das duas espécies.

O padrão de variação craniana em *K. rupestris* pode ser interpretado à luz do reconhecimento de unidades subespecíficas neste táxon. BARROWCLOGH (1982) e THORPE (1987) sugerem que subespécies não poderiam ser reconhecidas com base em variação clinal, mas que deveriam ser detectadas a partir de populações que ocupassem regiões discretas no espaço

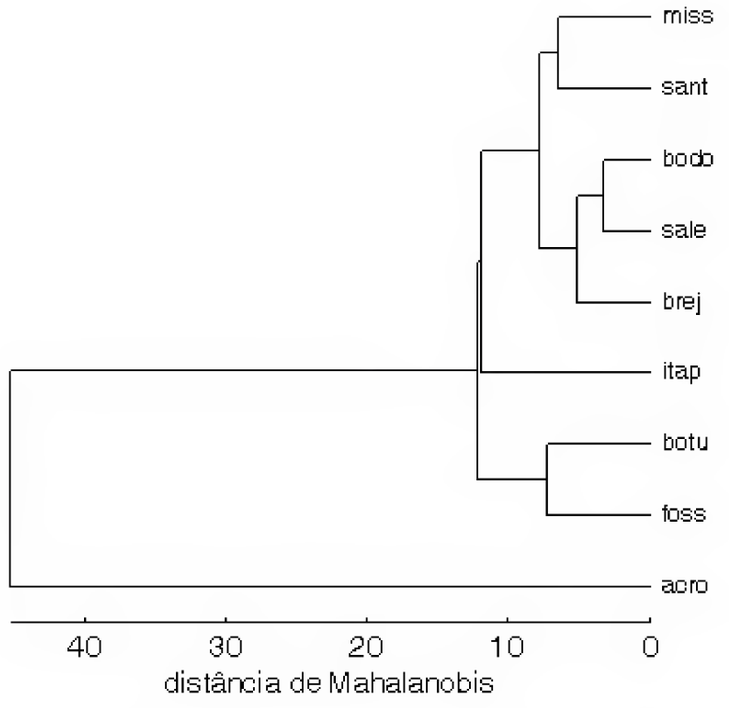

Fig.5- Dendrograma construído por UPGMA ilustrando os padrões de similaridade morfométrica de populações de *Kerodon rupestris* inferidos a partir das Distâncias de Mahalanobis. Abreviações das localidades: (miss) Missão Velha, (sant) Santana do Ipanema, (bodo) Exú-Bodocó, (sale) Campos Sales, (brej) Brejo Santo, (itap) Itapajé, (botu) Botumirim, (foss) Sub-fósseis, (acro) *Kerodon acrobata*.

multivariado de caracteres. Aos componentes de forma e tamanho têm sido atribuídos diferentes pesos na taxonomia e sistemática, sendo a variação na forma considerada como a mais relacionada à diferenciação genética entre populações (STRANEY, 1987). O tamanho craniano foi demonstrado ser fenotipicamente plástico no roedor *Thomomys bottae* como resposta à qualidade nutricional, enquanto que a variação da forma craniana mostrou-se correlacionada com diferenças genéticas entre subespécies reconhecidas (PATTON & BRYSKY, 1987). Posteriormente SMITH & PATTON (1988) relacionam o tamanho e a forma craniana com os componentes de diferenciação ecológicos e históricos (filogenéticos), sugerindo que unidades evolutivas independentes (subespécies, de acordo com estes autores) poderiam ser reconhecidas por unidades geográficas que mostrassem concordância no padrão da forma craniana e na variação genética. Este enfoque conceitual foi utilizado em alguns estudos de variação geográfica de pequenos mamíferos (PESSÔA & REIS, 1990; BANDOUCK & REIS, 1995; MOTOKAWA, 2003) tanto para distribuições continentais quanto para insulares.

Os dados craniométricos aqui estudados sugerem uma variação na forma e tamanho craniano estruturada geograficamente em *K. rupestris*. Embora ocorra sobreposição entre as populações geograficamente centrais, as análises de Componentes Principais e das Variáveis Canônicas evidenciaram que as populações de Botumirim (ao sul da distribuição geográfica) e a de Itapajé (ao norte da distribuição) estão completamente discriminadas no espaço multivariado. Estas populações do norte e do sul poderiam estar submetidas a processos de diferenciação em relação ao grupo populacional central, constituído por Campos Sales, Exú-Bodocó, Santana do Ipanema, Missão Velha e Brejo Santo.

MOTOKAWA (2003), estudando populações de *Crocidura dsinezumi* (Insectivora) distribuídas em ilhas no mar do Japão, associa a variação em cline de decréscimo de tamanho craniano entre as populações de norte para o sul daquela região a eventos históricos de separações geológicas entre as ilhas durante o Pleistoceno, época da ocupação e dispersão dos animais, e às modificações ambientais ao longo do tempo decorrido desde então. Se a diferenciação morfológica em *K. rupestris* for interpretada com base nas alterações ambientais ao longo do tempo geológico é possível relacioná-la à expansão da Caatinga no final do Pleistoceno e às atuais condições climáticas e isolamento dos afloramentos rochosos na região.

Kerodon rupestris é endêmico do semi-árido brasileiro, de ocorrência restrita a afloramentos rochosos (ALHO, 1982; GUIDON *et al.*, 1993). As modificações climáticas no final do Pleistoceno-Holoceno, introduziram mudanças no ecossistema dominante do Brasil intertropical, com a expansão das regiões semi-áridas (AB'SÁBER, 2003). Florestas tropicais que antes dominavam o cenário nordeste do Brasil teriam se retraído no sentido leste-oeste do continente em detrimento da expansão de "ilhas" anteriormente isoladas de Caatinga no nordeste e de Cerrado, expondo e isolando efetivamente os afloramentos rochosos. A presença de primatas atelídeos fósseis, que só poderiam ter vivido em grandes florestas úmidas, convivendo com formas pastadoras próprias de ambientes abertos, corroboram a hipótese de expansão da Caatinga nos últimos 11.000 anos (CARTELLE, 1994; CARTELLE & LESSA, 1988; OLIVEIRA-FILHO & RATTER, 1995; DE-OLIVEIRA *et al.*, 1997; VIVO, 1997). As condições climáticas das populações localizadas mais ao norte da distribuição de *K. rupestris* estão inseridas em um sistema definido por AB'SÁBER (2003) como semi-árido acentuado ou subdesértico, enquanto que as localizadas mais ao sul encontram-se nos domínios do semi-árido moderado ou de transição, com faixas sub-úmidas. Os fatos mencionados acima poderiam ser usados como argumentos na explicação da variação observada em *K. rupestris* ao longo da sua distribuição geográfica e no atual isolamento de *K. acrobata* em uma região de clima semi-úmido.

Processos ecológicos recentes ou históricos (filogenéticos) poderiam também ser utilizados para explicar esta variação, sendo possível identificar para os primeiros, causas oriundas de condições bióticas, mimetismo, deslocamento de caracteres e competição intraespecíficas, ou ainda as condições físicas como adaptação ao substrato ou às condições climáticas. Já os fatores históricos, quando resultantes do isolamento de populações como colonização de "ilhas" ou segmentação de uma espécie por um evento geológico, indicam que as linhagens divergentes podem ter sido derivadas por efeito do fundador ou deriva genética (THORPE, 1983). Mudanças subseqüentes na população podem resultar de isolamento e contato secundário de populações resultando em zonas de transição e sobreposição de linhagens.

A relação destes fenômenos com o que ocorre no gênero *Kerodon* já havia sido considerada por João Moojen em 1955 quando argumentou que a significativa diferenciação observada em uma nova forma do gênero, encontrada em Goiás, só poderia ser deduzida através de isolamento geográfico causado pela descontinuidade dos serrotes pedregosos distribuídos no Cerrado e na Caatinga (AVILA-PIRES, 1995). Estas considerações coincidem com o que se observa ao longo da distribuição de *K. rupestris*, cujos afloramentos rochosos, habitados por estes indivíduos, encontram-se isolados uns dos outros. Entretanto, será necessário avaliar geograficamente estes afloramentos ao longo de toda a distribuição da espécie no sentido de esclarecer se as distâncias entre eles estão correlacionados com a diferenciação morfológica evidenciada nas análises craniométricas.

O padrão clinal encontrado para *K. rupestris* não tem sido considerado para a delimitação de subspécies quando interpretado à luz dos critérios sugeridos por THORPE (1987). No entanto, níveis diferenciados de variação infraespecífica estão ocorrendo entre as populações estudadas. O padrão observado em *K. rupestris* sugere uma estrutura de variação que pode estar associada ao isolamento dos diferentes afloramentos rochosos habitados pela espécie. Ficou evidente que as amostras do norte e do sul ocuparam diferentes regiões do espaço multivariado de caracteres, sendo possível definir a disposição de três grupos populacionais discriminados com relação a um contínuo geográfico. Entretanto, para se definir o nível de diferenciação infraespecífica entre as amostras analisadas, serão necessários estudos adicionais associados com os limites de variação genética ao longo da distribuição geográfica destas populações.

AGRADECIMENTOS

Aos responsáveis pelos acervos do Museu Nacional (UFRJ), Museu de Zoologia (USP) e Museu de História Natural da PUC-Minas Gerais, pelo empréstimo de material e apoio durante os trabalhos nas respectivas coleções de mamíferos; à Stella Maris S. Franco (Museu Nacional/UFRJ – MN) e Dr. Alexandre R. Percequillo (MZUSP), pela orientação técnica nas citadas coleções; à Dra. Márcia Gomide (UFCE), Dra. Somália Vianna (UECE) e Dr. Danilo Souza (Secretaria de Saúde do Ceará), pelo apoio logístico nas coletas em Itapajé (CE); à Joelma de Lourdes Silva, pelas coletas em Botumirim (MG); a Aloísio Cardoso (CRA-BA), pelo apoio logístico em Iraquara; a M.F.Pessôa, pelo desenho do crânio; a José Ricardo Ribeiro (UFRJ), pela confecção do mapa. De forma muito especial, *in memoriam*, os autores agradecem ao Dr. João Moojen de Oliveira pela dedicação e competência no estudo dos roedores brasileiros, impressos em uma valiosa obra literária, e pela organização de imprescindíveis coleções científicas. Ao apoio financeiro da Coordenação de Aperfeiçoamento de Pessoal (CAPES) e do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

REFERÊNCIAS BIBLIOGRÁFICAS

AB'SÁBER, A.N., 2003. **Os Domínios de Natureza no Brasil: Potencialidades Paisagísticas**. São Paulo: Ateliê Editorial, 160p.

ALHO, C.J.R., 1982. Brazilian rodents: their habitats and habits. In: MARES, M.A & GENOWAYS, H.H. (Ed.) - **Mammalian Biology in South America**. Pittsburgh: Special Publication, Pymatuning Laboratory of Ecology, University of Pittsburgh, p.143-166.

AVILA-PIRES, F.D., 1995. Lei da Espécie. **Revista Brasileira de Zoologia**, Curitiba, **12**(4):1015-1023.

BANDOUK, A.C. & REIS, S.F., 1995. Craniometric variation and subespecific differentiation in *Thricomys apereoides* in northeastern Brazil (Rodentia: Echimyidae). **Zeitschrift fur Sauegetierkunde**, Jena, **60**:176-185.

BARROWCLOGH, J.F., 1982. Geographic variation, predictiveness and subspecies. **The Auk,** Albuquerque, **99**:601-603.

BERBERT-BORN, M. & KARMANN, I., 2000. Lapa dos Brejões – Vereda Romão Gramacho, Chapada Diamantina, Bahia. In: SCHOBBENHAUS, C.; CAMPOS, D.A.; QUEIROZ, E.T.; WINGE, M. & BERBERT-BORN, M. (Eds.) **Sítios Geológicos e Paleontológicos do Brasil**. Disponível em <http://www.unb.br/ig/sigep/sitio016/sitio016.htm>. Acesso em 18 abr. 2004.

CARTELLE, C., 1992. **Edentata e megamamíferos herbívoros extintos da Toca dos Ossos (Ourolândia, BA)**. Belo Horizonte. 301p. Tese (Doutorado). Programa de Pós-Graduação em Morfologia, Universidade Federal de Minas Gerais.

CARTELLE, C., 1994. Presença de *Lama* (Artiodactyla, Camelidae) no Pleistoceno Final-Holoceno da Bahia. **Acta Geologica Leopoldensia**, Porto Alegre, **17**(39/1):399-410.

CARTELLE, C. & LESSA, G., 1988. Descrição de um novo gênero e espécie de Macraucheniidae (Mammalia, Litopterna) do Pleistoceno do Brasil. **Paulacoutiana**, Porto Alegre. **3**:3-26.

DE-OLIVEIRA, P.E.; BARRETO, A.M.F. & SUGUIO, K., 1997. Paleovegetação e paleoclimas do Quaternário tardio da caatinga brasileira: o campo de dunas do médio Rio São Francisco. In: CONGRESSO BRASILEIRO DE ESTRATIGRAFIA DO QUATERNÁRIO, 6., Curitiba. **Anais...**, Curitiba: Universidade Federal do Paraná, p.473-477.

GUIDON, N.; DA-LUZ, M.; GUERIN, C. & FAURE, M., 1993. La toca de Janela da Barra do Antoniao et les autres sites paleolithiques karstiques de l'aire

archeologique de São Raimundo Nonato (Piaui, Bresil): et des recherches. In: XII CONGRES INTERNATIONAL DES SCIENCES PRÉHISTORIQUES ET PROTOHISTORIQUES, 3., Bratislava. **Actes...**, Bratislava: Institut Archeologique de l'Academie Slovaque des Sciences, p.483-491.

LACHER, T.E., 1979. Rates of growth in *Kerodon rupestris* and an assessment of its potential as a domesticated food source. **Papéis Avulsos de Zoologia**, São Paulo, **33**:67-76.

LESSA, G., 2004. **Variação morfométrica e citogenética em *Kerodon rupestris* (Wied, 1820) (Rodentia: Caviidae)**. 127p. Tese de Doutorado, Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro.

LESSA, G.; CARTELLE, C.; FARIA, H.D. & GONÇALVES, P.R., 1998. Novos achados de mamíferos carnívoros do Pleistoceno Final-Holoceno em grutas calcárias do estado da Bahia. **Acta Geologica Leopoldensia**, Porto Alegre, **21**(46/47):157-169.

MANLY, B.F.J., 1994. **Multivariate Statistical Methods - A primer**. 2.ed. Londres: Chapman & Hall. 215p.

MARES, M.A. & OJEDA, R.A., 1982. Patterns of diversity & adaptation in South American hystricognath rodents., In: MARES, M.A & GENOWAYS, H.H. (Eds.) **Mammalian Biology in South America**. Pittsburgh: Special Publication, Pymatuning Laboratory of Ecology, University of Pittsburgh, p.393-412.

MOOJEN, J.; LOCKS, M. & LANGGUTH. A., 1997. A new species of *Kerodon* Cuvier, 1825 from the State of Goiás, Brazil (Mammalia, Rodentia, Caviidae). **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (377):1-10.

MOTOKAWA, M., 2003. Geographic variation in the japanese white-toothed shrew *Crocidura dsinezumi*. **Acta Theriologica**, Varsóvia, **48**(2):145-156.

NEFF, N.A. & MARCUS, L.F., 1980. **A Survey of Multivariate Methods for Systematics**. New York: Publicação privada. 230p.

OLIVEIRA, J.A., 1992. **Estrutura da variação craniana em populações de *Bolomys lasiurus* (Lund, 1814) (Rodentia: Cricetidae) do Nordeste do Brasil**. Rio de Janeiro. 107p. Dissertação de Mestrado, Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro.

OLIVEIRA, J.A.; GONÇALVES, P.R. & BONVICINO, C.R., 2003. Mamíferos da Caatinga. In: LEAL, I.R.; TABARELLI, M. & DA-SILVA, J.M.C. (Eds.) **Ecologia e Conservação da Caatinga**. Recife: Publicação Especial, Universidade Federal de Pernambuco, 804p.

OLIVEIRA FILHO, A.T. & RATTER, J.A., 1995. A study of the origin of Central Brazilian forest by the analysis of plant species distribution patterns. **Edinburg Journal of Botanic**, Edinburgh, **52**(2):195-203.

PATTON, J.L. & ROGERS, M.A., 1983. Systematic implications of the non-geographic variation in spiny rats *Proechimys* (Echimyidae). **Zeitschrift fur Sauegetierkunde**, Jena, **48**:363-370.

PATTON, J.L. & BRYLSKI, P.V., 1987. Pocket gophers in alfafa fields: causes and consequences of habitat-related body size variation. **The American Naturalist**, Chicago, **130**(4):493-505.

PATTON, J.L. & SMITH, M.F., 1989. Population structure and the genetic and morphologic divergence among pocket gopher species (genus *Thomomys*). In: OTTE, D. & ENDLER, J.A (Eds.) **Speciation and its Consequences**. Sunderland: Sinauer Publications. p.284-304.

PESSÔA, L.M. & REIS, S.F., 1990. Geographic variation in *Proechimys dimidiatus* (Guenther) (Rodentia: Echimyidae). **Zoologisher Anzeiger**, Jena, **225**(5/6):383-390.

REIS, S.F.; DA-CRUZ, J.F. & VON-ZUBEN, C.J., 1988. Análise multivariada da evolução craniana em roedores caviíneos: convergências de trajetórias ontogenéticas. **Revista Brasileira de Genética**, Ribeirão Preto, **11**(3):633-641.

REIS, S.F.; PESSÔA, L.M. & STRAUSS, R.E., 1990. Application of size-free canonical discriminant analysis to studies of geographic differentiation. **Revista Brasileira de Genética**, Ribeirão Preto, **13**(3):509-520.

SMITH, M.F. & PATTON, J.L., 1988. Subspecies of pocket gophers: casual basis for geographic differentiation in *Thomomys bottae*. **Systematic Zoology**, Levittown, **37**:163-178.

SOKAL, R.R. & ROHLF, F.J., 1981. **Biometry**. Second Edition. San Francisco: Freeman. 887p.

STRANEY, D.O., 1987. Variance partitioning and nongeographic variation. **Journal of Mammalogy**, Provo, **59**:1-11.

STRAUSS, R.E., 1985. Static allometry and variation in body form in the South American catfish genus *Corydoras* (Callichthyidae). **Systematic Zoology**, Levittown, **34**:381-396.

STRAUSS, R.E.; ATANASSOV, M.N. & OLIVEIRA, J.A., 2003. Evaluation of the principal-component and the expectation-maximization methods for estimating missing data in morphometric studies. **Journal of Vertebrate Paleontology**, Northbrook, **23**(2):284-296.

THORPE, R.S., 1983. A review of numerical methods for recognising and analysing racial differentiation. In: FELSENSTEIN, J. (Ed.) **Numerical Taxonomy**. Nova Iorque e Londres: Springer Verlag, NATO Asi Series. Series G, Ecological Sciences 1. p.404-423.

THORPE, R.S., 1987. Geographic variation: a synthesis of cause, data, pattern and congruence in relation to subspecies multivariate analysis and phylogenesis. **Bollettino di Zoologia**, Modena, **54**:3-11.

VAN-GELDER, R.G., 1968. The genus *Conepatus* (Mammalia, Mustelidae): variation within a population. **American Museum Novitates**, Nova Iorque, **2322**:1-37

VIVO, M., 1997. Mammalian evidence of historical ecological change in the caatinga semiarid vegetation of Northeastern Brazil. **Journal of Comparative Biology**, Ribeirão Preto, **2**(1):65-73.

WOODS, C.A., 1983. Suborder Hystricognathi. In: WILSON, D.E. & REEDER, D.M. (Eds.) **Mammal Species of the World**. Washington: Smithsonian Institution Press. p.771-806.

APÊNDICE

EXEMPLARES EXAMINADOS

Kerodon rupestris – BRASIL - MINAS GERAIS: Botumirim (16°52'S 43°01'W) - MN 65142-65151, 67465-67468. BAHIA: Senhor do Bonfim (10°27'S 40°11'W) - MZUSP 2610-2612, 2614, 2615; Iraquara (12°15'S 41°36'W) - MN 68092-68094. ALAGOAS: Santana do Ipanema (9°22'S 37°14'W) - MN 2627, 26756-26760, 26763-26768, 26770-26774, 26761, 26762, 26769. CEARÁ: Brejo Santo (7°29'S 39°00'W) - MN 7825, 26314, 26316-26318, 26594-26610. Campos Sales (7°04'S 40°23'W) - MN 26220-26223, 26260-26264, 26267, 26268, 26279, 26283-26291, 26301-26304, 26309- 26312, 26320, 26342-26356, 26439, 26449-26451, 26457-26503, 26505-26535, 26537-26593, 26637, 26638, 43502-43508. Itapajé (3°41'S 39°34'W) - MN 22733, 26668-26685 26687-26691, 67469. Missão Velha (7°15'S 39°08'W) - MN 26277, 26366, 26367, 26433-26435, 26650-26652. PERNAMBUCO: Exú (7°47'S 39°55'W) - MN 25701, 25702, 26700-26704, 26710-26717. Bodocó (7°31'S 39°43'W) - MN 26705-26709, 26733, 26734, 26736, 26737, 26739, 26750, 26754, 26755, 26718-26720, 26721-26725, 26727. 26751. PIAUÍ: Guaribas (9°19'S 45°29'W) - PNSCO (número de campo - MZUSP) 6, ARP (número de campo - MZUSP) 65.

Sub-fósseis – BRASIL - BAHIA: Gruta dos Brejões (11°00'S 41°25'W) - Morro do Chapéu; Toca dos Ossos (10°58'S 40°45'W) - Ourolândia; Toca da Boa Vista (10°31'S 40°20'W) - Campo Formoso - MCL 1849, 11234, 11235, 11242-11249, 11251, 11254-11256, 11269.

Kerodon acrobata – BRASIL - GOIÁS: Posse de Goiás (13°50'S 46° 50'W) - MN 22728-22731 (série-tipo).

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.89-112, jan./mar.2005
ISSN 0365-4508

A NEW GENUS FOR *LONCHERES GRANDIS* WAGNER, 1845, WITH TAXONOMIC COMMENTS ON OTHER ARBOREAL ECHIMYIDS (RODENTIA, ECHIMYIDAE) [1]

(With 14 figures)

GILSON E. IACK-XIMENES [2, 4]
MARIO DE VIVO [2]
ALEXANDRE R. PERCEQUILLO [3]

ABSTRACT: A study of arboreal echimyids in Brazilian and European collections revealed a number of morphological traits supporting the recognition of *Loncheres grandis* Wagner, 1845, currently included in *Makalata* Husson, 1978, as a full genus. Our proposition of a new genus for *L. grandis* changed the species content of *Makalata*, what led us to reformulate the generic diagnosis for this genus and other arboreal echimyids as well. The new genus can be distinguished by several external characters including its color pattern, striking differences in tail pilosity, and palmar and plantar pad morphology. Osteological distinguishing traits includes the shape of nasals, the structure of the postorbital process of the zygomatic arch, petrosal morphology, the presence of a posterior maxillary foramen, the crown pattern of molariform teeth, and *baculum* morphology.

Key words: Rodentia, Hystricognathi, Echimyidae, *Loncheres grandis*, *Makalata, Phyllomys, Echimys*.

RESUMO: Novo gênero para *Loncheres grandis* Wagner, 1845, com comentários taxonômicos sobre outros equimídeos arborícolas (Rodentia, Echimyidae).

O estudo de equimídeos arbóreos em coleções brasileiras e européias revelou diversas características morfológicas sustentando o reconhecimento de *Loncheres grandis* Wagner, 1845, atualmente incluído em *Makalata* Husson, 1978, como um gênero válido. Nossa proposta de um novo gênero para *L. grandis* alterou o conteúdo específico de *Makalata*, o que nos levou a reformular a diagnose genérica para este gênero, assim como para outros equimídeos arbóreos. O novo gênero pode ser distinguido através de várias características externas tais como seu padrão de coloração, uma notável distinção da pilosidade caudal e a morfologia das almofadas das patas anteriores e posteriores. Características osteológicas distintivas incluem a forma dos nasais, a estrutura do processo pós-orbital do arco zigomático, a morfologia do petroso, a presença de um foramen maxilar posterior, a morfologia da coroa dos dentes molariformes e a forma do báculo.

Palavras-chave: Rodentia, Hystricognathi, Echimyidae, *Loncheres grandis*, *Makalata, Phyllomys, Echimys*.

INTRODUCTION

TATE (1935) created a broad concept for *Echimys* Cuvier, 1809, in which the genus occurred in all of the tropical South America to the east of the Andes, and included all species presently placed within the genera *Makalata* Husson, 1978, *Phyllomys* Lund, 1839, *Callistomys* Emmons & Vucetich, 1998, and *Echimys* itself. Despite MOOJEN's (1948, 1952) attempt to break *Echimys* by recognizing *Phyllomys* from eastern Brazil as a distinct genus, most authors (CABRERA, 1961; WOODS, 1993; NOWAK, 1999) simply continued to follow TATE (1935). HUSSON (1978) opened the way to a better understanding of the systematics of arboreal echimyids by creating *Makalata* to include *Echimys armatus* I. Geoffroy, 1838.

Since Husson's contribution several important steps have followed, all of them resulting in a much more refined view of groups of species within Tate's broad concept of *Echimys*: the separation of southeastern Brazilian species first under *Nelomys* Jourdan, 1837 (EMMONS & FEER, 1990) and later *Phyllomys* Lund, 1839 (LEITE, 2001; EMMONS *et al.*, 2002)

[1] Submitted on June 18, 2004. Accepted on January 25, 2005.
[2] Museu de Zoologia da Universidade de São Paulo, Mastozoologia. Av. Nazaré, 481, Ipiranga, 04263-000, São Paulo, SP, Brasil.
[3] Universidade Federal da Paraíba, Centro de Ciências Exatas e da Natureza, Departamento de Sistemática e Ecologia, Mastozoologia. Caixa Postal 5133, João Pessoa, 58051-970, PB, Brasil.
[4] E-mail: giliackx@yahoo.com.

and the erection of *Callistomys* by EMMONS & VUCETICH (1998) to include *Echimys pictus* from the coastal forests of the Brazilian State of Bahia.

Here we propose a new genus for *Loncheres grandis* Wagner, 1845. This species was part of the species content of TATE's (1935) *Echimys* and was later transferred to *Makalata* by EMMONS & FEER (1997). We believe that *Loncheres grandis* does not belong to neither *Makalata* nor *Echimys*, and in fact to no other currently available arboreal echimyid genus. The recognition of this new genus led us to a redefinition of the species content of both *Echimys* and *Makalata* and their generic diagnostic features.

Brief taxonomic history, with special reference to *Loncheres grandis* Wagner, 1845

WAGNER (1845) described *Loncheres grandis* based on a specimen collected by J. Natterer in Brazil, attributing his placement of the new species in *Loncheres* Illiger, 1811, on its "affinities" with *L. cristatus* (a junior synonym of *Echimys chrysurus*). A few years later, WAGNER (1850) distinguished two groups of species in *Loncheres*, the first including all species with hairy tails, namely *L. grandis*, *L. nigrispina*, and *L. unicolor* (the latter two species currently in *Phyllomys* Lund, 1839), and the second group including the naked-tailed species *L. macrura* and *L. armata* (both currently in *Makalata* Husson, 1978).

PELZELN (1883), in his contribution dealing with the material obtained by J. Natterer, was able to restrict the type locality of *L. grandis* as Manaqueri, Solimões River, Amazonas. This decision had some importance because *Loncheres* was a broad genus, containing arboreal echimyid species from the entire South American continent. The increase in knowledge on the geographic distribution of its species eventually led to the avoidance of errors such as that by TROUESSART (1880), who included *L. grandis* under *L. blainvillei* (*sic*; currently in *Phyllomys*).

ALLEN (1899), acting as first reviewer, fixed *Myoxus chrysurus* Zimmermann, 1780 as type species of *Loncheres* and *Echimys spinosus* Desmarest, 1817 as type species of *Echimys*. This act was intended to keep both genera as distinct and valid, however the fixation of the type species of *Echimys* was not made according to the rules of the zoological nomenclature (article 30 of the International Commitee of Zoological Nomenclature, see TATE, 1935), and TATE (1935) corrected this by fixing *Myoxus chrysurus*, as the type species of *Echimys*. This act made *Loncheres* definitely a synonym of *Echimys*.

Even before Tate's solution to the question of the validity of *Loncheres* and *Echimys*, authors begun to group many species of arboreal echimyids in the genus *Echimys*. TROUESSART (1905) was the first to transfer species that he had formerly (TROUESSART, 1880) placed in *Loncheres* to the genus *Echimys* Cuvier, 1809, and THOMAS (1916) included *L. grandis* in *Echimys*. Later, THOMAS (1928) described *E. saturnus* and compared it with *E. chrysurus* and *E. grandis*.

At the time of Tate's publication of the taxonomic history of "hystricoid" rodents (TATE, 1935), the genus *Echimys* included 24 valid species, which that author decided to distribute in two species groups, his "hairy" and "naked-tailed" groups. This division does not correspond to any of the currently recognized genera, but certainly indicates that Tate was aware of the diversity within *Echimys*. ELLERMAN (1940) also tried to group species within *Echimys*, but despite his employment of a number of external and cranial characters, his species groups were also heterogeneous by current standards.

MOOJEN (1948, 1952) was the first to group a number of species previously under *Echimys* in the genus *Phyllomys* Lund, 1839, but subsequent authors, notably CABRERA (1961), ignored his opinion. The recognition that *Echimys* was a heterogeneous assemblage of species became widely accepted only after HUSSON (1978) erected *Makalata* to contain *Echimys armatus* I. Geoffroy, 1838. This led to further studies of the many species contained in the genus *Echimys*. EMMONS & FEER (1990, 1997) adopted *Nelomys* Jourdan, 1837 for several eastern Brazilian species, an usage that was later corrected by EMMONS *et al.* (2002) through the use of *Phyllomys* for the same group of species. An additional consequence of the same trend was the creation of the genus *Callistomys* EMMONS & VUCETICH, 1998 for *Nelomys pictus* Pictet, 1838.

Evidently, changing the species content of *Echimys* by creating or revalidating genera to contain subsets of its species, made the definition of those an important issue, that it is still under progress. EMMONS & FEER (1997) included *E. grandis* in *Makalata* without offering justification. In our opinion this happened due to improper characterization of both *Echimys* and *Makalata*. We believe that *Echimys grandis* belong in a separate genus, which we describe bellow. Additionally we provide comparisons between our new monotypic genus and other genus level taxa which species were previously included within *Echimys*.

METHODS

We examined 317 specimens (Appendix I) of *Echimys*, *Makalata*, *Loncheres grandis* and *Phyllomys* deposited in the following collections: Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Nacional - Rio de Janeiro (MN); The Natural History Museum, London (BMNH); Museum für Naturkunde, Berlin (MNK); Naturhistorika Riksmuseet, Stockholm (NRM); Zoologische Staatsammlung, München (ZSM); Naturhistorisches Museum, Wien (NMW); Zoological Museum, University of Copenhagen (ZMUC), and Musée Nationale d´Histoire Naturelle, Paris (MNHN). Locality records for specimens examined can be found in Appendix II.

We have recorded the external measurements from the specimen's tags as follows: 1) head and body length (HB); 2) tail length (T); 3) ear length (E); and 4) hind foot length (HF). When the alternative "total length" was given instead of "head and body length", we have subtracted the tail length values from the total length.

We have recorded 15 skull measurements directly from skulls to the nearest 0.01mm. Measurements were based on PATTON & ROGERS (1983), and their definitions, as employed in this study are: 1) Skull length (SL): from the tip of the nasals to the posteriormost part of the occipital region; 2) Zygomatic breadth (ZB): largest distance across the external sides of the zygomatic arches; 3) Frontal constriction (FC): the smaller distance across the orbital border of frontals; 4) Nasal length (NL): greatest distance from the tip to the posteriormost part of nasals; 5) Squamosal breadth (SB): distance across the external projection of the squamosal crest taken at the level of the external auditory meatus; 6) Rostrum breadth (RB): distance across both sides of the rostrum at the premaxilar-maxilar suture; 7) Bullar length (BL): greatest length of the bulla, from anteriormost portion to the posterior border nearest to the paraoccipital process; 8) Postpalatal length (PPL): from the anteriormost border of the foramen magnum to the anteriormost edge of the mesopterygoid fossa; 9) Palatal length (PL): from the alveolar edge of incisors to the anteriormost edge of the mesopterygoid fossa; 10) Maxillary toothrow length (TRL): largest distance from the anteriormost border of the fourth premolar to the posteriormost border of the third molar; 11) Maxillary breadth (MB): greatest distance across the fourth premolars taken from their alveolar borders; 12) First molar breadth (M1B): greatest distance from lingual to buccal borders of the first upper molar at tip of crown level; 13) Braincase width (BW): taken across the outermost borders of parietals at their contact with the squamosals; 14) Mandible length (MBL): from the lingual border of the incisor's alveolus to the posteriormost border of the postcondyloid process; 15) Mandible height (MH): shortest distance taken vertically from the uppermost part of the condyloid process to a plane passing from the lower edge of the symphiseal suture to the lowermost edge of the angular process.

We recognized three dental age classes, based on the eruption of the maxillary teeth: 1) young: specimens with third upper molar unerupted; 2) subadult: specimens with the third upper molar in the process of eruption; 3) adult: specimens with all maxillary teeth erupted.

We employed WAHLERT (1974, 1983, 1985) and WOODS & HOWLANDS (1979) for the nomenclature of cranial foramina. Dental nomenclature (Fig. 1) is modified from LAVOCAT (1976) with further considerations of BUTLER (1985), JAEGER *et al.* (1985), FLYNN *et al.* (1986), JAEGER (1989), BRYANT & MCKENNA (1995), and CANDELA (1999a, b; 2002). We employed DIDIER (1962) and PATTON (1987) for *baculum* nomenclature.

RESULTS

Order Rodentia Bowdich, 1821
Suborder Hystricognathi Tullberg, 1899
Family Echimyidae Gray, 1825

Toromys gen.nov.

Loncheres: Wagner, 1845:145, part.
Echimys: Trouessart, 1905:504, part.
Makalata: Emmons & Feer, 1997:236, part.

Type-species: *Loncheres grandis* Wagner, 1845.

Geographic distribution – Known records of *Toromys grandis* are depicted in figure 2. The species was previously known to occur along both banks of the Rio Amazonas (EMMONS & FEER, 1990, 1997; EISENBERG & REDFORD, 1999). Here we extend its distribution to include the species' type locality, Manaqueri, at the lower Rio Solimões (Amazonas, Brazil) and the mid to lower sections of the Rio Tapajós (Pará, Brazil). EMMONS & FEER (1997) suggested that this rodent prefers the proximity of water, particularly the seasonally flooded forest ("várzea"), and the distribution here presented supports this claim. We believe that further collecting may demonstrate the presence of *Toromys* along other tributaries of Rio Amazonas.

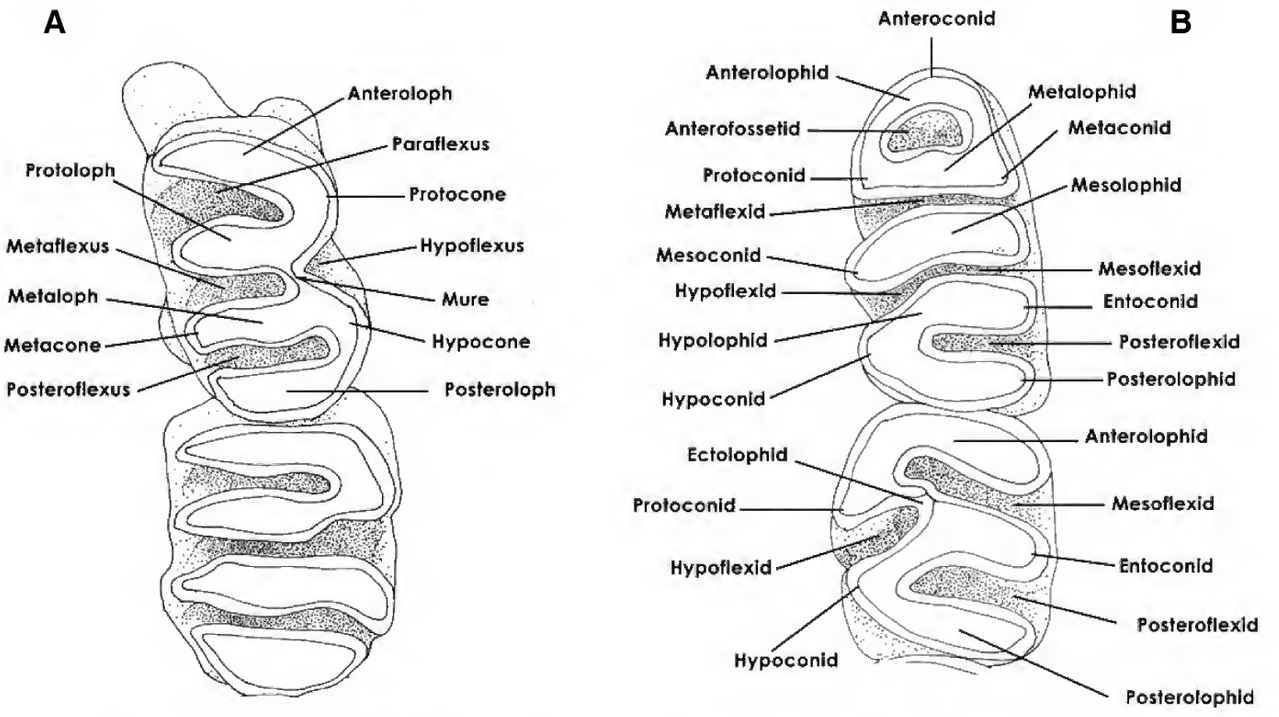

Fig.1- Dental nomenclature for the molariforms: (A) upper molariforms, (B) lower molariforms.

Etymology – "Toro" (= local name in Amazon region to arboreal echimyids) + "mys" (= rat). Arboreal Amazonian echimyins are locally known as "rato-toró" or "toró", which is the onomatopoeic Portuguese for the vocalizations of these rodents. *Toromys grandis* is specifically known as "Toró preto" (black Toró).

The genus is masculine.

Species included – Only the type species, *Loncheres grandis* Wagner, 1845 is currently included in the genus.

Diagnosis – *Toromys* is identifiable by its color pattern of body with golden and black upper parts, blackish head sprinkled with gold, and black tail; body covered with setiforms and aristiforms as soft spines (definition of "soft spines" is made under "Comparisons", below); tail fully covered by hairs (scales not visible) but without a distal hair tuft; small tubercular rugosities between plantar and palmar pads in hands and feet; nasals medially constricted; external auditory meatus of *Toromys* is separated from squamosal bone by a thin ridge of petrosal bone; posterior maxillary foramen present; upper molariform teeth with protoloph and metaloph connected by a slender mure.

Description

External Measurements: A large Echimyinae rodent with head and body length ranging from 275 to 354mm (mean=303mm, n=45), tail frequently shorter than head and body length ranging from 244 to 361mm (mean=285mm, n=42); ear round and short, from 15 to 25mm (mean=19.5mm, n=27); and hind foot length varying from 40 to 65mm (mean=52.8mm, n=45).

Pelage and coloration: Head darker than body; dorsally and laterally black sprinkled with gold; quantities of black and gold varying individually, from black slightly mottled with gold to uniformly sprinkled with gold and black; variation related to the number of monochromatic black hairs to black hairs with subterminal gold bands. Mystacial vibrissae thick and long, entirely black, reaching or extending beyond the pinnae. Mental region and throat lighter than sides and dorsum of head, with variable amounts of straw yellow. Ears round, hairs black; external face of pinnae slightly hirsute, with short black hair; internal face of pinnae slightly hirsute, with longer black hairs in the outer border of pinnae. Dorsal and lateral pelage of body composed largely by narrow and soft spines; general coloration from black sprinkled with gold to gold sprinkled with black; mid dorsum slightly darker; hairs from entirely black to black with a subterminal golden band; the amount of black and gold varying individually relatively to the amount of unicolored

black hairs and black hairs with subterminal gold band and to the width of the gold band; lateral parts of body similar to dorsum but slightly lighter. Shoulders and proximal parts of limbs indistinct from sides of the body; limbs ventrally less hirsute, proximally grading to the general ventral color. Hands and feet varying from black or dark brown mottled with gold to sprinkled with black and gold; two kinds of hair present: unicolored black hair and black hair with subterminal gold band. Ventrum gold yellowish to straw yellow, sometimes with a median gold yellowish line; hair bicolored, light brown at base and yellow to gold terminally. Tail fully haired; the color pattern of the posterior dorsum extends to the basal 1/6 portion of tail, which hairs are longer than in the remainder of the tail; distal 5/6 of tail covered with relatively shorter hairs; tail with basal one-sixth mottled with black and copper, the remainder jet-black; scales not visible covered by tail hairs; longest middle hair of the tail scale triad covers from 20 to 22 rows of scales at the base of tail, approximately 15 rows in the middle, and nine to 11 at the tip; tail tuft absent.

Cranial anatomy: Skull large and robust (SL range: 60.8-72.9mm); slender rostrum; nasals constricted medially. Lateral wings of frontal well-developed forming a roof over the orbital region. Postorbital process of zygoma formed by jugal and squamosal. Incisive foramina variable, generally moderately long and narrow, but in some individuals wide and short; septum of incisive foramina formed mainly by premaxillae. Palatal region long and slender; palatine extending up to M1. Mesopterygoid fossa with slit-shaped lateral openings. Alisphenoid region wide; alisphenoid canal incomplete, formed only by posterior opening; buccinator and masticator foramina separated from each other; foramen ovale medium sized; maxillary vein pass through foramina; transverse canal well-developed. Bullae with tiny styliform process, tegmen timpani short and wide; external auditory meatus separated from squamosal bone by a thin ridge of petrosal bone.

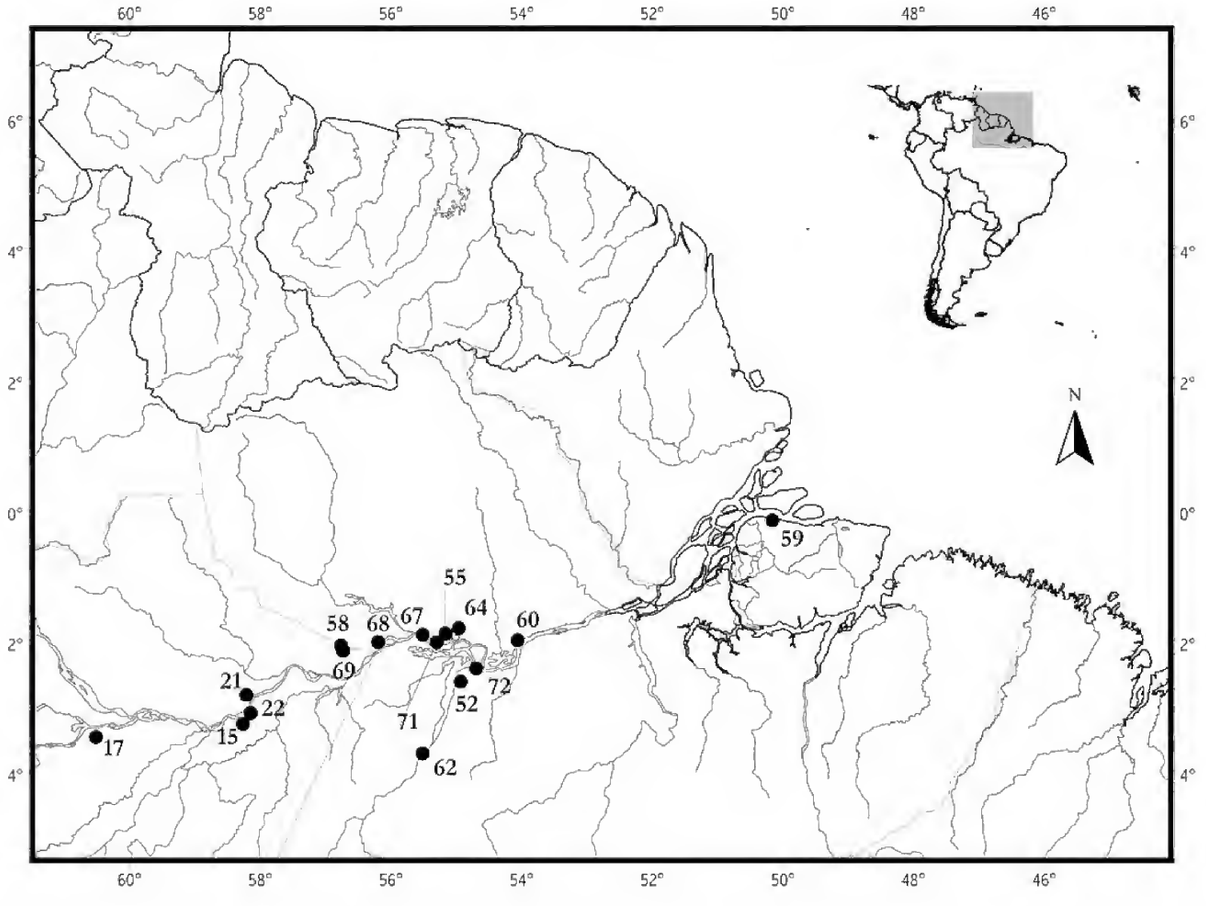

Fig.2- Geographic distribution of *Toromys grandis*. For localities names and geographical coordinates, see Appendix II.

Dental morphology: Upper molariforms tetralophodont; anteroloph, protoloph, and metaloph connected by slender mure. Lower dp4 tetralophodont, metalophid absent, mesolophid isolated; lower molars trilophodont. The holotype of *Loncheres grandis* (NMW B920) and two other specimens (NRM A587187, A597188) have a particular M3 morphology compared to other specimens: the M3 in the above cited material is smaller and trilophodont, but this seems to be anomalous and with no geographic or taxonomic significance.

Baculum: Baculum elongate (greatest length: 7.69mm; n=1; Fig.3) with a broad and thick shaft. Proximal end of baculum round, broader and thicker than distal end, which is pointed. The shaft does not present any dorsoventral curvature and apical wings are absent.

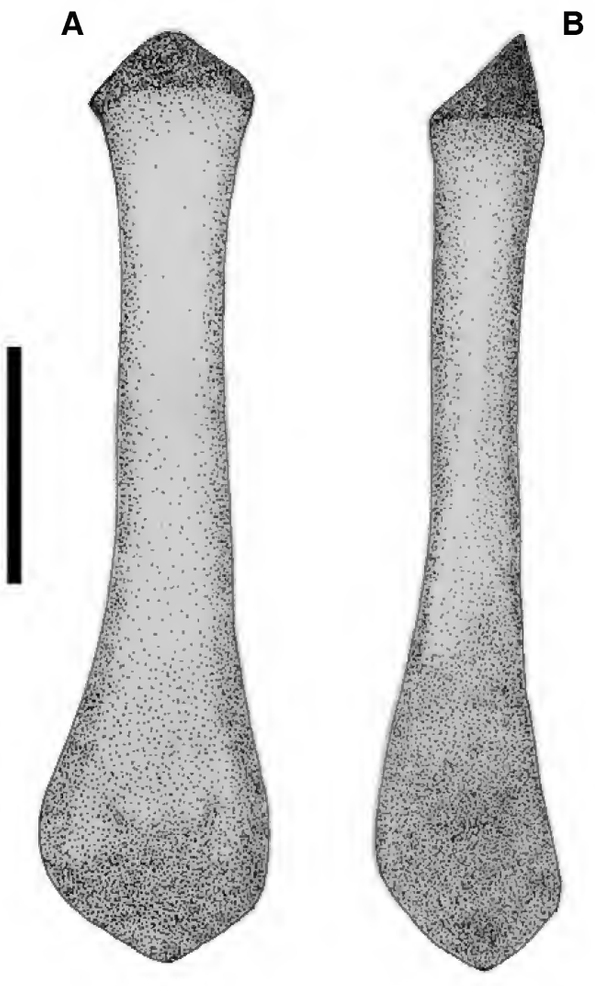

Fig.3- *Baculum* of *Toromys grandis* (MZUSP4722). Scale bar =2mm.

COMPARISONS

Table 1 presents the most relevant distinguishing characters of *Toromys*, *Echimys*, *Makalata*, and *Phyllomys*. More detailed morphological comparisons follow.

Body size and proportions: Head and body length and tail length distinguish *Toromys* and *Echimys* from *Makalata* and *Phyllomys*; *Toromys* and *Echimys* have larger body and tail lengths than the latter (Tabs.1-2). In *Makalata*, tail length ranges from 145 to 234mm, while in *Echimys* it ranges from 270 to 415mm, and in *Toromys* from 244 to 361mm. Tail length in *Phyllomys* is similar to that of *Makalata*, ranging from 180 to 275mm. Aside from absolute size, *Toromys* and *Makalata* have tails shorter than head and body length (89% and 94%, respectively); *Echimys* and *Phyllomys* generally have tails longer than head and body (118% and 106%, respectively). Thus, *Toromys* has a large body size and proportionally shorter tail; *Echimys* is also a large bodied form, but with a longer tail. On the other hand, *Makalata* and *Phyllomys* are small bodied forms of Echimyinae, but they do differ on tail size: the former having the tail shorter than head and body, and the latter a longer tail. Hind foot is smaller in *Makalata* and *Phyllomys* (HF range: 30-48mm, and 30-50mm, respectively) than in *Echimys* and *Toromys*. These have long and wide feet, ranging from 40 to 65mm in *Toromys* and from 45 to 60mm in *Echimys*.

Chromogenetic fields: *Toromys* and *Phyllomys* have three basic chromogenetic fields (as defined by HERSHKOVITZ, 1977) – 1- head, body (including limbs and fore and hindfeet) and proximal part of tail; 2- ventral region; 3- most of the tail except for its proximal region. In the three genera, coloration of each chromogenetic field is mostly uniform, sometimes gradually darkening or becoming lighter, but without clear-cut regional differentiation. *Makalata* is essentially similar to *Toromys* and *Phyllomys*, but with an additional field in the muzzle; all of its known species have reddish muzzles. These three genera have the head and body chromogenetic fields expressing their particular colors as "sprinkled" patterns, i.e. the hairs usually present two or more distinct bands of pigmentation, except for an additional field in the muzzle. *Echimys* differs from all of the

former in two important aspects; its chromogenetic fields are more complex, and they express color as uniformly monochromatic; the hairs have a single color throughout their length. The additional chromogenetic fields in *Echimys* include its complex head pattern, with long eye stripes and a distinctive stripe from the rostrum extending medially to the crown, up to the pinnae. Additionally, the tail is tricolored, with the proximal region similar to the dorsum and a middle section distinct from the distal third.

Body hair patterns: Echimyins possess two main basic types of body hair in upper and lateral surfaces: aristiforms and setiforms (MOOJEN, 1948), both with flattened shape. Aristiforms are wide and strong, and the dorsal margins are raised pronouncedly, forming a wide and shallow longitudinal groove. This type of hair is flat throughout its length and has thick borders, except at the tips. It also presents different degrees of hardness, and this characteristic is directly related to the width of the hair: broad aristiforms form hard spiny pelage and narrow aristiforms form a more flexible and soft pelage. The setiforms are narrower than aristiforms, and flattened with moderately raised margins; the longitudinal groove and the thick marginal borders are present with varied length along the setiforms; the width of the groove varies from a narrow groove to a slight indentation.

In *Toromys*, the body is covered by setiforms and aristiforms, the latter as narrow and soft spines (total length=30.44mm, maximum width=0.32mm); the setiforms (total length=34.13mm, maximum width=0.17mm) are longer than aristiforms, the

Table 1. Comparisons between *Toromys* , *Echimys*, *Makalata*, and *Phyllomys*.

	Toromys	*Echimys*	*Makalata*	*Phyllomys*
Tail/ Head and body ratio	94%	118%	88.08%	106%
Tail: tuft	absent	present	absent	present
Tail: chromogenetic fields	basal and distal	basal, medial and distal	basal; bicolored dorso-ventrally	basal
Palmar and plantar surface between pads	with small rugosities	smooth	smooth	smooth
Dorsal pelage	narrow and soft spines; hairs present	wide and hard spines; hairs totally concealed	spines and hairs equally distributed	spines and hairs equally distributed
Body chromogenetic fields	head, dorsal and ventral	mask and crown stripe on head	muzzle	none
Nasal shape	external margins strongly concave and sharpen angles	external margins concave	external margins straight, tapering posteriorly	external margins straight, slightly tapered posteriorly
Passage of maxillary vein	Passing through a foramen	Passing through a maxillary notch	Passing through a maxillary notch	Passing through a maxillary notch
External auditory meatus/squamosal	thin blade of petrosal	wide crest of petrosal	wide crest of petrosal	wide crest of petrosal
Teeth occlusal pattern	anteroloph, protoloph, and metaloph connected by a slender mure; dp4 tetralophodont	metaloph isolated from protoloph by a continuous hypoflexus-metaflexus; dp4 pentalophodont	metaloph isolated from protoloph by a continuous hypoflexus-metaflexus; dp4 pentalophodont or tetralophodont	lophs isolated; dp4 pentalophodont

longitudinal groove and the thick marginal borders are present almost along the entire setiforms, the basal portion is slightly wider than distal part which tapers to a short filamentous tip. *Makalata* and *Phyllomys* share the broader and harder aristiforms (*Makalata* total length=24.25-30.88mm, maximum width=0.89-1.66mm; *Phyllomys* total length=22-36mm, maximum width=0.4-1.6mm; LEITE, 2003) and thin short setiforms over the body (*Makalata* total length=21.55mm, maximum width=0.15mm; *Phyllomys* total length=22.83mm, maximum width=0.18mm), relative amounts of each kind of hair varying within different species. In these two genera the width of the aristiforms also varies among species. The morphology of setiforms of *Toromys*, *Makalata*, and *Phyllomys* are similar, but in *Makalata* and *Phyllomys* the setiforms are shorter than aristiforms. In *Toromys*, *Makalata*, and *Phyllomys* setiforms and aristiforms are evident on inspection. The relative amounts of aristiforms and setiforms vary among species in *Makalata* and *Phyllomys*. In *Echimys* the aristiforms are well developed (total length=30.59mm, maximum width=2.67mm), wide and hard. The setiforms in *Echimys* are shorter than aristiforms (total length=25.79mm) and they have a wide basal portion (maximum width=0.62mm) with a longitudinal groove, abruptly tapering in a long filamentous distal portion (maximum width=0.11mm); setiforms can be seen only under magnification.

Caudal hair patterns: The patterns of hair coverage, chromogenetic fields, and scale size of tails may easily distinguish the four genera. All genera possess well furred tails, but in *Toromys* and *Echimys* tails are entirely covered by long hairs, in such a way that visualization of scales is difficult. On the other side, the caudal hairs of *Makalata* and *Phyllomys* are shorter and thinner, and scales are more clearly visible through the fur. However, the tail hairs of *Echimys* and *Phyllomys* become increasingly longer from the base to the tip of the tail, thus forming distinct distal tufts, while the opposite occurs in *Toromys* and *Makalata*, which lack tufts. In *Toromys*, the longest middle hair of the tail scale triad covers from 20 to 22 rows of scales at the base of tail, approximately 15 rows in the middle, and 9 to 11 at the tip of tail. In *Echimys* and most species of *Phyllomys*, the longest hair covers 10 to 12 rows at the base of tail, reaching approximately 30 rows at the tip. In *Makalata*, hairs are present along the entire tail, but they are much shorter than in the previous genera; the number of scale rows covered by the longest hairs is 5 to 6 at the base of tail and 3 to 4 at the tip. In *Phyllomys* the development of the tuft is variable and in *P. dasythrix*, tuft is absent.

The coloration of posterior end of dorsum continues until the base of tail in the four genera. This chromogenetic field covers at least 10% of the entire tail in *Toromys* and *Echimys* and is shorter in *Makalata* and *Phyllomys*. In *Toromys* there is only one additional chromogenetic field for the remaining part of tail (hair entirely black in the only known species). In *Echimys* there are two additional chromogenetic fields, dividing the remaining part of the tail in two areas. The first begins posteriorly to the base and covers at least half of the tail and is dark brown in color; the second one extends to the tip, and its color is whitish or yellowish. There is no color differentiation in the dorsal and ventral regions of the tail. *Makalata* also presents two additional chromogenetic fields in the tail besides that of the base, but they express themselves dorso-ventrally, with a lighter tone below and a darker one above (countershading pattern). However, since the tail hair is short in *Makalata*, visualization of the pattern is not obvious. In *Phyllomys* the tail is variable, generally unicolored, but in *P. lundi* a weak countershading pattern occurs (LEITE, 2003).

Palmar and plantar morphology: *Toromys* presents a very distinct morphology of plantar and palmar surfaces relatively to *Echimys*, *Phyllomys*, and *Makalata*. In the latter three, the pads are relatively smooth, as is the skin between the pads. In *Toromys* the pads are likewise smooth, but the skin between the pads present small but distinct rugosities (Fig.4).

Cranial anatomy. There are few diagnostic qualitative cranial traits for the genera studied here. They all share a basic morphologic plan, with a remarkable differentiation on skull size and robustness. The most conspicuous traits that distinguish these genera are the nasal shape, the presence of maxillary foramen, and morphology of the bullae.

Toromys presents concave external margins of nasals; in *Echimys* the external margins of the nasals are also concave, but distinctly less so than in *Toromys*; *Makalata* presents external margins of the nasals almost longitudinally parallel, while *Phyllomys* presents them converging posteriorly (Fig.5). In *Toromys* the maxillary vein pass through a foramen formed by maxillar palatine and alisphenoid bones, the posterior maxillary foramen. The other genera have a posterior maxillary notch

Table 2. Descriptive statistics of *Toromys*, *Echimys*, *Makalata*, and *Phyllomys*. (N) $\bar{x}$ ± *s.d.* *Min.* - *Max.*

	Toromys	*Echimys*	*Makalata*	*Phyllomys*
HB	(45) 303 ± 15.58 275 - 354	(8) 280.63 ± 25.70 250 - 310	(39) 220.56 ± 27.90 168 - 294	(62) 212.58 ± 18.53 160 - 262
T	(42) 285.12 ± 22.06 244 - 361	(9) 330.55 ± 47.20 270 - 415	(29) 196.72 ± 20.86 145 - 234	(47) 226.55 ± 22.44 180 - 275
F	(45) 52.78 ± 4.71 40 - 65.00	(9) 52.89 ± 14.04 45 - 60	(39) 38.15 ± 4.73 30 - 48	(68) 37.08 ± 3.55 30 - 50
E	(27) 19.48 ± 2.01 15 - 25	(4) 20.50 ± 6.87 19 - 23	(20) 13.50 ± 2.09 10 - 17	(61) 15.54 ± 2.78 9 - 20
SL	(41) 67.15 ± 2.38 60.78 - 72.90	(9) 62.20 ± 16.17 59 – 65.89	(50) 53.54 ± 2.6 47.23 – 59.30	(42) 50.02 ± 3.12 41.03 – 58.25
ZB	(41) 32.31 ± 1.32 30.33 - 36.69	(11) 30.41 ± 5.67 25.96 - 33.33	(49) 25.65 ± 1.46 21.55 - 28.20	(49) 24.22 ± 1.74 20.93 - 29.41
FC	(45) 18.69 ± 1.25 15.570 - 21.36	(13) 15.29 ± 1.60 12.46 - 18.50	(54) 13.29 ± 0.97 11.35 - 15.08	(54) 11.28 ± 1.04 9.29 - 13.97
NL	(41) 22.24 ± 1.22 19.40 - 24.28	(12) 18.50 ± 2.42 16.20 - 21.96	(52) 16.47 ± 1.27 13.28 - 19.20	(44) 14.81 ± 1.94 10.38 - 21.34
BW	(43) 21.93 ± 1.35 18.40 - 24.72	(10) 21.44 ± 3.36 19.69 - 22.38	(55) 18.99 ± 1.15 16.40 - 21.43	(51) 18.26 ± 0.74 16.69 - 19.63
SB	(38) 25.62 ± 1.13 23.55 - 28.31	(9) 23.81 ± 4.53 21.59 - 24.83	(248) 21.04 ± 1.25 18.80 - 23.99	(46) 19.72 ± 1.14 17.86 - 23.77
RB	(43) 10.87 ± 0.67 9.60 - 12.48	(13) 10.51 ± 1.14 8.64 - 11.81	(55) 8.31 ± 0.68 6.49 - 9.70	(53) 7.46 ± 0.88 6.41 - 10.58
PL	(44) 28.65 ± 1.32 26 - 33.12	(11) 24.39 ± 4.03 21.60 - 27.34	(55) 20.97 ± 1.36 17.48 - 25.58	(53) 19.21 ± 1.81 15.27 - 26.02
PPL	(42) 25.23 ± 1.17 23.35 - 27.44	(9) 24.63 ± 4.78 21.80 - 26.17	(51) 20.22 ± 1.44 16.92 - 23.61	(49) 19.68 ± 1.49 16.02 - 23.84
TRL	(43) 15.56 ± 0.51 14.25 - 16.71	(11) 13.51 ± 1.05 12.65 - 14.89	(50) 11.26 ± 0.68 9.53 - 12.63	(51) 11.45 ± 1.09 10.19 - 15.10
M1B	(45) 3.24 ± 0.15 2.97 - 3.62	(13) 2.96 ± 0.25 2.53 - 3.55	(53) 2.28 ± 0.22 1.79 - 2.75	(54) 2.37 ± 0.21 1.88 - 2.96
MB	(45) 8.40 ± 0.44 7.60 - 9.21	(12) 8.92 ± 1.03 7.77 - 9.85	(55) 6.74 ± 0.62 5.50 - 9.44	(56) 6.48 ± 0.62 5.60 - 8.39
BL	(42) 13.00 ± 0.66 11.42 - 13.46	(11) 12.47 ± 0.71 11.42 - 13.46	(54) 11.36 ± 0.58 10.11 - 12.84	(51) 11.02 ± 0.93 9.40 - 13.17
MBL	(44) 36.51 ± 1.46 33.40 - 40.37	(10) 32.80 ± 6.75 27.60 - 35.30	(50) 27.56 ± 2.57 14.52 - 33.17	(50) 27.66 ± 2.38 22.04 - 35.69
MH	(45) 17 ± 1.04 15.23 - 19.77	(8) 16.21 ± 2.77 12.63 - 16.88	(49) 12.88 ± 1.23 9.86 - 15.43	(49) 13.01 ± 1.29 10.54 - 16.79

(N) number of specimens, ($\bar{x}$) average, (s.d.) standard deviation, (Min.-Max.) minimum and maximum.

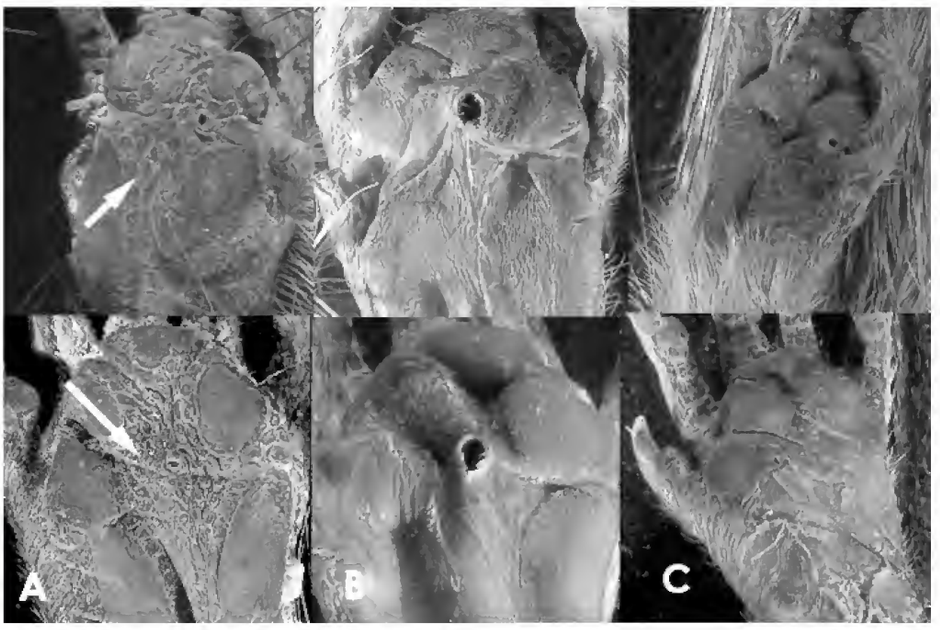

Fig.4- Palmar (upper) and plantar regions: (A) *Toromys grandis* (MZUSP4488; foot length=54mm), (B) *Echimys chrysurus* (foot: MZUSP4548; hand: MZUSP4558), (C) *Makalata didelphoides* (foot: MZUSP4559; foot length=44mm; hand: MZUSP24488), (→) rugosities between the pads.

embracing the maxillary vein (Fig.6). The external auditory meatus of *Toromys* is separated of the squamosal bone by a thin ridge of petrosal bone; *Phyllomys*, *Makalata*, and *Echimys* have the external auditory meatus separated by a well-developed crest of petrosal bone (Fig.7). The postorbital process of the zygoma in *Toromys* and *Makalata* is formed by the squamosal and the jugal; in *Echimys* and most species of *Phyllomys*, only by the jugal (Fig.8). The alisphenoid canal in *Toromys* is incomplete, usually appearing as a short canal with only the posterior opening differentiated; only the posterior opening is present in *Makalata*, while in *Echimys* the development of the alisphenoid canal is variable: most species have a complete canal with well developed anterior and posterior openings. In *Phyllomys* the alisphenoid canal is incomplete, formed by the posterior foramen and with a gutter extending through the sphenoidal fissure (Fig.9). In *Toromys*, the buccinator and masticator foramina are separated, while in *Echimys* and *Phyllomys* both foramina merge, and in *Makalata* this character is polymorphic but, in general, the buccinator and masticator foramina merge (Fig.9).

Cranial size: *Toromys* possess the largest and most robust skull of all Echimyinae rodents (Tab.2). The average skull length and molar toothrow length observed in *Toromys* exceed values found in all other genera. When compared to *Makalata* and *Phyllomys*, the differences are substantial (Fig.10; Tab.2); even relatively to *Echimys*, there are also obvious quantitative differences. *Phyllomys* is the smallest genus in almost all cranial variables.

Dental morphology: Figure 11 depicts upper and lower toothrows for the taxa here discussed. The upper molariforms of *Toromys* present the anteroloph, protoloph, and metaloph connected by a slender mure; in *Makalata* and *Echimys* the metaloph is isolated from the protoloph by a continuous hypoflexus-metaflexus. In *Phyllomys* all lophs are isolated from each other. *Toromys* has a tetralophodont lower fourth premolar (dp4), with an isolated mesolophid and lacking a metalophid. *Makalata* presents two distinct dp4 morphologies: the first is similar to the one just described for *Toromys*. The mesolophid may connect labially or lingually to the anterolophid in old individuals, a condition most easily found in the tetralophodont *Makalata*, but also present in very old *Toromys*. The second dp4 morphology found in *Makalata* is shared with *Phyllomys* and *Echimys*. In *Echimys* and pentalophodont *Makalata* the anterolophid is connected both lingually and labially with metalophid forming an anterofossetid, while in *Phyllomys* the anterolophid is connected labially to the metalophid.

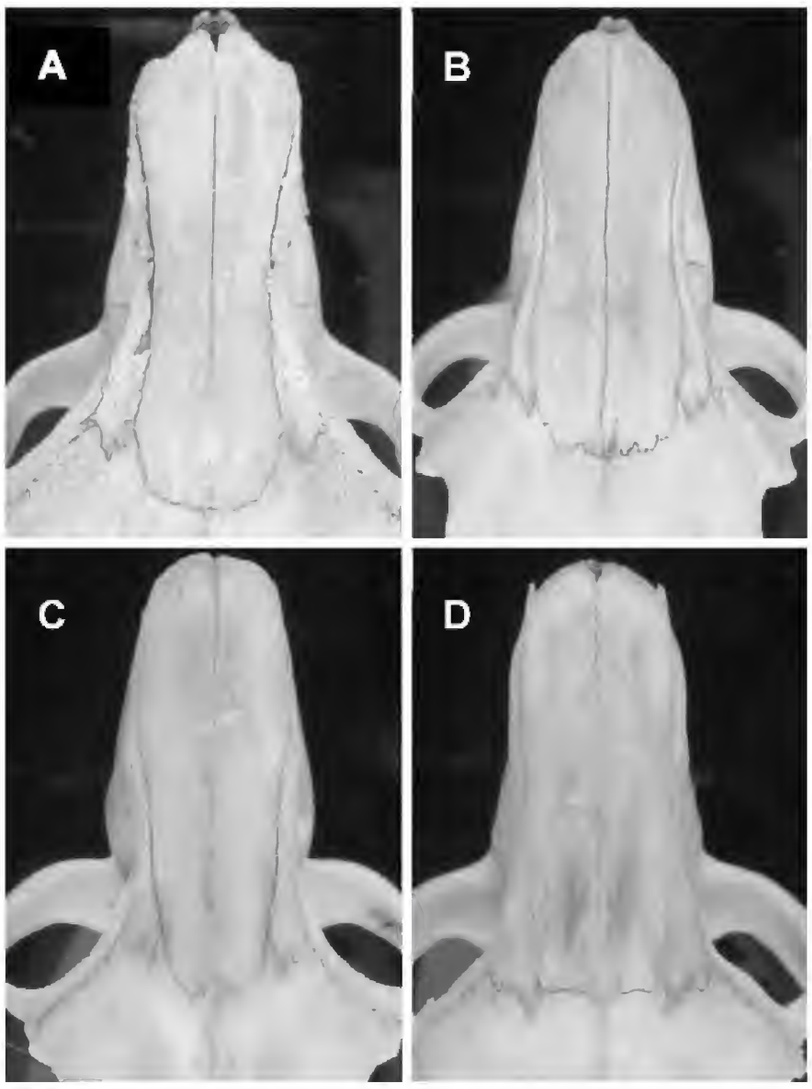

Fig.5- Shape of the nasals in dorsal view: (A) *Toromys grandis* (MZUSP4722; NL=21.6mm), (B) *Echimys chrysurus* (MZUSP4548; NL=18.3mm), (C) *Phyllomys nigrispinus* (MZUSP25858; NL=15.75mm), (D) *Makalata didelphoides* (MZUSP899; NL=15.4mm). Photos: C.Moreira.

Baculum: As bacula of *Echimys* and *Makalata* were not available for study, we limited our comparisons to Didier's descriptions of *Makalata* (DIDIER, 1962), and LEITE's (2003) description of *Phyllomys*.

DIDIER (1962) described and illustrated three quite different bacula for *Makalata* (treated as *Echimys* by that author), all three types notably differing from that of *Toromys* as follows: 1) the general shape of the *baculum* body (ventral view) is claviform in *Toromys grandis* and *M. semivillosus*; pyriform elongate in *M. rhipidurus* and straight with a wider proximal end in *M. didelphoides* (*E. armatus*, *sensu* DIDIER, 1962); 2) in *Toromys* the shaft is elongate, straight, thick, and broad; in *M. rhipidurus* the shaft is similar to that of *Toromys* except that it has a lateral indentation at the proximal end, which narrows abruptly distally; in *M. didelphoides* the shaft is elongate, straight and thin with a sinoidal curvature in lateral view; in *M. semivillosus* the shaft is elongate and thin with a lateral indentation at both proximal and distal extremities; 3) Proximal end of baculum is irregularly rounded, thick and broad in *Toromys*; in *M. didelphoides* the proximal end is V-notched; in *M. rhipidurus* the proximal end is evenly rounded; the *baculum* of *M. semivillosus* is fusiform proximally, with a slender median

depression; 4) The distal end of the baculum is pointed in *Toromys*; in *M. didelphoides* it is concave with apical wings and a median depression; in *M. rhipiddurus* it is evenly rounded; the distal extremity of the baculum of *M. semivillosus* is straight. *Phyllomys* has a baculum with a straight terminal extremity, the shaft is straight and slender from the distal to the middle portion, widening in the proximal third in an obovate shape, abruptly changing into a straight proximal extremity (LEITE, 2003).

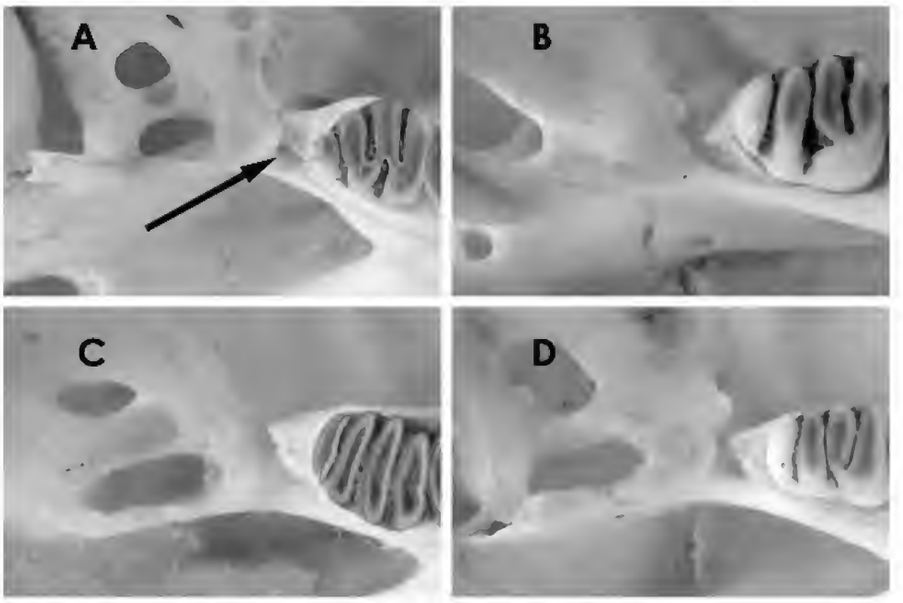

Fig.6- Passage of maxillary vein: (A) *Toromys grandis* (MZUSP4722; TL=62.7mm), (B) *Echimys chrysurus* (MZUSP4551; TL=59mm), (C) *Phyllomys nigrispinus* (MZUSP666; TL=48.82mm), (D) *Makalata didelphoides* (MZUSP899; TL=52.4mm), (→) passage of the vein in the postmaxillary foramen. Photos: C.Moreira.

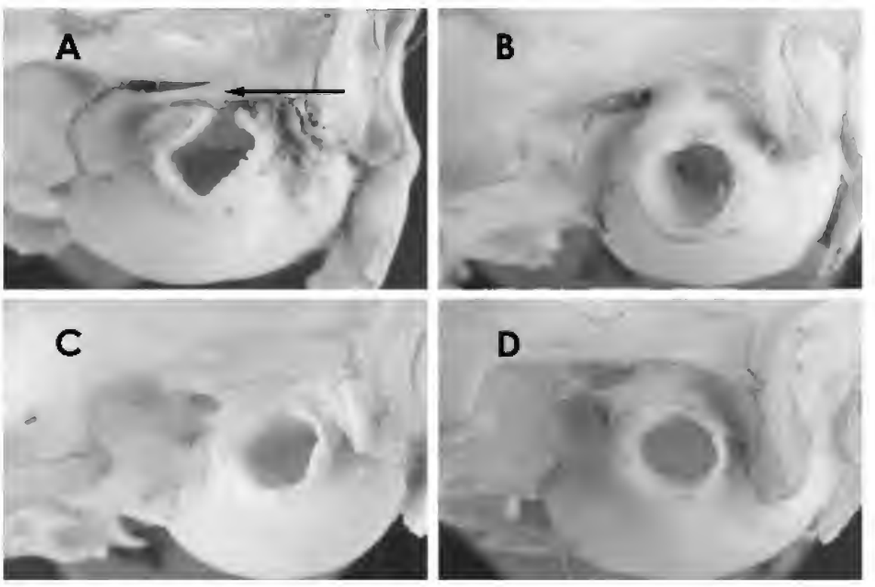

Fig.7- Bullar and petrosal morphology: (A) *Toromys grandis* (MZUSP4720; BL=13.3mm), (B) *Echimys chrysurus* (MZUSP4551; BL=12.2mm), (C) *Phyllomys nigrispinus* (MZUSP 25858; BL=10.53mm), (D) *Makalata didelphoides* (MZUSP899; BL=11.4mm), (→) external appearance of the petrosal bone. Photos: C.Moreira.

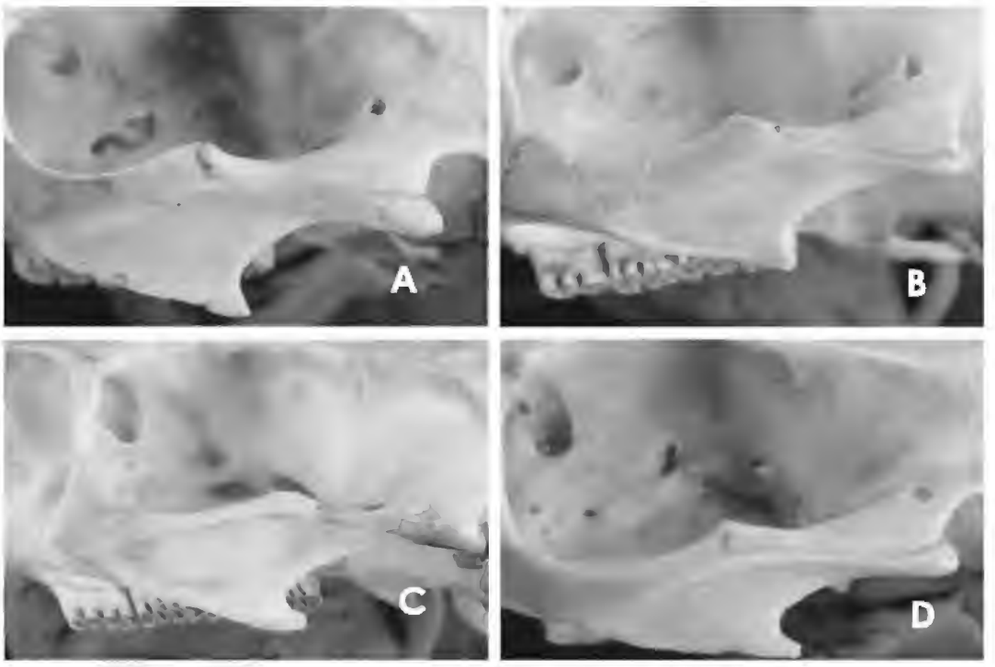

Fig.8- Postorbital process of zygoma: (A) *Toromys grandis* (MZUSP4720; TL=65.4mm), (B) *Echimys chrysurus* (MZUSP4551; TL=59mm), (C) *Phyllomys nigrispinus* (MZUSP 25858; TL=50.73mm), (D) *Makalata didelphoides* (MZUSP4546; TL=56.9mm). Photos: C.Moreira.

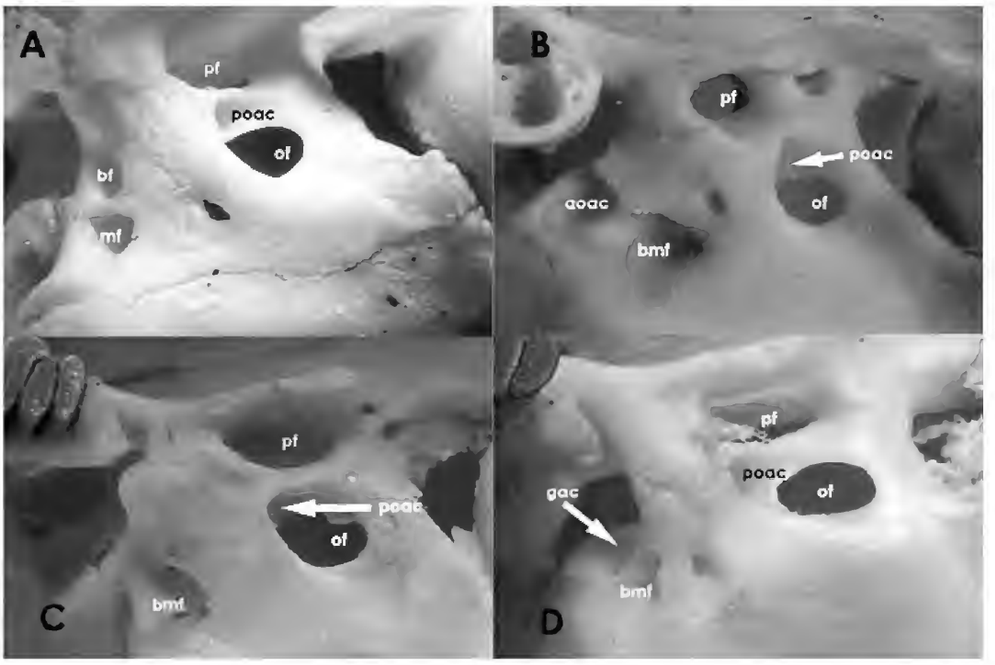

Fig.9- Alisphenoid region: (A) *Toromys grandis* (MZUSP4722), (B) *Echimys chrysurus* (MZUSP4642), (C) *Phyllomys thomasi* (MZUSP3197), (D) *Makalata didelphoides* (MZUSP899). Abbreviations for foramina and other structures: (bf) buccinator foramen, (mf) masticator foramen, (bmf) buccinator masticator foramina confluents, (of) oval foramen, (aoac) anterior opening of alisphenoid canal, (poac) posterior opening of alisphenoid canal, (gac) gutter of alisphenoid canal, (pf) pterygoid fossa.

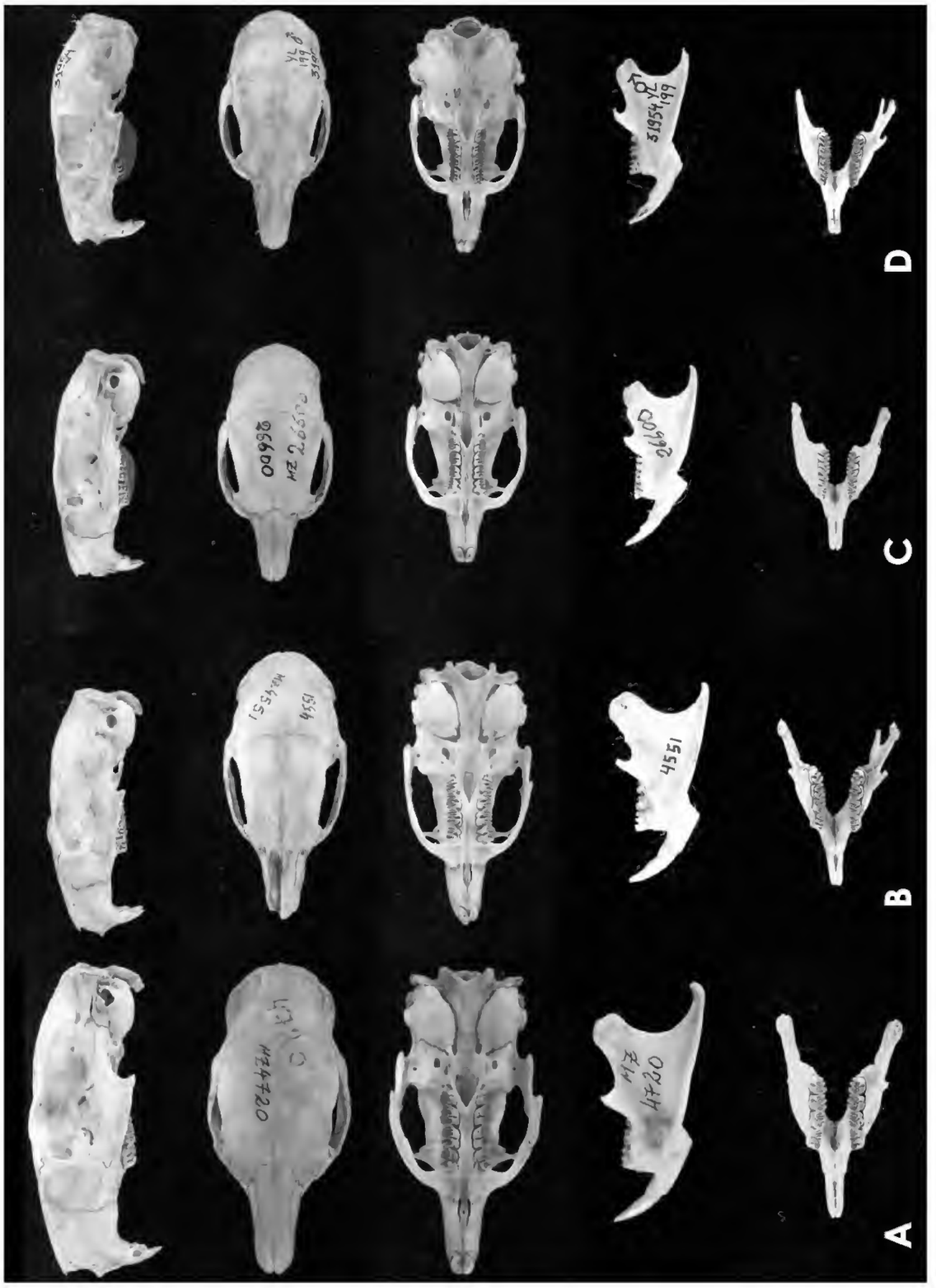

Fig.10- Skulls and mandibles: (A) *Toromys grandis* (MZUSP4720; TL=65.4mm; MBL=36.6mm), (B) *Echimys chrysurus* (MZUSP4551; TL=59mm, MBL=31.2mm), (C) *Makalata didelphoides* (MZUSP26600; TL=53mm, MBL=27.6mm), (D) *Phyllomys pattoni* (MZUSP31954; TL=53.3mm, MBL=26.6mm). Photos: C.Moreira.

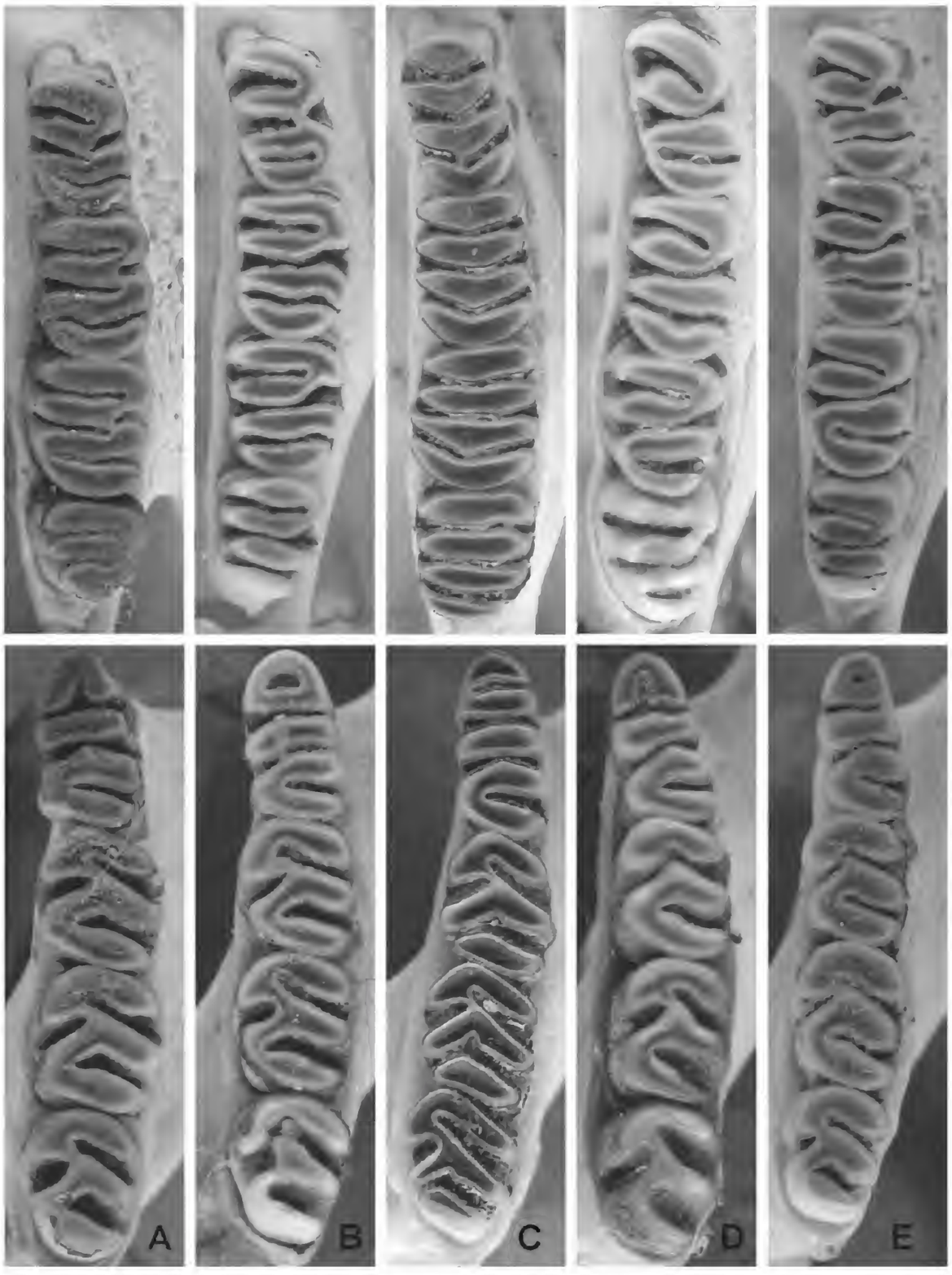

Fig.11- Toothrows: (A) *Toromys grandis* (MZUSP 4489; TRL=14.7mm), (B) *Echimys chrysurus* (MZUSP4551; TRL=12.9mm), (C) *Phyllomys nigrispinus* (MZUSP25858; TRL=12.92mm), (D) *Makalata* with pentalophodont dp4 (MZUSP899; TRL=11.4mm), (E) *Makalata* with tetralophodont dp4 (MZUSP22930; TRL=11.8mm). Photos: C.Moreira.

CHARACTERIZATION OF *ECHIMYS*, *MAKALATA*, AND *PHYLLOMYS*

The creation of *Toromys* for *Loncheres grandis* changes the species content of both *Echimys* and *Makalata*, since that species was alternatively placed in one or other genus (WOODS, 1993; EMMONS & FEER, 1997; EISENBERG & REDFORD, 1999; CARVALHO & SALLES, 2004). Additionally, since we make many comparisons with *Phyllomys* as well, we furnish emended diagnosis for the three genera bellow. Each generic diagnosis is followed by a list of species currently recognized as valid and their synonyms.

Genus *Echimys* Cuvier, 1809

Type-species – *Myoxus chrysurus* Zimmermann, 1780.

Diagnosis – A large sized echimyine with a long tricolored tail and with the white distal portion of tail extending over more than one third of tail length. Head with a black mask extending from the muzzle to above and bellow the eyes. Differentiated chromogenetic field extending from immediately behind the muzzle to the region between the ears. Septum of incisive foramen formed only by premaxillar; dp4 with anterolophid developed and connected to metalophid evenly both lingually and labially; upper molars with protoloph connected to protocone, deep groove formed by continuous hypoflexus and metaflexus; metaloph connected with posteroloph by hypocone; postorbital process of zygoma formed by jugal.

Distribution – Amazon basin and Guiana region (Fig.12).

Species included – *E. chrysurus* (Zimmermann, 1780); *E. paleaceus* (Olfers, 1818); and a third, new species (IACK-XIMENES *et al.*, in press). Synonym: *E. cristatus* Desmarest, 1817.

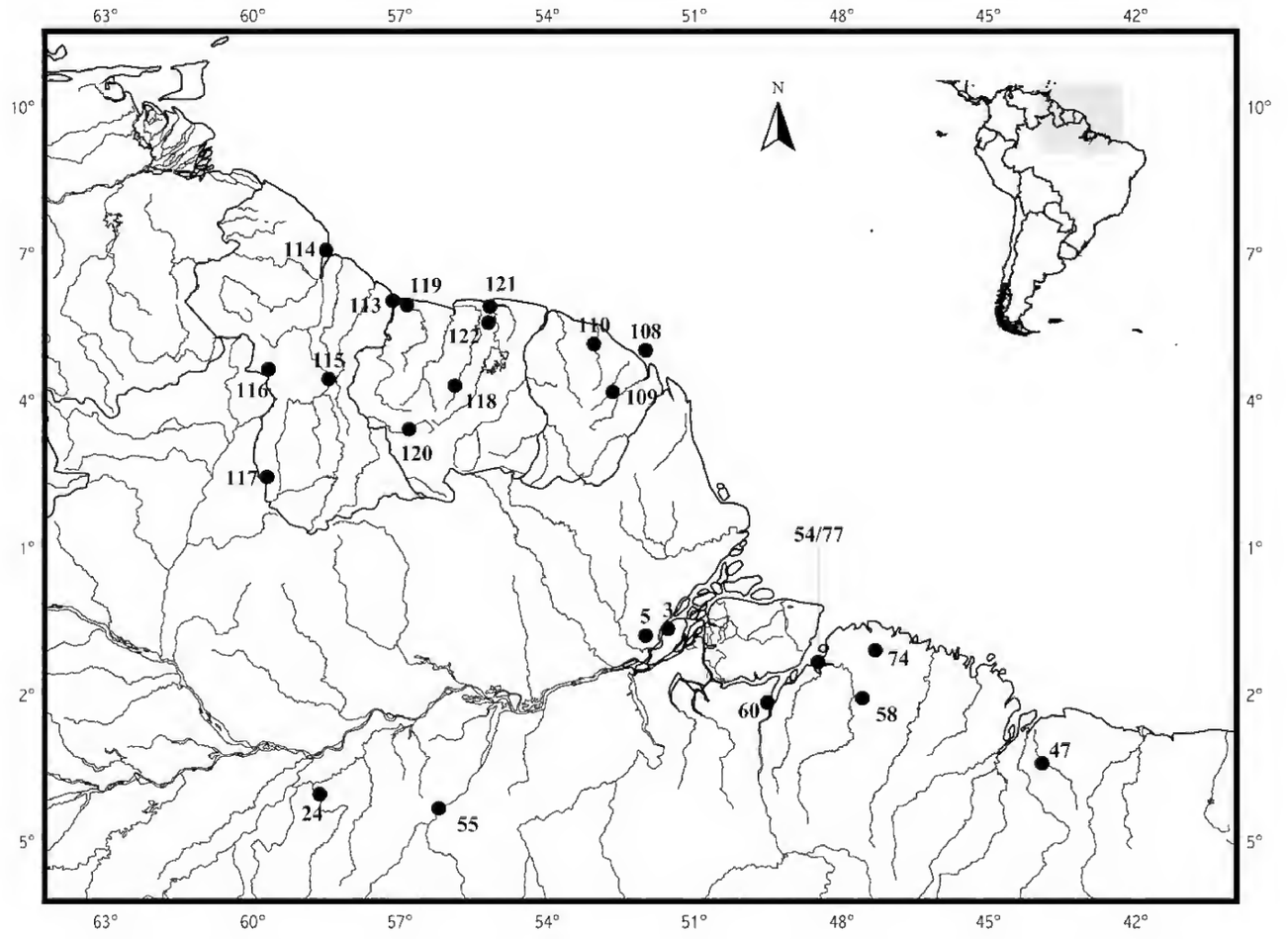

Fig.12- Geographic distribution of *Echimys*. For localities names and geographical coordinates, see Appendix II.

Genus *Makalata* Husson, 1978

Type-species – *Nelomys armatus* Geoffroy, 1838.

Diagnosis – An echimyid with mystacial region pheomelanic (rusty, from red to orange), tail with short hair, making scales plainly visible; postorbital process of zygoma formed mostly by jugal, squamosal projects below the postorbital process.

Distribution – Amazon basin, Northeastern Brazil and the Guiana region (see figure 13).

Species included – *M. didelphoides* (Desmarest, 1817); *M. macrura* (Wagner, 1842); *M. obscura* (Wagner, 1840); *M. occasius* (Thomas, 1921); *M. rhipidurus* (Thomas, 1928); *M. semivillosus* (I.Geoffroy, 1838). Synonyms: *Nelomys armatus* I. Geoffroy, 1838; *Loncheres carrikeri* Allen, 1911; *Loncheres castaneus* Allen and Chapman, 1897; *Loncheres flavidus* Hollister, 1914; *Loncheres guianae* Thomas, 1888; *Echimys longirostris* Anthony, 1921; *Loncheres punctatus* Thomas, 1899.

Genus *Phyllomys* Lund, 1839

Type-species – *Phyllomys brasiliensis* Lund, 1840.

Diagnosis – An echimyid with alisphenoid canal incomplete, formed by posterior foramen and a gutter extending until the sphenoidal fissure; upper molariformes formed by isolated lophs; dp4 pentalophodont with anterolophid and metalophid connected labially.

Distribution – East Brazil (Fig.14).

Species included: *P. blainvilii* (Jourdan, 1837); *P. brasiliensis* Lund, 1840; *P. dasythrix* Hensel, 1872; *P. kerri* (Moojen, 1950); *P. lamarum* (Thomas, 1916); *P. lundi* Leite, 2003; *P. mantiqueirensis* Leite, 2003; *P. medius* (Thomas, 1909); *P. nigrispinus* (Wagner, 1842); *P. pattoni* Emmons, Leite, Kock and Costa, 2002; *P. thomasi* (Ihering, 1897); *P. unicolor* (Wagner, 1842). Synonym: *Loncheres braziliensis* Waterhouse, 1848.

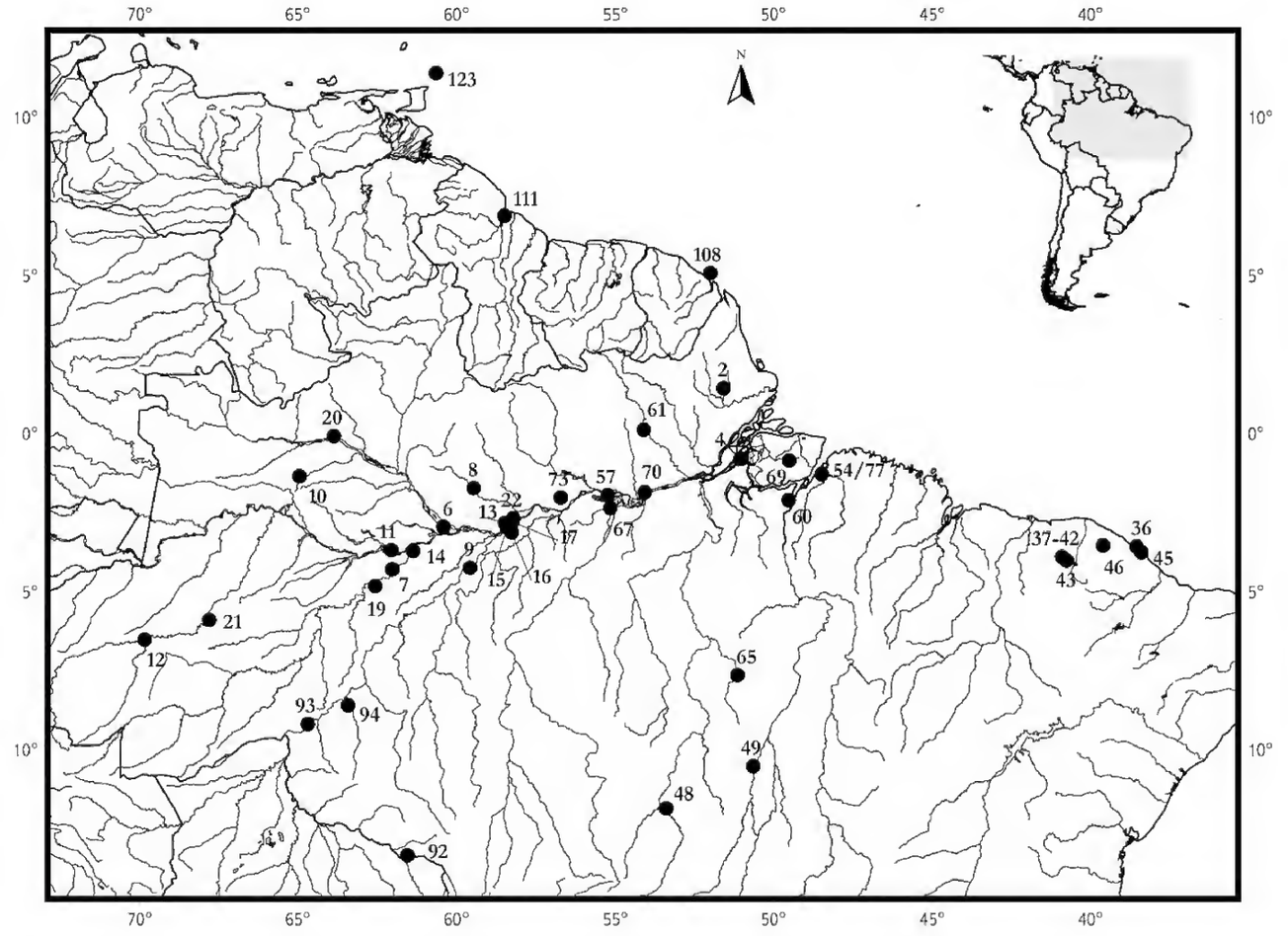

Fig.13- Geographic distribution of *Makalata*. For localities names and geographical coordinates, see Appendix II.

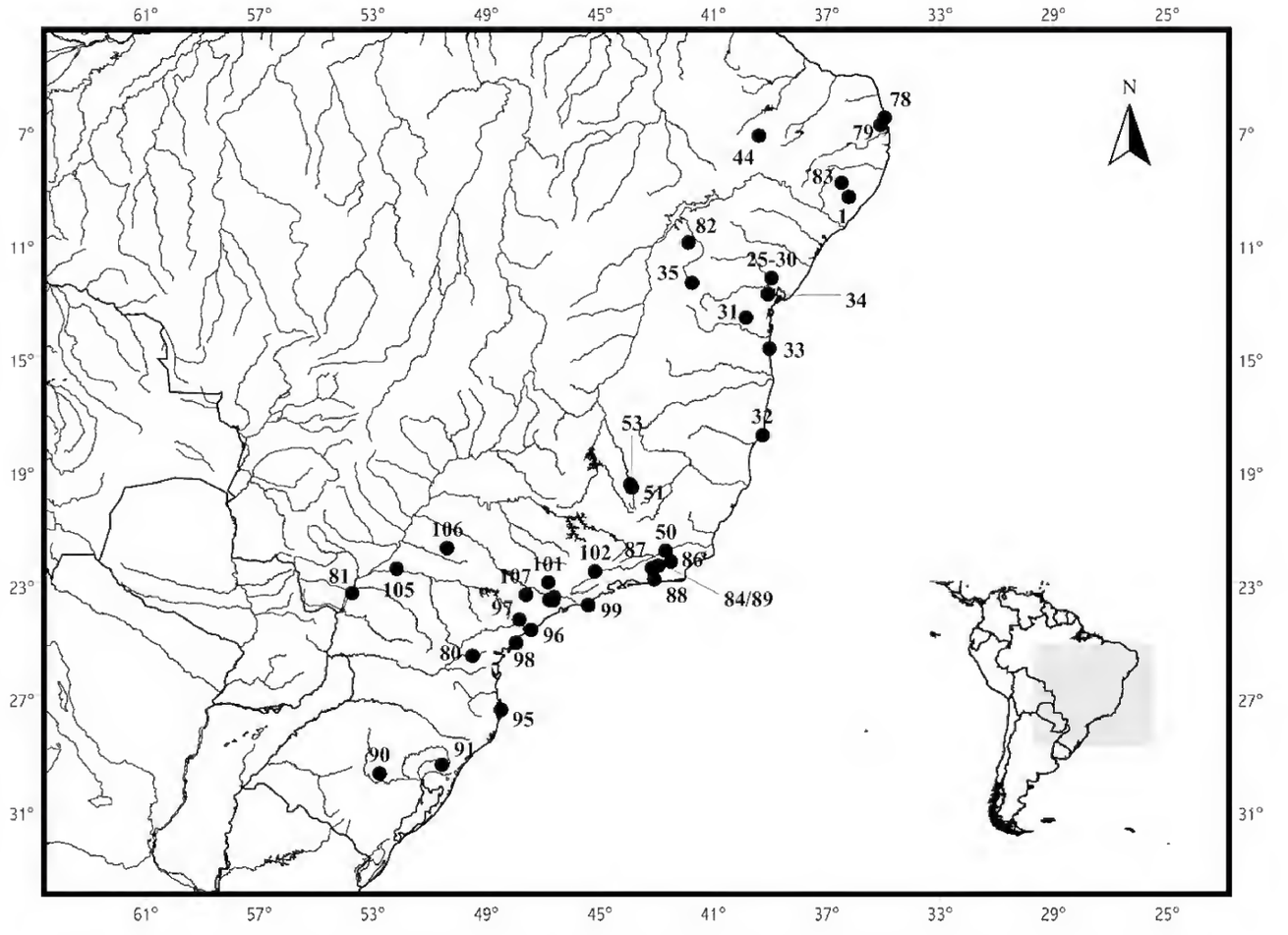

Fig.14- Geographic distribution of *Phyllomys*. For localities names and geographical coordinates, see Appendix II.

ACKNOWLEDGEMENTS

We are indebted to the curators of the several museums visited for their permission to study specimens under their care, namely Dr. João A. Oliveira (Museu Nacional - Rio de Janeiro); Dr. Paula Jenkins and Dr. Daphne Hills (Natural History Museum, London), Dr. Peter Giere (Museum für Naturkunde, Berlin), Dr. Olavi Grönwall (Naturhistorika Riksmuseet, Stockholm), Dr. Barbara Herzig, Dr. Friederike Spitzenberger, and Alexander Bibl (Naturhistorische Museum Wien), Dr. Richard.Kraft (Zoologische Staatsammlung München), Dr. Hans Jørgen Baagøe and Dr. Andersen Mogens (Zoological Museum University of Copenhagen), and Dr. Christiane Denys (Museum Nationale D´Histoire Naturelle, Paris). Research was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (Biota Program 98/05075-7; G.E. Iack-Ximenes – grant 99/07973-5; A.R. Percequillo – grant 98/12273-0). We would particularly like to thank Dr. M.G.Vucetich for advice concerning dental nomenclature and Cristiano R. Moreira for photographs.

LITERATURE CITED

ALLEN, J.A. 1899. The generic names *Echimys* and *Loncheres*. **Bulletin of the American Museum of Natural History**, New York, **115**:257-264.

BRYANT, J.D. & MCKENNA, M.C., 1995. Cranial anatomy and phylogenetic position of *Tsaganomys altaicus* (Mammalia; Rodentia) from the Hsanda Gol Formation (Oligocene), Mongolia. **American Museum Novitates**, New York, **3156**:1-42.

BUTLER, P.M., 1985. Homologies of molar cusps and crests, and their bearing on assessments of rodent morphology. In: LUCKETT, W.P. & HARTENBERGER, J.L. [Eds.] **Evolutionary relationships among rodents: a multidisciplinary analysis**. New York and London: Plenum Press. p.381-401.

CABRERA, A., 1961. Catálogo de los mamíferos de América del Sur. Volume II. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"**, Buenos Aires, **4**:309-732.

CANDELA, A.M., 1999a. **Los Erethizontidae (Rodentia, Hystricognathi) fósiles de Argentina. Sistemática e historia evolutiva y biogeográfica**. 357p. Ph.D. Dissertation, Facultad de Ciências Naturales y Museo.

CANDELA, A.M., 1999b. The evolution of the molar pattern of the Erethizontidae (Rodentia, Hystricognathi) and the validity of *Parasteiromys* Ameghino, 1904. **Palaeovertebrata**, Montpellier, **28**:53-73, figs.1-8.

CANDELA, A.M., 2002. Lower deciduous tooth homologies in Erethizontidae (Rodentia, Hystricognathi): evolutionary significance. **Acta Paleontologica Polonica**, Warszaw, **47**(4):717-723.

CARVALHO, G.A.S & SALLES, L.O., 2004. Relationships among extant and fossil echimyids (Rodentia, Hystricognathi). **Zoological Journal of the Linnean Society**, London, **142**:445-477.

CARVALHO, J.C.M., 1955. Notas de viagem ao Rio Paru do Leste. **Publicações Avulsas do Museu Nacional**, Rio de Janeiro, **14**:1-82, figs.1-18.

CUVIER, G.F., 1809. Extrait des premiers Mémoires de M.F.Cuvier, sur les dents des mammifères considérés comme charactères génerics. **Nouveau Bulletin des Sciences, par la Société Philomathique**, Paris, **1**(24):394-395.

CUVIER, G.F., 1812. Essai sur de nouveaux caractères pour les genres des mammifères. **Annales du Muséum d'Histoire Naturelle**, Paris, **19**:268-295.

DESMAREST, A.G., 1817. **Nouveau Dictionnaire d'Histoire Naturelle, appliquée aux arts, a l'Agriculture, à l'Économie rurale et domestique, à la Médecine, etc**. *EAL-EZE*. Par une société de Naturalistes et d'Agriculteurs. Nouvelle Édition. Paris: Abel Lanoir Imprimerie. Tome X. 591p.

DIDIER, R., 1962. Note sur l'os penien de quelques rongeurs de l'Amerique du Sud. **Mammalia**, Paris, **26**(3):408-430.

EMMONS, L.H., 1993. On the identity of *Echimys didelphoides* Desmarest, 1817 (Mammalia: Rodentia: Echimyidae). **Proceedings of Biological Society of Washington**, Washington, **106**(1):1-4.

EMMONS, L.H. & FEER, F., 1990. **Neotropical Rainforest Mammals: A field Guide**. Chicago: The University Chicago Press. 281p.

EMMONS, L.H. & FEER, F., 1997. **Neotropical Rainforest Mammals: A field Guide**. 2.ed. Chicago: The University Chicago Press, 307p.

EMMONS, L.H.; LEITE, Y.R.; KOCK, D. & COSTA, L.P., 2002. A review of the named forms of *Phyllomys* (Rodentia, Echimyidae), with the description of a new species from coastal Brazil. **American Museum Novitates**, New York, **3380**:1-40.

EMMONS, L.H. & VUCETICH, M.G., 1998. The identity of Winge's *Lasiuromys villosus* and the description of a new genus of echimyid rodent (Rodentia: Echimyidae). **American Museum Novitates**, New York, **3223**:1-12.

EISENBERG, J.F. & REDFORD, K.H., 1999. **Mammals of the Neotropics. The Central Tropics. Ecuador, Peru, Bolivia, Brazil**. v.3. Chicago: The University of Chicago Press, 609p.

ELLERMAN, J.R., 1940. **The families and genera of living rodents with a list of named forms**.v.1. London: British Museum of Natural History, 689p.

FLYNN, L.J.; JACOBS, L.L. & CHEEMA, I.U., 1986. Baluchimyinae, a new ctenodactyloid rodent subfamily from the Miocene of Baluchistan. **American Museum Novitates**, New York, **2891**:1-25.

GEOFFROY, I., 1838. Notices sur les rongeurs épineux désignés par les auteurs sous les noms d' *Echimys*, *Loncheres*, *Heteromys* et *Nelomys*. **Revue Zoologique**, Paris, **1**:99-101.

GEOFFROY, I., 1840. Notices sur les rongeurs épineux désignés par les auteurs sous les noms d' *Echimys*, *Loncheres*, *Heteromys* et *Nelomys*. **Magasin de Zoologie 2nd Serie**, Paris, **2**:1-57.

HUSSON, A.M., 1978. **The Mammals of Suriname**. Zoologische Monographieën van het Rijksmuseum van natuurlijke historie 2. Leiden: E.J.Brill. xxxiv, 569p., il.

IACK-XIMENES, G.E.; DE VIVO, M. & PERCEQUILLO, A.R. (in press) A new species of *Echimys* Cuvier, 1809 (Rodentia, Echimyidae) from Brazil. **Papéis Avulsos de Zoologia, São Paulo**, São Paulo.

JAEGER, J.J., 1989. L'évolution de la pentalophodontie chez les rongeurs caviomorphes (Mammalia, Rodentia) In: DAVIS-DOMERGES, J.L.; CHALINE, J. & LAURIN, B. (Eds.) **Ontogenèse et évolution**. Geobios, Mémoire Spéciale 12. Lyon: Elsevier Ed. p.235-244.

JAEGER, J.J.; DENIS, C. & COIFFAIT, B., 1985. New Phiomorpha and Anomaluridae from the late Eocene of North-West Africa: phylogenetics implications. In: LUCKETT, W.P. & HARTENBERGER, J.L. (Eds.) **Evolutionary relationships among rodents: a multidisciplinary analysis**. New York: Plenum Press, p.685-712.

JOURDAN, C., 1837. Mémoire sur quelques mammifères nouveaux. **Comptes Rendus Hebdomadaires des Sceànces de L'Academie des Sciences**, Paris, **15**:521-524.

LAVOCAT, R., 1976. Rongeurs caviomorphes de l'Oligocène de Bolivie. II Rongeurs du Bassin Deseadien de Salla-Luribay. **Palaeovertebrata**, Montpellier, **7**(3):15-90.

LEITE, Y.L.R., 2003. Evolution and systematics of the Atlantic tree rats, genus *Phyllomys* (Rodentia, Echimyidae) with description of two new species. **University of California Publications, Zoology**, Berkeley, **132**:1-118.

LUND, P.W., 1839. Nouvelles observations sur la faune fossile du Brésil; extraits d'une lettre adressée aux redacteurs par M.Lund. **Annales des Sciences Naturelles, ser.2**, Paris, **12**:205-208.

MAUFFREY, J.F. & CATZEFLIS, F., 2003. Ecological and isotopic discrimination of syntopic rodents in a neotropical rain forest of French Guiana. **Journal of Tropical Ecology**, Cambridge, **19**:209-214.

MOOJEN, J., 1948. Speciation in the Brazilian spiny rats (genus *Proechimys*, family Echimyidae). **University of Kansas Publications, Museum of Natural History**, Kansas, **1**(19):301-406.

MOOJEN, J., 1952. **Os Roedores do Brasil**. Rio de Janeiro: Instituto Nacional do Livro. Biblioteca Científica Brasileira, Série A-II., 214p., il.

NOWAK, E.M., 1999. **Walker's Mammals of the World**. 6.ed., v.2. Baltimore and London: The John Hopkins University Press. 1936p., il.

OLIVEIRA, T.G. & MESQUITA, E.R.L., 1998. Notes on the distribution of the white faced tree rat, *Echimys chrysurus* (Rodentia, Echimyidae) in northeastern Brazil. **Mammalia**, Paris, **62**(2):305-306.

PATTON, J.L., 1987. Species groups of spiny rats genus *Proechimys* (Rodentia: Echimyidae). **Fieldiana Zoology, n.s.**, Chicago, **39**:305-345.

PATTON, J.L. & ROGERS, M.A., 1983. Systematic implications of non-geographic variation in the spiny rat genus *Proechimys* (Echimyidae). **Zeitschrift für Saugertierkunde**, Jena, **48**:363-370.

PELZELN, A., 1883. Brasilische Säugerthiere. Resultate von Johann Natterers Reise in den Jahren 1817 bis 1835. **Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien**, Wien, **33**:1-140.

TATE, G.H.H., 1935. The taxonomy of the genera of Neotropical hystricoid rodents. **Bulletin of the American Museum of Natural History**, New York, **68**:295-447.

THOMAS, O., 1910. Mammals from the River Supinaam, Demerara, presented by Mr. F.V.McConnell to the British Museum. **Annals and Magazine of Natural History**, London, **8**(6):111-14.

THOMAS, O., 1916. Some notes on the Echimyinae. **Annals and Magazine of Natural History**, London, **8**(18):294-301.

THOMAS, O., 1928. A new *Echimys* from Eastern Ecuador. **Annals and Magazine of Natural History**, London, **10**(2):409-410.

TROUESSART, E.L., 1881[1888]. Catalogue des mammifères vivants et fossiles. Ordre des rongeurs. **Bulletin de la Société d'Etudes Scientifiques D'Angers**, Angers, **10**(1):58-144; (2):145-212 [for 1880].

TROUESSART, E.L., 1905. **Catalogum mammalium tam viventium quam fossilium**. Suppl. Pts. 3 & Ungulata to Monotremata. Berlin: Friedländer, 929p.

VANZOLINI, P.E., 1992. **A Supplement to the Ornithological Gazetteer of Brazil**. São Paulo: Museu de Zoologia, Universidade de São Paulo, 252p.

UNITED STATES BOARD ON GEOGRAPHICAL NAMES, 1993. **Gazetteer. Guyana**. Official Standard Names. Washington: Office of Geography, Department of the Interior, 123p.

WAGNER, J.A., 1845. Diagnosen einiger neuer Arten von Nagern und Handflüglern. **Archiv für Naturgeschichte**, München, **11**:145-149.

WAGNER, J.A., 1850. Beiträge zur Kentniss der Säugethiere Amerika's. **Abhandlungen der Königlichen Akademie der Wissenschaft**, München, **5**(2):271-332.

WAHLERT, J.H., 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. **Bulletin of the Museum of Comparative Zoology**, Cambridge, **113**:113-214.

WAHLERT, J.H., 1983. Relationships of Florentiamyidae (Rodentia, Geomyidae) based on cranial and dental morphology. **American Museum Novitates**, New York, **2769**:1-23.

WAHLERT, J.H., 1985. Cranial foramina of rodents. In: LUCKETT, W.P. & HARTENBERGER, J.L. (Eds.) **Evolutionary relationships among rodents: a multidisciplinary analysis**. New York: Plenum Press, p.311-333.

WATERHOUSE, G.R., 1848. **A Natural History of the Mammalia II**. London: Hyppolyte Bailliere Publisher, 500p., il.

WOLFHEIM, J.H., 1983. *Alouatta seniculus*. In: **Primates of the World - Distribution, Abundance, and Conservation**. Seattle and London: University of Washington Press. 831p.

WOODS, C.A., 1993. Hystricognathi. In: WILSON, D.E. & REEDER, D.A. (Eds.) **Mammals Species of the World. A taxonomic and geographic reference**. 2.ed. Washington: Smithsonian Institution Press. p.771-806.

WOODS, C.A. & HOWLANDS, E.B., 1979. Adaptative radiation of capromyid rodents: anatomy of the masticatory apparatus. **Journal of Mammalogy**, Provo, **60**(1):95-116.

ZIMMERMANN, E.A.W., 1780. **Geographische Geschichte des Menschen und der viersüßigen Thiere. Zweiter Band Enthalt ein vollständiges verzeichniß aller bekannten Quadrupeden von E. A. W Zimmermann**. Leipzig. In der Weygandschen Buchhandlung 1780.

APPENDIX I

Specimens examined (Abreviations: s&s = skin & skull, ♂ = males, ♀ =females, Faz.=Fazenda, Sit.=Sítio):

Echimys (N= 29): *Echimys chrysurus* (N= 27) – BRAZIL - PARÁ: Aurá, Belém, MN3847 (s&s); Cametá, Rio Tocantins: MZUSP4510, 4547, 4548, 4551, 4642, MN21504, NRM A587194-A587196 (♂, s&s), 4557, 4558 (♂, skin); Pará: MZUSP25809 (♂, skin), MNK1181 (♂, s&s, holotype of *Loncheres paleaceus*); Peixe-Boi: BMNH14.6.10.1 (♂, s&s); Utinga, Belém: MZUSP25810 (♂, skin); Rodovia BR-010 km 87-94: MZUSP26200 (skull); AMAPÁ - Rio Amapari: MN21505 (♀, s&s); Serra do Navio: MN20411 (s&s); GUYANA: Potaro Highlands, 1300ft.: BMNH7.6.10.4 (♂, skin); Supinaam river: BMNH10.5.4.21 (♂, skin); Upper County [Upper Corentyn]: BMNH43.8.19.14 (♀, s&s); SURINAM: Surinam: MNK1182 (♂, s&s); FRENCH GUIANA - Cayenne: MNHN 1995-1398 (♂, s&s, holotype of *Echimys cristatus*); rive droite du Petit Saut, Programme Faune Sauvage: MNHN1999-1082 (skin & skeleton); No locality: MZUSP4011 (skull); MN60538 (skeleton). *Echimys* sp. (N=2) – BRAZIL - PARÁ: Barreirinhas, Tapajós River: MZUSP26650 (♂, s&s); AMAZONAS: Virgem Guajará, Rio Madeira: MN67549 (alcohol).

Makalata (N= 93): *Makalata didelphoides* (N= 45) – BRAZIL - AMAPÁ: Igarapé do Braço, Rio Araguari: IEPA: 0174 (♂, s&s); AMAZONAS: Ayapua, Rio Purús, MNK35816, 35817 (♂, s&s); Balbina: MN26925 (♂, s&s); Igarapé Anibá, N. bank Rio Amazonas: MZUSP4641, 26553 (♀, s&s), 4549 (♂, s&s); Lago do Batista, Rio Amazonas: MZUSP4509, 4550, 26554, 26599 (♀, s&s), 4546, 4559, 26600 (♂, s&s), 26601 (s&s); Rio Juruá: MZUSP: 896 (skull), 899 (♂, s&s); Silves: MZUSP: 4553 (♂, s&s); 40km up to mouth of Rio Ariaú, right bank of Rio Negro: MN30487 (skull), 30475 (skull); Codajás, Rio Solimões (N): NRM A59 8016 (♀, s&s); Igarapé do Castanha, Rio Purús: NRM A591144, A591148 (♀, s&s); Itacoatiara, Rio Amazonas (N): NRM A581433 (♀, s&s); João Pessôa, Rio Juruá: NRM2117, 2163 (♂, s&s), 2333 (♀, s&s); Lago do Canaçari, Rio Amazonas (N): NRM A621453 (♂, s&s); Redempção, Rio Purús: NRM A591176 (♀, s&s); PARÁ: Boiuçu, N. bank Rio Amazonas: MZUSP4481, MN6450 (♀, skin); 26593 (♀ skull); Rio Ererê: MN6151 (♀ s&s); Irocanga, Rio Tapajós (W): NRM A588045, A598209 (♀, s&s), A608046 (♂, s&s); Paraná de Faro: MNK38814 (♂, s&s); FRENCH GUIANA: Cayenne: MNK1183 (♂, s&s, holotype of *Nelomys armatus*:); Environs immédiate du barrage de Petit Saut (Programme Faune Sauvage): MNHN1999-1082 (♀, s&s); GUIANA: Guiana: MNK8345 (♂, skull); BONASICA: Essequibo river: NRM1 (♂, s&s); DEMERARA: Plantation Providence: NRM2 (♂, s&s); No locality: MZUSP25854, ZSM54a (skulls); MN31530 (♀, skull); *Makalata castaneus* (N= 1): TOBAGO: ZMUC: CN2307 (s&s); *Makalata macrura* (N=2) – BRAZIL - AMAZONAS: Borba: NMW B921 (♀, skin, holotype:); Carvoeiro, próximo à boca do Rio Branco: NMW923 (♂, s&s); *Makalata* sp. (N= 45) – BRAZIL - AMAPÁ: Rio Tracajatuba: MN20412 (♂, skull), 20413 (♀, skull); AMAZONAS: Balbina: MZUSP22757, 22933, 22936, 22937, 26923, 26924 (♂, s&s), 22930, 22931, 22934, MN26922 (♀, s&s); CEARÁ: Fortaleza: MN8279 (♀, skin); Sit. Piraquara, São Benedito: MN21488, 21494 (♀, s&s), 21495 (♂, s&s); Sit. Macapá, São Benedito: MN21489 (♀, s&s), 21499 (♂, s&s); Sit. Cinta do S. José, São Benedito: MN21490 (♂, s&s); Sit. Guaribas do Amaral, São Benedito: MN21491 (♂, skin), 21500 (♀, s&s), 21501 (♂, skull); Sit. São José da Boa Vista, São Benedito: MN21496 (♀, s&s); Sit. Barra, São Benedito: MN11101 (♂, s&s), 21492 (♀, s&s); Sit. Trairuçu, Itapagé, Ceará: MN31541 (♀, skin) Sit. Trairuçú (córrego no litoral da praia) Aguiráz: MN21493 (♂, s&s); 31541 (♀, skull); Sit. Mazagão, Guaraciaba do Norte: MN21497 (♂, s&s); 21498 (♀, skin); Ceará: MNI p267 (♀, skull); MATO GROSSO: Jacaré, baixo Rio Kuluene, Alto Xingú: MN10394 (♂, s&s); Rio Tapirapé: MN6152 (♂, skin); PARÁ: Cametá, Rio Tocantins: MN4080 (♂, s&s); Coatacoará, Rio Parú do Leste, Almeirim: MN21502 (♀, skin); Gorotire, Rio Fresco: MZUSP25824 (♀, s&s); Monte Alegre: MN1929 (skull); 1971, 1972 (♂, skins); Marajó: MNK38813, 43570 (♀, s&s); Utinga, Belém: MN19619 (♀, s&s); RONDÔNIA: UHE Samuel: MZUSP27446 (♂, s&s); Campo dos Veados, Rio Guaporé: NMW ST182 (♀, s&s); Pedra de Amolar, Salto do Girão, Rio Madeira: NMW917 (♂, skin).

Phyllomys (N= 137): *Phyllomys blainvilii*: (N=39) BRASIL - ALAGOAS: Viçosa: MN21513 (♂, s&s); BAHIA: Lapa: MN4125-4127, 4132, 4137, 4140, (♂, s&s), 4133 (♂, skin), 4128, 4131 (♀, s&s), 4136 (s&s); Várzea da Canabrava, Seabra: MN21626, 21628, 21630, 21635, 21627, 21638, 21639,

21650 (♂, s&s), 31544 (♂, skull), 21631-21634, 21636, 21640, 21643-21645, 21649 (♀, s&s), 2P1641, 2P1647, 2P1664 (♀, skull); CEARÁ: Sit. Serra Bebida Nova, Crato: MN21572, 21574 (s&s), 21599, 21601 (♂, s&s); PERNAMBUCO: Sit. Barquinho, Garanhuns: 21516 (♂, s&s), No locality: NMW B1101 (♂, s&s); *Phyllomys brasiliensis* (N=3): BRAZIL: MINAS GERAIS: Rasquão do Azude: ZMK CN83 (♀, s&s); Lagoa Santa: ZMK81 (♀, s&s); Sumidouro: ZMK CN83 (♂, skeleton); *Phyllomys dasythrix*: (N= 2) BRAZIL - RIO GRANDE DO SUL: Pinheiros, Candelária: MN6238 (♂♂, s&s); São Francisco de Paula: MN21503 (♂, s&s). *Phyllomys* aff. *dasythrix*: (N= 1) BRAZIL - SÃO PAULO: Teodoro de Sampaio, Serra do Diabo: MZUSP8885 (♀, s&s). *Phyllomys lamarum*: (N=16) BRAZIL - BAHIA: Faz. Morro, Feira de Santana: MN21654 (♀, s&s); Faz. Estiva, Feira de Santana: MN21655 (♀, s&s), 21656 (♀, s&s); Faz. Salgado Quarta, Feira de Santana: MN21661 (♂, skin); Faz. Estrada Nova, Feira de Santana: MN21660 (♂, skull); Faz. Quituba, Feira de Santana: MN21662 (♀, skin), 21663 (♀, skin), 21664 (♂, s&s); Faz. Feira Nova 2ª, Feira de Santana: MN21667 (♂, skin), 21668 (♂, skin); PARAÍBA: Camaratuba, Mamanguape: MZUSP8413 (♀, s&s), 8415 (♂, s&s), 8416 (♂, s&s), 8417 (♂, s&s), 8418 (♀, skull); Uruba, Mamanguape: MZUSP8414 (♂, s&s).

Phyllomys medius: (N= 6) BRAZIL - PARANÁ: Porto Camargo, Rio Paraná: MZUSP7716 (♀ s&s); SANTA CATARINA: Florianópolis: MN31568, 31570-31572 (skins); SÃO PAULO: Barra do Onça Parda: MZUSP 10629 (♀, s&s); *Phyllomys nigrispinus*: (N=29) BRAZIL - PARANÁ: Guajuvira: MN6431 (skin); SÃO PAULO: Barra do Icaparra: MZUSP25862, 25863 (♀, s&s); Itatiba: MZUSP664, 666 (s&s), 665, 25819 (♂, s&s); São Paulo: MZUSP: 1949, 1952, 1953 (♀, s&s); Interlagos, São Paulo: MZUSP10311, 10312, 10316-10318, 25854-25857 (♀, s&s), 10319, 10320, 25853, 25858-25861 (♂, s&s); Taboão da Serra: MZUSP26652 (♀, s&s); Vanuire: MZUSP3738 (♀, s&s); Ypanema: NMW B918 (♂, skin, holotype). *Phyllomys pattoni*: (N= 26) BRAZIL - BAHIA: faz. Monte Castelo, ilha da Cassumba, 7km SW Caravelas: MZUSP 31953-31956 (♂, s&s, all paratypes); Pirataquissé, Ilhéus: MN10453, 11258 (♂, s&s), 11256, 11257, 21517 (♀, s&s); São Felipe: MN22264 (s&s); MINAS GERAIS: Faz. São Geraldo, Além Paraíba: MN4077 (♂, s&s); PERNAMBUCO: Dois Irmãos, Recife: MN8195 (s&s); RIO DE JANEIRO: São Francisco, Niterói: 6449 (♀, s&s); Teresópolis: MN2232 (skull), 2239 (♀, skull), 2240 (skull), 6440 (♂, skull), 6443 (♂, skull), 6742 (♂, s&s); Faz. Alpina, Teresópolis: MN: 1933 (s&s), 31522 (skull); Nova Friburgo: MN31564 (♂, skin), 31567 (♂, skin); Ilha Grande: MN31566 (s&s); Santa Cruz, Petrópolis: MN21508 (♂, s&s); SÃO PAULO: Piquete: MZUSP138 (alcohol); *Phyllomys thomasi*: (N=14) BRAZIL: SÃO PAULO: Ilha de São Sebastião: MZUSP45 (♂ skin), 47 (♂, s&s, holotype), 51 (♂, skin), 223 (♂, skull), 526 - 528 (♂, skull), 532 (♂, skin), 535 (♂, s&s), 2151 (♂, s&s), 3197 (♂, s&s), 3199 (♂, s&s), 6433 (♂, s&s), 27755 (♀♀, s&s); *Phyllomys* sp. (N=1) No locality: MN1930 (♂, skin).

Toromys (N= 57): *Toromys grandis* – BRAZIL - AMAZONAS: Lago Batista, N. bank Rio Amazonas: MZUSP4790 (♀, s&s), NRM A587189-A587193 (♂, s&s); Manaqueri im Mündungsbereich des Rio Solimões: NMW: B920 (s&s, holotype); Silves: MZUSP4487 (♀, s&s), 4488, 4489 (♂, s&s); Urucurituba, Rio Amazonas: NRM A587184-A587186 (♂, s&s); 556 (♂, skin); PARÁ: Belterra, Santarém: MN5751 (♂, s&s); Bravo, N. bank Rio Amazonas: MZUSP4719, 4720, 4722, 4723 (♂, s&s); Faz. Recreio, Ilha Caviana: MZUSP: 25815 (♀, s&s); Facienda Paraiso bei Faro: MNK38812 (♂, s&s); Lago Cuiteua, N. bank Rio Amazonas: MZUSP4786 (♀, s&s); Paraná do Bom Jardim, Paissandú, Nhamundá: MZUSP8960 (♂, s&s); 8961 - 8963 (♀, s&s); 25817 (♂, s&s); Paraná de Faro: MNK38811 (♀, s&s); BMNH11.12.22.12 (♂, s&s); Santarém: MN11922-11924, 11926, 11928, 11929, 11940, 11941 (♀, s&s); 11925, 11927, 11930-11939 (♂, s&s), BMNH: 5.6.3.4 (♂, skull); Igarapéassú, Santarém: MN11584 (♀, s&s); Faz. São Pedro, Monte Alegre: MN1944 (♂, s&s), 1945 (♀, s&s); Óbidos: MN5968 (♂, s&s); Santa Rita, Rio Amazonas: NRM A58 7187-A59 7188 (♂, s&s); Jardim Zoológico, Santarém: BMNH5.6.3.1 (♀, s&s).

APPENDIX II

Gazetteer

BRAZIL - ALAGOAS: 1- Viçosa 09°24'S 36°14'W. AMAPÁ: 2- Igarapé do braço, Rio Araguari 01°17'02"N 51°35'20"W; 3- Rio Amapari. 00°45'N 51°32'W; 4- Rio Tracajatuba 00°56'N 51°00' W; 5- Serra do Navio 00°53'44"N 52°00'08"W. AMAZONAS: 6- 40km up to mouth of Rio Ariaú right bank of Rio Negro *c.* 03°06'S 60° 26'W; 7- Aiapuá, Rio Purus 04°27'S 62°03'W; 8- UHE Balbina, Rio Uatumã 01°53'S 59°28'W; 9- Borba, Rio Madeira 04°24'S 59°35'W; 10- Carvoeiro, near mouth of Rio Branco 01°26'S 62°01'W; 11- Codajás, Rio Solimões 03°50'S 62°05'W; 12- Eirunepé (=João Pessôa), Rio Juruá 06°40'S 69°52'W; 13- Igarapé Anibá, N. bank Rio Amazonas 02°59'S 58°29'W; 14- Igarapé do Castanho, Rio Purús 3°52'S 61°23'W; 15- Itacoatiara Rio Amazonas, N. bank 03°08'S 58°25'W; 16- Lago do Batista, Rio Amazonas 03°17'S 58°16'W; 17- Lago do Canaçari 02°57'S 58°15'W; 18- Manaqueri, Rio Solimões 03°29'S 60°31'W; 19- Redenção, Rio Purús 04°58'S 62°35'W; 20- Rio Ererê, left bank Rio Negro 00°14'S 63°53'W; 21- Rio Xiruã, afl. right bank Rio Juruá 06°03'S 67°50'W; 22- Silves 02°50'S 58°13'W. 23- Urucurituba, Rio Amazonas 02°46'S 57° 49'W; 24- Virgem Guajará, Borba, Rio Madeira 04°19'44"S 59°42'26"W. BAHIA: Feira de Santana 12°15'S 38°57'W (includes 25- Faz. Estiva, 26- Faz. Estrada Nova, 27- Faz. Feira Nova 2ª, 28- Faz. Morro, 29- Faz. Quituba, 30- Faz. Salgado Quarta); 31- Lapa 13°39'S 39°51'W; 32- Faz. Monte Castelo, ilha da Cassumba, 7km SW Caravelas 17°48'06" 39°15'49" W; 33- Pirataquissé, Banco da Vitória, Ilhéus *c.* 14°45'S 39°04'W; 34- São Felipe 12°50'50" S 39°05'22"W; Seabra 12°25'S 41° 46'W (includes 35- várzea da Cana Brava, Seabra). CEARÁ: 36- Fortaleza 03°43'02"S 38°32'35"W; São Benedito 04°03'S 40°53'W (includes: 37- Sit. Barra; 38- Sit. Cinta do S. José, 39- Sit. Guaribas do Amaral, 40- Sit. Macapá, 41- Sit. Piraquara; 42- Sit. São José da Boa Vista); Guaraciaba do Norte 04°10' 01" S 40°44'51"W (includes 43- Sit. Mazagão, Guaraciaba do Norte); 44- Sit. Serra Bebida Nova, Crato 07°14'03"S 39°24'34"W; 45- Sit. Trairuçú (córrego no litoral da praia), Aquiráz 03°54'05"S 38°23'28"W; 46- Sit. Trairuçú, Itapagé 03°41'S 39°35'W. MARANHÃO: 47- Vargem Grande 03°30'S 43°55'W (Locality from OLIVEIRA & MESQUITA, 1998; Four specimens were collected). MATO GROSSO: 48- Jacaré, baixo Rio Kuluene, Alto Xingú 12°00'S 53°24'W; 49- Rio Tapirapé 10°40'54"S 50°39'22"W. MINAS GERAIS: Além Paraíba 21°52'S 42°41'W (includes 50- faz. São Geraldo, Além Paraíba); 51-Lagoa Santa 19°38'S 43°53'W; 52- Rasquão do Azude (not located; probably near to Lagoa Santa); 53- Sumidouro 19°32'28"S 43°56'28"W. PARÁ: Belém 01°26'S 48°29'W (includes 54- Aurá, Belém; 77- Utinga, Belém); 55- Barreirinhas, Rio Tapajós 04°25'S 56°13'W; 56- Belterra, Santarém 02°38'S 54° 56'W; 57- Boiuçu, N. bank Rio Amazonas 02°05'S 55°14'W; 58- BR-010 km 87-94 *c.* 02°10'S 47°35'W. 59- Bravo, N. bank Rio Amazonas 01°54'S 55°10'W; 60- Cametá, Rio Tocantins 02°15'S 49°31'W; 61- Coatacoará, Rio Parú do Leste, Almeirim 00°02'48"S 54°06'48"W (coordinates based on CARVALHO [1955] itinerary); 62- Faz. Paraíso, Faro, Rio Amazonas 02°05'S 56°46'W; 63- faz. Recreio, ilha Caviana 00°10'N 50°10'W; 64- Faz. São Pedro, Monte Alegre: See Monte Alegre; 65- Gorotire, Rio Fresco 07°47'S 51°08'W; 66- Igarapé Açú, left bank of Rio Tapajós, Santarém 03°44'S 55°31'W; 67- Iroçanga, Rio Tapajós 02°30'S 55°10'W; 68- lago Cuiteua, N. bank Rio Amazonas 01°49'S 54° 58'W; 69- Marajó 01°00'S 49°30'W; 70- Monte Alegre 02°00'28"S 54°04'09"W; 71- Óbidos 01°55'S 55°31'W; 72- Paraná de Bom Jardim, Nhamundá, Paissandú 02° 02'S 56°12'W (VANZOLINI , 1992); 73- Paraná de Faro 02°10'S 56°44'W; 74- Peixe-Boi 01°11'32"S 47°18'50"W; 75- Santa Rita, Rio Amazonas 02°02'S 55° 18'W (Paraná do Bom Jardim, near Bom Jardim (or Santa Rita) island. Located on map SA21 of Hispanic America); 76- Santarém 02° 26' S 54° 42' W. PARAÍBA: 78- Camaratuba, Mamanguape 06°35'32" S 34°58'12"W; 79- Mamanguape 06°50'19"S 35°07'34"W (includes Uruba, Mamanguape). PARANÁ: 80- Guajuvira 25°35'51"S 49°30'59"W; 81- Porto Camargo, Rio Paraná 23° 22'05"S 53°44'35"W; PERNAMBUCO: Recife 11°00'35"S 41°53'23"W (includes 82- Dois Irmãos, Recife); Garanhuns 08°53'25"S 36°29'34"W (includes 83- Sit. Barquinho, Garanhuns). RIO DE JANEIRO: 84- Faz. Alpina, Teresópolis 22°19'S 42°59'W; 85- Ilha Grande 23°09' S 44°14'W; 86- Nova Friburgo 22°16'55"S 42°31'52"W; Petrópolis 22°30'18"S 43° 10'43" W (includes 87- Santa Cruz, Petrópolis); Niterói 22°53'00"S 43°06'13"W (includes 88- São Francisco, Niterói); 89- Teresópolis 22°24'44"S 42°57'56"W. RIO GRANDE DO SUL: 90- Candelária 29°40'09"S 52°47'20"W (includes Pinheiros, Candelária 29°44'S 52°46'W); 91- São Francisco de Paula 29°26'53"S 50°35'01"W. RONDÔNIA: 92-

Campo dos Veados Rio Guaporé 13° 29' S 61° 34' W; 93- Pedra de Amolar Salto do Girão Rio Madeira 09°20'S 64°43'W; 94- UHE Samuel 08°45'S 63°27'W. SANTA CATARINA: 95- Florianópolis 27°29'S 48°29'W. SÃO PAULO: 96- Barra de Icaparra 24°41'S 47°26'W; 97- Barra do Onça Parda 24° 19'S 47°51'W (ribeirão Onça Parda); 98- Ilha do Cardoso 25°08'S 47°58'W; 99- Ilha de São Sebastião 23°48'S 45°25'W; 100- Interlagos, São Paulo (see São Paulo); 101- Itatiba 23°00'21"S 46°50'20"W; 102- Piquete 22°36'S 45°10'W; 103- São Paulo 23°32'S 46°37'W; 104- Taboão da Serra, 23°37'34"S 46°47'30"W; 105- Teodoro de Sampaio, near Serra do Diabo 22°31'57"S 52°10'03"W; 106- Vanuire, posto indígena 21°47'S 50°23'W; 107- Ypanema (currently Floresta Nacional de Ipanema, 20km NW Sorocaba) 23°26 07"S 47°37'41"W.

FRENCH GUIANA: 108- Cayenne 04°56'N 52°00'W; 109- Nouragues 04°05'N 52°40'W (MAUFFREY & CATZEFLIS, 2003); 110- rive droite du Petit Saut (Programme Faune Sauvage) 05°04'N 53°03'W.

GUYANA - DEMERARA-MAHAICA: 111- Bonasika creek, Essequibo River 06°45'N 58°30'W; 112- Plantation Providence (not located); 113- East Berbice Corentyne Upper County (here as Upper Corentyne Local Government Distric 5°57'N 57°09'W; Collected by Sir R. Schomburgh; According THOMAS (1916), the specimen of Sir Schomburgh came from Upper Corenty). POMEROON-SUPENAAM: 114- Supinaam river, 1300ft 06°59'N 58°31'W (Collected by McConnell/Cozier. In USBGN, 1976 as Supenaam River; see also THOMAS (1910) and WOLFHEIM (1983). POTARO-SIPARUNI: 115- Kabukalli, landing Iwokrama forest Potaro-Siparuni (not located, here as Akramukra falls 04°21'S 58°28'W; based on specimen ROM111578); 116-Potaro Highlands, 1300ft. (not located, here as Kowa Mountain 04°51'N 59° 41'W). UPPER TAKUTU-UPPER-ESSEQUIBO: 117- Tamton 02°21'N 59°43'W (based on specimen ROM36840).

SURINAM: (Localities based on 8 specimens examined by Husson, 1978) BROKOPONDO: 118- Bedoti, south of Gansee on West Bank of Suriname River, locality now submerged by the Brokopondo Lake 04°13'N 55°53'W. NICKERIE: 119- Groot Henarpolder South east of Nieuw Nickerie, northwestern Nickerie district 05°52'N 56°52'W; 120- Zuid River, near Kayserberg Airstrip, southern Nickerie District 3°20'N 56°49'W. PARA: 121- Republiek, about 35km South of Paramaribo 5°30'N 55°12'W. PARAMARIBO: 122- Agricultural Experimental Station (Cultuurtuin) 05°50'N 55°10'W.

TOBAGO: 123- Tobago 11°15'N 60°40'W.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.113-130, jan./mar.2005
ISSN 0365-4508

TAXONOMY OF PIGMY RICE RATS GENUS *OLIGORYZOMYS* BANGS, 1900 (RODENTIA, SIGMODONTINAE) OF THE BRAZILIAN CERRADO, WITH THE DESCRIPTION OF TWO NEW SPECIES [1]

(With 4 figures)

MARCELO WEKSLER [2]
CIBELE R. BONVICINO [3]

ABSTRACT: We present a taxonomic overview of the species of *Oligoryzomys* from the Brazilian Cerrado. We recognize seven species, including two described herein, making *Oligoryzomys* one of the most diverse mammalian genera of the Cerrado morphoclimatic domain. *Oligoryzomys chacoensis* occurs in the Cerrado and Chaco morphoclimatic domains. *Oligoryzomys flavescens* is distributed mainly in the Atlantic Forest of Brazil and the Pampas region of Argentina and Uruguay, but is also found in gallery forest in the Cerrado of Brazil near the border of the Atlantic Forest. *Oligoryzomys stramineus* and *O. fornesi* occur in the Cerrado and Caatinga morphoclimatic domains. *Oligoryzomys nigripes* is found in the Atlantic Forest and in the Southern portion of the Cerrado. The two new species are endemic to the Cerrado, and one of them is found only in "campo rupestre" vegetation. *Oligoryzomys eliurus* and *O. delticola* are placed tentatively as junior synonyms of *O. nigripes*. *Oligoryzomys fornesi* is recognized as a distinct species from *O. microtis*.

Key words: taxonomy, morphology, karyotype, *Oligoryzomys*, Cerrado.

RESUMO: Taxonomia dos camundongos-do-mato, gênero *Oligoryzomys* Bangs, 1900 (Rodentia, Sigmodontinae) do Cerrado brasileiro, com a descrição de duas novas espécies.

Apresentamos uma revisão taxonômica das espécies do gênero *Oligoryzomys* do Cerrado brasileiro. Reconhecemos sete espécies, incluindo duas aqui descritas, tornando *Oligoryzomys* um dos mais diversos gêneros de mamíferos do domínio morfoclimático do Cerrado. *Oligoryzomys chacoensis* ocorre nos domínios morfoclimáticos do Cerrado e do Chaco. *Oligoryzomys flavescens* se distribui principalmente na Mata Atlântica do Brasil e na região dos pampas da Argentina e Uruguai, mas é também encontrado em matas de galeria no Cerrado do Brasil próximo do limite com a Mata Atlântica. *Oligoryzomys stramineus* e *O. fornesi* ocorrem nos domínios morfoclimáticos do Cerrado e da Caatinga. *Oligoryzomys nigripes* é encontrado na Mata Atlântica e na porção sul do Cerrado. As duas novas espécies são endêmicas do Cerrado, e uma delas é encontrada apenas na vegetação de "campo rupestre". *Oligoryzomys eliurus* e *O. delticola* são tentativamente consideradas sinônimos juniores de *O. nigripes*. *Oligoryzomys fornesi* é reconhecida como uma espécie distinta de *O. microtis*.

Palavras-chave: taxonomia, morfologia, cariótipo, *Oligoryzomys*, Cerrado.

INTRODUCTION

Oligoryzomys Bangs, 1900 comprises a diverse group of small-sized Neotropical muroid rats distributed from northern Central America to the southernmost part of South America (MUSSER & CARLETON, 1993). The monophyly of *Oligoryzomys* is supported by morphologic data (CARLETON & MUSSER, 1989) and analyses of allozymes (DICKERMAN & YATES, 1995), mitochondrial genes (MYERS, LUNDRIGAN & TUCKER, 1995), and nuclear genes (WEKSLER, 2003). Delimitations of *Oligoryzomys* species, however, are still problematic due to lack of comprehensive revisions.

Fifty-eight specific and subspecific names are associated with *Oligoryzomys* (MUSSER & CARLETON, 1993). The latest taxonomic summary of the genus (CARLETON & MUSSER, 1989) recognized 12 species divided in five groups: the *fulvescens* group, with *O. fulvescens* (Saussure, 1860), *O. arenalis* (Thomas, 1932), and *O. vegetus* (Bangs, 1902); the *microtis* group

[1] Submitted on June 15, 2004. Accepted on January 14, 2005.
[2] American Museum of Natural History, Department of Mammalogy. 79th Street at Central Park West, 10024, NY, USA.
[3] Fundação Instituto Oswaldo Cruz, Departamento de Medicina Tropical, Laboratório de Biologia e Controle da Esquistossomose. Av. Brasil, 4365, Manguinhos, 21045-900, Rio de Janeiro, RJ, Brasil.
Instituto Nacional de Câncer (INCA), Divisão de Genética. Rua André Cavalcanti, 37, 4° andar, 20231-050, Rio de Janeiro, RJ, Brasil.
Fellow of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

with *O. microtis* (Allen, 1916); the *andinus* group with *O. andinus* (Osgood, 1914) and *O. chacoensis* (Myers and Carleton, 1981); the *flavescens* group with *O. flavescens* (Waterhouse, 1837) and three undescribed species; and the *nigripes* group with *O. nigripes* (Olfers, 1818), *O. eliurus* (Wagner, 1845), *O. destructor* (Tschudi, 1844), *O. longicaudatus* (Bennet, 1832), and *O. delticola* (Thomas, 1917). GALLARDO & PALMA (1990) subsequently recognized *O. magellanicus* (Bennet, 1836) as a distinct species from *O. longicaudatus* based on phallic morphology and karyotypic and morphometric data. In their checklist of muroid species, MUSSER & CARLETON (1993) considered *O. griseolus* (Osgood, 1912) as a valid species apart from *O. fulvescens*, and included the extinct *O. victus* (Thomas, 1898) in the genus *Oligoryzomys*.

More recently, CARLETON & MUSSER (1995) recognized four subspecies in *O. fulvescens* based on phenetic and karyotypic distinctiveness while MYERS *et al.* (1995) considered *O. fornesi* (Allen, 1916) as a valid species distinct from *O. microtis* based on molecular data. Finally, SILVA & YONENAGA-YASSUDA (1997) reported two new karyotypes attributed to presumably undescribed species, while BONVICINO & WEKSLER (1998) described a new species, *O. stramineus*. Thus, the genus *Oligoryzomys*, at this time, comprises 17 recognized species, in addition to five other undescribed species and four subspecies of *O. fulvescens*.

Seven species of *Oligoryzomys* presumably occur in the Cerrado region of Central Brazil, eastern Bolivia, and Northern Paraguay: *O. chacoensis*, *O. eliurus*, *O. microtis*, *O. nigripes*, *O. stramineus*, *O. fornesi*, and *O. flavescens*. Thus, *Oligoryzomys* is one of most species-rich mammalian genus of the Cerrado, a morphoclimatic domain that is considered as a biodiversity hotspot (MYERS *et al.*, 2000). In 1996, we conducted a series of inventory expeditions to the Parque Nacional da Chapada dos Veadeiros and collected specimens clearly belonging to two different species of *Oligoryzomys*. Analyses of morphologic characters and karyotypic data indicated that they belong to two undescribed species. In the process of recognizing the distinctiveness of these taxa, we reviewed the material used in our previous report on *Oligoryzomys* (BONVICINO & WEKSLER, 1998) and incorporated new information from subsequent expeditions and from other sources (*e.g.*, SILVA & YONENAGA-YASSUDA, 1997). Here we present the description of the two new species, and provide a taxonomic summary of the remaining species of *Oligoryzomys* of the Cerrado morphoclimatic domain.

MATERIAL AND METHODS

Examination of external, cranial, and dental morphology was performed in 370 specimens of *Oligoryzomys*. Part of these specimens (284) is listed in BONVICINO and WEKSLER (1998). In addition, 86 specimens have been obtained recently from several Brazilian localities (Fig.1; Appendix 1). Skins and skulls are housed in the mammal collection of Museu Nacional, Rio de Janeiro (MN). The following acronyms refer to field numbers: C.R.Bonvicino (CRB), R.T.Santori (RTS), Laboratório de Vertebrados - Universidade Federal do Rio de Janeiro (LV), Laboratório de Biologia e Controle da Esquistossomose - Fundação Instituto Oswaldo Cruz, Rio de Janeiro (LBCE).

Oligoryzomys sp.nov.1 – Goiás State, 65km SSW Cavalcante, Fazenda Fiandeira 14°04'S 47°45'W (unsexed MN 50312, 50316-17, ♀ MN 50310, 50313, 50315, 50318, 50319, 50320, 50321; ♂ MN 50307, 50308, 50309, 50311, 50314, 50287, CRB 928, 937); Mimoso de Goiás, Fazenda Cadoz 15°03'22"S 48°09'41"W (♀ MN 67087).

Oligoryzomys sp.nov.2 – Goiás State, 5km N Alto Paraíso, Pouso Alto 14°07'57"S 47°30'36"W (unsexed MN 50328, ♀ CRB 1077, MN 50322, 50324, 50327, 50286; ♂ MN 50323, 50325, 50326).

O. nigripes – São Paulo State, Pedreira 22°43'S 46°55'W (unsexed CRB 1234, ♂ CRB 1209, 1247, 1407, 1427, 1435, 1436-37, ♀ CRB 1232, 1406, 1414, 1422, 1424-25, 1428); Fazenda Intervales (♀ INT 5, ♂ EM 1036); Rio Claro 22°45'S 47°33'W, Faz. São José (♂ RTS 5, CRB 1366, ♀ RTS 10); Araraquara 21°47'S 48°01'W (unsexed RTS 17, ♀ RTS 25). Rio de Janeiro State, Nova Friburgo 22°16'S 42°32'W (♂ CRB 1368, ♀ CRB 1369); Teresópolis 22°26'S 42°59'W, Vieira (♂ CRB 1271, 1441-44, ♀ CRB 1274, 1440, LBCE 495, 549, 551); Sumidouro 22°03'S 42°40'W (♂ LBCE 427, 439, 450, 455, 458, 474, 475, 478, 480-483, ♀ LBCE 445, 449).

O. flavescens – São Paulo State, Pedreira (♂ CRB 1405, 1408, 1419, 1430). Minas Gerais State, Itamonte 22°17'02"S 44°52'12"W (♀ CRB 1308).

O. fornesi – Bahia State, Fazenda Sertão do Formoso, Jaborandi 14°48'00"S 45°57'40"W (♂ MN 62637, 62638).

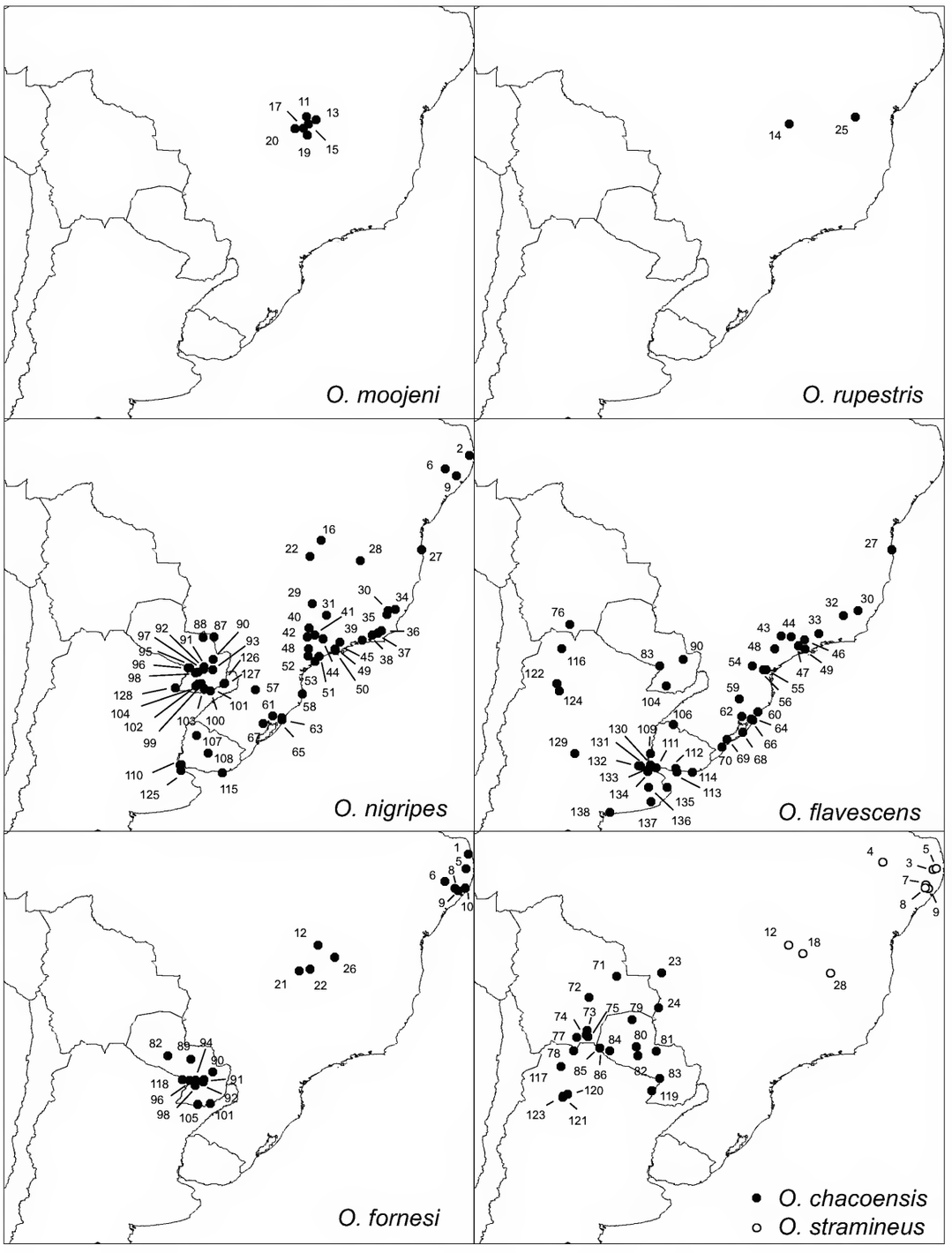

Fig.1- Geographic distribution of *Oligoryzomys* species that occur in the Brazilian Cerrado, Caatinga, and Atlantic Forest. Numbered symbols correspond to collection localities listed in the Appendix. *Oligoryzomys moojeni* sp.nov. and *O. rupestris* sp.nov. are endemic to the Cerrado, the latter being found only in "campo rupestre" vegetation. *Oligoryzomys nigripes* is found in the Atlantic Forest and in the Southern portion of the Cerrado, while *O. flavescens* is distributed mainly in the Atlantic Forest and Pampas, but is also found in gallery forest in the Cerrado of Brazil near the border of the Atlantic Forest. *Oligoryzomys chacoensis* occurs in the Cerrado and Chaco morphoclimatic domains, while *O. stramineus* and *O. fornesi* occur in the Cerrado and Caatinga morphoclimatic domains.

O. stramineus – Minas Gerais State, Juramento 16°50'S 43°35'W, Fazenda Canoas (♂ CRB 1380-81, ♀ LV-FC 156, CRB 1383).

We provide the mean, standard deviation, and range of 5 external and 18 skull measurements: head-and-body length (HB), tail length (T), length of feet with claws (F), maximum length of internal side of ear (E), weight (W), greatest skull length (GSL), condylo-incisive length (CIL), breadth of the occipital condyles (BOC), length of diastema (LD), palatal bridge (PB), length of incisive foramen (LIF), breadth of incisive foramen (BIF), length of maxillary molars (LM), breadth of first maxillary molar (BM1), external alveolar breadth (M1M), cranial height (CH), rostrum length (RL), rostrum breadth (BRO), least interorbital breadth (LIB), orbital length (ORL), zygomatic breadth (ZB), breadth of braincase (BB), and breadth of the zygomatic plate (BZP). External measurements (in millimeters) were recorded only from field-captured animals; we excluded pregnant females for weight values. Skulls were measured with digital calipers to the 0.01mm. Definitions of these measurements are the same as in BONVICINO & WEKSLER (1998). For morphometric characterization, we considered only adult specimens (all teeth erupted and with minimal wear) and grouped males and females.

Chromosome preparations were obtained from bone marrow cultures in RPMI 1640, 20% fetal calf serum, ethidium bromide (5µg/ml) and 10^{-6} M colchicine for two hours), following ANDRADE & BONVICINO (2003).

RESULTS

Oligoryzomys moojeni sp.nov.
(Figs.1, 2A, 3A, 4A)

Holotype – Adult ♂, MN 50309 (field number CRB 948). Skin, skull and partial skeleton, plus karyotype, collected in August 1996, by C.R.Bonvicino, M.Weksler, B.Lemos, and S.Lindbergh (Fig.2A).

Type-locality – Fazenda Fiandeira in "Morro do Chapéu" region, in the lowest part of the Chapada dos Veadeiros National Park, 65km SSW Cavalcante (14°04'S 47°45'W, altitude ranging from 550 to 740m), Goiás State, Brazil.

Paratypes – ♂ MN 50287, 50307, 50308, 50311, 50314, 50318, 50377, 50378, ♀ MN 50310, 50313, 50315, 50319, 50320, 50321, unsexed MN 50312, 50316, 50317.

Other specimens examined – MN 67087 from Faz. Cadoz, Mimoso de Goiás, Goiás State, Brazil.
External measurements – HB 89±4 (84-96, n=10), T 121±6 (112-132, n=9), F 23±2 (21-25, n=10), E 15±1.3 (13-17, n=10), W 16.9±5.3 (10-25, n=9).

Cranial measurements – See table 1.

Diagnosis – A medium-sized *Oligoryzomys* species characterized by: (1) brown-orange dorsal pelage, not contrasting with the creamy ventral pelage; (2) small incisive foramina; and (3) the highest diploid number (2n=70) among *Oligoryzomys* species.

Geographic distribution – Cerrado of Goiás and Minas Gerais States, in lower altitudes (less than 800m).

External characters – Adult dorsal pelage grizzled reddish-brown to yellowish-brown, composed of long and wholly guard hairs and slightly shorter overhairs with a sub-apical brown-yellowish or brown-reddish band. Lateral color lighter than in dorsum and without a defined limit with the creamy ventral pelage. Ventral hairs creamy at their upper half and gray at their basal half. Ventral regions of neck and limbs with entirely cream hairs. Inner side of pinnae with brown-reddish hairs. Dorsal surface of feet covered with lighter hairs, the tufts of longer hairs at base of pedal claws silvery. Tail slightly bicolored, dorsal surface dark gray and ventral surface light gray. Superciliary, genal, and mysticacial vibrissae not extending beyond ears. In juveniles, dorsum is reddish-brown to dark brownish-gray, ventral and lateral surfaces are gray, and the hairs of ventral surfaces of neck and limbs have a light gray base. There are eight mammae in inguinal, abdominal, postaxial, and pectoral pairs.

Cranial characters – Delicate skull, medium and narrow rostrum with similar width to interorbital constriction. Interorbital region hourglass-shaped. Braincase without supraorbital and postorbital ridges and with weakly developed lambdoidal ridge. Interparietal bone as broad as parietal. Large zygomatic plate relative to skull size, leading to deep zygomatic notch. Jugal bone absent, thus the zygomatic process of squamosal is in contact with the zygomatic process of maxillary. Incisive foramina with elongated teardrop shape, the posterior borders not extending beyond the anterior plane of the first molars, but sometimes almost reaching it. Palate with large posterolateral pits within fossa (absent in younger specimens). Palatal bridge broad and long; distance between the anterior border of mesopterygoid fossa and third molar similar to length of second molar. Mesopterygoid fossa usually perforated dorsally by large sphenopalatine vacuities, but partially ossified in some old animals. Width of parapterygoid plate slightly greater than width of mesopterygoid fossa. Stapedial foramen present (Fig.3), squamoso-alisphenoid groove and sphenofrontal

foramen absent (carotid circulatory pattern 2; VOSS, 1988). Medium or small subsquamosal fenestra and large postglenoid foramen. Alisphenoid strut absent. Large mastoid fenestra. Capsular projection of lower incisor alveolus present.

Dental characters – Upper and lower incisors opisthodont; molars pentalophodont. Superior molar rows parallel but with M3-M3 distance slightly broader than M1-M1 distance when taken from lingual side. Procingulum of first upper molar (M1) with anteromedian flexus; anterolabial and anterolingual conules of approximately equal size. Anteroloph reduced; posteroloph distinct but joined to metacone even in slightly worn molars. M3 reduced, with hypoflexus absent or very reduced, except in one animal where it is present.

Karyotype – Karyotypic analyses of 12 specimens of *Oligoryzomys moojeni* sp.nov. showed 2n=70, AN=74 (Fig.4A). The autosome complement comprised 3 pairs of small-sized biarmed chromosomes and 31 acrocentric pairs (one large pair and 30 varying in size from medium to small). The X chromosome is a large submetacentric, and the Y chromosome a small acrocentric. The 2n=70, AN=74 karyotype was described by ANDRADES-MIRANDA *et al.* (2001; see also LIMA *et al.*, 2003).

Table 1. Sample size, mean, standard-deviation, and range of cranial variables from *Oligoryzomys stramineus*, *O. nigripes*, *O. chacoensis*, *O. rupestris* sp.nov., *O. moojeni* sp.nov., *O. fornesi*, and *O. flavescens*.

	stramineus n=36	*chacoensis* n= 5	*nigripes* n=35	*rupestris* sp. nov. n=8	*moojeni* sp. nov. n=8	*fornesi* n=26	*flavescens* n=41
GSL	(33) 25.7±1.1 (23.3-28.3)	(3) 23.8±0.6 (23.2-24.3)	(31) 25.5±1.3 (23.1-28.4)	(7) 23.8±1.0 (22.7-25.2)	23.96±0.9 (25.0-22.1)	(25)22.8±0.8 (21.0-24.0)	(38) 22.5±1.1 (20.1-24.3)
CIL	(34) 23.2±1.1 (20.4-25.8)	(3) 21.2±0.7 (20.6-21.9)	(31) 22.9±1.3 (20.7-25.9)	(8) 20.9±1.1 (19.3-22.5)	21.58±0.9 (22.5-19.9)	(25)20.3±0.8 (18.7-21.6)	(41) 20.0±1.0 (17.4-22.0)
BOC	(33)5.7±0.2 (5.4-6.1)	(3) 5.7±0.3 (5.5-6.0)	(33) 5.7±0.2 (5.3-6.5)	(8) 5.6±0.2 (5.2-5.8)	5.29±0.3 (5.6-4.9)	(25) 5.4±0.2 (5.1-5.9)	(41) 5.4±0.2 (5.2-5.8)
LD	(36) 6.4±0.4 (5.3-7.5)	(5) 5.7±0.5 (5.2-6.3)	(35) 6.3±0.4 (5.4-7.6)	(8) 5.7±0.4 (4.3-4.9)	6.08±0.4 (6.4-5.3)	(26) 5.6±0.3 (5.0-6.2)	(39) 5.4±0.4 (4.5-6.0)
PB	(36) 4.7±0.3 (4.2-5.4)	(5) 4.1±0.2 (3.8-4.2)	(34) 4.5±0.3 (3.9-5.2)	(8) 4.5±0.2 (4.1-4.5)	4.28±0.3 (4.69-3.7)	(26) 4.0±0.2 (3.6-4.5)	(41) 3.8±0.2 (3.1-4.2)
LM	(36) 3.7±0.2 (3.3-4.2)	5 3.5±0.1 (3.3-3.7)	35 3.7±0.1 (3.5-4.0)	8 3.3±0.1 (3.2-3.5)	3.28±0.1 (3.4-3.1)	26 3.1±0.2 (2.8-3.6)	41 3.2±0.1 (3.0-3.5)
LIF	36 4.9±0.4 (4.2-5.7)	5 4.1±0.3 (3.9-4.5)	35 4.8±0.3 (4.1-5.9)	8 3.9±0.2 (3.5-4.1)	4.16±0.3 (4.7-3.7)	26 3.9±0.3 (3.4-4.9)	41 4.3±0.3 (3.4-4.9)
BIF	36 1.8±0.2 (1.5-2.4)	5 1.6±0.1 (1.4-1.8)	35 1.8±0.1 (1.5-2.1)	8 1.7±0.2 (1.5-2.0)	1.82±0.2 (2.1-1.5)	26 1.7±0.1 (1.4-1.9)	41 1.5±0.1 (1.3-1.8)
M1M	35 4.7±0.2 (4.3-5.3)	5 4.5±0.1 (4.5-4.6)	35 4.6±0.2 (4.3-5.1)	8 4.3±0.2 (3.5-4.1)	4.34±0.1 (4.5-4.2)	25 4.2±0.2 (3.9-4.6)	41 4.2±0.2 (3.8-4.5)
BM1	36 1.1±0.1 (1.0-1.3)	5 1.1±0.1 (1.1-1.2)	35 1.1±0.1 (1.0-1.2)	8 1.0±0.1 (1.0-1.1)	1.01±0.1 (1.13-0.89)	26 0.9±0.1 (0.8-1.1)	41 1.0±0.1 (0.9-1.1)
CH	36 7.8±0.3 (7.3-8.4)	5 7.5±0.2 (7.2-7.8)	35 7.8±0.3 (7.3-8.8)	8 7.2±0.2 (6.9-7.4)	7.36±0.35 (7.7-6.9)	25 7.0±0.3 (6.5-7.5)	41 7.1±0.3 (6.5-8.0)
RL	(35) 9.3±0.6 (7.8-10.7)	(4) 8.7±0.6 (8.3-9.5)	(35) 9.1±0.7 (7.7-10.6)	(7) 8.4±0.5 (7.9-9.3)	8.49±0.4 (9.1-7.6)	(26) 7.9±0.4 (7.3-8.7)	(38) 7.6±0.5 (6.4-8.6)
BRO	(35) 4.7±0.3 (4.2-5.6)	(5) 4.5±0.3 (4.2-4.8)	(35) 4.6±0.3 (4.0-5.4)	(8) 4.3±0.4 (3.7-4.6)	4.61±0.3 (4.9-4.2)	(26) 4.1±0.2 (3.7-4.7)	(40) 4.1±0.3 (3.5-4.5)
LIB	(36) 3.8±0.1 (3.5-4.0)	(5) 3.9±0.1 (3.8-4.0)	(35) 3.8±0.2 (3.5-4.1)	(8) 3.7±0.1 (3.4-3.9)	3.69±0.1 (3.8-3.6)	(25) 3.7±0.2 (3.3-4.2)	(41) 3.4±0.2 (3.2-3.9)
ORL	(36) 8.8±0.4 (7.6-9.6)	(5) 8.3±0.2 (8.0-8.5)	(35) 8.7±0.3 (8.1-9.5)	(8) 8.1±0.3 (7.8-8.6)	8.29±0.2 (8.6-8.0)	(26) 7.7±0.4 (6.8-8.6)	(41) 7.6±0.4 (6.6-8.2)
ZB	(36) 13.2±0.6 (11.9-14.8)	(4) 12.8±0.3 (12.3-13.1)	(35) 13.3±0.6 (12.3-14.9)	(7) 12.0±0.7 (10.8-12.8)	12.43±0.3 (12.7-11.9)	(26)12.0±0.6 (10.5-12.8)	(37) 12.0±0.7 (10.3-13.3)
BB	(35) 10.7±0.4 (10.1-11.6)	(3) 10.6±0.1 (10.4-10.6)	(32) 10.9±0.3 (10.2-11.5)	(7) 10.2±0.2 (9.9-10.4)	10.02±0.3 (10.7-9.8)	(24)10.0±0.4 (9.1-10.7)	(41) 10.1±0.3 (9.5-11.0)
BZP	(36) 2.8±0.2 (2.3-3.5)	(5) 2.4±0.3 (1.9-2.7)	(34) 2.6±0.2 (2.1-3.0)	(8) 2.2±0.2 (1.8-2.3)	2.34±0.2 (2.7-2.1)	(26) 2.3±0.1 (2.0-2.5)	(40) 2.2±0.2 (1.8-2.6)

See methods to variable abbreviations. (n) sample size.

Habitat – Specimens of *Oligoryzomys moojeni* sp.nov. were captured at lower altitudes (500-700m) in the Parque Nacional da Chapada dos Veadeiros. This species was captured primarily in open vegetation formations, like "cerrado *sensu stricto*" (6 individuals) and "campo úmido" in the border with "cerrado *sensu stricto*" (2 individuals), but also in forest formations like open gallery forest with bamboo trees (3 individuals) and in the border of disturbed "cerradão" (1 individual).

Reproduction – Two pregnant females were captured in August 1996 with three fetuses each. One of them was captured in the same trap with a young adult male.

Comparisons – *Oligoryzomys moojeni* sp.nov. differs from all other *Oligoryzomys* species by its unique karyotype. Other differences include: (1) a creamy ventral pelage without a defined limit between dorsal and ventral pelage color, contrary to a whitish venter and a sharply defined limit between dorsal and ventral coloration in adult specimens of *O. nigripes*, *O. chacoensis*, and *O. stramineus*; (2) absence of yellow hairs at ventral region between forelimbs, opposite to presence of patch of yellow hairs in *O. nigripes* and *O. stramineus*; (3) bicolored tail, contrary to unicolored tail in *O. nigripes* and *Oligoryzomys* sp.nov. 2 (see below); (4) entirely creamy ventral side of limbs, contrary to the dark coloration in *O. fornesi* and *O. flavescens*; (5) lighter and heterogeneous dorsal coloration (alternating dark and lighter hairs), opposite to darker and homogeneous dorsal coloration in *O. flavescens*; and (6) small incisive foramina (not reaching plane of first molar), opposite to longer foramina reaching first molar in *Oligoryzomys* sp.nov. 2, *O. flavescens, O. stramineus, O. nigripes*, and *O. chacoensis*.

Etymology – This species is named in honor to João Moojen, one of the foremost mammalogists of Brazil.

Remarks – LIMA *et al.* (2003) described a karyotypic variant of *Oligoryzomys* with the same diploid number of 70 as *O. moojeni* sp.nov., but with a different fundamental autosome number (AN=76). We did not examine those specimens, but the similar karyotype indicates that the variant might be closely related to *O. moojeni* sp.nov.

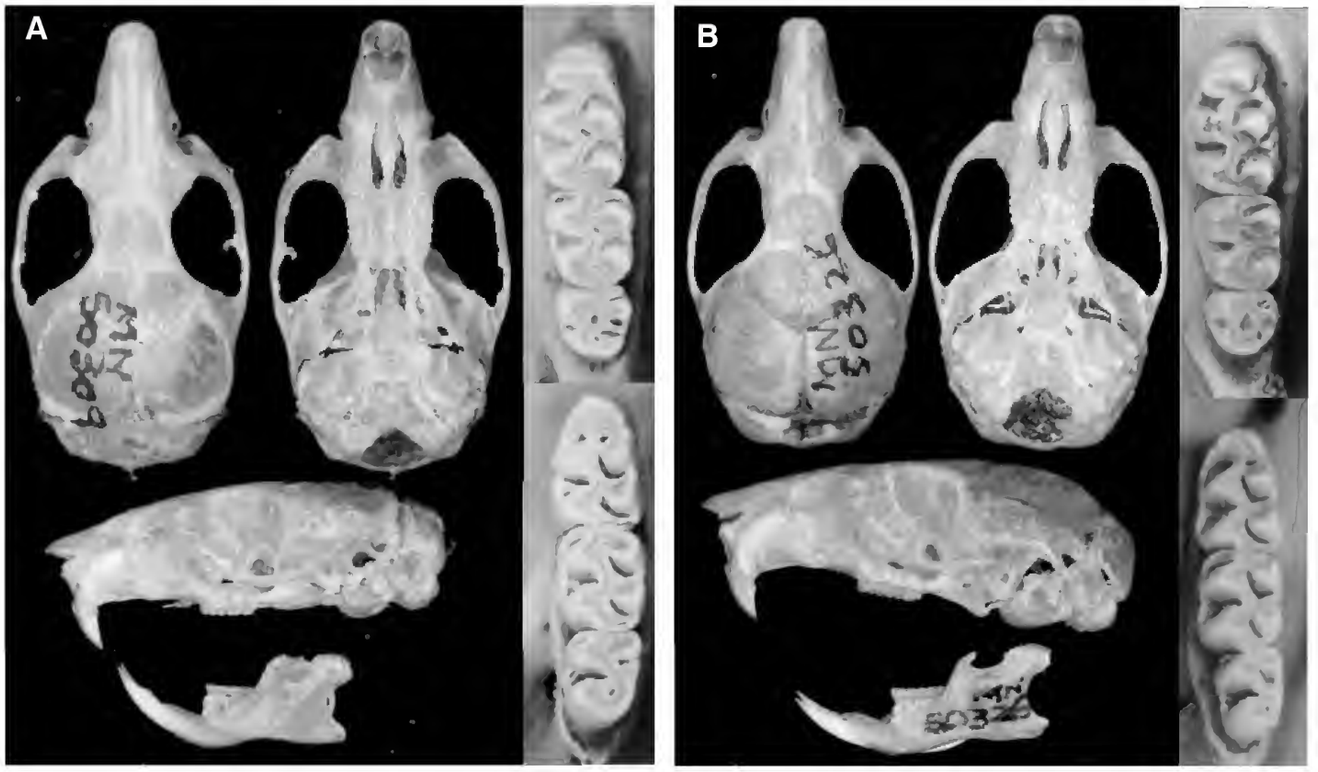

Fig.2- Dorsal, ventral and lateral views of skull of the holotypes of (A) *Oligoryzomys moojeni* sp.nov. (MN50309) and (B) *Oligoryzomys rupestris* sp.nov. (MN50286). The superior and molar row of *Oligoryzomys moojeni* sp.nov. is from MN50287.

Oligoryzomys rupestris, sp.nov.
(Figs.1, 2B, 3B, 4B)

Holotype – Adult ♀ MN 50286 (field number CRB 1141). This specimen was captured in November 1996 by C.R.Bonvicino, J.Freitas, L.Maroja, B.Lemos, and S.Lindbergh (Fig.2B). Skin, skull, partial skeleton, bone marrow cells and liver were preserved.

Type-locality – Pouso Alto (14°01'S 47°31'W), in the highest part of the Chapada dos Veadeiros National Park, at 1,500m altitude, 14km NNW of Alto Paraíso, Goiás State, Brazil.

Paratypes (same locality and collectors) – ♀ MN 50322, 50324, 50327, ♂ MN 50323, 50325, 50326, unsexed MN 503228.

External measurements – HB=82.9±10.0 (76-99, n=6), T=121.1±11.1 (114-138, n=6), F= 23.6±2.0 (20-25, n=6), E=14.5±2.0 (10-16, n=6), W=13.8±4.9 (10-20, n=6).

Cranial measurements – See table 1.

Diagnosis – A small-sized *Oligoryzomys* species, characterized by: (1) gray head contrasting with a lighter yellow-brownish dorsal body coloration; (2) small tufts of whitish hairs anterior to pinna base; (3) stapedial foramen reduced or absent, squamosal-alisphenoid groove and sphenofrontal foramen absent (carotid circulatory pattern 3; VOSS, 1988); and (4) the lowest known diploid number (2n=46, AN=52) among *Oligoryzomys* species.

Geographic distribution – Species known from only two localities, Alto Paraíso, Goiás State, and Pico das Almas, Bahia State, both with "campo rupestre" vegetation, at high altitudes.

External characters – Adult dorsal pelage grizzled yellowish-brown, with gray head and light gray cheeks, composed of long and dark guard hairs and slightly shorter over-hairs with distal part (1/3 of total length) brownish-yellow and light gray base (2/3 of total length). Lateral color yellowish, with less and lighter guard hairs than dorsum, and with a moderately defined limit with ventral pelage. Base of ventral hairs light gray, except for a small region of the neck with completely white hairs. Inner side of pinnae with light brown hairs. Subauricular patches, areas of whitish coloration immediately ventral to the pinnae base, present. Dorsal foot surface covered with white hairs, with tufts of longer hairs at base of pedal claws. Tail unicolored, dorsal and ventral surface gray. Young individuals with gray dorsal and lateral pelage. Eight mammae in inguinal, abdominal, postaxial, and pectoral pairs.

Cranial characters – Delicate skull, medium and narrow rostrum with similar breadth to interorbital constriction. Interorbital region hourglass-shaped. Braincase without supraorbital and postorbital ridge; lambdoidal ridge weakly developed. Interparietal bone as broad as parietal. Large zygomatic plate relative to skull size, with deep zygomatic notch. Jugal bone absent, thus the zygomatic process of squamosal is in contact with the zygomatic process of maxillary. Extension of posterior borders of incisive foramina variable, reaching or not the plane of first molar up to the anterocone. Posterolateral palatal pits varying in number and morphology, from single and large to multiple within a shallow fossa, or without fossa. Palatal bridge broad and long; distance between the anterior border of mesopterygoid fossa and the third molar similar to length of second molar. Mesopterygoid fossa dorsally perforated by large sphenopalatine vacuities. Width of parapterygoid plate slightly greater than width of mesopterygoid fossa. Stapedial foramen reduced or absent (Fig.3), squamosal-alisphenoid groove and sphenofrontal foramen absent (carotid circulatory pattern 3; VOSS, 1988). Medium or small subsquamosal fenestra and large postglenoid foramen. Alisphenoid strut absent. Large mastoid fenestra. Capsular projection of lower incisor alveolus present but not pronounced.

Dental characters – Upper and lower incisors opisthodont; molars pentalophodont. Superior molar rows parallel but with M3-M3 distance slightly broader than M1-M1 distance when taken from lingual side. Procingulum of first upper molar (M1) forming a continuous conule without anteromedian flexus. Anteroloph reduced, posteroloph distinct but joined to metacone even in slightly worn molars. M3 reduced, with hypoflexus usually present in younger specimens, but absent in very old exemplars.

Karyotype – Karyotypic analyses of 8 specimens of *Oligoryzomys rupestris* sp.nov. showed 2n=46, AN=52 (Fig.4B), one of the lowest known diploid number of the genus (Tab.2). The autosome complement comprised 4 pairs of biarmed chromosomes (2 large- and 2 small-sized) and 18 acrocentric pairs (one very large and 17 small). The X chromosome is a medium sized submetacentric and the Y chromosome a small acrocentric. The karyotype herein reported is similar to the one reported by SILVA & YONENAGA-YASSUDA (1997) in specimens identified as *Oligoryzomys* sp.1.

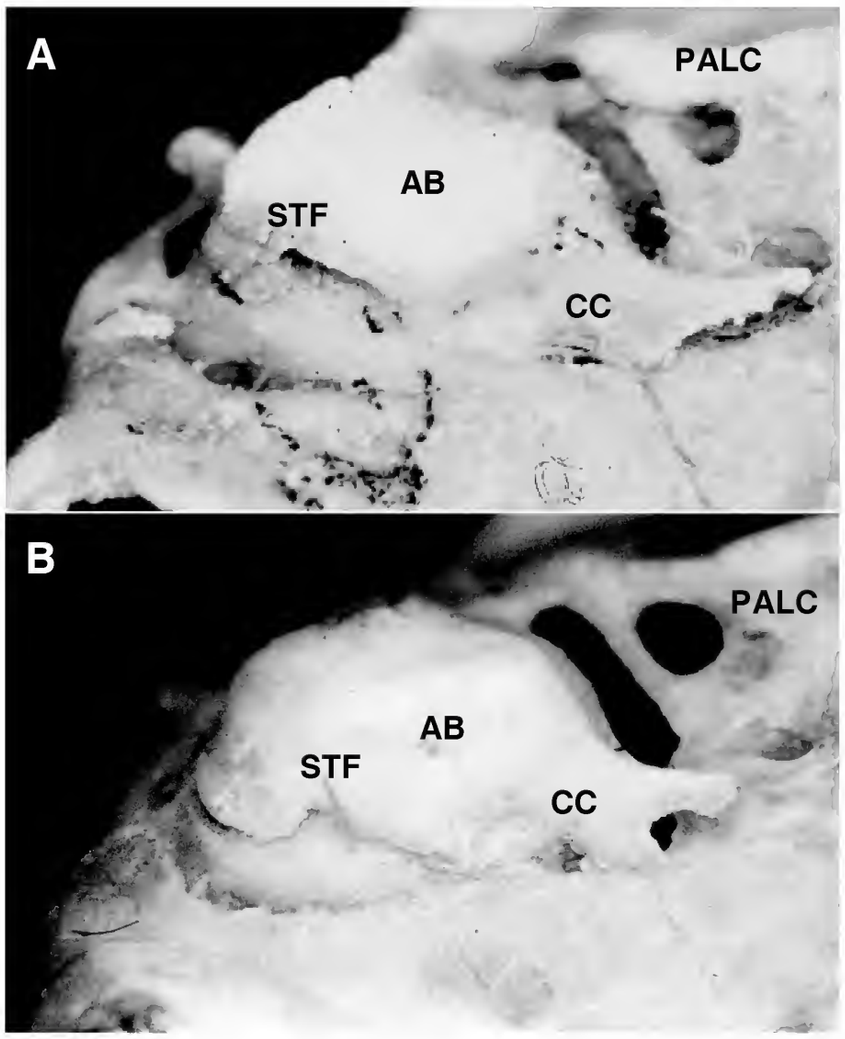

Fig.3- Ventral view of the ectotympanic region showing the different condition of carotid circulation in *Oligoryzomys moojeni* sp.nov. (A) and *Oligoryzomys rupestris* sp.nov. (B). Abbreviations: (AB) auditory bulla, (CC) carotid canal, (PALC) posterior opening of alisphenoid canal, (STF) stapedial foramen.

Habitat – *Oligoryzomys rupestris* sp.nov. is a habitat specialist. Although we sampled all vegetation types in the Pouso Alto region, this species was captured only at high altitude (1,500m) in "campo rupestre" or in the border of adjacent vegetation. Specimens karyotyped by SILVA & YONENAGA-YASSUDA (1997) were also captured in "campo rupestre". "Campo rupestre" is a type of vegetation typical of the Central Brazilian Cerrado, with outcrop rocks in scarce, 2-5m tall, cerrado vegetation (EITEN, 1994).

Comparisons – *Oligoryzomys rupestris* sp.nov. differs from all other *Oligoryzomys* species by its gray head contrasting with the remaining body coloration, absent or reduced stapedial foramen, and unique karyotype. Differences from other species includes: (1) a whitish ventral coloration with a moderate limit between lateral and ventral coloration, against a creamy coloration with a less clearly limit between lateral and ventral coloration in *Oligoryzomys moojeni* sp.nov., *O. flavescens*, and *O. fornesi*; (2) absence of yellow hairs in ventral region between forelimbs, contrary to it presence as a yellow patch in adult specimens of *O. nigripes* and *O. stramineus*; and (3) unicolored tail, against bicolored tail in *O. stramineus*, *Oligoryzomys moojeni* sp. nov., *O. flavescens*, and *O. fornesi*.

Etymology – *rupestris*, from "campo rupestre", a type of high altitude Cerrado vegetation with outcrop rocks, the typical habitat of this species.

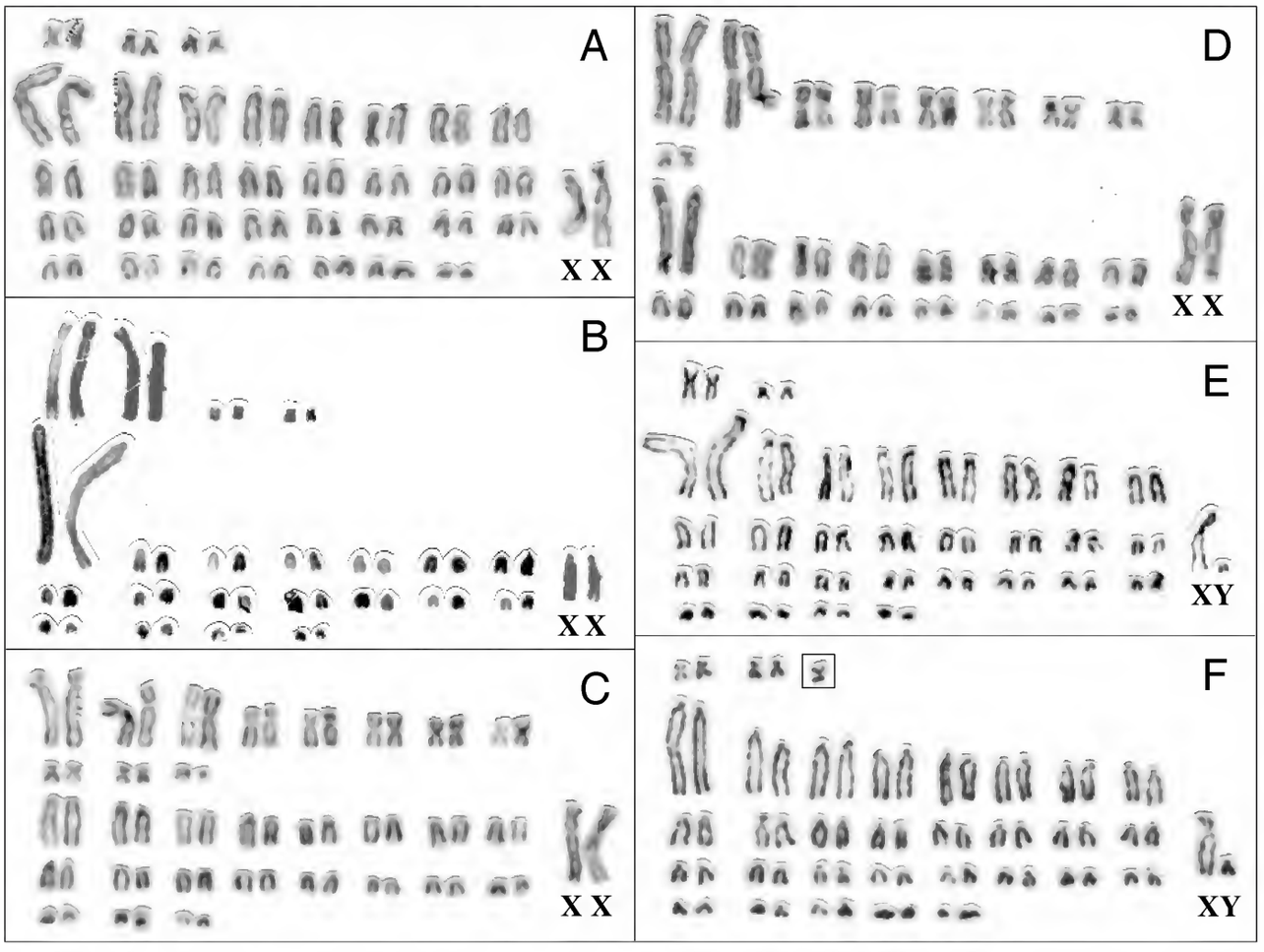

Fig.4- Conventional Giemsa coloration of (A) *Oligoryzomys moojeni* sp.nov., (B) *Oligoryzomys rupestris* sp.nov., (C) *O. nigripes*, (D) *O. stramineus*, (E) *O. fornesi*, and (F) *O. flavescens* karyotypes.

Remarks – The two specimens (MZUSP 29015, 29016), karyotypically identical to *O. rupestris* sp.nov. described by SILVA & YONENAGA-YASSUDA (1997), could not be found in the MZUSP (Museu de Zoologia da Universidade de São Paulo) collection. However, karyotypic and habitat similarities indicate that they are probably referable to *O. rupestris* sp.nov. The same authors described a second karyotype, 2n=44-45, AN=52-53, for another *Oligoryzomys* species (MZUSP 27423, 29013, and 29014) of the "campos rupestres" habitat of Serra do Cipó (19°18'S 43°35'W), State of Minas Gerais. Although this karyotype differs from the one described for *O. rupestris* sp.nov., the only available specimen (MZUSP 27423) is morphologically similar to *O. rupestris* sp.nov., also sharing the distinctive carotid circulatory pattern, indicating a close phylogenetic relationship.

Oligoryzomys nigripes (Olfers, 1818).
(Figs.1, 4C)

Type-locality – Paraguay - Department of Paraguarí, Ibicuy National Park, 85 km SSE Atyra (restricted by MYERS & CARLETON, 1981).

Diagnosis – A large sized *Oligoryzomys* species, characterized by (1) dark-brown to dark-yellowish dorsal pelage color, with defined limit with whitish ventral coloration, and often with an orange pectoral band, (2) long ears, and (3) a 2n=62, AN=78-82 karyotype.

Distribution – In Brazil, this species occurs in the Atlantic Forest, from the State of Pernambuco in the North to the Rio Grande do Sul State in the South, and in the Southern portion of the Cerrado in Federal District, Minas Gerais, and São Paulo states. It also occurs in Paraguay (east of Paraguay River), Uruguay (Departments of Salto, Durazno,

Colonia, and Maldonado), and Argentina (Provinces of Buenos Aires, Misiones, and Chaco).

External measurements – HB 92.0±9.9 (70-120, n=44), T 116±10.5 (96-144, n=43), F 24.8±1.8 (21-29, n=42), E 17±1.4 (14.5-20, n=44), W 25.4±4.7 (18-40, n=29).

Cranial measurements – See table 1.

Karyotype – Karyotypic analysis of 38 specimens showed 2n=62, AN=81-82 (Fig.4C); variation in autosome fundamental number due to pericentric inversions as previously described (YONENAGA *et al.*, 1976; MYERS & CARLETON, 1981).

Habitat – *O. nigripes* was captured at altitudes ranging from 100m (present study) to 2,000m (BONVICINO *et al.*, 1997) in the Atlantic Forest. It is the most habitat-generalist of all Brazilian *Oligoryzomys* species, occurring in primary and secondary vegetation, mainly in forest vegetation, like the montane and sub-montane forest of the Atlantic Forest and gallery forest of the Cerrado. It may be sympatric with *O. stramineus* (BONVICINO & WEKSLER, 1998) though not in the same trap line. It can be syntopic with *O. flavescens* and sympatric with *O. fornesi*, this latter species being an open vegetation inhabitant. We only collected *O. nigripes* on the ground level despite that MYERS & CARLETON (1981) collected specimens in trees and suggested some arboreal activity, also based on their relatively shorter feet than other *Oligoryzomys* species.

Reproduction – Pregnant females were collected in September and November with an average of 4.7 embryos (range 4-6) was recorded in a sample of 21 pregnant females. MYERS & CARLETON (1981) reported an average of 3.57 (range 2-5) in 32 pregnant females, and noted that reproduction occurs around June and August, with a hiatus in July.

Remarks – *Oligoryzomys nigripes* could not be separated from *O. delticola* and *O. eliurus* based on morphologic and karyotypic data (MYERS & CARLETON, 1981; BONVICINO & WEKSLER, 1998). Previous morphometric analyses did not detect differences between samples assigned to *O. delticola* and *O. nigripes* (BONVICINO & WEKSLER, 1998). Size alone does not provide a distinctive criterion for separating these species because *O. nigripes* exhibits a large variability, even within populations. We tentatively placed *O. delticola* and *O. eliurus* as junior synonyms of *O. nigripes*, but examination of the holotypes of these species is necessary to corroborate our taxonomic arrangement.

Oligoryzomys stramineus
Bonvicino and Weksler, 1998
(Figs.1, 4D)

Type-locality – Brazil - Goiás State: Teresina de Goiás, Fazenda Vão dos Bois.

Diagnosis – A large body-sized *Oligoryzomys* species characterized by (1) paler dorsal color, with defined limit between lateral and whitish ventral pelage, (2) long incisive foramen, (3) broad zygomatic plate, and (4) a 2n=52, AN=68-70 karyotype.

Distribution – Endemic to Brazil, from the Cerrado of Northern Goiás and Northern Minas Gerais states, and the Caatinga of Paraíba and Pernambuco states.

External measurements – HB=94.3±10.2 (70-111, n=33); T=118.6±=9.2 (95-134, n=32); F=25.5±1.4 (23-29, n=33); E=16.1±1.6 (12-20, n=32).

Cranial measurements: See table 1.

Karyotype – Karyotypic analyses of 5 specimens showed 2n=52, AN=68-69 (Fig.4D), similar to the one previously found in 30 specimens (BONVICINO & WEKSLER, 1998; Tab.2); differences in autosome fundamental number being due to an inversion in one small acrocentric pair.

Habitat – This species was collected mainly in gallery forest in the Cerrado morphoclimatic domain (BONVICINO & WEKSLER, 1998); data for Caatinga habitats are unavailable. *Oligoryzomys stramineus* is sympatric with *O. fornesi* (in the same line trap) and with *O. nigripes* (but never in the same line trap).

Reproduction – We collected young juveniles in August 1995, suggesting that reproduction occurred around June-July. One pregnant female captured in September 1997 produced 4 fetuses.

Oligoryzomys chacoensis
(Myers and Carleton, 1981).
(Fig.1)

Type-locality – Paraguay - Department of Boquerón, 419km by road NW Villa Hayes (alongside the Trans Chaco Highway).

Diagnosis (MYERS & CARLETON, 1981) – "A medium-sized species (of the subgenus) *Oligoryzomys*, unique by its whitish underside, with hair white to the base on the chin and throat, relatively long ears with hairs on inner surface with unusually short or absent dark basal bands, small but distinctive tuffs of orange hairs anterior to ears, and karyotype with 2n=58, AN=74".

Table 2. Data on *Oligoryzomys* karyotypes.

SPECIES GROUP	TAXON	2n	AN	LOCALITY	REFERENCE
andinus	*O. andinus*	60	70	Peru: Ancash	GARDNER & PATTON, 1976
andinus	*O. chacoensis*	58	74	Paraguay: Presidente Hayes	MYERS & CARLETON, 1981
andinus	*O. chacoensis* (*O. cf. longicaudatus*)	58	74	AR: Tucuman and Jujuy	ESPINOSA & REIG, 1991
flavescens	*O. flavescens*	64	68	BR: MG	BONVICINO & WEKSLER, 1998
flavescens	*O. flavescens*	64	66	BR: SP, Pedreira	this study
flavescens	*O. flavescens*	66	68	AR: Buenos Aires and Cordoba	ESPINOZA & REIG, 1991
flavescens	*O. flavescens*	66	70	Argentina and Uruguay	BRUM-ZORRILA *et al.* ,1988; VIDAL RIOJA *et al.*, 1988
flavescens	*O flavescens*	64-66	66-68	Bolivia: Tarija	ANISKIN & VOLOBOUEV, 1999
flavescens	*O. flavescens*	64-66	66-68	BR: RS, PR, and SC	ANDRADES-MIRANDA *et al.*, 2001
flavescens	*O. flavescens*	64-66	66-68	AR: Buenos Aires; Uruguay	BRUM-ZORRILA *et al.*, 1988
flavescens	*O. flavescens*	64-66	66-68	BR: PR, SC and RS	SBALQUEIRO *et al.*, 1991
flavescens	*O. flavescens* (*O.* cf. *flavescens*)	66-68	68-70	AR: Jujuy and Tucuman	ESPINOSA & REIG, 1991
flavescens	*O. flavescens* (*O. fornesi*)	64-66	66-68	Paraguay: Caaguazú, Canendiyu, Misiones, and Presidente Hayes	MYERS & CARLETON, 1981
flavescens	*O. fornesi*	62	64	BR: GO	BONVICINO & WEKSLER, 1998
flavescens	*O. fornesi*	62	64	Paraguay: Caaguazú and Canendiyu	MYERS & CARLETON, 1981
flavescens	*O. fornesi* (*O. aff. eliurus*)	62	64	BR: PE	FURTADO, 1981
flavescens	*O. fornesi* (*O. eliurus*)	62	64	BR: DF and GO	SVARTMAN, 1989; ANDRADES-MIRANDA *et al.*, 2001
flavescens	*O. microtis* (*O. longicaudatus* var. 2)	64	66	Peru: Loreto	GARDNER & PATON, 1976
flavescens	*O. microtis*	64	66	BR: AM	PATTON *et al.*, 2000
flavescens	*O. microtis*	64	66	Peru: Ucayali and Loreto	ANISKIN & VOLOBOUEV, 1999
flavescens	*O. moojeni* sp. nov. (*Oligoryzomys* sp.)	70	74	BR: GO, Minaçu, Niquelândia, Colinas do Sul, Uruaçú	ANDRADES-MIRANDA *et al.*, 2001
flavescens	*O. moojeni* sp. nov. (*Oligoryzomys* sp.)	70	74	BR: GO, Cavalcante and Mimoso do Goiás	LIMA *et al.*, 2003
flavescens	*Oligoryzomys* sp.	70	76	BR: TO, Lajeado and Porto Nacional	LIMA *et al.*, 2003
fulvescens	*O. fulvescens*	60	72	Venezuela: Miranda	KIBLISKY, 1969
fulvescens	*O. fulvescens costaricensis*	54	68	Costa Rica: San José	GARDNER & PATON, 1976; CARLETON & MUSSER, 1995
fulvescens	*O. fulvescens fulvescens*	60	74	Mexico: Veracruz	HAIDUK *et al.*, 1979; CARLETON & MUSSER, 1995
fulvescens	*O.* gr. *fulvescens* (*O. longicaudatus* var.3)	62	74,76	Venezuela: Bolivar	GARDNER & PATON, 1976
nigripes	*O. destructor* (*O. longicaudatus* var. 4)	60	76	Peru: Ayacucho	GARDNER & PATON, 1976
nigripes	*O. longicaudatus* (*O. l. philippii*)	56	66	Chile: Valdívia	GALLARDO & PATTERSON, 1985
nigripes	*O. magellanicus* (*O. l. magellanicus*)	54	66	Chile: Punta Arenas	GALLARDO & PATTERSON, 1985
nigripes	*O. nigripes*	62	82	Paraguay	MYERS & CARLETON, 1981

continued...

... conclusion

Species Group	Taxon	2n	AN	Locality	Reference
nigripes	*O. nigripes*	62	82	BR: SP and RJ	YONENAGA *et al.*, 1976
nigripes	*O. nigripes* (*O. delticola*)	62	82	AR: Parana River Delta	ESPINOSA & REIG, 1991
nigripes	*O. nigripes*	62	78	BR: BA	ZANCHIN, 1988
nigripes	*O. nigripes*	61-62	78, 80-82	BR: GO, BA, ES, PR, SC, and RS	ANDRADES-MIRANDA *et al.*, 2001
nigripes	*O. nigripes*	62	81-82	BR: MG and RJ	BONVICINO & WEKSLER, 1998
nigripes	*O. nigripes*	62	80-82	BR: RJ, SP, ES, and RS	ZANCHIN, 1988; BONVICINO *et al.*, 2001
nigripes	*O. nigripes*	62	80-82	BR: SP and RJ	ALMEIDA & YONENAGA-YASSUDA, 1991
nigripes	*O. nigripes* (*O. delticola*)	62	80-81	Uruguay	BRUM-ZORRILA *et al.*, 1988
nigripes	*O. stramineus*	52	68	BR: MG, Juramento	this study
nigripes	*O. stramineus*	52	68	BR: GO	ANDRADES-MIRANDA *et al.*, 2001
nigripes	*O. stramineus* (*O. aff. eliurus*)	52	68	BR: PE	MAIA *et al.*, 1983; FURTADO, 1981
nigripes	*O. stramineus* (O. *aff. eliurus*)	52	68	BR: PE	FURTADO, 1981
nigripes	*O. stramineus*	52	68-70	BR: GO	BONVICINO & WEKSLER, 1998
nigripes	*Oligoryzomys* sp. (*O. delticola*)	60	76	Uruguay: Río Queguay	BRUM-ZORRILA *et al.*, 1988
nigripes	*Oligoryzomys* sp. (*O. longicaudatus* var.1)	68	74,76	Peru: Ayacucho	GARDNER & PATON, 1976
rupestris	*O. rupestris* sp. nov.	46	52	BR: GO, Alto Paraíso	this study
rupestris	*O. rupestris* sp. nov. (*Oligoryzomys* sp.1)	46	52	BR: BA, Pico da Almas	SILVA & YONENAGA-YASSUDA, 1997
rupestris	*Oligoryzomys* sp. (*Oligoryzomys* sp.2)	44-45	52-53	BR: MG, Serra do Cipó	SILVA & YONENAGA-YASSUDA, 1997
ungrouped	O. *cf. messorius*	56	58	BR: RR	ANDRADES-MIRANDA *et al.*, 2001
ungrouped	*Oligoryzomys* sp. (*O. microtis*)	66	74	BR: AP	ANDRADES-MIRANDA et al., 2001

Names used in the cited references are in brackets. Country and state acronyms read as follows: (AR) Argentina, (BR) Brazil; (AM) Amazonas, (AP) Amapá, (BA) Bahia, (ES) Espírito Santo, (GO) Goiás, (MG) Minas Gerais, (PE) Pernambuco, (PR) Paraná, (RJ) Rio de Janeiro, (RS) Rio Grande do Sul, (RR) Roraima, (SC) Santa Catarina, (SP) São Paulo, and (TO) Tocantins.

Distribution – Paraguayan Chaco, Bolivian Chaco (Departments of Beni, Santa Cruz, and Tarija), Argentina (Provinces of Jujuy, Formosa, Chaco, Salta, and Tucumán) and Brazil (Mato Grosso do Sul and southwestern part of the State of Mato Grosso) (MYERS & CARLETON, 1981; CARLETON & MUSSER, 1989). CARLETON & MUSSER (1989) extended its distribution to Ceará and Pernambuco states in Brazil, but as argued by BONVICINO & WEKSLER (1998), this assessment was based on misidentification of specimens that actually belong to *O. stramineus* (USNM 528416 and USNM 304583).

External measurements (in mm, from MYERS & CARLETON, 1981) – Total length=223.4 (185-280, n=90), T 129.0 (105-150, n=90), F 24.8 (18-30, n=90), E 16.6 (13-19, n=90).

Cranial measurements – See table 1.

Karyotype – 2n=58, AN=74 (MYERS & CARLETON, 1981; Tab.2).

Habitat – *Oligoryzomys chacoensis* occurs in forest, thorn scrub, and grassland in Chaco. MYERS & CARLETON (1981) commented that hind feet of *O. chacoensis,* as in *O. nigripes*, are relatively short when compared to more terrestrial *Oligoryzomys* species.

Reproduction – MYERS & CARLETON (1981) reported an average of 4.6 embryos (range 2-5) in 10 pregnant females and suggested that reproduction occurred around January, February, July, with few births in June (winter).

Oligoryzomys fornesi (Massoia, 1973).
(Figs.1, 4E)

Type-locality – Argentina - Province of Formosa: Department of Río Pilcomayo, Naineck, Ceibo 13.

Distribution – In Brazil, it occurs in Cerrado (Distrito Federal, Minas Gerais, and Goiás states) and Caatinga (Pernambuco State). It also occurs in Argentina (Province of Formosa) and Paraguay.

Diagnosis – One of the smallest *Oligoryzomys* species, characterized by (1) chestnut-brown-yellowish dorsal coloration, with abundant dark guard hairs resulting in a heterogeneous pelage, ventral color light yellow-gray, (2) short incisive foramen not reaching M1, (3) mesopterygoid fossa distant from M3, and (4) a 2n=62, AN=64 karyotype.

External measurements – HB 75.3±8.9 (60-84, n=8); T 100.1±8.0 (90-111, n=8); F 22.6±0.7 (22-24, n=8); E 12.7±0.5 (12-13, n=7); W 14.0 ±3.1 (9-20, n=11).

Cranial measurements – See table 1.

Karyotype – 2n=62, AN=64 (Fig.4E), as previously reported (BONVICINO & WEKSLER, 1998; Tab.2 and taxonomic remarks). The karyotype of *O. fornesi* has been erroneously attributed to either *O. flavescens* or *O. eliurus* in previous studies. MYERS & CARLETON (1981) attributed 2n=62-66 to *O. fornesi*, though their sample actually consisted of two karyotypically discontinuous species: *O. fornesi* (2n=62, AN=64) and *O. flavescens* (2n=64-66, AN=66-68) (BONVICINO & WEKSLER, 1998). Karyotypes of *O. fornesi* and *O. flavescens* are discontinuous because a 2n=63 karyotype has not been reported. Furthermore, these two taxa also differ in morphological traits (such as length of incisive foramen that is greater in *O. flavescens* than in *O. fornesi*). ANDRADES-MIRANDA *et al.* (2001) considered the 2n=62, AN=64 karyotype as belonging to *O. eliurus*, but we disagree from their interpretation. Specimens with 2n=62, AN=64 analyzed by us showed the same morphological attributes described for *O. fornesi* (BONVICINO & WEKSLER, 1998) and are different from those attributed to *O. eliurus* in its original description (WAGNER, 1845). Furthermore, we agree with MYERS & CARLETON (1981) that *O. eliurus* is conspecific with *O. nigripes* (see above). Finally, the type locality of *O. eliurus* is Ytararé, State of São Paulo, in the Atlantic Forest, while the 2n=62, AN=64 karyotype has been recorded only in specimens from the core of the open vegetation morphoclimatic domains in Brazil and Paraguay (Cerrado, Caatinga, and Chaco; Fig.1) but never in the Atlantic Forest or in its limits with the Cerrado.

Habitat – In Brazil, this species mainly occurs in open vegetation formations but is also found in forest formations of the Cerrado (data on the habitat utilization in Caatinga are unavailable). It is sympatric (in the same line trap) with *O. nigripes* and *O. stramineus*. MYERS & CARLETON (1981) reported that *O. fornesi* is sympatric with *O. chacoensis* in Paraguay, while BONVICINO & WEKSLER (1998) found that *O. fornesi* and *O. flavescens* are sympatric in one locality (Curuguaty).

Reproduction – No reproductive data is available.

Taxonomic remarks – The taxonomy history of *O. fornesi* is complex. Initially described as a subspecies of *O. microtis*, *O. fornesi* was raised to full specific status by MYERS & CARLETON (1981). OLDS & ANDERSON (1987) placed it again as a subspecies of *O. microtis* and CARLETON & MUSSER (1989) placed it as a junior synonym of *O. microtis*. We consider *O. fornesi* and *O. microtis* as different species because they are karyotypically different (Tab.2). Phylogenetic analyses of cytochrome *b* sequence data corroborated this proposition, placing *O. microtis* and *O. fornesi* in different evolutionary lineages (MYERS *et al.*, 1995). Furthermore, these species occupy different morphoclimatic domains (*O. fornesi* in Cerrado, Chaco, and Caatinga, *O. microtis* in the Amazon biome). Although the present taxonomic arrangement is supported by karyotypic, molecular, and biogeographic data, it is clear that a thorough morphological analysis will facilitate species diagnoses.

Oligoryzomys flavescens (Waterhouse, 1837).
(Figs.1, 4F)

Type-locality – Uruguay - Maldonado.

Diagnosis – A small-sized species, characterized by (1) dorsum with bright brownish-orange hairs finely intermixed with dark hairs, (2) lateral brighter orange coloration, without defined limits with yellow-gray ventral coloration, (3) incisive foramen long usually reaching first molar, (4) fossa mesopterygoid distant from M3, and (5) an 2n=64-66, AN=66-70 karyotype.

Distribution – In Brazil, it occurs in Atlantic Forest, from the State of Bahia to the State of Rio Grande do Sul, and in gallery forest (a link to the Atlantic Forest) in the Cerrado of Central Brazil. It also occurs in Paraguay, Uruguay, and Argentina.

External measurements – HB 87.8.3±5.7 (81-93, n=4); T 109.7±17.7 (97-1304, n=3); F 23.5±1.3 (22-24, n=4); E 15.0±0.8 (15-16, n=4), W 18.8±2.6 (15-21, n=4).

Cranial measurements – See table 1.

Karyotype – Karyotypic analysis of 6 specimens of *O. flavescens* showed 2n=64-66, AN=66-68 (Fig.4F, Tab.2). As described by SBALQUEIRO *et al.* (1991), the basic diploid and autosome fundamental numbers of this species are 2n=64, AN=66; variation in diploid and autosome fundamental number being due to acrocentric or metacentric B chromosomes. The *O. microtis* karyotype, 2n=64, AN=66, apparently shares a similarity in 2n and AN with one karyotypic variant of *O. flavescens*. However, there are some differences in the morphology of biarmed autosomes: in *O. microtis,* one of the two biarmed chromosome pairs is the largest of the autosome complement and the other is a small pair, while in *O. flavescens* the two biarmed pairs are small-sized.

Habitat – *Oligoryzomys flavescens* was captured at lower altitudes in disturbed Atlantic forest regions, although this species also occurs at high altitudes (1,800m) in Parque Nacional de Caparaó.

Reproduction – Data on pregnant females were never reported.

DISCUSSION

Significant morphological and karyotypic differences were observed between *Oligoryzomys rupestris* sp.nov. and other species of *Oligoryzomys*, while *O. moojeni* sp.nov. was similar to other species of the genus, especially those of small body-size group (*sensu* BONVICINO & WEKSLER, 1998). Additionally, *O. moojeni* sp.nov. is found in habitats of the Cerrado morphoclimatic domain, like "cerrado *sensu stricto*" and "campo úmido", which also harbor other congeneric species, such as *O. stramineus* and *O. fornesi*. Conversely, *O. rupestris* sp.nov. is one of only two mammal species known to be endemic to "campos rupestres" (see next).

Oligoryzomys rupestris sp.nov. shows a unique pelage pattern among *Oligoryzomys*, with a contrasting coloration between head and body. The head is gray, while the remaining of the body is of a lighter yellow-brownish coloration, similar to the other *Oligoryzomys* species. The presence of a white fur patch behind the ears is another distinctive characteristic of *O. rupestris* sp.nov. in respect with other *Oligoryzomys* species. Both characteristics are found in some oryzomyine taxa (*e.g.*, *Oryzomys subflavus* and *Nesoryzomys*, respectively) but is the first time to be reported for *Oligoryzomys*.

The cranial morphology of *O. rupestris* sp.nov. drastically differs in respect to the carotid circulatory pattern of all other *Oligoryzomys* because *O. rupestris* sp.nov. exhibits a reduced stapedial foramen in its auditory bullae. This, coupled with lack of sphenofrontal foramen and the alisphenoid-squamosal groove, characterizes the derived pattern 3 of the carotid circulation, as defined by VOSS (1988; see also CARLETON, 1980; CARLETON & MUSSER, 1993 for illustrations). Conversely, all species of *Oligoryzomys* examined to date show a well-developed stapedial foramen but still lack the sphenofrontal foramen and groove characteristic of the derived pattern 2. This pattern was considered to be one of the diagnostic characters of *Oligoryzomys* by CARLETON & MUSSER (1989), and is a synapomorphic trait of this genus (WEKSLER, 2004). Within oryzomyines, pattern 2 is found only in *Oligoryzomys* and in the *Oryzomys megacephalus* species group (*e.g.*, *O. megacephalus*, *O. perenensis*, *O. yunganus*, *O. seuanezi*, and *O. oniscus*), while pattern 3 is found among some oryzomyine taxa (*e.g.*, *Nectomys*, *Holochilus*, *Oryzomys palustris*, *Oryzomys subflavus*, *Pseudoryzomys*). Pattern 2 is, apparently, an evolutionary intermediary state between the primitive condition (a carotid circulation with stapedial and sphenofrontal foramina plus a groove; pattern 1 of VOSS, 1988) and the pattern 3. According to this interpretation, the pattern observed in *O. rupestris* sp. nov. can be interpreted as a autapomorphy in respect with pattern 2 observed in the presumed *Oligoryzomys* ancestor of *O. rupestris* sp.nov.

Oligoryzomys rupestris sp.nov. shows the smallest diploid and fundamental numbers among *Oligoryzomys* species described to date (Tab.2). While *O. rupestris* sp.nov. shows 2n=46, diploid number in remaining *Oligoryzomys* species varies from 52 to 70, encompassing all likely diploid numbers between these extremes (52, 54, 56, 58, 60, 62, 64, 66, 68, 70). Similar differences are observed in autosome fundamental number that accounts for 52 in *O. rupestris* sp.nov. but varies from 58 to 82 in other congeneric species, suggesting a series of Robertsonian rearrangements and inversions for deriving the karyotype of *O. rupestris* sp.nov. from other *Oligoryzomys* karyotypes. A similar reduction of diploid and fundamental numbers was also observed in the karyotype of another, undescribed, species of *Oligoryzomys* (Tab.2; *Oligoryzomys* sp.2) reported by SILVA & YONENAGA-YASSUDA (1997). These authors pointed that *Oligoryzomys* sp.1 (= *O. rupestris* sp.nov.) and *Oligoryzomys* sp.2 were karyotypically very similar, probably sister taxa.

Oligoryzomys rupestris and its putative sister species (*Oligoryzomys* sp.2 of SILVA & YONENAGA-YASSUDA, 1997) are found only in a vegetation type known as "campos rupestres" (literally 'rocky fields'). This consists of thin and small wooded savanna vegetation with rocky outcrops (EITEN, 1994). The main cluster of "campos rupestres" is located in the Serra do Espinhaço formation, in the Brazilian states of Bahia and Minas Gerais, where the collecting sites of *Oligoryzomys* sp.1 (= *O. rupestris* sp.nov.) and *Oligoryzomys* sp.2 reported by SILVA & YONENAGA-YASSUDA (1997) were located. The Chapada dos Veadeiros, the second largest formation of "campos rupestres", is the only other place where *Oligoryzomys rupestris* sp.nov. has been collected. "Campos rupestres" show a high endemicity of plant species belonging to the Velloziaceae, Eriocaulonaceae and Melastomataceae (EITEN, 1994) while *Oligoryzomys rupestris* sp.nov. and *Oligoryzomys* sp.2 are the only mammalian taxa apparently endemic to this vegetational type. This might be due to dearth of knowledge on the taxonomy of the mammalian fauna of the Cerrado, especially in respect with two other small mammals predominantly collected in "campos rupestres" of Chapada dos Veadeiros: *Galea aff. flavidens* and *Thrichomys* sp.nov. (BONVICINO *et al.*, in press).

ACKNOWLEDGMENTS

To Dr. J.A.Oliveira (Museu Nacional - Rio de Janeiro – MN) for helping with skulls photographs; to Drs. L. Flamarion B. de Oliveira (MN), A.Langguth (Universidade Federal da Paraíba), J.Marinho (Universidade de Brasília), P.Myers (University of Michigan Museum Zoology), D.Oren (Museu Paraense Emílio Goeldi), and M.Carleton (United States National Museum) for access to collections, and to H.Seuánez for reviewing the manuscript. We are indebted to R.Santori (Universidade do Estado do Rio de Janeiro), P.S.D´Andrea, E.Vieira (Fundação Instituto Oswaldo Cruz) and G.Marroig (Universidade de São Paulo) for supplying specimens collected in Araras, Rio Claro, Sumidouro, Faz. Intervales, Teresópolis, Nova Friburgo, and Faz. Canoas; to R.Finoti, J.Freitas, B.Lemos, S.Lindbergh, L.Maroja (Universidade Federal do Rio de Janeiro), and A.C.Paula (IBAMA) for helping in field work. License for collect specimens were supplied by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA). This work was supported by IBAMA, Conselho Nacional de Desenvolvimento Científico e Tecnológico, Instituto Oswaldo Cruz, and Smithsonian Institution.

LITERATURE CITED

ALMEIDA, E.J.C. & YONENAGA-YASSUDA, Y., 1991. Pericentric Inversion and sexual chromosome heteromorphisms in *Oryzomys nigripes* (Rodentia, Cricetidae). **Caryologia**, Florence, **44**:63-73.

ANDRADE, A.F.B & BONVICINO, C.R., 2003. A new karyologic variant of *Oecomys* (Rodentia: Sigmodontinae) and its phylogenetic relationship based on molecular data. **Genome,** Ottawa, **46**(2):195-203.

ANDRADES-MIRANDA, J.; OLIVEIRA, J.F.B.; LIMA-ROSA, C.A.V.; NUNES, A.P.; ZANCHIN, N.I.T. & MATTEVI, M.S., 2001. Chromosome studies of seven species of *Oligoryzomys* (Rodentia: Sigmodontinae) from Brazil. **Journal of Mammalogy**, Provo, **82**(4):1080-1091.

ANISKIN, V.M. & VOLOBOUEV, V.T., 1999. Comparative chromosome banding of two South-American species of rice rats of the genus *Oligoryzomys* (Rodentia, Sigmodontinae). **Chromosoma Research**, Dordrecht, New York and London, **7**:557-562.

BONVICINO, C.R.; LANGGUTH, A.; LINDBERGH, S.M. & PAULA, A.C., 1997. An elevational gradient study of small mammals at Caparaó National Park, Southeastern Brazil. **Mammalia**, Paris, **61**(4):547-560.

BONVICINO, C.R. & WEKSLER, M., 1998. A new species of *Oligoryzomys* (Rodentia, Sigmodontinae) from Northeastern and Central Brazil. **Zeitschrift für Saugetierkunde**, Jena, **63**:90-103.

BONVICINO, C.R.; D´ANDREA, P.S. & BORODIN P., 2001. Pericentric inversions: a study in natural populations of *Oligoryzomys nigripes* (Rodentia: Sigmodontinae). **Genome**, Toronto, **44**:791-796.

BONVICINO, C.R.; LEMOS, B. & WEKSLER, M., in press. Small mammals of Chapada dos Veadeiros National Park (Cerrado of Central Brazil). Ecologic, karyologic and taxonomic considerations. **Brazilian Journal of Biology**, São Carlos, **66**.

BRUM-ZORILLA, N.; FRONZA, T.G; WAINBERG, R.; VIDAL, L. & ZWIRNER, N., 1988. *Oryzomys flavescens* and *O. delticola* chromosomes (Rodentia, Cricetidae) from Uruguai and Argentina. **Caryologia**, Florence, **41**:275-288.

BUENO, A.M.; AGOSTINI, J.M.S.; MORAES, J. & RAMOS, A.P.D., 1987. Estudos cromossômicos preliminares de roedores da família Cricetidae coletados na Ilha de Santa Catarina. **Ciência e Cultura (suplemento)**, São Paulo, **39**:746.

CARLETON, M.D., 1980. Phylogenetics relationship in neotomine-peromyscine rodents (Muroidea) and a reappraisal of the dichotomy within new world Cricetinae. **Miscellaneous Publications Museum Zoology University of Michigan**, Ann Arbor, **17**:1-146.

CARLETON, M.D. & MUSSER, G.G., 1989. Systematics studies of oryzomyine rodents (Muridae, Sigmodontinae) - a synopsis of *Microryzomys*. **Bulletin of the American Museum of Natural History**, New York, **191**:1-83.

CARLETON, M.D. & MUSSER, G.G., 1995. Systematic studies of oryzomyine rodents (Muridae: Sigmodontinae): definition and distribution of *Oligoryzomys vegetus* (Bangs, 1902). **Proceedings of the Biological Society of Washington**, Washington, **108**(2):338-369.

DIKERMAN, A.W. & YATES, T.L., 1995. Systematic of *Oligoryzomys*: protein-electrophoretic analyses. **Journal of Mammalogy**, Provo, **76**:172-182.

EITEN, G., 1994. Vegetação do Cerrado. In: PINTO, M.N. (ed.). **Cerrado**. Brasília: Sematec, Editora UnB. 681p.

ESPINOZA, M.B. & REIG, O.A., 1991. Cytogenetics and karyosystematics of South America oryzomyine rodents (Cricetidae, Sigmodontinae). III. Banding karyotypes of Argentinean *Oligoryzomys*. **Zeitschrift für Saugetierkunde**, Jena, **56**:306-317.

FURTADO, V., 1981. **Diversidade cromossômica em roedores das famílias Cricetidae e Caviidae de Pernambuco, Brasil**, Porto Alegre. 185p. Ph.D. Thesis. Universidade Federal do Rio Grande do Sul.

GALLARDO, M.H. & PALMA, E., 1990. Systematics of *Oryzomys longicaudatus* (Rodentia: Muridae) in Chile. **Journal of Mammalogy**, Provo, **71**:333-342.

GALLARDO, M.H. & PATTERSON, B.D., 1985. Chromosomal differences between two nominal subspecies of *Oryzomys longicaudatus* Bennett. **Mammalian Chromosomes Newsletter**, Houston, **25**:49-53.

GARDNER, A.L. & PATTON, J.L., 1976. Karyotypic variation in oryzomyine rodents (Cricetinae) with comments on chromosomal evolution in the Neotropical cricetine complex. **Occasional Papers Museum Zoology, Louisiana State University**, Baton Rouge, **49**:1-47.

HAIDUK, M.W.; BICKHAM, J.W. & SCHMIDLY, D.J., 1979. Karyotypes of six species of *Oryzomys* from Mexico and Central America. **Journal of Mammalogy**, Provo, **60**:610-615.

KIBLISKY, P., 1969. The chromosomes of two species of the genus *Oryzomys* (Rodentia – Cricetidae). **Experientia**, Hünenberg, **25**:1338-1339.

LIMA J.F.S.; BONVICINO, C.R. & KASAHARA, S., 2003. A new karyotype of *Oligoryzomys* (Sigmodontinae, Rodentia) from Central Brazil. **Hereditas**, Lund, **139**:1-6.

MAIA, V.; LAFAYETTE, J.M. & PINTO, M.W., 1983. Dados cromossômicos (bandas G, C e RONS) em *Oryzomys aff. eliurus* (Cricetidae, Rodentia) em Pernambuco. **Ciência e Cultura (suplemento)**, São Paulo, **35**:317.

MASSOIA, E., 1973. Descripción de *Oryzomys fornesi*, nueva espécie y nuevos datos sobre algunos espécies y subespécies argentinas del subgénero *Oryzomys* (*Oligoryzomys*) (Mammalia - Rodentia - Cricetidae). **Revista de Investigaciones Agropecuarias, INTA, Serie 1, Biologia y Producción Animal**, Buenos Aires, **10**:21-37.

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**, 2.ed. Washington: Smithsonian Institution Press, p.501-755.

MYERS, P. & CARLETON, M.D., 1981. The species of *Oryzomys* (*Oligoryzomys*) in Paraguay and the identity of Azara's "Rat sixième ou Rat à Tarse Noir". **Miscelaneous Publications of the Museum of Zoology University of Michigan**, Ann Arbor, **161**:1-41.

MYERS, P., LUNDRIGAN, B. & TUCKER, P.K., 1995. Molecular phylogenetics of oryzomyine rodents: the genus *Oligoryzomys*. **Molecular Phylogenetics and Evolution**, New York, **4**:372-382.

MYERS, N.; MITTERMEIER, R.A.; MITTERMEIER, C.G.; FONSECA, G.A.B. DA & KENT, J., 2000. Biodiversity hotspots for conservation priorities. **Nature,** London, **403**:853-858.

OLDS, N. & ANDERSON, S., 1987. Notes on Bolivian mammals 2. Taxonomy and distribution of rice rats of the genus *Oligoryzomys*. In: PATTERSON, B.D. & TIMM, R.M. (Eds.) **Studies in Neotropical mammalogy: essays in honor of Philip Hershkovitz**. Fieldiana Zoology, New Series, Chicago, **39**:261-281.

PATTON, J.L.; SILVA, M.N.F. & MALCON, J.R., 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. **Bulletin of the American Museum of Natural History**, New York, **244**:1-306.

SBALQUEIRO, I.J.; MATTEVI, M.S.; OLIVEIRA, L.F. & SOLANO, M.J.V., 1991. B chromosome system in populations of *Oryzomys flavescens* (Rodentia, Cricetidae) from southern Brazil. **Acta Theriologica**, Bialowieza, **36**:193-199.

SILVA, M.J. & YONENAGA-YASSUDA, Y., 1997. New karyotype of two related species of *Oligoryzomys* genus (Cricetidae, Rodentia) involving centric fusion with loss of NORs and distribution of telomeric $(TTAGGG)_n$ sequences. **Hereditas**, Lund, **127**:217-229.

SVARTMAN, M., 1989. **Levantamento cariotípico de roedores da região do Distrito Federal**, São Paulo. M.Sc. Dissertation, Universidade de São Paulo.

VIDAL-RIOJA, L.; FRONZA, T.G.; WAINBERG, R.; BRUM-ZORILLA, N.; WALLACE, F. & ZAMBELLI, A., 1988. C-banding pattern and satellite DNA localization on the chromosomes of *Oryzomys flavescens* (Rodentia, Cricetidae). **Caryologia**, Florence, **41**:323-328.

VOSS, R.S., 1988. Systematic and ecology of ichthyomyine rodents (Muroidea) - patterns of morphological evolution in a small adaptative radiation. **Bulletin of the American Museum of Natural History**, New York, **188**:259-493.

WAGNER, A., 1845. Diagnosen eineger neuen Arten von Nagen und Handfluglern. **Archiv für Naturgeschichte**, Berlin, **1**:145-149.

WEKSLER, M., 2003. Phylogeny of Neotropical oryzomyine rodents (Muridae: Sigmodontinae) based on the nuclear IRBP exon. **Molecular Phylogenetics and Evolution**, New York, **29**(2):331-349

WEKSLER, M., 2004. **Phylogenetic analysis of the tribe Oryzomyini (Muroidea: Sigmodontinae) based on morphological and molecular data**. New York. 408p. PhD Thesis, City University of New York.

YONENAGA, Y.; FROTA-PESSOA, O.; KASAHARA, S. & ALMEIDA, E.J.C., 1976. Cytogenetic studies on Brazilian rodents. **Ciência e Cultura**, São Paulo, **28**:202-211.

ZANCHIN, N.I.T., 1988. **Estudos cromossômicos em orizominos e equimídeos da Mata Atlântica**. Porto Alegre. 162p. M.Sc. Dissertation, Universidade Federal do Rio Grande do Sul.

APPENDIX 1

Gazzetter of localities shown in figure 1. In addition to the localities reported in the present analysis, the following studies were also consulted: ANISKIN & VOLOBOUEV (1999), ANDRADES-MIRANDA *et al.* (2001), ALMEIDA & YONENAGA-YASSUDA (1991), BONVICINO *et al.* (2001), BUENO *et al.* (1987), BONVICINO & WEKSLER (1998), BRUM-ZORRILA *et al.* (1988), ESPINOSA & REIG (1991), LIMA *et al.* (2003), MASSOIA (1973), MYERS & CARLETON (1981), OLDS & ANDERSON (1989), SBALQUEIRO *et al.* (1991), SILVA & YONENAGA-YASSUDA (1997), and YONENAGA *et al.* (1976).

BRAZIL – PARAÍBA, (1) Mamanguape 6°50'19"S 35°07'34"W, (2) Pirauá 7°31'07"S 35°30'18"W, (3) Natuba 7°38'29"S 35°32'00"W; PERNAMBUCO, (4) Exú 7°30'43"S 39°43'27"W, (5) Macaparana 7°33'17"S 35°27'11"W, (6) Buíque 8°37'S 37°09'W, (7) Angelim 8°53'25"S 36°17'09"W, (8) Correntes 9°07'44"S 36°19'49"W, (9) Bom Conselho 9°10'11"S 36°40'47"W; ALAGOAS, (10) Matriz Camaragipe 9°09'06"S 35°32'00"W; GOIÁS, (11) Minaçu 13°31'59"S 48°13'12"W, (12) Fazenda Vao dos Bois, Teresina de Goiás 13°46'35"S 47°15'53"W, (13) Cavalcante 13°47'51"S 47°27'30"W, (14) Alto Paraíso de Goiás 14°07'57"S 47°30'36"W, (15) Colinas do Sul 14°09'05"S 48°04'42"W, (16) Flores de Goiás 14°26'55"S 47°03'01"W, (17) Niquelândia 14°28'26"S 48°27'35"W, (18) Mambaí 14°29'16"S 46°06'47"W, (19) Uruaçu 14°31'29"S 49°08'27"W, (20) Mimoso de Goiás 15°03'22"S 48°09'41"W, (21) Corumbá de Goiás 15°55'25"S 48°48'31"W; DISTRITO FEDERAL, (22) Brasília 15°46'47"S 47°55'47"W; MATO GROSSO, (23) Cáceres 16°04'14"S 57°40'44"W; MATO GROSSO DO SUL, (24) Corumbá 19°00'33"S 57°39'12"W; BAHIA, (25) Pico das Almas 13°33'S 41°56'W, (26) Fazenda Sertao do Formoso, Jaborandi 14°48'00"S 45°57'40"W, (27) Rio Una, 10km ESE Sao José 15°13'S 39°02'W; MINAS GERAIS, (28) Fazenda Canoas, Juramento 16°50'53"S 43°35'13"W, (29) Peirópolis 19°44'S 47°45'W, (30) Caparaó National Park 20°19'S 41°43'W, (31) Passos 20°43'S 46°37'W, (32) Viçosa 20°45'14"S 42°52'55"W, (33) Itamonte 22°17'02"S 44°52'12"W; ESPÍRITO SANTO, (34) Venda Nova 20°20'23"S 41°08'05"W, (35) Monte Verde 20°39'S 41°48'W; RIO DE JANEIRO, (36) Sumidouro 22°02'59"S 42°40'29"W, (37) Nova Friburgo 22°15'S 42°31'W, (38) Teresópolis 22°24'44"S 42°57'46"W, (39) Itaguaí 22°51'08"S 43°46'31"W; SÃO PAULO, (40) Araraquara 21°47'40"S 48°01'32"W, (41) Río Claro 22°24'41"S 47°33'41"W, (42) Santa Maria da Serra 22°34'02"S 48°09'38"W, (43) Americana 22°44'25"S 47°20'04"W, (44) Pedreira 22°44'31"S 46°54'05"W, (45) Taubaté 23°01'35"S 45°33'19"W, (46) Caçapava 23°06'S 45°43'W, (47) Guararema 23°25'S 46°02'W, (48) Itapetininga 23°35'50"S 48°03'11"W, (49) Casa Grande 23°37'S 45°57'W, (50) Guaratuba 23°45'S 45°55'W, (51) Intervales 24°13'S 48°05'W, (52) Pedro de Toledo 24°16'29"S 47°13'58"W, (53) Iguape 24°42'29"S 47°33'19"W; PARANÁ, (54) Ponta Grossa 25°05'42"S 50°09'43"W, (55) Curitiba 25°25'4'0' 49°16'23"W, (56) Piraquara 25°26'30"S 49°03'48"W; SANTA CATARINA, (57) Itá 27°12'16"S 52°19'23"W, (58) Florianópolis 27°35'48"S 48°32'57"W; RIO GRANDE DO SUL, (59) Esmeralda 28°03'13"S 51°11'25"W, (60) Torres 29°20'07"S 49°43'37"W, (61) Alto Ferrabraz 29°35'S 50°56'W, (62) Sapiranga 29°38'17"S 51°00'25"W, (63) Pontal do Morro Alto 29°46'15"S 50°11'15"W, (64) Osório 29°53'12"S 50°16'11"W, (65) Emboaba 29°58'S 50°12'W, (66) Tramandaí 29°59'05"S 50°08'01"W, (67) Faxinal 30°18'S 51°41'W, (68) Mostardas 31°06'25"S 50°55'16"W, (69) Pelotas 31°46'19"S 52°20'33"W, (70) Taím 32°30'S 52°35'W; BOLIVIA – SANTA CRUZ, (71) San Ignacio 16°23'S 60°59'W, (72) Ingeniero Mora 18°08'S 63°12'W; TARIJA, (73) Tiqupa 20°56'S 63°21'W, (74) Villa Montes 21°19'S 63°25'W, (75) Taringuiti 21°28'S 63°17'W, (76) Tarija 21°31'S 64°45'W, (77) Entre Rios 21°32'S 64°12'W, (78) Río Lipeo 22°41'S 64°26'W; PARAGUAY – ASUNCIÓN, (79) Agua Dulce 20°01'S 59°46'W; PRESIDENTE HAYES, (80) Estancia Laguna Porá 22°20'S 59°26'W, (81) Puerto Piñasco 22°43'S 57°50'W, (82) Juan de Zalazar 23°06'S 59°18'W, (83) La Golondrina 25°06'S 57°34'W; BOQUERON, (84) Dr. Pedro P. Peña 22°27'S 62°21'W, (85) Fortín Guachalla 22°27'S 62°20'W, (86) Fortín Teniente Pratts Gil 22°41'S 61°33'W; AMAMBAY, (87) Pedro Juan Caballero 22°34'S 55°37'W, (88) Cerro Corá 22°37'S 56°30'W; CONCEPCIÓN, (89) Concepción 23°24'23"S 57°26'04"W; CANENDIYU, (90) Curuguaty 24°31'S 55°42'W; CAAGUAZÚ, (91) Carayaó 25°11'S 56°24'W, (92) Coronel Oviedo 25°25'S 56°27'W, (93) Sommerfeld Colony 25°26'S 55°43'W; CORDILLERA, (94) Tobatí 25°15'S 57°04'W; CENTRAL, (95) Asunción 25°16'S 57°40'W, (96) Luque 25°16'S 57°34'W; PARAGUARI, (97) Sapucay 25°40'S 56°55'W, (98) Parque Nacional Ybicuí 25°42'S 57°06'W; ITAPUA, (99) Río Pirapó 26°40'S 56°38'W,

(100) San Rafael 27°08'S 56°23'W, (101) Encarnación 27°20'S 55°54'W; MISIONES, (102) San Antonio 26°42'S 56°53'W, (103) San Francisco 26°52'S 57°03'W, (104) San Pablo 26°52'S 57°03'W, (105) Ayolas 27°24'S 56°54'W; URUGUAY – ARTIGAS, (106) Artigas 30°24'S 56°28'W; SALTO, (107) Salto 31°25'S 57°00'W; DURAZNO, (108) Durazno 33°05'S 56°05'W; RIO NEGRO, (109) Fray Bentos 33°08'S 58°18'W; COLONIA, (110) Martin Chico 34°10'S 58°13'W, (111) Colonia del Sacramento 34°28'S 57°51'W; CANELONES, (112) Canelones 34°32'S 56°17'W; MONTEVIDEO, (113) Montevideo 34°53'S 56°11'W; MALDONADO, (114) Maldonado 34°54'S 54°57'W, (115) Punta del Este 34°58'S 54°57'W; ARGENTINA – JUJUY, (116) Maimara 23°35'S 65°24'W, (117) Léon 24°03'S 65°26'W; FORMOSA, (118) Naineck 25°13'S 58°07'W, (119) Riacho Pilagra 26°11'S 58°11'W; TUCUMÁN, (120) Burruyacu 26°30'S 64°55'W, (121) El Cadillal 26°40'S 65°16'W, (122) El Infiernillo 26°40'S 65°46'W, (123) Horco Molle 26°47'S 65°18'W, (124) Concepción 27°20'S 65°35'W; MISIONES, (125) Caraguatay 34°44'00"S 58°15'19"W, (126) Río Paranay 26°37'S 54°46'W, (127) Río Urugua-í, 30 km Pto. Bertoni 26°41'S 54°49'W; CHACO, (128) Las Palmas 27°04'S 58°42'W; CÓRDOBA, (129) Río Cuarto 33°08'S 64°21'W; BUENOS AIRES, (130) Parana Delta River 34°12'S 58°18'W, (131) Diego Gaynor 34°17'S 59°14'W, (132) Capilla del Señor 34°18'S 59°06'W, (133) 25 km SE Buenos Aires 34°36'S 58°27'W, (134) Ezeiza, Punta Lara 34°50'17"S 58°31'02"W, (135) Berazategui 36°24'S 56°58'W, (136) General Lavalle 36°24'S 58°27'W, (137) Balcarce 37°50'S 58°15'W, (138) Monte Hermoso 38°55'S 61°33'W.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.131-146, jan./mar.2005
ISSN 0365-4508

A NEW SPECIES OF *RHIPIDOMYS* (RODENTIA, MUROIDEA) FROM NORTH-EASTERN BRAZIL [1]

(With 7 figures)

CHRISTOPHER J. TRIBE [2]

ABSTRACT – The collections of mammals made in the 1950s by the Serviço Nacional de Peste (National Plague Service) in north-eastern Brazil include some 240 specimens of climbing mice, genus *Rhipidomys*, from the states of Ceará and Pernambuco. Morphological and morphometric analyses reveal the presence among them of a new species, *Rhipidomys cariri* sp.nov., described herein with two subspecies, namely the nominotypical subspecies and *R. cariri baturiteensis* ssp.nov., respectively from the mesic enclaves of Cariri and Baturité within the semi-arid caatinga of Ceará. The species may be distinguished from both the population of *R. mastacalis* found in eastern Pernambuco and that of *R. macrurus* occurring in the Serra de Ibiapaba on the western border of Ceará through its larger body size, greyer and coarser pelage, longer vibrissae and larger molars. Although the separation of the enclaves from the Atlantic forest to the east and the Amazonian forest to the west probably dates back only to the mid-Holocene or late Pleistocene, the new endemic species may well have a much more remote origin; molecular data would be needed to test this hypothesis.

Key words: Ceará, morphology, morphometrics, mesic enclaves, caatinga.

RESUMO – Uma nova espécie de *Rhipidomys* (Rodentia, Muroidea) do Nordeste brasileiro.

O material mastozoológico coletado no Nordeste pelo Serviço Nacional de Peste, na década de 1950, inclui cerca de 240 exemplares de ratos arborícolas do gênero *Rhipidomys* provenientes do Ceará e de Pernambuco. A utilização de métodos morfológicos e morfométricos permitiu distinguir entre eles uma nova espécie, *R. cariri* sp.nov., descrita aqui com duas subespécies, a nominotípica e *R. cariri baturiteensis* ssp.nov., respectivamente provenientes dos brejos (zonas úmidas) do Cariri e de Baturité, isolados na caatinga do Ceará. A espécie se distingue tanto da população de *R. mastacalis* encontrada no leste de Pernambuco quanto daquela de *R. macrurus* que ocorre na Serra de Ibiapaba, no extremo ocidental do Ceará, pelo seu tamanho corporal maior, sua pelagem mais cinzenta e menos lisa, suas vibrissas mais compridas e sua série molar maior. Apesar de a separação entre os brejos cearenses e a mata atlântica, ao leste, e a amazônica, ao oeste, remontar apenas até o meio do Holoceno ou o final do Pleistoceno, é possível que a nova espécie endêmica tenha origem bem mais antiga, hipótese esta que poderia ser testada com dados moleculares.

Palavras-chave: Ceará, morfologia, morfometria, brejos, caatinga.

INTRODUCTION

Mice of the muroid genus *Rhipidomys* Tschudi, 1845 are among the lesser known arboreal mammals of the Neotropics, yet they are widespread in South America. The twenty or more recognisable species inhabit most types of wooded habitat north of latitude 24°S, from rainforest to semi-deciduous woodland, as well as plantations and even the rafters of rural dwellings. In Brazil they are found from Roraima to São Paulo and from Pernambuco to Acre (TRIBE, 1996).

In his book on the rodents of Brazil (MOOJEN, 1952), João Moojen listed four species of *Rhipidomys* from Brazil: *R. maculipes* (Pictet & Pictet, 1844), distributed in the '*matas do sul da Bahia. Ilhéus*' ('forests of southern Bahia. Ilhéus'); *R. macrurus* (Gervais, 1855), found in northern

[1] Submitted on September 15, 2004. Accepted on December 20, 2004.

[2] Affiliated Researcher, University Museum of Zoology Cambridge, Department of Zoology, Downing Street, Cambridge CB2 3EJ, United Kingdom. E-mail: cjt14@cam.ac.uk.

Goiás; *R. mastacalis* (Lund, 1840), in the states of Minas Gerais and Rio de Janeiro; and *R. cearanus* Thomas, 1910, in the State of Ceará. Apart from very brief notes on their coloration and a table of measurements of the type specimens, he gave no indication as to how these forms might be distinguished other than geographically. Moojen's book was written, however, before he could see the full results of the collections of rodents made by the Serviço Nacional de Peste (SNP – the National Plague Service) in north-eastern Brazil, which were conducted under his overall direction mostly between 1951 and 1956 (OLIVEIRA & FRANCO, this volume). Examination of the hundreds of *Rhipidomys* specimens contained in these collections reveals that the pattern of species in north-eastern Brazil is more complex than Moojen's book suggested (CERQUEIRA, VIEIRA & SALLES, 1989). Indeed, a new species with two subspecies based on SNP material is described below.

MATERIAL AND METHODS

Localities and specimens

The 1st Region (*1ª Circunscrição*) of the Serviço Nacional de Peste covered the four states of Ceará, Paraíba, Pernambuco and Alagoas, located north of the São Francisco river in north-eastern Brazil. Most of the area lies within the *polígono das secas* or drought zone, characterised by irregular, infrequent rainfall and covered mainly by the thorn scrub vegetation known as *caatinga*. Within the *caatinga*, ranges of hills and isolated massifs that intercept moisture-bearing winds provide more mesic habitats, known locally as *brejos*, which support mesophytic forests. A relatively narrow strip along the east coast receives high rainfall; this is the *zona da mata* or forest zone, originally covered by the northern end of the Atlantic forest but now almost entirely devoted to intensive farming. A band known as the *agreste*, originally occupied by semi-deciduous forest, buffers the *zona da mata* from the *caatinga*.

Within this region, *Rhipidomys* specimens were collected in the moister parts but not in the *caatinga* proper. Substantial series were obtained in four areas:

a) Crato (07°14'S 39°23'W), in the Cariri *brejo* of southern Ceará, where 24 *Rhipidomys cariri cariri* ssp.nov. are known to have been collected by the SNP in July-August 1946 and between July 1952 and April 1953. Freitas refers to 21 '*Holochilus sciureus*' (see the species description for discussion of this misidentification), but does not include four specimens collected in a preliminary survey in 1946 (FREITAS, 1957, Tab.1).

b) Pacoti (04°13'S 38°56'W), in the Serra de Baturité *brejo* in northern Ceará, where 17 *Rhipidomys cariri baturiteensis* ssp.nov. were captured between July 1953 and November 1954. Freitas mentions 22 *R. cearanus* from Baturité district (FREITAS, 1957).

c) the Serra de Ibiapaba, western Ceará, especially at São Benedito (04°03'S 40°53'W) and Guaraciaba do Norte (04°10'S 40°46'W); 141 specimens of *Rhipidomys macrurus* are known to have been collected here between August 1952 and June 1954. Freitas, however, refers to 292 *R. cearanus* from the corresponding SNP district of Ipu (FREITAS, 1957); this number may include discarded and/or misidentified specimens. The hamlet of São Paulo in the Serra de Ibiapaba is the type locality of *R. cearanus* Thomas, regarded here as a junior synonym of *R. macrurus*.

d) the area of Caruaru (08°17'S 35°58'W), in eastern Pernambuco, where 58 *Rhipidomys mastacalis* were caught between April 1952 and November 1953. In addition, one *R. mastacalis* was taken at Garanhuns in eastern Pernambuco (08°54'S 36°29'W) in October 1952, and one at Anádia in Alagoas (09°42'S 36°18'W) in July 1955. Freitas lists 120 *R. mastacalis* from Caruaru and 5 from Garanhuns, but the Anádia specimen, which was marked as 'unidentified rat' on its record card, is not mentioned (FREITAS, 1957). For the purposes of analysis, the Anádia and Garanhuns specimens were included with the Caruaru series on the basis of morphological similarity and geographical proximity.

All but three of the 242 specimens located are now in the collections of the Museu Nacional, Rio de Janeiro (MN), mostly in the form of study skins with cleaned skulls; the University of Kansas Natural History Museum (KU) has one and the National Museum of Natural History, Washington, D.C. (USNM) two specimens of *R. c. cariri* from Crato. The SNP material includes most of the *Rhipidomys* specimens known from north-eastern Brazil, relatively few individuals having been collected in the region before or since. This material was studied by the author as part of a broader investigation into the whole genus (TRIBE, 1996).

References to *R. macrurus* and *R. mastacalis* in the following sections denote only the samples and populations mentioned above unless the context requires a more comprehensive interpretation.

Analyses

Specimens were examined and compared for the size and proportions of external, cranial and dental characters and for pelage colour and texture. External measurements recorded on specimen labels were accepted as approximations to the true values unless clearly in error; hind foot length was usually rechecked on the dry foot where possible. Specimens were allocated to dental age classes on the basis of their molar wear (see TRIBE, 1996, for details). Juveniles (those in which wear had not yet exposed the dentine in the lophs of the upper second molar) and old individuals (those in which the main enamel features of the M2 occlusal surface had been obliterated) were excluded from morphometric analyses, leaving 107 adults in classes 2-4 (11 *R. c. cariri*, 7 *R. c. baturiteensis*, 67 *R. macrurus* and 27 *R. mastacalis*). For the multivariate analysis, four of these *R. macrurus* specimens and one *R. mastacalis* for which missing values could not be imputed satisfactorily (TRIBE, 1996) were omitted from the adult dataset.

The following 30 skull dimensions were measured (see TRIBE, 1996, for definitions of measurement end points): occipito-nasal length (ONL); condylo-incisive length (CIL); palatal length (PL); post-palatal length (PPL); upper molar row – crown length (MRC); upper molar row – alveolar length (MRA); 1st upper molar breadth (M1B); palatal bridge length (PBL); temporal fossa length (TFL); diastema length (DL); incisive foramen length (IFL); incisive foramen breadth (IFB); palatal breadth at M1 (PB1); palatal breadth at M3 (PB3); mesopterygoid fossa breadth (MFB); breadth across incisor tips (BIT); bullar width (BW); bullar length (BL); braincase breadth (BCB); skull height (SH); rostral height (RH); rostral breadth (RB); rostral length (RL); nasal length (NL); zygomatic plate length (ZPL); interorbital breadth (IOB); zygomatic breadth (ZB); greatest length of mandible (GLM); mandibular molar row – alveolar length (MMR); depth of mandibular ramus (DR).

For each of the four taxa, descriptive statistics (range, mean and standard deviation) were calculated for each variable and for a number of bivariate ratios of interest. Student's *t*-tests were used to compare these means for each pair of taxa.

Principal components analysis (PCA) was performed to provide a low-dimensional representation of the data (REYMENT, BLACKITH & CAMPBELL, 1984). PCA was chosen since it does not impose any *a priori* structure on the data; that is, the specimens are not analysed according to their geographical groups of origin, as would be necessary with techniques such as discriminant analysis or MANOVA. The appearance in the results of any groupings congruent with the geographical origin of the specimens would thus demonstrate that the samples were morphometrically distinct along at least one major axis of variation of the pooled data. This would support the four-taxon arrangement described above on the basis of morphology and geographical origin.

In PCA, linear combinations (components) of the original variables are calculated sequentially so as to be uncorrelated with each other and to maximise the variance they contain; thus the major part of the variation present in all the original variables is expressed in a small number of components. The individual measurement values for a specimen (log-transformed and standardised) are multiplied by the coefficients that make up the latent vector (eigenvector) corresponding to each component, and the products are summed to produce a score for the specimen on that component. Bicomponent plots of the resulting specimen scores can then be examined in the light of groupings based on parameters such as sex, age or, as here, geographical provenance. In most cases, the first component in PCAs performed on vertebrate specimens predominantly represents variation in general specimen 'size' (REYMENT, BLACKITH & CAMPBELL, 1986), a large proportion of which will be of ontogenetic origin. The variation in 'shape' reflected in subsequent components is often more informative for phylogenetic purposes.

Since the number of specimens analysed must always exceed the number of variables (REYMENT, BLACKITH & CAMPBELL, 1984), a reduced set of 15 variables (PL, MRC, PBL, TFL, PB1, MFB, BW, BCB, SH, RB, NL, ZPL, IOB, MMR and DR) was used in PCAs involving fewer than 30 specimens, the dimensions excluded being those previously found to display the highest measurement errors or greatest sexual or ontogenetic variation among adults (TRIBE, 1996). Principal components are specific to the samples analysed and will change when specimens are added to or subtracted from the dataset (NEFF & MARCUS, 1980); the latent vector weightings therefore have to be interpreted anew for each subset of specimens analysed separately.

RESULTS

Morphologically, each of the four series of SNP specimens – *R. c. cariri* ssp.nov., *R. c. baturiteensis* ssp.nov., *R. macrurus* and *R. mastacalis* – was relatively homogeneous and there was no evidence from visual examination or univariate analyses of measurements (such as clear bimodality in distributions) to suggest that more than one taxon might be present in each sample. On the basis of specimen size and pelage, the four series fell clearly into two groups. The two separated by the greatest distance, *R. macrurus* and *R. mastacalis*, resembled each other in their moderate size and in their sleek, reddish-brown dorsal pelage with only a slight agouti effect. In contrast, *R. c. cariri* and *R. c. baturiteensis* were larger, with coarser, duller, more agouti pelage.

No single variable or bivariate ratio provided unambiguous separation of the four series, since the ranges of values for the different taxa always overlapped. The *t*-test results, however, showed that the sample means for many variables were significantly different, several with a probability $p < 0.001$ of falsely rejecting the null hypothesis of equality of population means (see table 1 for a selection of significant variables and ratios). In the pairwise comparisons, the variable means that differentiated *R. c. cariri* and *R. c. baturiteensis* on the one hand from *R. macrurus* and *R. mastacalis* on the other, with a probability $p < 0.05$, were MRC, MRA, TFL, BW, BL, RB, RL and DR. *Rhipidomys c. cariri* and *R. c. baturiteensis* had the larger means in each case. A number of bivariate ratios also had distinct means, including RL/ONL (rostral length as a proportion of skull length, greater in *R. c. cariri* and *R. c. baturiteensis*), RH/RL (relative height of the rostrum, shallower in *R. c. cariri* and *R. c. baturiteensis*) and PBL/MRC (relative length of the palatal bridge to the molar row, shorter in *R. c. cariri* and *R. c. baturiteensis*). Several other individual variables and bivariate ratios had means that distinguished either *R. c. cariri* or *R. c. baturiteensis* from both *R. macrurus* and *R. mastacalis*: ONL, CIL, PPL, PB1, MFB, ZB, GLM, PB1/PBL and BW/BCB were all larger in *R. c. cariri*; and DL, BCB, ZPL, MMR and IFB/IFL were all larger in *R. c. baturiteensis*.

The *R. c. cariri* and *R. c. baturiteensis* samples also differed from each other in several of these characters. Molar lengths and breadth were significantly greater in *R. c. baturiteensis*, which also had longer and narrower incisive foramina, a narrower palate and mesopterygoid fossa, and a rather shallower rostrum than *R. c. cariri*.

Principal components analysis reflected the craniometric distinctness of the four samples. In an analysis of all valid specimens together, a plot of specimen scores on the third principal component (PC3) against the second (Fig.1) could

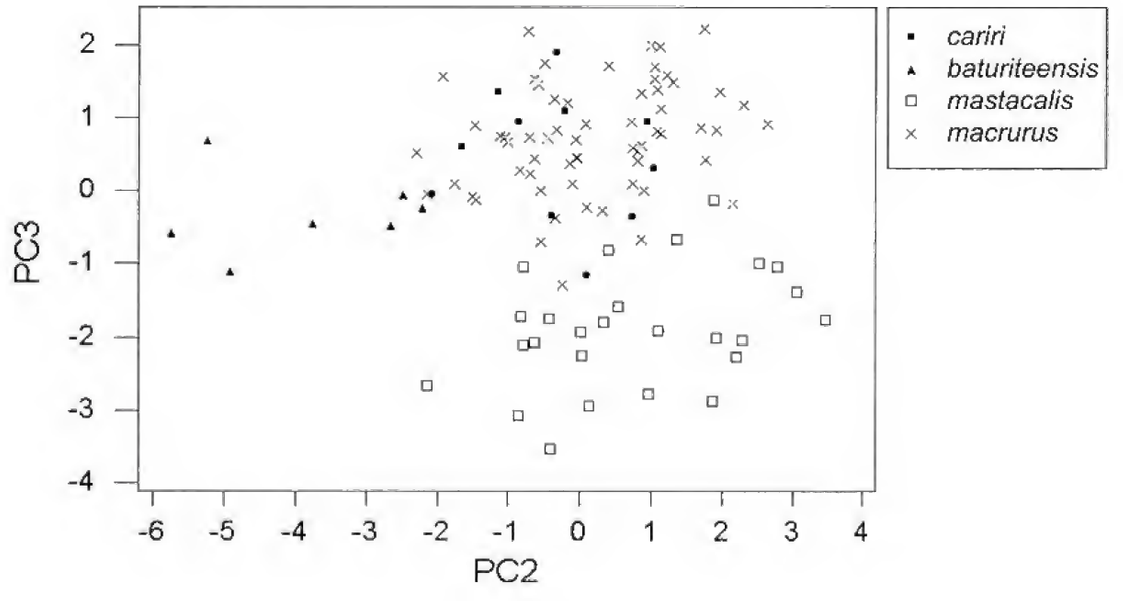

Fig.1- Principal components analysis, using 30 variables, of all analysable specimens: *Rhipidomys cariri cariri* ssp.nov. (n = 11), *R. c. baturiteensis* ssp.nov. (n = 7), *R. macrurus* from Serra de Ibiapaba, Ceará (n = 63), and *R. mastacalis* from Pernambuco (n = 26). Plot of scores on the second and third components.

be divided into three main areas, occupied respectively by the *R. c. baturiteensis* sample, the *R. mastacalis* sample, and the *R. c. cariri* plus *R. macrurus* samples. *Rhipidomys c. baturiteensis* was separated from the remainder mainly along the PC2 axis, while *R. mastacalis* clustered apart mainly on PC3, with little overlap in each case. The size of the coefficients on the second latent vector (see table 2 for all latent vectors discussed) suggested that *R. c. baturiteensis* was distinguished by its larger molars and bullae compared with incisive foramen breadth and rostral height. The third latent vector was more complex to interpret, with large positive loadings particularly for bullar dimensions and a large negative one for palatal bridge length; since the *R. mastacalis* specimens clustered at the negative end of the component, they might be expected to have a relatively longer palatal bridge and/or smaller bullae than the rest.

Clearer separations resulted when only two or three groups were included in the dataset analysed. The large series of *R. macrurus* and *R. mastacalis*, for instance, when analysed together, formed separate ellipsoid clusters in a plot of PC3 against PC2. The second latent vector contrasted molar and palatal bridge lengths with bullar dimensions and incisive foramina length, *R. mastacalis* having relatively smaller bullae, a longer palatal bridge and shorter incisive foramina on average than *R. macrurus*. The third latent vector emphasised a combination of bullar plus molar variables against a collection of breadth variables from the central portion of the skull (IFB, IOB, MFB, PB3), suggesting that in *R. mastacalis* that region might be broader for a given molar/bullar size than in *R. macrurus* skulls.

Separate analyses of *R. c. baturiteensis* with *R. macrurus* and of *R. c. baturiteensis* with *R. mastacalis* resulted in clearly distinct clusters in plots of PC2 against PC1. In each case, as in the analysis illustrated in figure 1, virtually all the separation was along the second component axis and was due to the larger molars and bullae of *R. c. baturiteensis* in contrast to variables that showed no appreciable difference between the samples, such as rostral height. *Rhipidomys c. baturiteensis* also clustered towards the more negative end of the PC1 axis in each case, whereas the *R. macrurus* and *R. mastacalis* specimens spanned the whole range of values. The corresponding latent vector consisted of large negative loadings for major skull dimensions with smaller, also negative, contributions from basicranial and molar variables. It could thus be interpreted as a general (negative) skull size component (REYMENT, BLACKITH & CAMPBELL, 1986). *Rhipidomys c. baturiteensis* skulls therefore lay at the larger end of the size range included in the analysis.

When the *R. c. baturiteensis* and *R. c. cariri* specimens were analysed together, the two groups occupied separate but contiguous areas in plots of PC2 against PC1 (Fig.2) and of PC4 against PC2. *Rhipidomys c. baturiteensis* tended to score higher than *R. c. cariri* on all three components. The first latent vector contained large positive loadings for the molar rows and most skull dimensions except for variables concentrated in the central portion of the skull, which were much less important. The second contrasted these (palatal breadth at M1, temporal fossa length, mesopterygoid fossa breadth and interorbital breadth, all with large negative coefficients) with molar size (positive), while the fourth latent vector contrasted interorbital breadth (negative loadings) with length variables (nasal, palatal bridge and temporal fossa – positive). These results suggest that the central portion of the skull in *R. c. cariri* might be broader, whereas *R. c. baturiteensis* has larger molars and a longer, more slender rostral part. Indeed, the raw skull measurements show that, on average, *R. c. cariri* has a broader palatal bridge and mesopterygoid fossa, while *R. c. baturiteensis* has longer and broader molars, and longer and more slender incisive foramina.

The fact that the *R. c. cariri* sample had a preponderance of males (8 out of 11) and an average dental age class of 3.3, compared with only 3 males out of 7 and an average dental age class of 2.6 in the *R. c. baturiteensis* sample, might at first sight suggest that the differences between the groups could be due to sexual and ontogenetic variation. It is significant, however, that molar dimensions and variables located in the central portion of the *Rhipidomys* skull are less influenced by sex and age than most longitudinal measurements, which tend to be larger in males and older specimens (TRIBE, 1996). Since the latent vectors suggest that relatively larger longitudinal measurements characterise *R. c. baturiteensis* whereas *R. c. cariri* has relatively larger central skull dimensions (and this is borne out by the raw data), the differences cannot be attributed solely to the sex/age composition of the samples.

When *Rhipidomys c. cariri* and *R. mastacalis* were analysed together, a plot of scores on the first two principal components placed them in two distinct but contiguous clusters. The first component showed that the *R. c. cariri* specimens were larger on average, while the second suggested they had larger molars and bullae, a shorter palate and a relatively shallower rostrum than *R. mastacalis*.

Table 1 A. Descriptive statistics for a selection of variables and ratios of untransformed data for four *Rhipidomys* samples: means and standard deviations (in mm), and number of specimens (*n*). Table 1 B. Probabilities (*p*) calculated from Student's *t*-tests for the equality of population means. *p* values ≤ 0.05 but >0.01 (▪) indicate a remote probability, and those ≤ 0.01 (□) indicate a very remote probability, that the populations in question have equal means.

A. DESCRIPTIVE STATISTICS

Taxon sample	Variable or ratio	ONL	MRC	M1B	IFL	IFB	MFB	BW	IOB	RL/ ONL	PBL/ MRC	PB1/ PBL	RH/ RL	IFB/ IFL
R. c. cariri	mean	35.733	5.185	1.425	7.117	2.907	2.413	4.468	5.468	0.308	0.944	0.665	0.596	0.409
(Crato)	s.d.	0.709	0.135	0.035	0.305	0.132	0.190	0.138	0.211	0.007	0.058	0.041	0.022	0.016
	n	9	23	23	11	11	11	8	11	9	11	11	11	11
R. c. baturiteensis	mean	35.223	5.447	1.507	7.593	2.727	2.090	4.520	5.321	0.315	0.942	0.592	0.565	0.359
(Pacoti)	s.d.	1.176	0.121	0.048	0.314	0.117	0.160	0.235	0.214	0.006	0.036	0.036	0.036	0.016
	n	7	15	15	7	7	7	7	7	7	7	7	7	7
R. macrurus	mean	34.021	4.992	1.393	6.951	2.757	2.149	4.254	5.260	0.298	0.978	0.633	0.635	0.397
(Serra de Ibiapaba)	s.d.	1.580	0.144	0.054	0.387	0.169	0.184	0.124	0.266	0.008	0.045	0.045	0.023	0.027
	n	63	108	119	67	67	67	66	67	63	67	67	64	67
R. mastacalis	mean	33.674	4.984	1.375	6.637	2.783	2.244	4.030	5.446	0.300	1.037	0.580	0.629	0.419
(Pernambuco)	s.d.	1.660	0.130	0.044	0.400	0.219	0.212	0.129	0.255	0.008	0.059	0.049	0.031	0.024
	n	27	37	40	27	27	27	27	27	27	25	26	27	27

B. STUDENT'S *t*-TESTS: VALUES OF *p*

Populations compared	Variable or ratio	ONL	MRC	M1B	IFL	IFB	MFB	BW	IOB	RL/ ONL	PBL/ MRC	PB1/ PBL	RH/ RL	IFB/ IFL
R. c. cariri - *R. c. baturiteensis*		0.299	□0.000	□0.000	□0.006	□0.009	□0.002	0.601	0.171	▪0.041	0.941	□0.002	▪0.033	□0.000
R. c. cariri - *R. macrurus*		□0.002	□0.000	□0.007	0.170	□0.007	□0.000	□0.000	▪0.014	□0.000	▪0.026	▪0.026	□0.000	0.209
R. c. cariri - *R. mastacalis*		□0.001	□0.000	□0.000	□0.001	0.089	▪0.028	□0.000	0.803	▪0.011	□0.000	□0.000	□0.003	0.175
R. c. baturiteensis - *R. macrurus*		0.051	□0.000	□0.000	□0.000	0.618	0.419	□0.000	0.528	□0.000	▪0.042	▪0.041	□0.000	□0.000
R. c. baturiteensis - *R. mastacalis*		▪0.027	□0.000	□0.000	□0.000	0.523	0.084	□0.000	0.243	□0.000	□0.000	0.525	□0.000	□0.000
R. macrurus - *R. mastacalis*		0.368	0.771	0.057	□0.001	0.585	▪0.031	□0.000	□0.002	0.233	□0.000	□0.000	0.312	□0.001

(ONL) occipito-nasal length, (MRC) upper molar row – crown length, (M1B) 1st upper molar breadth, (IFL) incisive foramen length, (IFB) incisive foramen breadth, (MFB) mesopterygoid fossa breadth, (BW) bullar width, (IOB) interorbital breadth, (RL) rostral length, (PBL) palatal bridge length, (PB1) palatal breadth at M1, (RH) rostral height.

An analysis of *R. c. cariri* with all the *R. macrurus* specimens, however, failed to provide complete separation of the two groups. In case the different sizes and sex/age compositions of the samples might be affecting the analysis, the 11 *R. c. cariri* specimens were then analysed simultaneously with subsets of 11 *R. macrurus* and 11 *R. mastacalis* specimens, each of which matched the composition of the *R. c. cariri* sample as closely as possible in terms of sex and dental age class. Where more specimens were available in a particular sex/age category than were required for the subset, the appropriate number of individuals was selected at random. In the resulting analysis, a plot of scores on PC2 and PC3 provided good separation of the three groups, with minimal overlap (Fig.3). *Rhipidomys c. cariri* was distinguished almost entirely along the second component axis on the basis of its larger molars and bullae and broader palate and mesopterygoid fossa, and its relatively shallower rostrum and shorter palatal bridge.

The results of both univariate and multivariate analyses thus demonstrate the distinctness of the four geographical series of *Rhipidomys* specimens examined, confirming the morphologically based taxonomic hypothesis that they belong to four distinct taxa. Most of the variation between the four groups seems to be concentrated in dimensions of the molars, bullae, palate, incisive foramina, and rostrum. The larger molars and bullae of *Rhipidomys cariri* as a species are particularly important in distinguishing it from its neighbours, while at a subspecies level *R. c. baturiteensis* differs in its narrower palate and longer, more slender rostrum from *R. c. cariri.* It is unfortunate, however, that the overlap between the four taxa in their ranges of measurements means that there is no variable or ratio that could serve as an unambiguous marker to identify a specimen from its skull. *R. cariri* therefore has to be determined on the basis of a somewhat subjective assessment of skin and skull characters.

Rhipidomys cariri sp.nov.

Rhipidomys cearanus – MOOJEN, 1943 (not *Rhipidomys cearanus* Thomas, 1910).

Holochilus sciureus – FREITAS, 1957 (part; not *Holochilus sciureus* Wagner, 1842).

Rhipidomys mastacalis – MARES *et al.*, 1981 (part; not *Mus mastacalis* Lund, 1840).

Holotype – BRAZIL - CEARÁ: Crato (07°14'S 39°23'W), Sítio Caiana; MN 10170; adult ♂; collected by Batista for the Serviço Nacional de Peste on 20 August 1946, in a palm tree; field number 3. Condition: round study skin in good condition; cleaned skull and mandible (rami joined at symphysis), slightly damaged (left pterygoid process separated; left jugal and both lacrimals missing, left nasal tip chipped).

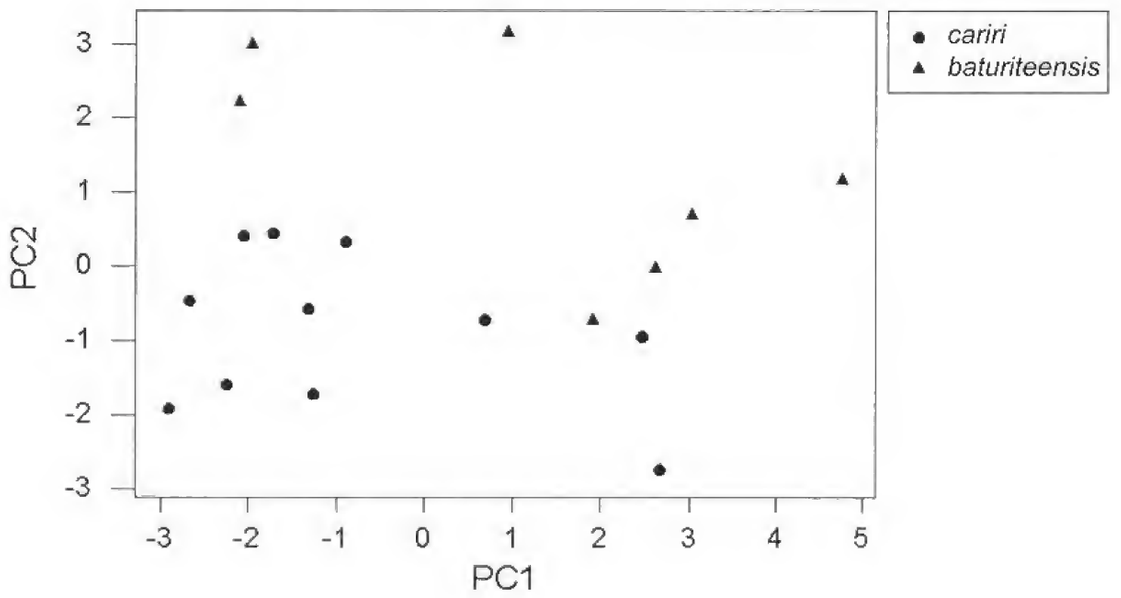

Fig.2- Principal components analysis of all analysable specimens of *Rhipidomys cariri cariri* ssp.nov. (n = 11) and *R. c. baturiteensis* ssp.nov. (n = 7), using 15 variables. Plot of scores on the first and second components.

Table 2. Selected latent vectors from principal components analyses discussed in the text (coefficients rounded to two decimal places for clarity).

SAMPLES ANALYSED	*cc-cb-mc-ms*		*mc-ms*		*cb-mc*		*cb-ms*		*cc-cb*			*cc-mc*		*cc-mc-ms*	
NO OF SPECIMENS	107		89		70		33		18			37		33	
NO OF VARIABLES	30		30		30		30		15			30		30	
LATENT VECTOR / VARIABLE	LV2	LV3	LV2	LV3	LV1	LV2	LV1	LV2	LV1	LV2	LV4	LV1	LV2	LV2	LV3
ONL	0.04	0.03	-0.02	-0.02	-0.24	-0.08	-0.23	0.05				-0.24	0.01	0.00	-0.04
CIL	0.06	0.05	-0.05	-0.01	-0.24	-0.09	-0.24	0.05				-0.24	0.03	0.04	-0.05
PL	0.08	-0.15	0.08	0.12	-0.23	-0.04	-0.23	0.10	0.34	-0.15	0.21	-0.21	0.22	0.17	0.14
PPL	0.07	0.21	-0.17	-0.10	-0.21	-0.17	-0.22	0.04				-0.22	-0.05	0.00	-0.17
MRC	-0.42	-0.18	0.36	-0.39	-0.16	0.38	-0.15	-0.35	0.37	0.19	0.00	-0.13	-0.40	-0.45	0.15
MRA	-0.36	-0.30	0.44	-0.24	-0.16	0.38	-0.15	-0.31				-0.13	-0.31	-0.43	0.23
M1B	-0.36	0.00	0.10	-0.35	-0.09	0.36	-0.16	-0.27				-0.14	-0.18	-0.18	-0.15
PBL	0.01	-0.44	0.31	0.08	-0.17	0.06	-0.09	0.03	0.23	-0.06	0.36	-0.01	0.32	0.19	0.38
TFL	0.03	-0.07	0.06	0.01	-0.21	0.00	-0.22	0.07	0.11	-0.41	0.35	-0.21	0.06	0.01	0.11
DL	0.10	0.06	-0.12	0.07	-0.22	-0.09	-0.23	0.06				-0.22	0.18	0.22	-0.05
IFL	-0.04	0.23	-0.21	-0.05	-0.21	0.01	-0.20	-0.09				-0.21	-0.08	0.04	-0.25
IFB	0.22	0.02	-0.05	0.28	-0.09	-0.21	-0.13	0.27				-0.19	0.04	-0.02	-0.11
PB1	0.11	0.10	-0.07	0.04	-0.12	-0.17	-0.12	0.14	0.09	-0.53	0.08	-0.16	-0.13	-0.20	0.00
PB3	0.11	-0.14	0.10	0.19	-0.13	-0.11	-0.07	0.16				-0.12	-0.08	-0.20	0.20
MFB	0.18	-0.09	0.12	0.21	-0.08	-0.15	-0.06	0.33	-0.13	-0.39	-0.10	-0.15	-0.04	-0.19	-0.01
BIT	0.10	-0.09	0.05	0.13	-0.17	-0.07	-0.19	0.12				-0.17	0.27	0.18	0.09
BW	-0.26	0.34	-0.31	-0.33	-0.14	0.22	-0.16	-0.30	0.27	0.14	-0.14	-0.16	-0.32	-0.25	-0.30
BL	-0.34	0.39	-0.26	-0.46	-0.12	0.30	-0.10	-0.36				-0.09	-0.43	-0.29	-0.37
BCB	-0.07	-0.05	0.07	-0.05	-0.20	0.08	-0.21	-0.03	0.29	0.09	-0.10	-0.21	-0.02	-0.06	0.08
SH	0.10	0.02	-0.04	0.01	-0.21	-0.13	-0.22	0.08	0.34	-0.20	-0.03	-0.22	0.13	0.13	0.02
RH	0.21	0.03	-0.05	0.02	-0.18	-0.24	-0.16	0.23				-0.20	0.21	0.20	0.09
RB	0.01	-0.10	0.10	0.09	-0.19	-0.03	-0.21	0.03	0.25	-0.19	-0.20	-0.22	-0.05	-0.14	0.17
RL	-0.02	0.04	-0.04	0.02	-0.23	0.03	-0.22	-0.03				-0.22	-0.01	-0.04	-0.14
NL	0.07	0.03	-0.04	0.03	-0.21	-0.06	-0.20	0.07	0.25	-0.02	0.40	-0.18	0.18	0.15	-0.06
ZPL	-0.04	0.20	-0.24	-0.03	-0.17	0.05	-0.21	-0.07	0.35	0.14	-0.14	-0.20	0.05	0.05	-0.09
IOB	0.14	-0.28	0.18	0.23	-0.13	-0.12	-0.10	0.20	0.12	-0.30	-0.50	-0.12	0.05	-0.04	0.40
ZB	0.08	-0.02	0.01	0.03	-0.22	-0.11	-0.22	0.08				-0.22	0.04	0.06	0.03
GLM	0.03	0.07	-0.05	-0.03	-0.23	-0.05	-0.22	0.04				-0.22	0.06	0.06	-0.08
MMR	-0.37	-0.28	0.38	-0.23	-0.15	0.38	-0.14	-0.30	0.34	0.31	-0.06	-0.06	-0.11	-0.22	0.30
DR	-0.01	0.09	-0.10	0.00	-0.18	0.00	-0.19	-0.02	0.12	-0.18	-0.43	-0.17	-0.07	-0.05	-0.13

Samples analysed: (*cc*) *Rhipidomys cariri cariri*, (*cb*) *R. c. baturiteensis*, (*mc*) *R. macrurus*, (*ms*) *R. mastacalis*. See the text for the abbreviations of the variables.

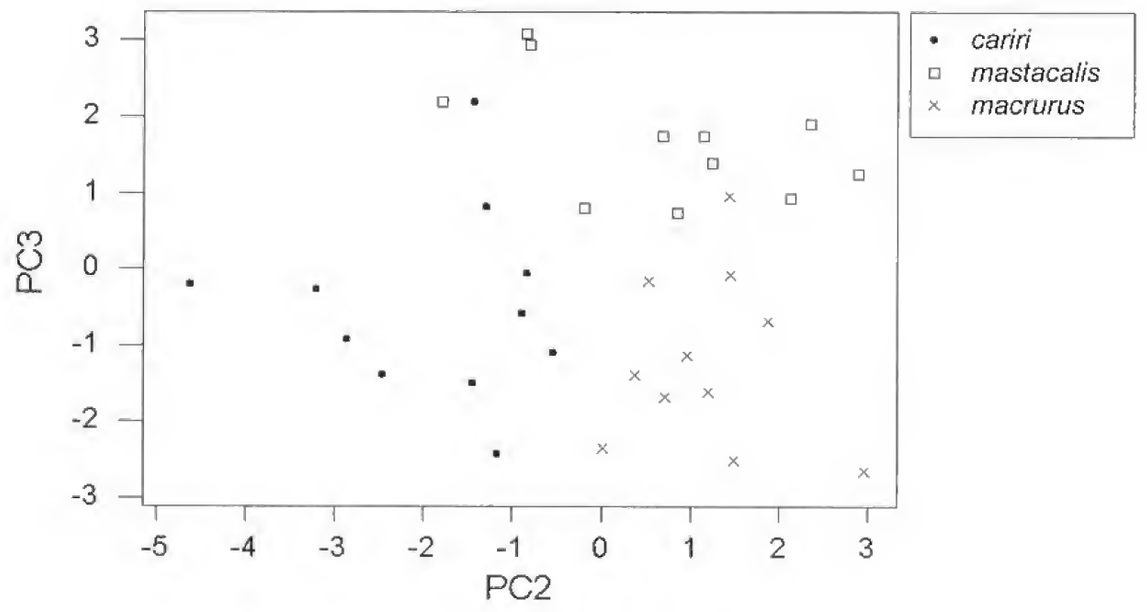

Fig.3- Principal components analysis, using 30 variables, of all analysable *Rhipidomys cariri cariri* ssp.nov. (n = 11) and an equal number each of *R. mastacalis* and *R. macrurus* matching the *R. c. cariri* sample in terms of sex and dental age class. Plot of scores on the second and third components.

Diagnosis – Moderately large *Rhipidomys* specimens with conspicuously agouti, yellowish-grey-brown dorsal pelage and cream underparts; ventral pelage rather woolly in texture; tail longer than head and body, with short to medium-length pencil; hind foot large, broad, with short toes; ears large; vibrissae very long and thick. Skull large and robust, with well-developed supraorbital ridges and broad occiput; palatal bridge very short; bullae and molars moderately large. Carotid circulatory pattern derived (VOSS, 1988: "pattern 3").

Description – Moderate to large-bodied rats, with adult head-and-body length usually 130-160mm, the largest in the sample being 190mm; tail length equals 110-140% of head-and-body length (Fig.4). Dorsal pelage is yellowish-grey-brown, sometimes a little greyer, sometimes a little redder, but always with conspicuous flecking from the dark guard hairs and dark tips to the body hairs. Dorsal body hairs have mid-grey bases (about 62% of the hair length), an orange subterminal band (about 29%) and a dark tip (8-9%). The ventral pelage is white or pale cream in appearance; some specimens have pale to mid-grey hair bases especially towards the sides and occasionally (as in the holotype) right across the abdomen, as well as in a midline pectoral spot. The pelage texture is slightly coarse and woolly, especially on the ventral surface. Females have six mammae, as in all *Rhipidomys*. The tail is uniformly coloured, varying among specimens from pale to rather dark; the tail hairs are dark and short (1-2mm) especially along the proximal half of the tail, but may be rather longer at the tip forming a terminal tuft or pencil up to 15mm in length (Fig.4a, c). The hind foot is broad and relatively long compared with other *Rhipidomys* of similar size, measuring 27-30mm including the claw; unfortunately, the collectors' measurements as given on the specimen labels and SNP record cards for this locality are of little use (they were taken to the nearest centimetre), and the feet of some specimens were deformed too much on drying to be remeasured accurately. The dark patch on the dorsal surface of the metatarsals varies from narrow to broad, but is often poorly defined; the ungual tufts are usually approximately the same length as the claws. The ears seem to be larger in area than in other eastern Brazilian species, although they are barely a millimetre longer on average. The mystacial vibrissae are long (> 50mm) and coarse; genal and supraorbital vibrissae are sparse.

The skull (Figs.5-7, a-b) is large and robust with well-developed, straight supraorbital ridges diverging from the front of the interorbital region. The rostrum is moderately long and the zygomatic

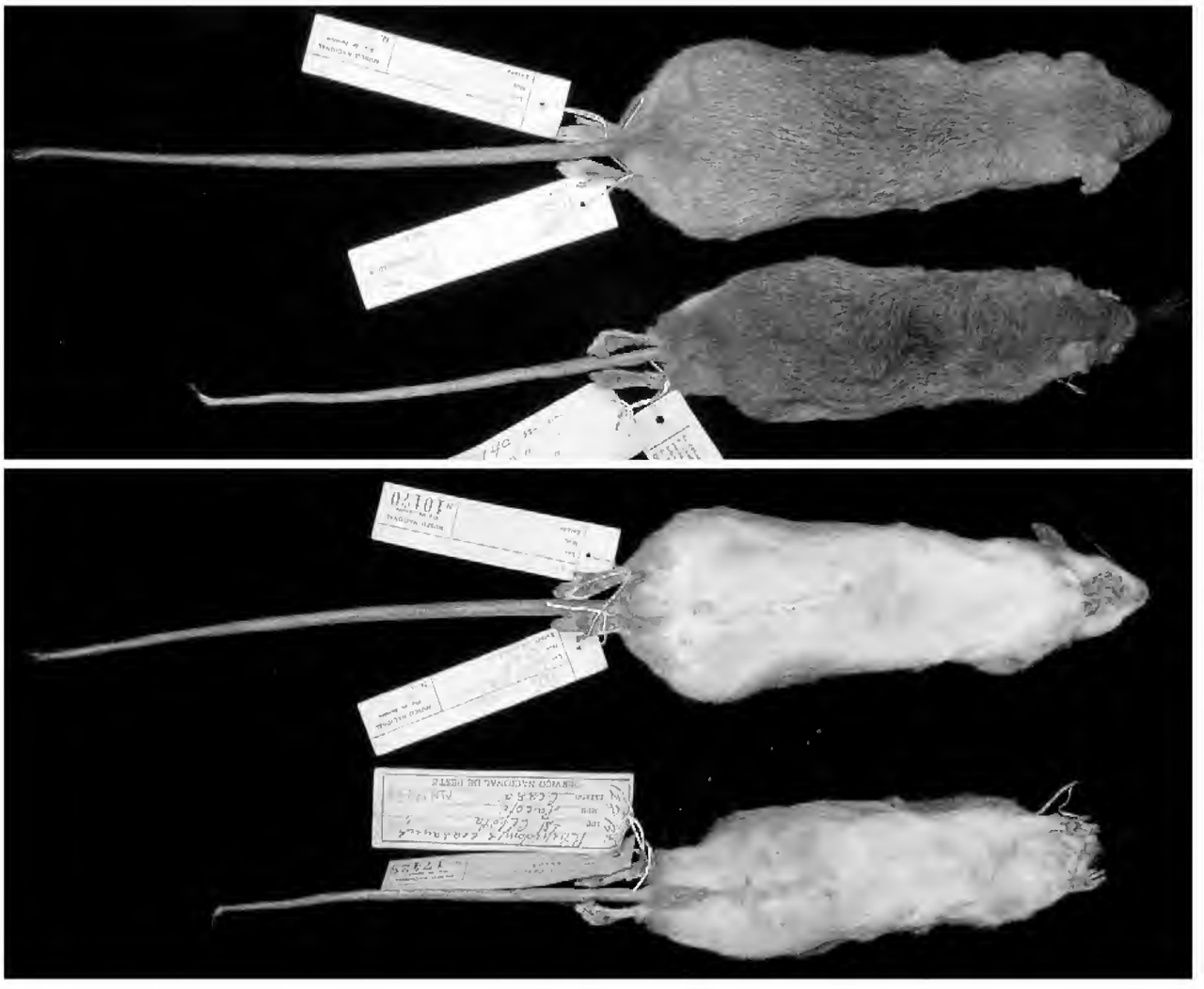

Fig.4- Dorsal and ventral views of skins of *Rhipidomys cariri* sp.nov. Upper specimen in each pair: *R. cariri cariri* ssp.nov. holotype, adult ♂ , MN 10170; lower specimen: *R. cariri baturiteensis* ssp.nov. holotype, adult ♀ , MN 17428.

plate broad, generally with a shallow zygomatic notch visible in dorsal view. The braincase is large and rather angular rather than rounded, with a broad occiput relative to the greatest breadth across the squamosals; the lateral process of the parietal (the part of the parietal extending below the parietal ridge) is rectangular; the hamular process of the squamosal is long and almost horizontal. The roughly elliptical incisive foramina terminate between the anterior roots of the first molars while the mesopterygoid fossa penetrates between the posterior roots of the third molars, making the palatal bridge shorter than the molar row. Sphenopalatine vacuities are absent. The bullae are relatively large for the genus and slightly inflated. The carotid circulation pattern is derived (VOSS, 1988: "pattern 3"), with a small stapedial foramen, no translucent internal groove across the squamosal and alisphenoid, and no sphenofrontal foramen.

The upper incisors are robust and more opisthodont than in most *Rhipidomys*. The molars are moderately large for *Rhipidomys* from eastern Brazil (Tab.1, MRC). The first upper and lower molars (M1, m1) have a well-defined antero-median flexus/flexid; oblique paralophules are present in M1-3; M3 is not greatly reduced in size and occlusal structure.

Comparisons – External and cranial characters

serve to distinguish *R. cariri* from the nearest *Rhipidomys* to the east and west, *R. mastacalis* and *R. macrurus* respectively. The body size of *R. cariri* is larger for equivalently aged specimens, the hind foot is longer and broader, and the mystacial vibrissae are much longer and coarser. The dorsal colour is greyer with a stronger agouti effect (*R. mastacalis* from Pernambuco tends to be a more intense red, and *R. macrurus* from the Serra de Ibiapaba in western Ceará is browner), and the ventral pelage tends to be a little woolly rather than sleek. *Rhipidomys cariri* skulls are generally larger and more robust than all but the oldest *R. macrurus* and *R. mastacalis* (Figs.5-7); in these, however, the zygomatic arches tend to bow outwards so that the greatest breadth lies across the jugals, whereas in *R. cariri* the arches tend to converge forwards from a point on the zygomatic process of the squamosal close to the root. In *R. cariri* the third upper molar is less reduced.

In pelage colour and texture *R. cariri* somewhat resembles *R. leucodactylus*, a species found throughout much of the Amazon basin; *R. leucodactylus* is larger, however, with a hind foot length of at least 32mm, and has considerably larger teeth, its molar row length being in excess of 6mm.

Distribution – Known from the vicinity of Crato, in the large mesic enclave of the Cariri, southern Ceará State, NE Brazil. The specimens were misidentified by SNP personnel in the Crato district as *Holochilus sciureus* and were tallied as such by Freitas in his table of animals caught between 1952 and 1955 (FREITAS, 1957, Tab.1); the Museu Nacional collections demonstrate that no *Holochilus* specimens were in fact taken at Crato. Specimens from the Baturité massif in northern Ceará are described below as a distinct subspecies of *R. cariri*.

Ecological notes – Specimen labels indicate that nine of the Crato specimens were taken in fields, five in palms and two in trees (presumably broadleaf). The SNP individual record cards list the crops grown on the farms where they were caught (rice, beans, maize, manioc, sugarcane) but do not specify whether or not the specimen was found in any one of them. The cards also show that soils varied from sandy and stony to 'black earth'; at some sites rivers were permanent, at others intermittent.

Local names – Names given by collectors on specimen labels are *rato guagipó* and *rato palmeira* (palm rat).

Etymology – The specific epithet refers to the Cariris, a group of indigenous peoples in north-eastern Brazil, whose name is attached to the mesic enclave in southern Ceará where the nominotypical subspecies was collected. Grammatically, *cariri* is treated as a noun in apposition to the genus name, in the nominative case. It is pronounced with the stress on the last syllable (ka-ree-REE).

Material examined – BRAZIL - CEARÁ: Crato (07°14'S 39°23'W, includes Sítio Arisco, Sítio Baixa do Maracujá, Sítio Belo Horizonte, Sítio Caiana, Sítio Grangeiro, Sítio Passagem 1ª, Sítio Passagem 2ª, Sítio Recreio 1º): MN 1530, 10170 (holotype), 17298, 17299, 17347, 17348, 17349, 17351, 17353, 17378, 17379, 17380, 17417 to 17423, 30012, 30013; KU 27308; USNM 304587, 304588. Total: 24.

Rhipidomys cariri baturiteensis ssp.nov.

Rhipidomys cearanus – FREITAS, 1957 (part; not *Rhipidomys cearanus* Thomas, 1910).

Holotype – BRAZIL - CEARÁ: Pacoti (04°13'S 38°56'W), Sítio Cebola; MN 17428; adult ♀, collected by Mario Pereira for the Serviço Nacional de Peste on 25 July 1953, in a coffee plantation; field number Bt128; pregnant with four embryos. Condition: round study skin in good condition; cleaned skull and mandible (rami separated at symphysis), slightly damaged (tip of left pterygoid process broken; left zygomatic arch split; left bulla glued out of position).

Diagnosis – The tail has relatively short hairs on its distal half and the tail pencil is short; the skull has a short and relatively narrow palatal bridge; and the molars are large and broad.

Description – The dorsal pelage of the holotype of *Rhipidomys cariri baturiteensis* is rather redder-brown than in the nominotypical subspecies *R. c. cariri*, but other specimens are more yellowish-grey-brown, all conspicuously agouti. The ventral pelage is white or pale cream to the hair bases; grey bases only occur ventrally at the extreme sides of the abdomen and in the pectoral spot. The tail hairs are shorter than in *R. c. cariri*, especially along the distal half of the tail, and the pencil extends only a few millimetres beyond the tail tip (Fig.4b, d).

The rostrum is longer compared with skull length, and the incisive foramina are notably more slender than in *R. c. cariri* (Tab.1, ratios RL/ONL and IFB/IFL). The zygomatic plate is broad. The palatal bridge is shorter than the molar row but narrower than in *R. c. cariri* (Tab.1, ratio PB1/PBL); the mesopterygoid

Fig.5- Dorsal view of skulls of *Rhipidomys* from north-eastern Brazil. From left to right: *R. cariri cariri* ssp.nov. holotype, adult ♂, MN 10170; *R. cariri baturiteensis* ssp.nov. holotype, adult ♀, MN 17428; *R. macrurus*, adult ♀, MN 12579; *R. mastacalis*, adult ♂, MN 17367. Scale bar = 10mm.

fossa is also narrower. The molars are larger than in *R. c. cariri* on average (Tab.1, MRC), although not in the holotype, and M1 is significantly broader (Tab.1, M1B). In the upper molars, particularly M2, the hypoflexus often penetrates into the median mure, almost meeting the inner tip of the mesoflexus.

Distribution – Known only from the vicinity of Pacoti, in the isolated mesic enclave of the Serra de Baturité massif, northern Ceará State, NE Brazil, some 330km north of Crato, the type locality of *Rhipidomys cariri*.

Ecological notes – Specimen labels indicate that 12 specimens were taken in sugar cane fields, two in coffee plantations, two in second-growth forest and one in a quarry. Two females (the holotype and MN 17445) each had four embryos in late July 1953. Six males captured between mid-August and early September 1954 had enlarged testes and one did not.

Etymology and local name – The subspecies is named after the Serra de Baturité, an isolated massif in northern Ceará where it was collected, with the suffix *-ensis* denoting provenance; the two '*e*'s in the epithet *baturiteensis* should therefore be pronounced separately. Local name given by collectors on the specimen labels: *rato de cana* (sugar cane rat).

Material examined – BRAZIL - CEARÁ: Pacoti (04°13'S 38°56'W, includes Sítio Cebola, Sítio Ladeira, Sítio Ouro, Sítio Pirajá, Sítio Santa Rosa): MN 17373, 17428 (holotype), 17431, 17440 to 17446, 30005 to 30011. Total: 17.

DISCUSSION

Rhipidomys cariri sp.nov. is known only from two isolated areas of mesophytic forest, or *brejos*, within the xerophytic *caatinga* domain of north-eastern Brazil. Although at present there are no mesic corridors linking these habitats with either the Atlantic forest to the east or the Amazon forest to the west, it has long been hypothesised that such connections existed in the past, based on the presence in the *brejos* of many plant species also found in those larger forest systems (*e.g.*, RIZZINI, 1963; ANDRADE-LIMA, 1982). Pollen from swamp or lake-bed cores taken at localities currently occupied by Amazon forest (Carajás, Pará) and cerrado (Salitre de Minas, Minas Gerais) shows that the predominant vegetation types fluctuated several times during the late Pleistocene and Holocene: mesophytic floras alternated with xerophytic ones that expanded in approximate synchrony with the temperature and rainfall minima of the Northern Hemisphere Late Glacial (ABSY *et al.*, 1991; LEDRU, 1993). Even in the driest periods, however, mesic areas dependent on orographic precipitation are unlikely to have been severely affected (CLAPPERTON, 1993); the Baturité *brejo* comes into this category. Similarly, since the humidity of the Cariri *brejo* is due to the permanent springs that emerge along the northern and eastern face of the large Araripe mesa, fed from permeable rocks overlying gently sloping impermeable strata within

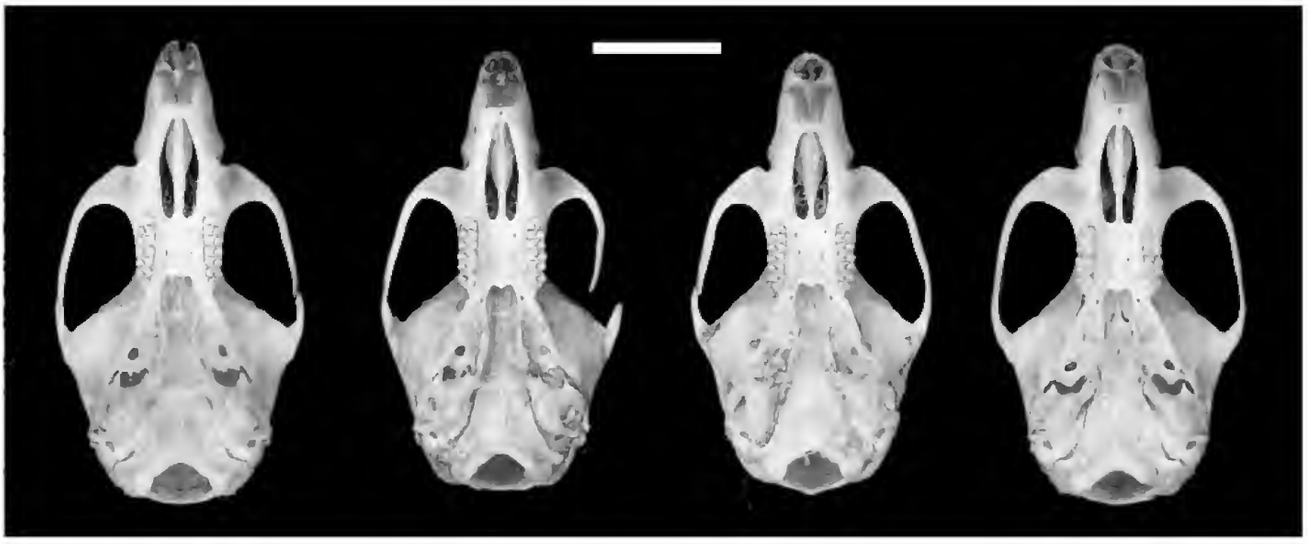

Fig.6- Ventral view of the same skulls illustrated in figure 2. Scale bar = 10mm.

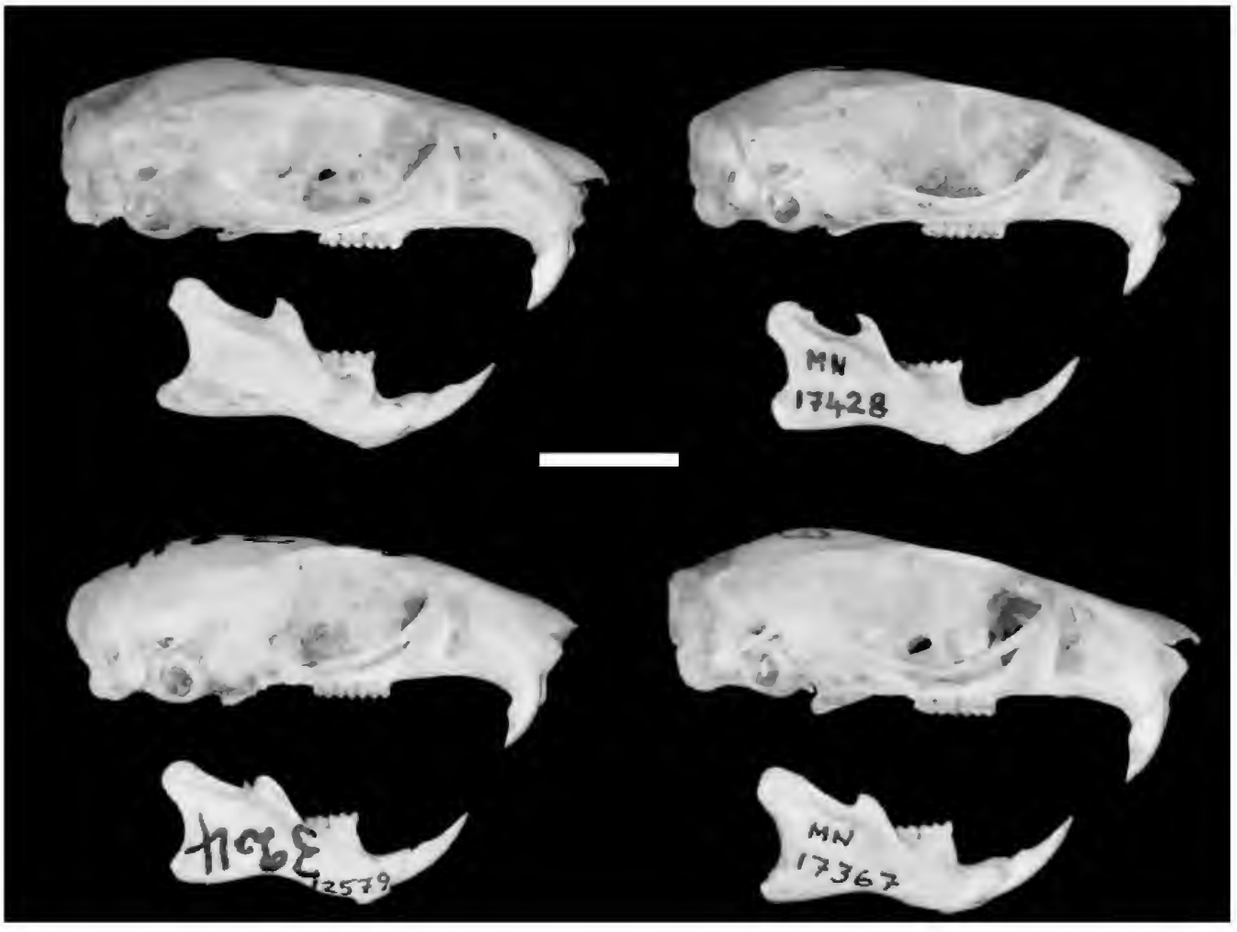

Fig.7- Lateral view of the skulls illustrated in figure 2. Top left: *R. cariri cariri* ssp.nov.; top right: *R. c. baturiteensis* ssp.nov.; bottom left: *R. macrurus*; bottom right: *R. mastacalis*. Scale bar = 10mm.

the mesa (VANZOLINI, 1981; BORGES-NOJOSA & CARAMASCHI, 2003), here too mesic conditions could have continued to provide suitable habitat for *R. cariri* while the remainder of the region experienced even greater aridity than today.

During the wetter phases, forest cover is likely to have been more continuous, linking the present-day *brejos* with both the Amazon and Atlantic forests (VIVO, 1997). At a gallery forest site in the Icatu valley within the *caatinga* in north-western Bahia, pollen evidence points to a humid forest populated with both Amazonian and Atlantic tree species in the period 10 990-10 540 yrs BP, when temperatures were some 5°C cooler than at present (OLIVEIRA, BARRETO & SUGUIO, 1999). Such gallery forests are likely to have persisted as continuous links between the Amazon and Atlantic forests across central Brazil even outside the periods of peak humidity (MEAVE *et al.*, 1991; OLIVEIRA FILHO & RATTER, 1995).

Given the relative recency of the probable connection between the current *brejos* and the more extensive forests to the west and east, it might perhaps be expected that most forest-dwelling small mammal species would be found in all three regions. Even in apparently continuous habitats such as the Amazon and Atlantic forests, however, individual species are not necessarily widespread and phylogeographic patterns within genera vary considerably (PATTON *et al.*, 1997; PATTON, SILVA & MALCOLM, 2000). Divergence estimates based on the mitochondrial cytochrome-*b* gene revealed a complex pattern of relationships among several *Rhipidomys* species in the Atlantic and the Amazonian forests and the region between them, with most genetic divergences dating back to before the Pleistocene (COSTA, 2003). *Rhipidomys cariri* was not represented in the study, unfortunately. These findings preclude a general explanation of diversity based on the Pleistocene forest refuge theory (HAFFER, 1969; VANZOLINI & WILLIAMS, 1970). Although a late Pleistocene/Holocene origin for *R. cariri*, subsequent to the latest isolation of the *brejos* in which it occurs, cannot yet be ruled out, such molecular work does suggest that the species may be much older and survives there as a relict for reasons currently unknown.

Rhipidomys cariri is not the only instance of vertebrate endemism in the *brejos*: a growing number of species restricted to these areas has been described in recent years. They include the forest frogs *Adelophryne baturitensis* and *A. maranguapensis* from the Baturité and Maranguape ranges, respectively (HOOGMOED, BORGES & CASCON, 1994); the lizards *Mabuya arajara*, from the Cariri, and *Colobosauroides cearensis* and *Leposoma baturitensis*, both found in several *brejos* in Ceará (REBOUÇAS-SPIEKER, 1980; CUNHA, LIMA-VERDE & LIMA, 1991; and RODRIGUES & BORGES, 1997, respectively); and the bird *Antilophia bokermanni*, the Araripe manakin, endemic to the Cariri (COELHO & SILVA, 1998). Apart from *Rhipidomys cariri*, however, no mammal truly endemic to the *brejos* has yet been formally described, although several taxa commonly regarded as local populations of more widespread species may in fact prove to be distinct (OLIVEIRA, GONÇALVES & BONVICINO, 2003).

In the past it was common to refer any specimen of *Rhipidomys* from north-eastern Brazil indiscriminately to *R. cearanus* or *R. mastacalis*, on the assumption that there was a single, widespread species present throughout the region. With the identification of *R. cariri* from the mesic forests isolated within the *caatinga*, and confirmation that *R. macrurus* in western Ceará is distinct from *R. mastacalis* in eastern Pernambuco, three species are now known from the area north of the Rio São Francisco alone. Additional work is still needed in fields such as karyology and DNA research, however, in order to characterise them more fully and to test phylogeographic hypotheses of their relationships and origins. Larger series of specimens suitable for both morphological and molecular work are also needed from forests further south, within and adjacent to the *caatingas* of Bahia, to help elucidate the relationships of these three species with the *Rhipidomys* populations found there.

To summarise, *Rhipidomys* species in north-eastern Brazil are restricted to the mesic *brejos* and, despite the fluctuations in the general climate and vegetation of the region during the Pleistocene and Holocene, these areas are likely to have provided suitable habitat at all times. The Amazon forest, the *brejos* and the Atlantic forest were probably last connected fairly recently, in the early Holocene, but even today spatial continuity of forest does not preclude endemism or restricted ranges, so it is possible that *R. cariri* was confined to this region even when mesophytic forests were more continuous. Indeed, phylogeographic patterns within *Rhipidomys* suggest splitting events that predate the Pleistocene. Further work is therefore needed to show when and how *R. cariri* originated and to clarify its relationships with other *Rhipidomys* taxa.

ACKNOWLEDGEMENTS

To J.A.Oliveira (Museu Nacional - Rio de Janeiro – MN) for inviting me to submit this contribution to the volume in honour of Prof. João Moojen, and for his willingness to photograph the *Rhipidomys* specimens for me; together with S.M.Franco (MN), he provided access to the collections of the Museu Nacional and generously facilitated my work there. R.M.Timm (University of Kansas Natural History Museum), M.D.Carleton and A.L.Gardner (National Museum of Natural History) kindly enabled me to examine other specimens. The manuscript benefited greatly from constructive comments by B.D.Patterson (Field Museum) and R.S.Voss (American Museum of Natural History). I am grateful to R.Cerqueira (Universidade Federal do Rio de Janeiro) for first drawing my attention to the question of *Rhipidomys* in NE Brazil. Part of this research was carried out while the author held a doctoral award from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Brasília.

LITERATURE CITED

ABSY, M.L.; CLEEF, A.; FOURNIER, M.; MARTIN, L.; SERVANT, M.; SIFEDDINE, A.; FERREIRA DA SILVA, M.; SOUBIES, F.; SUGUIO, K.; TURCQ, B. & VAN DER HAMMEN, T., 1991. Mise en évidence de quatre phases d'ouverture de la forêt dense dans le sud-est de l'Amazonie au cours des 60 000 dernières années. Première comparaison avec d'autres régions tropicales. **Comptes Rendus de l'Académie des Sciences**, Paris, Série II, **312**:673-678.

ANDRADE-LIMA, D., 1982. Present-day forest refuges in northeastern Brazil. In: PRANCE, G.T. (Ed.) **Biological Diversification in the Tropics**. New York: Columbia University Press. p.245-251.

BORGES-NOJOSA, D.M. & CARAMASCHI, U., 2003. Composição e análise comparativa da diversidade e das afinidades biogeográficas dos lagartos e anfisbenídeos (Squamata) dos brejos nordestinos. In: LEAL, I.R.; TABARELLI, M. & SILVA, J.M.C. (Eds) **Ecologia e Conservação da Caatinga**. Recife: Ed. Universitária da UFPE. p.463-512.

CERQUEIRA, R.; VIEIRA, M.V. & SALLES, L.O., 1989. Habitat and reproduction of *Rhipidomys cearanus* at São Benedito, Ceará (Rodentia, Cricetidae). **Ciência e Cultura**, São Paulo, **41**:1009-1013.

CLAPPERTON, C.M., 1993. **Quaternary Geology and Geomorphology of South America**. Amsterdam: Elsevier. 779p., il.

COELHO, G. & SILVA, W., 1998. A new species of *Antilophia* (Passeriformes: Pipridae) from Chapada do Araripe, Ceará, Brazil. **Ararajuba**, Londrina, **6**:81-84.

COSTA, L.P., 2003. The historical bridge between the Amazon and the Atlantic Forest of Brazil: a study of molecular phylogeography with small mammals. **Journal of Biogeography**, Oxford, **30**:71-86.

CUNHA, O.R.; LIMA-VERDE, J.S. & LIMA A.C.M., 1991. Novo gênero e espécie de lagarto (*Colobosauroides cearensis*) no Estado do Ceará (Lacertilia: Teiidae). **Boletim do Museu Paraense Emilio Goeldi**, Belém, **7**:163-176.

FREITAS, C.A., 1957. Notícia sôbre a peste no Nordeste. **Revista Brasileira de Malariologia e Doenças Tropicais**, Rio de Janeiro, **9**:123-133.

HAFFER, J., 1969. Speciation in Amazonian forest birds. **Science**, New York, **165**:131-137.

HOOGMOED, M.S.; BORGES, D.M. & CASCON, P., 1994. Three new species of the genus *Adelophryne* (Amphibia: Anura: Leptodactylidae) from northeastern Brazil, with remarks on the other species of the genus. **Zoologische Mededelingen**, Leiden, **68**:271-300.

LEDRU, M.-P., 1993. Late Quaternary environmental and climatic changes in Central Brazil. **Quaternary Research**, New York, **39**:90-98.

MARES, M.A.; WILLIG, M.R.; STREILEIN, K.E. & LACHER, T.E., 1981. The mammals of northeastern Brazil, a preliminary assessment. **Annals of Carnegie Museum**, Pittsburgh, **50**:81-137.

MEAVE, J.; KELLMAN, M.; MACDOUGALL, A. & ROSALES, J., 1991. Riparian habitats as tropical refugia. **Global Ecology and Biogeography Letters**, Oxford, **1**:69-76.

MOOJEN, J., 1943. Alguns mamíferos colecionados no nordeste do Brasil com a descrição de duas espécies novas e notas de campo. **Boletim do Museu Nacional, Nova Série, Zoologia**, Rio de Janeiro (5):1-14, lâm.1-3.

MOOJEN, J., 1952. **Os Roedores do Brasil**. Rio de Janeiro: Instituto Nacional do Livro. 214p., il.

NEFF, N.A. & MARCUS, L.F., 1980. **A Survey of Multivariate Methods for Systematics**, New York, privately published. x, 243p.

OLIVEIRA FILHO, A.T. & RATTER, J.A., 1995. A study of the origin of central Brazilian forests by the analysis of plant species distribution patterns. **Edinburgh Journal of Botany**, Edinburgh, **52**:195-203.

OLIVEIRA, J.A. & FRANCO, S.M., 2005. A coleção de mamíferos do Serviço Nacional de Peste. **Arquivos do Museu Nacional**, Rio de Janeiro, **63**:13-20.

OLIVEIRA, J.A.; GONÇALVES, P.R. & BONVICINO, C.R., 2003. Mamíferos da Caatinga. In: LEAL, I.R.; TABARELLI, M. & SILVA, J.M.C. (Eds.) **Ecologia e Conservação da Caatinga**. Recife: Editora Universitária da UFPE. p.275-333.

OLIVEIRA, P.E., BARRETO, A.M.F. & SUGUIO, K., 1999. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: the fossil dunes of the middle São Francisco River. **Palaeogeography Palaeoclimatology, Palaeoecology**, Amsterdam, **152**:319–337.

PATTON, J.L.; SILVA, M.N.F.; LARA, M.C. & MUSTRANGI, M.A., 1997. Diversity, differentiation, and the historical biogeography of nonvolant small mammals of the Neotropical forests. In: LAURANCE, W.F. & BIERREGAARD, R.O., JR. (Eds.) **Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities**. Chicago: University of Chicago Press. p.455-465.

PATTON, J.L.; SILVA, M.N.F. & MALCOLM, J.R., 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. **Bulletin of the American Museum of Natural History**, New York, **244**:1-306.

REBOUÇAS-SPIEKER, R., 1980. Sobre uma nova espécie de *Mabuya* do Nordeste do Brasil. **Papéis Avulsos de Zoologia**, São Paulo, **39**:121-123.

REYMENT, R.A.; BLACKITH, R.E. & CAMPBELL, N.A., 1984. **Multivariate Morphometrics**, 2nd ed. London: Academic Press. 233p., il.

RIZZINI, C.T., 1963. Nota prévia sobre a divisão fitogeográfica do Brasil. **Revista Brasileira de Geografia**, Rio de Janeiro, **25**:1-64.

RODRIGUES, M.T. & BORGES, D.M., 1997. A new species of *Leposoma* (Squamata: Gymnophthalmidae) from a relictual forest in semiarid Northeastern Brazil. **Herpetologica**, Chicago, **53**:1-6.

TRIBE, C.J., 1996. **The Neotropical rodent genus *Rhipidomys* (Cricetidae, Sigmodontinae) – a taxonomic revision**. London. 316p., il. Thesis submitted for the degree of Doctor of Philosophy, University College London.

VANZOLINI, P.E., 1981. A quasi-historical approach to the natural history of the differentiation of reptiles in tropical geographic isolates. **Papéis Avulsos de Zoologia**, São Paulo, **34**:189-204.

VANZOLINI, P.E. & WILLIAMS, E.E., 1970. South American anoles, the geographic differentiation and evolution of the *Anolis chrysolepis* species group (Sauria, Iguanidae). **Arquivos de Zoologia**, São Paulo, **19**:291-298.

VIVO, M., 1997. Mammalian evidence of historical ecological change in the Caatinga semiarid vegetation of northeastern Brazil. **Journal of Comparative Biology**, Ribeirão Preto, **2**:65-73.

VOSS, R.S., 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. **Bulletin of the American Museum of Natural History**, New York, **188**:259-493.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.147-159, jan./mar.2005
ISSN 0365-4508

NEW INSIGHTS ON THE PHYLOGENETIC RELATIONSHIPS OF THE TWO GIANT EXTINCT NEW WORLD MONKEYS (PRIMATES, PLATYRRHINI) [1]

(With 1 figure)

PATRÍCIA GONÇALVES GUEDES [2, 3]
LEANDRO DE OLIVEIRA SALLES [2]

ABSTRACT: The phylogenetic position of the genera *Caipora* and *Protopithecus* within the Platyrrhini was investigated within a cladistic framework based on morphological characters with emphasis on patterns of tooth variation. A data matrix of 102 characters and 23 terminal taxa was subjected to analysis using a branch and bound option of the PAUP 4.0 Software. As a result, 40 equally most parsimonious trees were obtained. A strict consensus of these trees yielded a topology with 15 components with five unresolved trichotomies. The phylogenetic results show that the giant monkeys *Caipora* and *Protopithecus* should be recognized as typical atelins, belonging to the tribe Atelini, being both closely related to *Ateles*. The cranio-dental evidence supporting the Atelini clade are: 1) a rounded basal portion of the incisors; 2) I_{1-2} similar in size (height); 3) hypocone smaller than protocone in M^2 and similar in size in M^1; 4) metacone smaller than paracone in M^{1-2}; 5) metacrista developed in M^{1-2}; and 6) postglenoid foramen reduced. Based on this phylogenetic data, the taxonomical interpretation that indicates *Protopithecus* as a member of Alouattini is refuted.

Key words: *Protopithecus*, *Caipora*, Platyrrhini, primates, phylogenetics, tooth morphology.

RESUMO: Novos dados sobre as relações filogenéticas de dois macacos gigantes extintos do Novo Mundo (Primates, Platyrrhini).

A posição filogenética de *Caipora* e *Protopithecus* dentro de Platyrrhini foi investigada a partir de uma abordagem cladística baseada em caracteres morfológicos, com ênfase nos padrões de variação dentária. Uma matriz de dados com 102 caracteres e 23 táxons terminais foi submetida a uma análise de parcimônia usando a opção *branch and bound* do Programa PAUP 4.0. Como resultado desta análise, foram obtidas 40 árvores igualmente parcimoniosas. O consenso estrito das árvores resultou numa topologia contendo 15 componentes, sendo cinco tricotomias não resolvidas. De acordo com os resultados *Caipora* e *Protopithecus* são reconhecidos como atelinos, pertencentes a Tribo Atelini, ambos filogeneticamente associados ao gênero *Ateles*. As evidências crânio-dentárias que suportam o clado Atelini são as seguintes: 1) porção basal dos incisivos abaulada; 2) I_{1-2} similares em tamanho (altura); 3) hipocone menor que o protocone em M^2 e com tamanho similar em M^1; 4) metacone menor que o paracone em M^{1-2}; 5) metacrista desenvolvida em M^{1-2}; e 6) forame pós-glenóide reduzido. Baseado nestas informações, a interpretação taxonômica de *Protopithecus* como membro de Alouatini é refutada.

Palavras-chave: *Protopithecus*, *Caipora*, Platyrrhini, primatas, sistemática filogenética, morfologia dentária.

INTRODUCTION

Primates are primarily arboreal placental mammals presently distributed along tropical forests of Africa, Asia, Central and South America. During the Tertiary epochs, however, their geographical distribution extended through major parts of the European and the North American continents (SZALAY & DELSON, 1979). Among living primates, Eusimiiformes (*sensu* GROVES, 2001; "Anthropoids" in FLEAGLE, 1988; KAY, ROSS & WILLIAMS, 1997; and ROSS, 2000) comprise the most specious and studied primate group that encompasses Old World monkeys and apes (Catarrhini) and New World monkeys (Platyrrhini).

Platyrrhine monkeys represent at least 30% of the living primate species (MITTERMEIER *et al.*, 1988). Living platyrrhines are found from southern Mexico to northern Argentina, but paleontological records have been encountered in Patagonia and as far north as to the Greater

[1] Submitted on June 18, 2004. Accepted on February 16, 2005.
[2] Museu Nacional/UFRJ, Departamento de Vertebrados. Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil. Brasil. E-mail: losalles@mn.ufrj.br.
[3] Fellow of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Antilles (HOROVITZ & MACPHEE, 1999). These mammals inhabit remarkably different ecological niches, and show great variability in size, diet, and ecological adaptations. They range from the 100g *Callithrix* (*Cebuella*) *pygmaea* (Spix, 1823) to the 14kg *Brachyteles arachnoides* (E.Geoffroy, 1806).

A series of morphological attributes, shared by all species of the group, sustains an uncontroversial monophyletic status for the group (*e.g.*, KAY, ROSS & WILLIAMS, 1997). Conversely, historical relationships within platyrrhines remain the focus of heated debates. Part of the problem lies in the fossil record that, until about fifty years ago, was limited to a few fossil fragments, many assigned to the genus *Homunculus* Ameghino, 1891. At the present time, a few hundred specimens are catalogued and classified into approximately twenty genera (MCKENNA & BELL, 1997; TEJEDOR, 1998). Most of these fragments, however, are represented by isolated maxillary and mandibular fragments. A formal cladistic analysis including most of these fossil taxa was performed by HOROVITZ (1999).

There are, however, two remarkably complete and well preserved platyrrhine skeletons that have been recently discovered. They are the largest known specimens of New World monkeys: *Caipora bambuiorum* Cartelle & Hartwig, 1996 and *Protopithecus brasiliensis* Lund, 1838. These atelid monkeys were found next to one another in a cave in the Northeastern Brazil, in the State of Bahia (HARTWIG, 1995; CARTELLE, 1996; CARTELLE & HARTWIG, 1996; HARTWIG & CARTELLE 1996).

Caipora is hypothesized to have weighed approximately 20kg (CARTELLE, 1996; CARTELLE & HARTWIG, 1996). According to the authors, this species resembles atelin monkeys in both cranial and postcranial features, but it is distinctive in having a more spherical neurocranium with a much larger braincase and skeleton. They also indicated that the *Caipora* skeleton and teeth are more similar to *Ateles* E. Geoffroy, 1806 than to any other living platyrrhine genera (CARTELLE & HARTWIG, 1996).

Protopithecus is also remarkable for its large size, which is calculated to be a gigantic 25kg (CARTELLE, 1996; HARTWIG & CARTELLE, 1996). *Protopithecus* is also unquestionably supported as an atelid, but within atelids it exhibits a puzzling mosaic of characters with a cranial morphology that resembles alouattins and a postcranial skeleton similar to atelins (HARTWIG, 1995; CARTELLE & HARTWIG, 1996; HARTWIG & CARTELLE, 1996). This evolutionary puzzle was left unresolved by Cartelle and Hartwig, but they did suggest the possibility that typical atelin postcranial adaptations to suspensory locomotion may be a primitive condition for the ateline radiation (CARTELLE & HARTWIG, 1996; HARTWIG & CARTELLE, 1996). By suggesting that, the authors implied that the cranial similarities that *Protopithecus* shares with howler monkeys (*i.e.*, Alouattini) are to be interpreted as evidence favoring a close phylogenetic relationship of this giant monkey with the alouatines.

Here, we present the first formal phylogenetic study relative to the emergence of these two extinct species within platyrrhines. We hope to shed some light on the puzzle concerning the cladistic position of these giant monkeys within platyrrhines. In this first evaluation, we have focused on patterns of variation observed in the masticatory apparatus, while supplemental morphological information was gathered from HOROVITZ (1999). In future studies we expect to present more comprehensive assessments to platyrrhine phylogeny and evolution.

MATERIAL AND METHODS

Following MCKENNA & BELL (1997), the 20 genera are representing the terminal taxa of the present phylogenetic study. These include the two giant fossil species and two other extinct taxa (†), plus all currently recognized extant playtyrrhini genera: *Alouatta* Lacépède, 1799; *Aotus* Illiger, 1811; *Ateles* E. Geoffroy, 1806; *Brachyteles* Spix, 1823; *Cacajao* Lesson, 1840; *Caipora*† Cartelle & Hartwig, 1996; *Callicebus* Thomas, 1903; *Callimico* Miranda-Ribeiro, 1911; *Callithrix* Erxleben, 1777; *Carlocebus*† Fleagle, 1990; *Cebuella* Gray, 1866; *Cebus* Erxleben, 1777; *Chiropotes* Lesson, 1840; *Lagothrix* E.Geoffroy, 1812; *Leontopithecus* Lesson, 1840; *Pithecia* Desmarest, 1804; *Protopithecus*† Lund, 1838; *Saguinus* Hoffmannsegg, 1807; *Saimiri* Voigt, 1831; and *Stirtonia*† Hershkovitz, 1970.

The genus *Callithrix* presents interesting taxonomical questions. GROVES (2001), for example, divides *Callithrix* into the following subgenera: *Cebuella* Gray, 1866; *Mico* Lesson, 1840 (= *argentata* group of HERSHKOVITZ, 1977

and VIVO, 1991); and *Callithrix* Erxleben, 1977 (= *jachus* group of HERSHKOVITZ, 1977 and VIVO, 1991). Here we adopt MCKENNA and BELL´s classification in order to evaluate the controversial taxonomic status of *Cebuella*, and two *Callithrix* species were included as terminal taxa, representing the subgenera *Mico* and *Callithrix*. Unfortunately, however, no specimens of *Callithrix humilis*, only recently recognized as the new genus *Callibella* (VAN ROOSMALEN & VAN ROOSMALEN, 2003), were included in the material examined.

Carlocebus and *Stirtonia* were included in the analysis based on the fact that they are among the few available platyrrhine fossils represented by relatively complete upper and lower jaws with teeth in good conditions (see APPENDIX I for a detailed list of the material examined). The inclusion of these two fossil taxa has implied a minimal number of missing data cases to the analysis regarding the evaluation of the tooth morphology. Dental terminology is based on HERSHKOVITZ (1977).

The platyrrhines used as reference material in this study are from the following collections: Museu Nacional, Rio de Janeiro (MN); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Paraense Emilio Goeldi (MPEG); and Instituto de Geociências da Universidade Federal de Minas Gerais (IGC-UFMG). Illustrations of *Carlocebus* and *Stirtonia* published by SZALAY & DELSON (1979); HERSHKOVITZ (1970); SETOGUCHI, WATANABE & MOURI (1983); KAY *et al.* (1987); KAY, MADDEN & GUERRERO-DÍAZ (1989) and FLEAGLE (1990) were consulted.

We employed standard cladistic procedures (FARRIS, 1983) in order to carry out the phylogenetic analysis. The *branch and bound* algorithm was applied using the PAUP* 4.0 b10 program (SWOFFORD, 2002), and Bremer indices were calculated to evaluate branch stability.

The characters selected for this study were chosen in order to represent in detail the full range of patterns of variation in platyrrhine tooth morphology. We employ this strategy in the interest of developing a starting point for a better assessment of the taxon's paleodiversity. A total of 102 unordered characters were the basis of the study, distributed across 23 taxa, with two non-platyrrhines antropoid outgroups added: *Aegyptopithecus* Simons, 1965 which is a basal anthropoid representative, and one cercopithecoid catarrhine, *Pygathrix* E. Geoffroy, 1812.

RESULTS

Tooth morphology: patterns of variation

Even though platyrrhines are known to have rich diversity in their tooth morphology (HERSHKOVITZ, 1977; ROSENBERGER, 1981), most have retained the primitive dental formula of anthropoid primates – upper jaw with I^1, I^2, C, P^2, P^3, P^4, M^1, M^2 and M^3, and lower jaw with I_1, I_2, C, P_2, P_3, P_4, M_1, M_2 and M_3. Third molars are absent in callitrichines and *Xenothrix* Williams and Koopman, 1952 which is not included here. They generally have also maintained a quadritubercular upper molar crown pattern, except in the tritubercular callitrichines.

Since the 80's, a number of authors have been using dental features in their phylogenetic analyses of New World monkeys, such as ROSENBERGER (1977, 1981), KAY (1990); MACPHEE *et al.* (1995); KAY & MELDRUM (1997); HOROVITZ & MACPHEE (1999); HOROVITZ (1999); and GUEDES (2000). In the following we provide a general summary of the information on tooth morphology based on our direct observation of the specimens. Nearly half of the characters here hypothesized represent original data and/or reformulations of previously proposed characters. The other half is nearly identical to the information presented by HOROVITZ (1999). The details of such character formulations are a subject of a future, broader study on the evolution of the New World monkeys. A synthetic list of the characters formulated for this study is presented below:

1) Upper incisors, relative position: 0 – incisors placed in a wide U-shape liked dental arch; 1 – incisors placed in a narrow V-shape liked dental arch.
2) I^1, development of the metastyle: 0 – absent; 1 – present (Note: The metastyle may be reduced in some species of *Callithrix* group *jacchus*).
3) I^2, development of the parastyle and metastyle: 0 – absent; 1 – parastyle and metastyle present (Note: Metastyle is rounded in all platyrrhine genera except *Callithrix* and *Cebuella*, where it is cuspiform).
4) Upper incisors, anteroposterior inclination in relation to the sagittal plane of the palate (labial face): 0 – incisors have a perpendicular position in relation to the sagittal plane of the palate; 1 – incisors have a anterior inclination in relation to the sagittal plane of the palate; 2 – incisors

have a drastic inclination, almost parallel to the sagittal plane of the palate.

5) Upper incisors, development of the basal portion (buccal): 0 – weakly developed; 1 – developed, curve (rounded). (Note: A more basal portion analogous to the protocone, considered by HERSHKOVITZ (1977) as the protocone, may also be present independently of the entocingulum development).

6) Upper incisors, spatial orientation of the crowns: 0 – crowns are oriented to the posterior portion of the palate, almost in lateral alignment; 1 – I^1 crown is oriented to the posterior portion of the palate and I^2 crown is somewhat rotated internally; 2 – crowns are rotated to the internal region, anteriorly (I^1 slightly rotated and I^2 more accentuated way). (Note: Although incisors of *Callithrix* and *Cebuella* are organized in two rows, one composed by the central incisors and another composed by the lateral ones, crowns of lateral incisors are oriented internally to the tooth row, in a convergent direction. In *Leontopithecus* incisors are displaced in two rows also but they are oriented relative to the posterior region of the palate).

7) I^{1-2}, development of an accessory cusp (protocone): 0 – no cusp or accessory crest is developed at the entocingulum; 1 – a cusp is developed in I^1 and is vestigial or absent in I^2; 2 – a cusp is developed in both I^{1-2}.

8) Upper incisors, relative dimensions of the paracone: 0 – the maximum length is similar to the maximum width; 1 – the maximum length is bigger than the maximum width.

9) Premaxilla, development of the anterior portion (lateral view from the labial face): 0 – without any anterior projection of the premaxilla; 1 – with a drastic anterior projection of the premaxilla, from a transversal axis at the base of nasal bone.

10) Upper incisors, relative size: 0 – both incisors similar in size; 1 – I^1 bigger than I^2 (Note: This size relationship among upper incisors is independent from the shape, even when central and lateral incisors are differently shaped).

11) Upper incisors, development of the crown (paracone): 0 – low crowns; 1 – high crowns.

12) Development of crests over the palatine bone in the region of the major palatine foramen: 0 – absent; 1 – present, but reduced; 2 – present, well developed.

13) I_2-C, relative position: 0 – teeth separated by a diastema; 1 – teeth in contact.

14) I_{1-2}, relative size: 0 – both teeth similar in size; 1 – I_1 smaller than I_2.

15) Lower incisors, dorsoventral dimensions of the occlusal buccal surface: 0 – short paraconid; 1 – elongated paraconid; 2 – more prolongated paraconid.

16) Lower incisors, development of the buccal base of the paraconid: 0 – reduced or absent in I_{1-2}; 1 – reduced or absent in I_1 and developed in I_2; 2 – developed in both incisors.

17) I_2, development of a projection at the supra-distal (lateral) portion of the paraconid: 0 – absent; 1 – present.

18) Lower incisors, morphological general pattern of the crown: 0 – spatulate; 1 – bunodont; 2 – presenting a shape almost cylindrical, with I_2 in a caniniform trend (Note: Platyrrhine lower incisors are spatulate in general, with a variable degree of spatulation where pitheciins have the most extreme condition. Morphology of lower incisors of *Cebuella* is similar to those ones in *Callithrix* with the exception of I_2 being more caniniform and both incisors being more cylindrical and sharp – in *Callithrix* only I_2 is cylindrical. This trend to the cylindrical shape is the result of a condition where the I_2 buccal surface has a perpendicular position relative to I_1, with an apparent twist internally to the tooth row).

19) I_2, curvature of the internal surface: 0 – teeth without any apparent anterior curvature; 1 – teeth curved anteriorly.

20) Lower incisors, angle of projection in relation to its insertion axis over the mandible: 0 – non-evident anterior projection of the incisors; 1 – incisors drastically projected anteriorly.

21) I_2, development of the distal border of the metacingulid: 0 – vestigial or absent; 1 – present.

22) Development of the basal region of the lower incisors at the buccal surface: 0 – basal portion of incisors without any evidence of a developed conid; 1 – protoconid developed, forming a conid at the buccal extremity of the incisors.

23) Lower incisors, displacement: 0 – incisors located in V-shaped, in alignment with the rest of dental row; 1 – incisors displaced in a narrow arch; 2 – incisors aligned among themselves and displaced in a wider dental arch.

24) Lower incisors, development of parastylid (mesostylid) and distostylid: 0 – absent; 1 – present.

25) I_2, paraconid relative width: 0 – narrow; 1– enlarged.

26) Upper canine, entocingulum development: 0 – vestigial or absent; 1 – present.
27) Upper canine, parastyle and metastyle development: 0 – both parastyle and metastyle reduced or absent; 1 – parastyle absent, metastyle present; 2 – both parastyle and metastyle present.
28) Lower canine, entocingulid development at the anterior region of the buccal surface: 0 – vestigial or absent; 1 – present (Note: This is a sexually dimorphic character in both *Cebus* and *Saimiri*).
29) Lower canine, entocingulid development at the posterior region of the buccal surface: 0 – vestigial or absent; 1 – present, weakly developed; 2 – present, well developed.
30) Shape of the canines viewed from the labial surface: 0 – triangular, in a conical shape; 1 – pyramidal, laterally compressed ("pitheciine pattern"); 2 – cylindrical.
31) Lower canines, lateral projection: 0 – without any apparent lateral projection; 1 – with a slight lateral projection; 2 – canines extremely projected laterally.
32) C-P_2, relative position: 0 – teeth in contact; 1 – teeth separated by a diastema (Note: This is a variable condition in some species of *Callithrix*, *Saguinus* and *Aotus*. In species of *Pithecia*, *Chiropotes* and *Cacajao* all degrees can be found, from teeth in contact to total separation of teeth by different diastema sizes).
33) Premolars and molars, texture of the external layer of the enamel: 0 – smooth surface; 1 – crenulated surface (Note: In *Callicebus* there are different degrees of crenulation of the enamel).
34) P^2, protocone development: 0 – vestigial or absent; 1 – developed.
35) P^{3-4}, protocone relative development: 0 – present, developed; 1 – reduced or absent.
36) Upper premolars, relative size (labial surface): 0 – all premolars have the same height; 1 – P^2 is the biggest tooth of the series; 2 – P^4 is the biggest tooth of the series.
37) Premolars, relative position of the protocone: 0 – protocone has an anterior position in all premolars; 1 – protocone has a mesial position in P^2 and an anterior position in P^{3-4}; 2 – protocone has a more mesial position in all premolars, parallel to the paracone.
38) Lower premolars, entocingulid development: 0 – reduced or absent; 1 – present, developed.
39) Upper molars, hypocone relative position: 0 – hypocone aligned to the protocone; 1 – hypocone located more buccally to the protocone (not aligned).
40) Upper molars, mesostyle development: 0 – absent; 1 – present.
41) M^{1-2}, entocingulum development: 0 – reduced or absent; 1 – developed.
42) M^{1-2}, relative size of hypocone and protocone: 0 – hypocone and protocone have similar size in both molars; 1 – hypocone and protocone have similar size in M^1 and hypocone is smaller than protocone in M^2; 2 – hypocone is smaller than protocone in both molars; 3 – hypocone is absent.
43) M^{1-2}, relative size of metacone and paracone: 0 – metacone and paracone have similar size in both molars; 1 – metacone and paracone have similar size in M^1 and metacone is smaller than paracone in M^2; 2 – metacone is smaller than paracone in both molars.
44) M^3, development: 0 – M^3 bigger than M^1; 1 – M^3 smaller than M^1, until its half-size; 2 – M^3 reduced, smaller than half-size of M^1; 3 – M^3 absent.
45) M^{1-2}, epimetacrista development: 0 – developed; 1 – reduced or absent.
46) Upper molars, metaconule development: 0 – vestigial or absent; 1 – present.
47) M^{1-2}, paracone and metacone relative position: 0 – cones somewhat separated by a space; 1 – cones presenting a contact at their internal bases; 2 – both internal cusp walls are in full contact, and the basal portions are immersed each other.
48) Upper molars, prehypocrista development: 0 – vestigial or absent; 1 – present, reduced.
49) Upper molars, general shape pattern of the cusps: 0 – typically cuspiform (sharp), high; 1 – rounded, typically bunodont; 2 – the cusps are low, not detached from the crown.
50) Upper molars, preprotocrista development: 0 – present; 1 – vestigial or absent (Note: This crest appears to present a trend to reduction in Platyrrhini).
51) Upper molars, postprotocrista type of contact: 0 – it is connected to the hypocone; 1 – it is extended to the distal portion of the metacone base, oriented to the metacingulum; 2 – it is connected directly to the metacone (hypometacrista).
52) Upper molars, entocingulum development: 0 – reduced or absent; 1 – developed, forming a detached border (Note: This character is variable among *Callicebus* species).

53) P_2, metaconid development: 0 – vestigial or absent; 1 – present.
54) Lower molars, general shape of the cusps (talonid and trigonid depth): 0 – cylindrical cusps (high crown); 1 – elongated cusps, cuspiform (high crowned); 2 – bunodont cusps, rounded (low crown); 3 – cusp reduced and pratically non-detached from the crown.
55) Lower molars, epiprotocristid development: 0 – well developed; 1 – poorly developed (reduced).
56) P_3, entoconid and hypoconid development: 0 – vestigial or absent; 1 – present.
57) P_4, entoconid and hypoconid development: 0 – both conids developed; 1 – developed entoconid and reduced hypoconid; 2 – both conids vestigial or absent.
58) P_3, metaconid development: 0 – present; 1 – absent.
59) Lower premolars, relative size: 0 – P_2 is the biggest tooth in the size-decreasing premolars series; 1 – P_2 is the biggest tooth of the series, and P_{3-4} are of similar size; 2 – all three premolars have similar height.
60) M_{1-2}, hypoconulid development: 0 – developed in both molars; 1 – developed in M_1 and vestigial or absent in M_2; 2 – vestigial or absent in both molars.
61) Lower premolars, buccal projection of the talonid: 0 – non-evident; 1 – evident.
62) Lower premolars, basal portion development (labial surface): 0 – absence of a projection of the labial wall; 1 – presence of a curved prominence at the basal portion of the labial wall.
63) M_{1-2}, relative size of entoconid and hypoconid: 0 – entoconid bigger than hypoconid; 1 – entoconid with similar size in relation to the hypoconid; 2 – entoconid smaller than hypoconid.
64) M_{1-2}, entocristid development connecting entoconid to metaconid: 0 – deep, forming a "V" shape; 1 – flat.
65) Lower molars, pre-hypocristid relative position: 0 – it connects to the trigonid external wall and does not expand to the crown; 1 – it extends to the molar crown and is connected to the talonid internal wall.
66) M_3, development: 0 – M_3 is the biggest tooth in a decreasing series; 1 – M_3 has similar size of M_{1-2}; 2 – M_3 is the smallest tooth in an increasing series; 3 – M_3 absent.
67) Lower molars, protoconid / hypoconid relative height: 0 – both cuspids similar in height; 1 – hypoconid lower than protoconid.
68) Lower molars, relative width of trigonid and talonid (labio-buccal axis): 0 – both similar in width; 1 – talonid larger than trigonid.
69) P_2, entocingulid development: 0 – developed; 1 – absent.
70) Lower molars, relative position of protoconid and metaconid: 0 – both cuspids aligned; 1 – metaconid placed more distally in relation to the protoconid.
71) Lower molars, paraconid development: 0 – present; 1 – vestigial or absent.
72) M_3, epi-hypocristid development: 0 – present; 1 – vestigial or absent.
73) P_2, inclination of the labial wall towards the interior part of the arch: 0 – non-evident; 1 – evident.
74) Lower molars, development of a fossa between the labial cusps: 0 – present; 1 – vestigial or absent.
75) Mandible, relative position of coronoid and condylar processes: 0 – one process away from another one; 2 – processes placed closer to each other.
76) Mandible, relative height between coronoid and condylar process: 0 – coronoid process slightly higher than the condylar process, but similar in general aspect; 1 – coronoid process higher than the condylar process; 2 – coronoid process lower than the condylar process.
77) Mandibular ramus, shape of the ventro-distal border: 0 – rectangular; 1 – rounded; 2 – rounded and with a distal projection.
78) Mandible, angular process development: 0 – vestigial or absent; 1 – detached as an extremity (Note: This character is variable in *Aotus* specimens).
79) Mandible, development of the symphyseal region: 0 – with a narrow area of contact; 1 – with a wide area of contact, resulting in a relatively wide anterior upper surface.
80) Mandible, *pterigoideus internus* area of insertion: 0 – poorly detached, without any external marks; 1 – well developed and forming a detached concavity, visible from the external mandible surface.

As previously mentioned, other non-dental morphological characters gathered from the literature by HOROVITZ (1999), except the last two, were included in the data matrix in order to allow a broader morphological context to our analysis. These characters are the following:

81) Offspring per birth, number: 0 – one; 1 – two.

82) Lumbar vertebrae, number: 0 – more than five; 1 – five or fewer.
83) External thumb: 0 – absent or reduced; 1 – present.
84) Tail, ventral glabrous surface: 0 – absent; 1 – present.
85) Claws on manual and pedal digits except hallux: 0 – absent; 1 – present.
86) Postglenoid foramen: 0 – absent; 1 – reduced; 2 – large.
87) Middle ear, pneumatization of anteroventral region: 0 – absent; 1 – present.
88) Middle ear, paired prominences on cochlear housing: 0 – absent; 1 – present.
89) Pterygoid fossa, depth: 0 – deep; 1 – shallow.
90) Canal connecting sigmoid sinus and subarcuate fossa: 0 – absent; 1 – present.
91) Vomer, exposure in orbit: 0 – absent; 1 – present.
92) Temporal emissary foramen: 0 – present and large; 1 – small or absent.
93) Eyeball physically enclosed: 0 – absent; 1 – present.
94) Cranial capacity: 0 – less than $15cm^3$; 1 – more than $15cm^3$.
95) Zygomatical arch, ventral extent: 0 – below plane of alveolar level; 1 – above plane of alveolar level.
96) Pterion region, contacts: 0 – zygomatic-parietal; 1 – frontal-alisphenoid.
97) Infraorbital foramen, vertical position relative to the maxillary check teeth in Frankfurt plane: 0 – above interval between (or caudal to) $M^1$and P^4; 1 – above interval between P^4 and P^3; 2 – above (or rostral to) anteriormost premolar.
98) Zygomaticofacial foramen, size relative to maxillary M^1 breadth: 0 – small; 1 – large.
99) Number of premolars: 0 – two; 1 – three.
100) Carpometacarpal joint of thumb: 0 – non-saddle; 1 – saddle.
101) Orientation of the nares: 0 – parallel (narrow nose); 1 – lateral (broad nose).
102) Cheek, development: 0 –absent; 1 – present.

Parsimony analysis

The data matrix (APPENDIX II) built with these 102 characters and the 23 terminal taxa was submitted to a *branch and bound* algorithm. The results generated 40 equally parsimonious trees with a length of 290 steps, and consistency and retention indices of 0.483 and 0.677, respectively (complete statistics of the analysis are available upon request). A strict consensus of these 40 trees was retrieved, yielding a tree with 15 components (clades), with five unresolved trichotomies (Fig.1).

In the consensus tree in figure 1, two major clades diverge from the platyrrhine basal node. One includes Cebinae and Callitrichinae, representing the family Cebidae. The other represents the family Atelidae, composed of Pitheciinae and Atelinae, with Alouattini and Atelini as sister taxa within the later. Among cebids, Cebinae is formed by a trichotomous clade joining *Cebus*, *Saimiri*, and *Carlocebus*. They are phylogenetically related to the branch that joins *Aotus* as the sister taxon of *Callicebus*. The Callitrichinae clade has *Callimico* rooted at the basal node and then *Saguinus* as the next basal taxon, followed by *Leontopithecus*. *Leontopithecus* is the sister taxon of the clade represented by a polytomy with the three subgenera of *Callithrix*: *Cebuella*, *Mico*, and *Callithrix*. The two clades that stand as particularly well supported with Bremer values equal or higher than five are the Callitrichinae and Pitheciinae. Since the fossils in question are atelids, more information is provided here on the morphological basis of their interrelationships. Atelidae is composed of the pitheciine and ateline clades. The former is subdivided into two clades: the first one is represented by a polytomy with *Alouatta*, *Brachyteles*, and *Stirtonia*, and another one has *Lagothrix* rooted at the basal node as sister of a trichotomy with *Ateles*, *Caipora*, and *Protopithecus*. The synapomorphies, consistency indices and transformations for each character supporting Atelinae are: 13 (0.25; 0'↑1), 16 (0.33; 0'↑2), 25 (0.50; 0'↑1), 26 (0.40; 0'↑2), 36 (0.33; 1'↑2), 57 (0.40; 0'↑1), 59 (0.33; 0'↑2), 62 (0.33; 0'↑1), 79 (0.25; 1'↑0), 82 (1.00; 0'↑1), 84 (1.00; 0'↑1), 92 (0.67; 1'↑0), 97 (0.50; 2'↑1), and 98 (0.33; 0'↑1). On the other hand, the tribe Alouattini is supported by the following synapomorphies: 10 (0.50; 1'↑0), 39 (0.33; 0'↑1), 40 (0.33; 0'↑1), 46 (0.40; 0'↑1), 47 (0.33; 2'↑0), 51 (0.67; 2'↑1), 52 (0.50; 0'↑1), 61 (0.50; 0'↑1), 64 (0.33; 1'↑0), 66 (0.60; 2'↑0), 68 (0.25; 0'↑1), and 73 (0.33; 1'↑0).

Our analysis, therefore, shows that the two giant fossil platyrrhines are closely related to *Ateles* and fall within the tribe Atelini, along with *Lagothrix*. The following six apomorphic characters support the monophyly of the tribe Atelini: 5 (0.50; 0'↑1), 14 (1.00; 1'↑0), 42 (0.75; 2'↑1), 43 (0.33; 1'↑2), 45 (0.25; 1'↑0), and 86 (0.50; 0'↑1). The clade composed by the two giant fossils and *Ateles* is supported by the following eight

transformation series: 18 (0.50; 0'↑1), 49 (0.67; 0'↑1), 53 (0.33; 0'↑1), 54 (0.60; 0'↑2), 63 (1.00; 0'↑2), 71 (0.25; 0'↑1), 72 (0.33; 1'↑0), and 83 (0.50; 1'↑0). According to the alternatives observed among the 40 equally parsimonious trees, *Ateles* consistently occupies a sister position either to *Caipora* or *Protopithecus*.

DISCUSSION

The cladistic patterns that arose from our analysis of platyrrhine relationships agree well with previous morpho- and molecular-based arrangements proposed. This is especially true for the following:

1) The affinities between *Cebus* and *Saimiri* is an outcome that reinforces relationships proposed by ROSENBERGER (1981), BARROSO *et al.* (1997), HARADA *et al.* (1995), PORTER *et al.* (1997), HOROVITZ *et al.* (1998), CANAVEZ *et al.* (1999) and HOROVITZ (1999).
2) *Aotus* and *Callicebus* as sister taxa (ROSENBERGER, 1981; FORD, 1986; SORCI *et al.*, 1997); conversely, *Carlocebus* emerged as a component of the clade Cebinae, in contrast with HOROVITZ's proposal (1999) that places *Carlocebus carmemensis* together with the calitrichines. However, much is need to know about the taxonomical status of the two species currently recognized as part of the genus *Carlocebus* (*C. carmemensis* and *C. intermedius*).
3) The monophyletic status of Callitrichinae is well corroborated, with *Callimico* rooted at the basal node, followed by *Saguinus* and *Leontopithecus* (ROSENBERGER, 1981; FORD, 1986; KAY, 1990) and the "*Callithrix*" clade, encompassing the subgenera *Cebuela*, *Mico*, and *Callithrix* (BARROSO *et al.*, 1997).

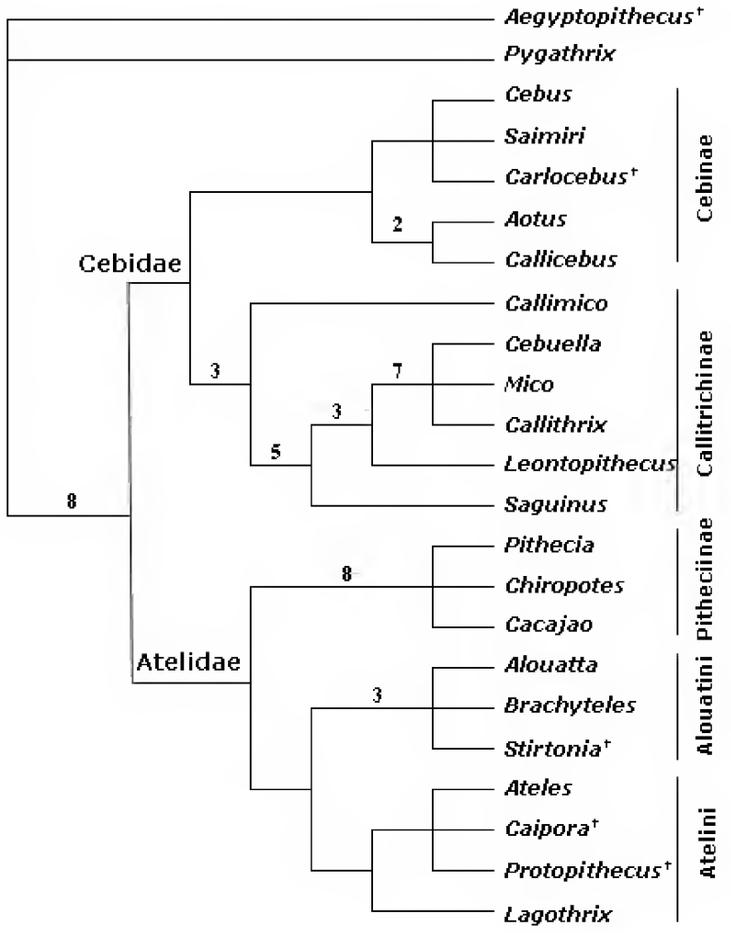

Fig.1- Strict consensus tree of 40 equally parsimonious trees showing relationships within the platyrrhines (CI= 0.483; RI= 0.677). Bremer support is indicated for clades with values higher or equal to 2.

4) The monophyletic status of Atelidae is pointed out, as widely accepted in the current literature.
5) Subfamily Pithecinae, with *Pithecia*, *Chiropotes* and Cacajao, has received full support from all sources of data. On the other hand, our analysis does not confirm the position of *Callicebus* at the subfamily's basal node, as many have recently found.
6) The monophyly of Atelinae is indicated, as widely supported by various studies.
7) *Alouatta* and *Stirtonia* have close affinities as alouattines, as is widely agreed. Conversely, the idea that *Brachyteles* is more closely related to the Alouattini than to *Ateles* has not received much support, with a few exceptions (KAY, 1990; MACPHEE *et al.* 1995).
8) Close affinities between *Ateles* and *Lagothrix* are pointed out (KAY, 1990; MACPHEE *et al.*, 1995).

Our results, which are largely based on dental morphology, are in agreement with CARTELLE & HARTWIG (1996) and HARTWIG & CARTELLE (1996) to the extent that *Caipora* and *Protopithecus* should be recognized as atelines and that *Caipora* is closely related to *Ateles*. However, our data provides no support for the interpretation of *Protopithecus* being an alouattin. We suspect that more progress on uncovering the phylogenetic relationships of these unique giant monkeys will be possible as we untangle the mosaic pattern found in their craniodental and postcranial structures.

To conclude, these two unique giant Brazilian subfossil monkeys, *Caipora* and *Protopithecus*, offer a special opportunity for new phylogenetic and paleontological enterprises to be undertaken, which will definitely open new avenues for the understanding of the New World monkeys' evolutionary history.

ACKNOWLEDGEMENTS

The authors wish to thank financial support from the CNPq and FAPERJ and comments by Claudia A.M. Russo (UFRJ) and Anwar Janoo (UFRJ). We are also grateful to Cástor Cartelle (PUC – Minas Gerais) for permission to access the fossil material, for computer facilities provided by CNPq grants to Claudia Russo and for the valuable comments provided by the reviewers, Alfred Rosenberger and Inés Horovitz.

LITERATURE CITED

BARROSO, C.M.L.; SCHNEIDER, H.; SCHNEIDER, M.P.C.; SAMPAIO, I.; HARADA, M.L.; CZELUSNIAK, J. & GOODMAN, M., 1997. Update on the phylogenetic systematics of New World monkeys: further DNA evidence for placing the pygmy marmoset (*Cebuella*) within the Genus *Callithrix*. **International Journal of Primatology**, New York, **18**(4):651-674.

CANAVEZ, F.C.; MOREIRA, M.A.M.; LADASKY, J.J.; PISSINATTI, A.; PARHAM, P. & SEUÁNEZ, H.N., 1999. Molecular phylogeny of New World primates (Platyrrhini) based on β_2-microglobulin DNA sequences. **Molecular Phylogenetics and Evolution**, San Diego, **12**(1):74-82.

CARTELLE, C., 1996. Updating two Pleistocene primates from Bahia, Brazil. **Neotropical Primates**, Belo Horizonte, **4**(2):46-48.

CARTELLE, C. & HARTWIG, W.C., 1996. A new extinct primate among the Pleistocene megafauna of Bahia, Brazil. **Proceedings of the National Academy of Sciences**, Washington, **93**:6405-6409.

FARRIS, J.S., 1983. The logical basis of phylogenetic systematics. In: PLATNICK, N.I. & FUNK, V.A. (Ed.): **Advances in Cladistics 2**. Second Meeting of the Willi Hennig Society. New York: Columbia University Press, p.7-36.

FLEAGLE, J.G., 1988. **Primate Adaptation and Evolution**. New York: Academic Press. 486p., il.

FLEAGLE, J.G., 1990. New fossil platyrrhines from the Pinturas Formation, southern Argentina. **Journal of Human Evolution**, London, **19**(1/2):61-85.

FORD, S.M., 1986. Systematics of the New World monkeys. In: SWINDLER, D.R. & ERWIN, J. (Eds.) **Comparative Primate Biology**, Volume 1, Systematics, Evolution and Anatomy. New York: A.R.Liss. p.73-135.

GROVES, C., 2001. **Primate Taxonomy**. Washington: Smithsonian Institution Press. 350p., il.

GUEDES, P.G., 2000. **Sistemática dos primatas do Novo Mundo e a evolução do aparelho mastigatório (Primates, Platyrrhini)**. 175p., il. M.Sc. Dissertation, Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Museu Nacional, Universidade Federal do Rio de Janeiro.

HARADA, M.L.; SCHNEIDER, H.; SCHNEIDER, M.P.C.; SAMPAIO, I.; CZELUSNIAK, J. & GOODMAN, M., 1995. DNA evidence on the phylogenetic systematics of New World monkeys: support for the sister-grouping of *Cebus* and *Saimiri* from two unlinked nuclear genes. **Molecular Phylogenetics and Evolution**, San Diego, **4**(3):331-349.

HARTWIG, W.C. & CARTELLE, C., 1996. A complete skeleton of the giant South American primate *Protopithecus*. **Nature**, London, **381**:307-311.

HARTWIG, W.C., 1995. A giant New World monkey from the Pleistocene of Brazil. **Journal of Human Evolution**, London, **28**:189-195.

HERSHKOVITZ, P., 1970. Notes of Tertiary platyrrhine monkeys and description of a new genus from the late Miocene of Colombia. **Folia Primatologica**, Basel, **12**:1-37.

HERSHKOVITZ, P., 1977. **Living New World Monkeys (Platyrrhini), with an Introduction to Primates**. Chicago: University of Chicago Press. 1117p., il.

HOFFSTETTER, R.,1977. Primates: filogenia e historia biogeografica. **Studia Geologica**, Salamanca, **13**:211-253.

HOROVITZ, I.; ZARDOYA, R. & MEYER, A., 1998. Platyrrhine systematics: a simultaneous analysis of molecular and morphological data. **American Journal of Physical Anthropology**, New York, **106**:261-281.

HOROVITZ, I., 1999. A phylogenetic study of living and fossil platyrrhines. **American Museum Novitates**, New York, **3269**:1-40.

HOROVITZ, I. & MACPHEE, R.D.E., 1999. The Quaternary Cuban platyrrhine *Paralouatta varonai* and the origin of Antillean monkeys. **Journal of Human Evolution**, London, **36**:33-68.

KAY, R.F.; MADDEN, R.H.; PLAVCAN, J.M.; CIFELLI, R.L. & GUERRERO-DÍAZ, J., 1987. *Stirtonia victoriae*, a new species of Miocene Colombian primate. **Journal of Human Evolution**, London, **16**:173-196.

KAY, R.F.; MADDEN, R.H. & GUERRERO-DÍAZ, J., 1989. Nuevos hallazgos de monos en el Mioceno de Colombia. **Ameghiniana**, Buenos Aires, **25**(3):203-212.

KAY, R.F., 1990. The phyletic relationships of extant and fossil Pithecinae (Platyrrhini, Anthropoidea). **Journal of Human Evolution**, London, **19**(1-2):175-208.

KAY, R.F. & MELDRUM, D.J., 1997. A new small platyrrhine and the phyletic position of Callitrichinae. In: KAY, R.F.; MADDEN, R.H.; CIFELLI, R.L. & FLYNN, J.J. (Eds.) **Vertebrate Paleontology in the Neotropics. Miocene Fauna of La Venta, Colombia**. Washington: Smithsonian Institution Press. p.435-472.

KAY, R.F.; ROSS, C. & WILLIAMS; A.B., 1997. Anthropoid origins. **Science**, Washington, **275**:797-804.

MACPHEE, R.D.E; HOROVITZ, I.; ARREDONDO, O. & VASQUEZ, O.J., 1995. A new genus for the extinct Hispaniolan monkey *Saimiri bernensis* Rimoli, 1977, with notes on its systematic position. **American Museum Novitates**, New York, **3134**:1-21.

MCKENNA, M.C. & BELL, S.K., 1997. **Classification of Mammals Above the Species Level**. New York: Columbia University Press. 631p.

MITTERMEIER, R.A.; RYLANDS, A.B.; COIMBRA-FILHO, A. & FONSECA G.A.B. (Ed.), 1988. **Ecology and Behavior of Neotropical Primates**, Volume 2. Washington: World Wildlife Foundation. 610p., il.

PORTER, C.A.; PAGE, S.L.; CZELUSNIAK, J.; SCHNEIDER, H.; SCHNEIDER, M.P.C.; SAMPAIO, I. & GOODMAN, M., 1997. Phylogeny and evolution of selected primates as determined by sequences of the T-globin locus and 5' flanking regions. **International Journal of Primatology**, New York, **18**(2):261-295.

ROSENBERGER, A.L., 1977. *Xenothrix* and ceboid phylogeny. **Journal of Human Evolution**, London, **6**:461-481.

ROSENBERGER, A.L., 1981. Systematics: the higher taxa. In: COIMBRA FILHO, A.F. & MITTERMEIER, R. (Eds.) **Ecology and Behavior of Neotropical Primates**, Volume 1. Rio de Janeiro: Academia Brasileira de Ciências. p.9-27.

ROSS, C.F., 2000. Into the light: the origin of Anthropoidea. **Annual Review of Anthropology**, Palo Alto, **29**:147-194.

SETOGUCHI, T.; WATANABE, T. & MOURI, T., 1983. La dentadura superior de *Stirtonia* (Ceboidea, Primates) del Mioceno de Colombia y del origen de la cúspide postero-interna de los molares superiores em los monos ahulladores (*Alouatta*). **Kyoto University Overseas Research, Reports of New World Monkeys**, Kyoto, **1983**:1-11.

SORCI, G.; MORAND, S. & HUGOT, J.P., 1997. Host-parasite coevolution: comparative evidence for covariation of life history traits in primates and oxyurid parasites. **Proceedings of the Royal Society of London**, London, **B264**(1379):285-289.

SWOFFORD, D.L., 2002. **Phylogenetic analysis using parsimony (PAUP*)**. Version 4.0 b10. Sunderland: Sinauer.

SZALAY, F.S. & DELSON, E., 1979. **Evolutionary History of the Primates**. New York: Academic Press. 595p., il.

TEJEDOR, M.F., 1998. The evolutionary history of platyrrhines: old controversies and new interpretations. **Neotropical Primates**, Belo Horizonte, **6**(3):77-82.

VAN ROOSMALEN, M.G.M. & VAN ROOSMALEN, T., 2003. The description of a new marmoset genus, *Callibella* (Callitrichinae, Primates), including its molecular phylogenetic status. **Neotropical Primates**, Belo Horizonte, **11**(1):1-10.

VIVO, M., 1991. **Taxonomia de *Callithrix* Erxleben, 1777 (Callitrichidae, Primates)**. Belo Horizonte: Fundação Biodiversitas para Conservação da Diversidade Biológica. 105p., il.

APPENDIX I

SPECIMENS EXAMINED

Alouatta belzebul (Linnaeus, 1766) – BRASIL, MARANHÃO, Imperatriz: MN21089 (♀).
Alouatta caraya (Humboldt, 1812) – BRASIL, MATO GROSSO, Alto Xingu: MN11704 (♀).
Alouatta seniculus (Linnaeus, 1766) – BRASIL, PARÁ, Almeirim: MN2774 (♂); BRASIL, RORAIMA, Boa Vista: MN21129 (♀), MN 23155 (♂).
Aotus infulatus Kuhl, 1820 – BRASIL, MATO GROSSO: MN2701 (sex indet.).
Aotus nigriceps Dollman, 1909 – BRASIL, RONDÔNIA, Rio Jamari: MN28495 (♂).
Aotus vociferans (Spix, 1823) – BRASIL, AMAZONAS, Rio Purus: MN2695 (♀).
Ateles paniscus (Linnaeus, 1758) – BRASIL, AMAZONAS, Paraná do Manhana: MN2500 (♀); BRASIL, AMAZONAS, Norte do Rio Amazonas: MN6035 (♂), MN6037 (♀); BRASIL, AMAZONAS, Fonte Boa: MN21058 (♀); BRASIL, MATO GROSSO, Rio Jaurú: MN506 (♀); BRASIL, MATO GROSSO, Alto Tapajós: MN32701 (♂); BRASIL, MATO GROSSO, Cáceres: MN33615 (sex indet.); unknown locality: MN1093 (sex indet.), MN2476 (♂).
Brachyteles aracnoides (E. Geoffroy, 1806) – BRASIL, RIO DE JANEIRO, Parati: MN8513 (♀), MN6699 (♂), MN7724 (♂); unknown locality: MN8514 (♂), MN30188 (♂).
Cacajao calvus (I. Geoffroy, 1847) – BRASIL, AMAZONAS, Paraná do Manhana: MN2444 (♀), MN2452 (♀).
Cacajao melanocephalus (Humboldt, 1811) – VENEZUELA, Serra do Imery: MN2437 (♂), MN2439 (♀).
Callicebus moloch (Hoffmannsegg, 1807) – COLOMBIA: MN2486 (sex indet.); BRASIL, AMAZONAS, Aripuanã: MN2480 (sex indet.); BRASIL, PARÁ, Vila Braga: MN2472 (♂); BRASIL, PARÁ, Santarém: MN11592 (♀), MN11593 (♂); BRASIL, PARÁ: MN21062 (♂); unknown locality: MN414 (sex indet.).
Callicebus personatus (E. Geoffroy, 1812) – BRASIL, ESPÍRITO SANTO, São Domingos: MN21053 (♂); BRASIL, ESPÍRITO SANTO: MN30181 (♂).
Callicebus torquatus (Hoffmannsegg, 1807) – BRASIL, AMAZONAS, Foz do Castanho: MN2482 (sex indet.); BRASIL, AMAZONAS, Fonte Boa: MN21047 (♂).
Callimico goeldii (Thomas, 1904) – BRASIL, ACRE, Porongaba, margem direita do Alto Rio Juruá: MPEG22969 (♂);PARÁ, BRASIL: MN23736 (♂); BRASIL, Rio Juruá, Seringal Oriente, próximo à Vila Taumaturgo: MPEG214 (♂); Rio Yaco, cabeceira do Rio Purus: MPEG443 (♂); unknown locality: MUZUSP 11355 (♂).
Callithrix argentata (Linnaeus, 1766) – BRASIL, PARÁ, Piquiatuba: MN5946 (♀); BRASIL, PARÁ, Cametá: MN5954 (♂); BRASIL, MATO GROSSO, Córrego do Cabral: MN2855 (sex indet.); BRASIL, MATO GROSSO, São Luiz de Cáceres: MN5845 (♂).
Callithrix aurita (E. Geoffroy, 1812) – BRASIL, MINAS GERAIS, Além Paraíba: MN1354 (♀), MN1355 (♂).
Callithrix flaviceps (Thomas, 1903)– BRASIL, ESPÍRITO SANTO, Santa Teresa: MN5875 (♀); MN178 (sex indet.): unknown locality.
Callithrix geoffroyi (Humboldt, 1912) – BRASIL, MINAS GERAIS, Conceição do Mato Dentro: MN13481 (♂), MN13482 (♀); BRASIL, ESPÍRITO SANTO, Morro da Argola: MN3958 (♂), MN3962 (♀), MN3970 (♂).
Callithrix humeralifer (Humboldt, 1812) – BRASIL, AMAZONAS, Lago do Baptista, Rio Amazonas: MN5944 (♀), MN5948 (♂); BRASIL, PARÁ, Rio Tapajós, Vila Braga: MN2838 (♀), MN2839 (♂).
Callithrix jacchus (Linnaeus, 1758) – BRASIL, SERGIPE, Cristinópolis: MN30541 (♂), MN30544 (♀); BRASIL, RIO DE JANEIRO, Parque Nacional da Tijuca: MN5570 (♀); unknown locality: MN5566 (sex indet.).
Callithrix penicillata (E. Geoffroy, 1812) – BRASIL, BAHIA, Barreiras: MN4260 (♀), MN4261 (♂); BRASIL, BAHIA, Ilhéus: MN8527 (♂), MN8535 (♂), MN8538 (♀); BRASIL, MINAS GERAIS, Uberaba: MN7565 (♀); BRASIL, MINAS GERAIS, Araguari: MN7566 (♂).
Cebuella pygmaea (Spix, 1823) – PERU, LORETO, Territorio Yahuas: MN2781 (♂), MN2782 (♂); PERU, IQUITOS: MPEG 201 (♀), MPEG 848 (♂); PERU, CHIMBOTE, Rio Solimões: MPEG 283 (♂); BRASIL, AMAZONAS, Alto Solimões: MN11910 (♂); ACRE, OCIDENTE, margem direita, Alto Rio Juruá: MPEG 22951 (♀); unknown locality: MN2783 (sex indet.).
Cebus apella (Linnaeus, 1758) – BRASIL, PARÁ, Paragominas: MN23336 (sex indet.), MN23337 (sex indet.); BRASIL, PARÁ, Nova Timboteua: MN23344 (♀), MN23346 (♀); BRASIL, RIO DE JANEIRO, Parque Nacional de Itatiaia: MN21171 (♂).
Cebus olivaceus Schomburgk, 1848 – BRASIL, RONDÔNIA, Boa Vista: MN23525 (F), MN23526 (♂).
Chiropotes albinasus (I. Geoffroy and Deville, 1848) – BRASIL, PARÁ, Serra do Cachimbo: MN21067 (♀), MN25718 (♀).

Chiropotes satanas (Hoffmannsegg, 1807) – BRASIL, RORAIMA, Parecis: MN454 (♂); BRASIL, AMAZONAS, Rio Catrimani: MN2909 (♂); BRASIL, PARÁ, Nova Timboteua: MN21056 (♀).
Lagothrix lagothricha (Humboldt, 1812) – BRASIL, AMAZONAS, Baixo Solimões: MN2722 (♂); BRASIL, AMAZONAS, São Manoel: MN2729 (♀); unknown locality: MN518 (♀), MN30196 (♂), MN30198 (sex indet.).
Leontopithecus crhysomelas (Kuhl, 1820)– BRASIL, BAHIA, Ilhéus: MN8518 (♂); BRASIL, BAHIA, Pontal: MN8521 (♀).
Leontopithecus rosalia (Linnaeus, 1766)– BRASIL, RIO DE JANEIRO, Marica: MN3964 (♂), MN3965 (♀), MN3966 (♂); unknown locality: MN186 (sex indet.), MN5491 (♀).
Pithecia irrorata Gray, 1842 – BRASIL, AMAZONAS, Rio Purus: MN3317 (♀); BRASIL, AMAZONAS, São Manuel: MN3339 (♂).
Pithecia monachus (E. Geoffroy, 1812) – BRASIL, AMAZONAS, Fonte Boa, Rio Solimões: MN3312 (♀); unknown locality: MN7662 (sex indet.).
Saguinus bicolor (Spix, 1823) – BRASIL, AMAZONAS, Manaus, Flores: MN23859 (sex indet.), MN23862 (sex indet.); unknown locality: MN2864 (sex indet.).
Saguinus fuscicollis (Spix, 1823) – COLOMBIA, CAQUETA, Rio Mecaya: MN24797 (♀); RORAIMA, UHE Samuel: MN28483 (♂), MN28484 (♀); BRASIL, AMAZONAS, Rio Juruá: MN5934 (♀), MN5937 (♂); BRASIL, AMAZONAS, Rio Juruá, Lago Grande: MN5956 (♂); BRASIL, AMAZONAS, Rio Juruá, Santo Antônio: MN5957 (♀); BRASIL, AMAZONAS, Tefé, Mata Patrimônio: MN23848 (♂); BRASIL, AMAZONAS, Coari: MN23850 (♂); BRASIL.
Saguinus geoffroyi (Pucheran, 1845) – COLOMBIA, UNGUIA, Choco: MN24771 (♂).
Saguinus imperator (Goeldi, 1907) – BRASIL, AMAZONAS, Rio Juruá, Santo Antônio: MN5929 (♂), MN5930 (♀).
Saguinus labiatus (Humboldt, 1812) – BRASIL, AMAZONAS, Rio Purus: MN2481 (♀), MN2482 (♂).
Saguinus leucopus (Günther, 1876) – COLOMBIA, PURI, Antioquia: MN28845 (♂).
Saguinus midas (Linnaeus, 1758) – BRASIL, AMAPÁ, Serra do Navio: MN20546 (♀), MN20547 (♂); BRASIL, AMAZONAS, Fonte Boa: MN23853 (♀), MN23854 (♂); BRASIL, PARÁ, Paragominas: MN23830 (♀), MN23831 (♂).
Saguinus pileatus (I. Geoffroy and Deville, 1848) – BRASIL, AMAZONAS, Tefé: MN23846 (♀), MN23847 (♀).
Saimiri sciureus (Linnaeus, 1758) – BRASIL, AMAPÁ, Oiapoque: MN20592 (♂); BRASIL, AMAPÁ, Rio Tracajatuba: MN20563 (♂); BRASIL, AMAZONAS, Lago do Batista: MN6056 (sex indet.), MN6079 (♂); BRASIL, PARÁ, Nova Timboteua: MN23532 (sex indet.).
Pygathrix sp. – unknown locality: MN61604 (sex indet.).
Tarsius sp. – unknown locality: MN2711 (♂).

EXTINCT SPECIES

Caipora bambuiorum Cartelle & Hartwig, 1996 – BRASIL - BAHIA: Campo Formoso, Toca da Boa Vista (type-locality) – (40°51'39"W, 10°09'36"S); Pleistocene: IGC-UFMG 05. Material: caudal vertebrae, incomplete pelvis and scapula, long bones from both upper and lower limbs, carpals, metacarpals, tarsals and phalanges. Skull (maxilla with I^1-P^3; right P^4; left M^1; right M^2; M^3) and mandible (with right I_{1-2}; C-P_2; right P_3; P_4-M_1; left M_2; M_3).
Protopithecus brasiliensis Lund, 1838 – BRASIL - BAHIA: Campo Formoso, Toca da Boa Vista (type-locality) – (40°51'39"W, 10°09'36"S); Pleistocene: IGC-UFMG 06. Material: several vertebrae, scapulae, long bones from upper and lower limbs, carpals, metacarpals, tarsals, metatarsals, pahalanges, skull (maxilla containing I^1-C; P^3 isolated; left P^4; part of left M^1; left M^2; M^3) and mandible (with I_1-C; right P_2; P_3-P_4).
Carlocebus carmenensis Fleagle, 1990 –Pinturas Formation, SANTA CRUZ PROVINCE, ARGENTINA; Lower Miocene. (FLEAGLE , 1990).
Carlocebus intermedius Fleagle, 1990 – Pinturas Formation, SANTA CRUZ PROVINCE, ARGENTINA; Lower Miocene. (FLEAGLE , 1990).
Stirtonia tatacoensis Hershkovitz, 1970 – LA VENTA, COLOMBIA; Middle Miocene. (HERSHKOVITZ, 1970; SETOGUCHI *et al.*, 1983; KAY *et al.*,1987; 1989).
Stirtonia victoriae Kay et al., 1987 Locality – LA VENTA, COLOMBIA; Middle Miocene. (KAY *et al.*, 1987).
Aegyptopithecus zeuxis Simons, 1965 – Fayum Depression, EGYPT; Middle Oligocene. (SZALAY & DELSON, 1979).

APPENDIX II

DATA MATRIX (23 TAXA & 102 CHARACTERS)

```
                        0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888999999999
                        1234567890123456789012345678901234567890123456789012345678901234567890123456789012345678901356789

Aegyptopithecus         1?0101001100?????????????00????0?0?01001?00002010?0?????????????????????????????????20000?0111000
Pygathrix               0000000000000?00?000?010?00000100?0000000000000000000000000000000?000?000001000100000000111000
Cebus                   1001100001001?1021110002000?0010010020000112012111201211001100011200100100100110001002010110110001
Saimiri                 0001100001000102111000200l0?1010010101101212001110200101000211010200000100100000001002010110110201
Aotus                   1000110001001?1010000001001?00200?0102000???120021102002111002000112010001001l2?0100100201010110020l
Callicebus              1001112001000111000000100101100011021100120111111001??2011020?001?2010001001120010010000111011002l1
Pithecia                1002021111110120000110100001212?1101200002011020212003110002000112001001010020110010010111001102O1
Chiropotes              1002022111120120000110100001212?1101200002111020212003110002000112001001110010110010O?00?100110201
Cacajao                 1002021111120120000110100001212?1101200002011020212003110002000112001001110010110010O?001100110201
Alouatta                1001000010000101000000101?0020010102001102111101011110011012110000010001000210100111010011001100l1
Brachyteles             0001000000101102010000101?1020010102001102111010001100011102?1000010000100000100001010100110011011l
Ateles                  1001110011000001010000100?0020010110000001110020112012110010012112000010100010000101000010?00110111
Lagothrix               0001100001001002000000101?0020010102000?0121002001200001l0?2010102000001100210000111O?001100110111
Callimico               1001000001100101001000100100200101000O??120200000020010120120000020000010011011000101?010101010211
Cebuella                1111010001100100020000010020120100l111?113130000002101002102001003110101000101101010121111010010201
Mico                    1111010000110?1000200000100202207001111?113130000002101002102001013110101000001101010121111010102O1
Callithrix              1111010000110?1000200000100002207001111?113130000002101002102001013110101000001101010121111010102O1
Saguinus                1001000001100101000001100000100?010011??131300000021010120020010030101010011011010101201l101010201
Leontopithecus          1001000001101101000001100100200001110l?013130000002101112002001013010101001101101010121111010102O1
Caipora                 1001100011001002010O?0101200200101022000012100201??0120110220l?10000001?10001000?????????????????1
Carlocebus              ??????????????????????????????????0?00?01????200?1112??20????20????????01?????????????????????????1
Stirtonia               ??????????????????????????????????0002201112??01000011??0100?210??0??1?01??0?????????????????????1
Protopithecus           0001100011001002010000101?00??0?0?021000011100201??012?1002201???????00??1????0?????????????????1
```

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.161-168, jan./mar.2005
ISSN 0365-4508

CHROMOSOMAL CHARACTERIZATION OF TAXA OF THE GENUS *TRINOMYS* THOMAS, 1921, (RODENTIA: ECHIMYIDAE) IN THE STATES OF RIO DE JANEIRO AND SÃO PAULO [1]

(With 3 figures)

LEILA MARIA PESSÔA [2, 3, 4]
MARGARET MARIA DE O. CORRÊA [2]
EMERSON BITENCOURT [5]
SÉRGIO F. DOS REIS [3, 6]

ABSTRACT: Ten species of spiny rats of the genus *Trinomys* are currently recognized in eastern Brazil. Although most taxa known in the genus *Trinomys* have been characterized on the basis of craniodental, pelage, and bacular traits, data on chromosomal morphology are available for only four taxa, two from the State of Bahia, one from the State of São Paulo, and one from the State of Espírito Santo. Here we describe the normal chromosomal complement for three additional taxa, namely, *Trinomys gratiosus bonafidei* (Fazenda Boa Fé, Teresópolis, Rio de Janeiro, type-locality), *Trinomys eliasi* (Barra de Maricá, Maricá, Rio de Janeiro, type-locality), and *Trinomys dimidiatus* (Rio Bonito, Rio de Janeiro, and Ubatuba, São Paulo). The specimens analyzed here from the locality of Ubatuba were identified on the basis of craniodental, pelage, and bacular traits as *T. dimidiatus*, extending the known range of this species at least 100km south into the State of São Paulo. The three taxa for which chromosomal data are presented differ in their diploid and fundamental numbers and, therefore, can be diagnosed on the basis of their karyotypes. The significance and implications of chromosome numbers and morphology as diagnostic markers are evaluated in the framework of the molecular phylogenetic relationships and of the data on geographic distribution currently available for the genus *Trinomys*.

Key words: Echimyidae, karyotypes, Rodentia, spiny rats, taxonomy, *Trinomys*.

RESUMO: Caracterização cromossômica de taxa do gênero *Trinomys* Thomas, 1921, (Rodentia, Echimyidae) nos Estados do Rio de Janeiro e São Paulo.

Dez unidades taxonômicas no nível de espécie são atualmente reconhecidas para os roedores do gênero *Trinomys* no leste do Brasil. Embora a maioria dos taxa conhecidos tenham sido caracterizados com base em caracteres do crânio, da dentição, da pelagem e do báculo, a informação sobre a morfologia dos cromossomos limita-se até o momento apenas a quatro taxa, dois provenientes do Estado da Bahia, um de São Paulo e um do Espírito Santo. Neste trabalho são descritos os complementos cromossômicos para mais três taxa, *Trinomys gratiosus bonafidei* (Fazenda Boa Fé, Teresópolis, RJ, localidade tipo), *Trinomys eliasi* (Barra de Maricá, Maricá, RJ, localidade tipo) e *Trinomys dimidiatus* (Rio Bonito, RJ, and Ubatuba, SP). Os espécimes analisados neste estudo provenientes de Ubatuba foram identificados como *T. dimidiatus* com base em caracteres craniodentais, da pelagem e do báculo, estendendo a distribuição da espécie pelo menos 100km ao sul na direção do Estado de São Paulo. Os taxa analisados neste trabalho diferem nos seus números diplóide e fundamental e, por conseguinte, podem ser diagnosticados com base nos seus cariótipos. As implicações da variação nos cromossomos para a diagnose dos taxa do gênero *Trinomys* que ocorrem nos estados do Rio de Janeiro e São Paulo são avaliadas no contexto das relações filogenéticas deste grupo, inferidas a partir de seqüências do genoma mitocondrial e da informação disponível sobre a distribuição geográfica de suas espécies.

Palavras-chave: Echimyidae, cariótipos, Rodentia, taxonomia, *Trinomys*.

INTRODUCTION

In his monograph "Speciation in Brazilian spiny rats (Genus *Proechimys*, Family Echimyidae)", MOOJEN (1948) established the foundations for the study of the taxonomy of spiny rats of the genus *Proechimys* Allen, 1899, distributed in Brazil. MOOJEN (1948) assessed morphological variation in craniodental and pelage traits and used this evidence to define taxa at the subgeneric, specific, and subspecific levels. Based primarily on the condition of the mainfold

[1] Submitted on May 26, 2004. Accepted on Janeiro 4, 2005.
[2] Universidade Federal do Rio de Janeiro, IB, Depto. de Zoologia. 21941-590, Rio de Janeiro, RJ, Brasil.
[3] Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).
[4] E-mail: pessoa@acd.ufrj.br.
[5] Instituto Osvaldo Cruz, Depto. de Entomologia. Av. Brasil, 4365, Manguinhos, 21045-900, Rio de Janeiro, RJ, Brasil.
[6] Universidade Estadual de Campinas, IB, Depto. de Parasitologia, IB. 13083-970, Campinas, SP, Brasil.

in the molariform teeth and on the patterns of geographic distribution, MOOJEN (1948) recognized two subgenera, *Proechimys*, distributed in the Amazon and Central Brazil, and *Trinomys* Thomas, 1921, distributed in eastern Brazil. Within each subgenus, taxa at the species and subspecies levels were characterized by a combination of traits in cranial character complexes, involving mainly the shape and configuration of the postorbital process of zygoma and the incisive foramen and patterns of pelage color. MOOJEN (1948) constructed his taxonomic structure on the basis of overall morphological similarity, following the prevailing theoretical paradigm of his time (SIMPSON, 1961) and, therefore, no phylogenetic information content should be expected or inferred from his taxonomic structure. MOOJEN's (1948) taxonomic structure and the diagnoses at the morphological, organismal level have served as the primary source for the identification of spiny rats in eastern Brazil and also as the basis for the discovery of new taxa (PESSÔA, OLIVEIRA & REIS, 1992; PESSÔA & REIS, 1993; REIS & PESSÔA, 1995; ROCHA, 1995; LARA, PATTON & HINGST-ZAHER, 2002).

Recently, evidence from molecular sequences sampled from the mitochondrial genome indicated that the subgenera *Trinomys* and *Proechimys*, as conceived and defined by MOOJEN (1948) on the basis of dental traits and distribution patterns, do not share a most recent common ancestor (LARA, PATTON & SILVA, 1996; LARA & PATTON, 2000; LEITE & PATTON, 2002). As a corollary to the molecular approach, the subgenera *Proechimys* and *Trinomys* were granted genus status. Furthermore, the specific and infraspecific taxonomic structure for *Trinomys* is currently based on the phylogenetic relationships of haplotype lineages, derived from 726 base pairs of the cytochrome *b* gene in the mitochondrial genome (LARA & PATTON, 2000). Three major clades are recognized in the molecular taxonomic structure (LARA & PATTON, 2000): the first clade includes the monotypic taxa *Trinomys dimidiatus* (Günther, 1877), *Trinomys iheringi* Thomas 1911, *Trinomys mirapitanga* Lara, Patton & Hingst-Zaher, 2002, and the polytypic *Trinomys gratiosus* Moojen, 1948; the second clade includes the monotypic *Trinomys yonenagae* Rocha, 1995, *Trinomys paratus* Moojen, 1948, *Trinomys eliasi* Pessôa and Reis, 1993, and the polytypic *Trinomys setosus* Desmarest 1817; and the third clade is represented only by *Trinomys albispinus* (Is. Geoffroy, 1838). These molecular clades also have morphological cohesion as defined in LARA & PATTON (2000). One taxon originally described in MOOJEN's (1948) taxonomic structure, *Proechimys iheringi panema* Moojen, 1948, and another described more recently, *Proechimys moojeni* Pessôa, Oliveira & Reis, 1992, have not been sampled for molecular sequences.

Whereas data on morphological and molecular variation have become available for most taxa in the genus *Trinomys*, information on chromosomal variation has been available only for four taxa of *Trinomys*, namely, *T. albispinus* (LEAL-MESQUITA *et al.*, 1992), and *T. yonenagae* (LEAL-MESQUITA *et al.*, 1992) from Bahia, *T. iheringi* (YONENAGA-YASSUDA *et al.*, 1985) from São Paulo, and *T. gratiosus gratiosus* Moojen, 1948 (ZANCHIN, 1988) from Espírito Santo. Here we focus our attention on chromosome morphology and characterize the chromosomal complement of additional three taxa of the genus *Trinomys* from Rio de Janeiro and São Paulo. We identified the taxa of interest by diagnostic features of the postorbital process of zygoma, incisive foramen, and pelage (MOOJEN, 1948; PESSÔA & REIS, 1992a) and of the baculum (PESSÔA & REIS, 1992b; PESSÔA, REIS & PESSÔA, 1996). The entities thus defined bear names in the morphological taxonomic structure (MOOJEN, 1948), which we then mapped onto names in the current molecular taxonomic structure (LARA & PATTON, 2000). Finally, we use the names and implied relationships available in the molecular taxonomic structure to convey information on chromosomal morphology and variation. The primary aim is to evaluate whether chromosomal morphology can be useful as markers in the diagnosis of taxa of spiny rats of eastern Brazil.

MATERIAL AND METHODS

Morphological diagnoses of *Trinomys* taxa

All specimens karyotyped in this study were deposited as skins and skulls as vouchers in the mammal collection of Museu Nacional - Rio de Janeiro (MN). Morphological diagnoses provided below for the *Trinomys* taxa are based on MOOJEN (1948), PESSÔA & REIS (1992a,b) and PESSÔA, REIS & PESSÔA (1996).

Proechimys dimidiatus – Maxillary part of vomerine septum wide and strong, vomer not visible ventrally; postorbital process of zygoma formed entirely by squamosal; proximal and distal ends of

baculum round, lateral indentation on mid-shaft; setiforms on mid-dorsal region gradually blackening toward tip but interrupted by Ochraceous-Buff subapical zone, setiforms on outer thighs white on basal half then gradually becoming gray on middle part and finally Light Ochraceus-Buff on distal third, or with tip blackish and Ochraceous-Buff subapical zone. The name *P. dimidiatus* in the morphological taxonomic structure (MOOJEN, 1948) maps onto *Trinomys dimidiatus* in the molecular taxonomic structure (LARA & PATTON, 2000). The following specimens of *T. dimidiatus* were analyzed: Rio Bonito, Rio de Janeiro (MN67553, MN67554), and Ubatuba, São Paulo (MN67550-67552).

Proechimys iheringi bonafidei – Maxillary part of vomerine septum long and thin, vomer not visible ventrally; post-orbital process of zygoma formed mostly by squamosal; proximal end of baculum square and distal end convex, lateral indentation on mid-shaft; setiforms on mid-dorsal region gradually blackening toward tip but interrupted by Ochraceous-Buff subapical zone, setiforms on outer thighs gray basally, gradually blackening toward the tip but interrupted by Ochraceous-Buff subapical zone, only a short blackened tip, setiforms on outer thighs gray basely gradually blackening toward tip, but interrupted by a Cinnamon-Buff subapical zone. The name *P. iheringi bonafidei* in the morphological taxonomic structure (MOOJEN, 1948) maps onto *T. gratiosus bonafidei* in the molecular taxonomic structure (LARA & PATTON, 2000). The following specimens of *T. gratiosus bonafidei* from Fazenda Boa Fé, Rio Bengalas, Teresópolis, Rio de Janeiro, were analyzed (MN43807, MN43821 and MN54153).

Proechimys iheringi eliasi – Maxillary part of vomerine septum narrow and short, vomer visible ventrally between the premaxillary and maxillary parts of vomerine septum; post-orbital process of zygoma formed mostly by jugal; proximal end of baculum tapered and distal end straight, lateral indentation on proximal third of shaft; setiforms on mid-dorsal region gradually blackening toward tip but not interrupted Ochraceous-Buff subapical zone. The name *P. iheringi eliasi* in the morphological taxonomic structure (MOOJEN, 1948) maps onto *T. eliasi* in the molecular taxonomic structure (LARA & PATTON, 2000). One specimen of *T. eliasi* from Restinga da Barra de Maricá, Rio de Janeiro, was analyzed (MN43822).

Chromosomal analysis

The nine specimens of *Trinomys* listed earlier in the text were studied morphologically and cytogenetically. A total of 446 metaphase cells were analyzed.

Cytogenetic analyses were done on mitotic metaphase chromosomes from bone marrow according FORD & HAMERTON (1956) with modifications. The chromosomes were stained with Giemsa and classified following LEVAN, FREDGA & SANDBERG (1964). The metacentric and submetacentric chromosomes are considered biarmed and subtelocentric and acrocentric ones are uniarmed.

RESULTS

Cytogenetic analyses of one female and one male of *T. dimidiatus* collected in Rio Bonito and two females and one male collected in Ubatuba, revealed a diploid number of 2n=60 and FN=116. This karyotype comprises 29 pairs of metacentric and submetacentric autosomes. Pair 10 has a secondary constriction on the long arm, probably coincident with the nucleolar organizer regions (NORs). The X chromosome is a large submetacentric (corresponding to the second pair of the complement) and the Y is a metacentric intermediary to pairs 20 and 21 (Fig.1a, b).

One female and two males of *T. g. bonafidei* collected in Teresópolis had a diploid number of 2n=56 and FN=108. The karyotype comprises 27 pairs of metacentric and submetacentric autosomes. Pair 10 showed a secondary constriction on the long arm, probably coincident with the NORs. The X-chromosome is a large submetacentric (corresponding to the second pair of the complement) and the Y is a metacentric intermediary to pairs 20 and 21 (Fig.2).

Cytogenetic analyses of one male of *T. eliasi* collected in Maricá showed a diploid number of 2n=58 (FN=112) with 28 pairs of metacentric and submetacentric autosomes. Pair ten also had a secondary constriction on the long arm, probably coincident with the NORs. The X chromosome is a large submetacentric (corresponding to the second pair of the complement) and the Y is a metacentric intermediary to pairs 21 and 22 (Fig.3). Diploid and fundamental numbers are summarized in table 1.

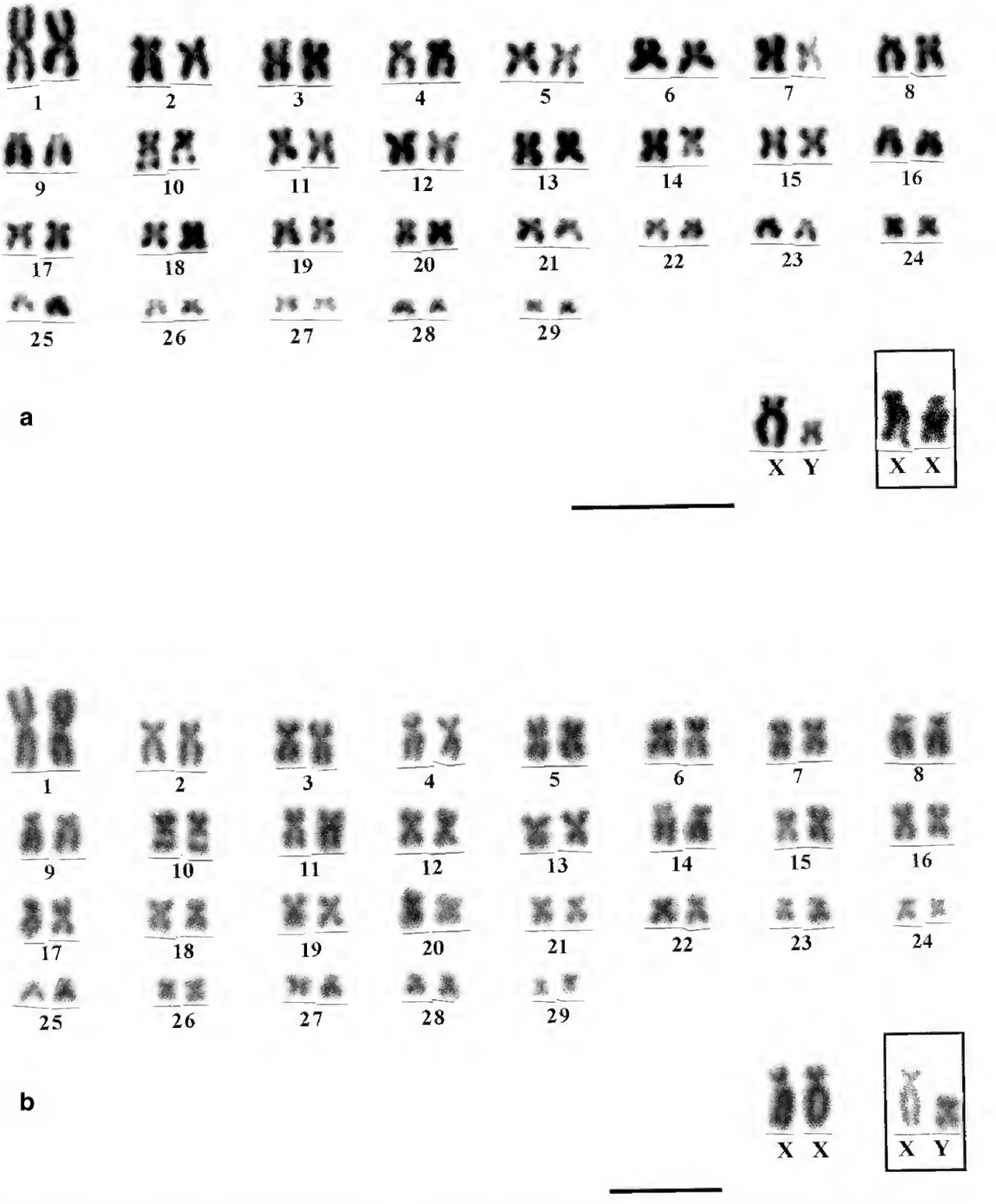

Fig.1- (a) karyotype of male (MN67553) *Trinomys dimidiatus* (2n=60, FN=116) from Rio Bonito, RJ. Pair ten shows a secondary constriction. In the inset, sex chromosomes of a female (MN 67554); (b) karyotype of female (MN67551) *T. dimidiatus* (2n=60, FN=116) from Ubatuba, SP. Pair ten shows a secondary constriction. In the inset, sex chromosomes of a male (MN67552). Scale bars = 10μm.

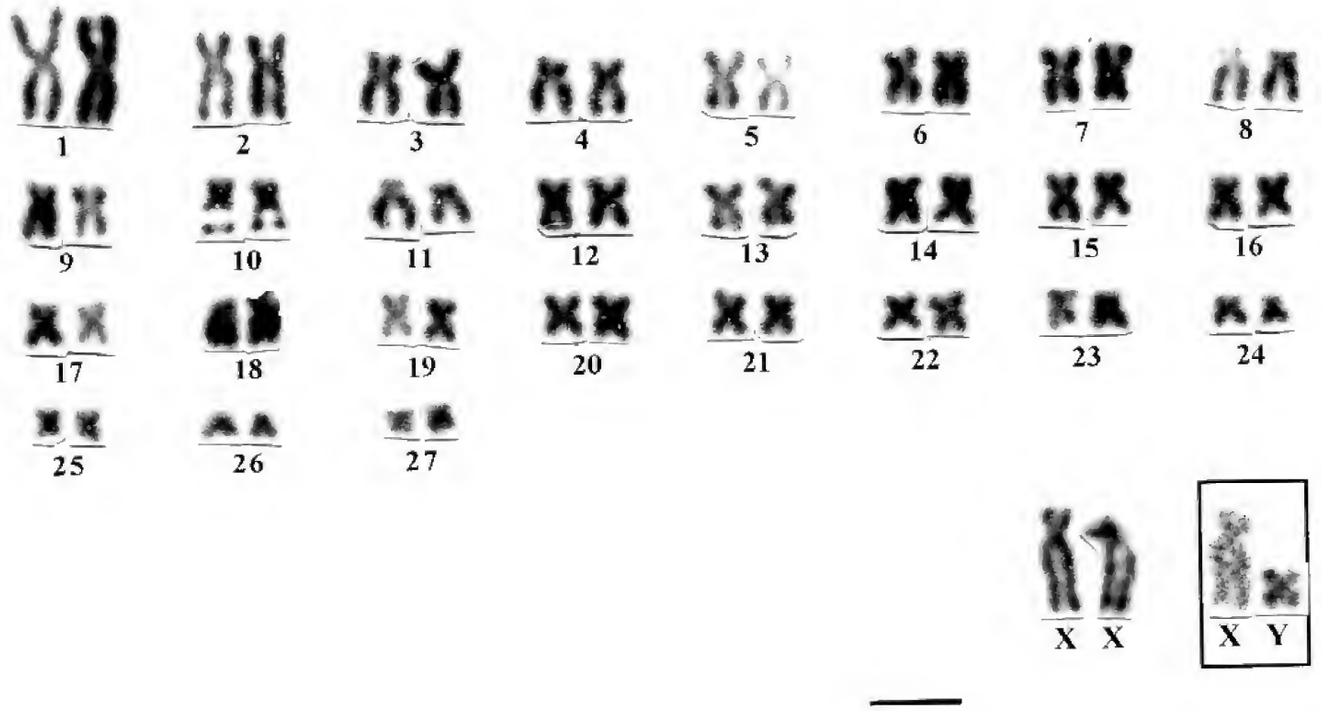

Fig.2- Karyotype of female (MN43807) *Trinomys gratiosus bonafidei* (2n=56, FN=108) from Teresópolis, RJ. Pair ten shows a secondary constriction. In the inset, sex chromosomes of a male (MN54153).

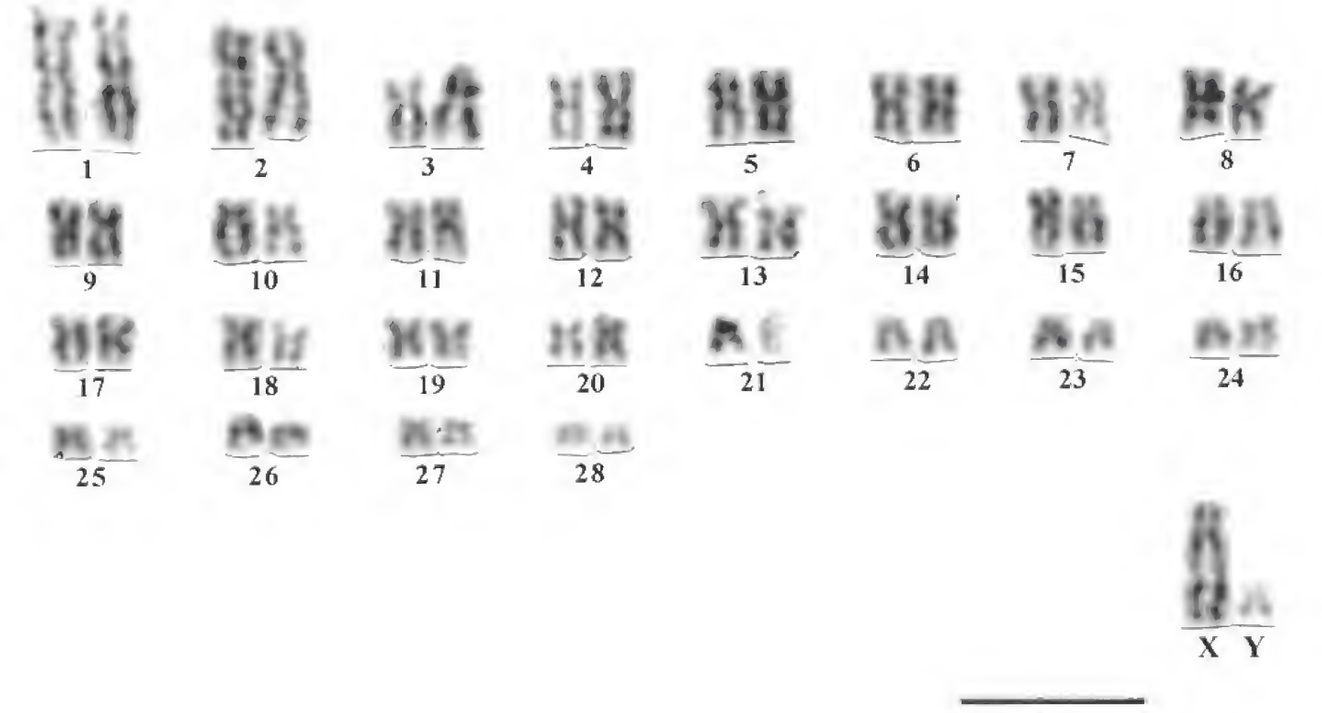

Fig.3- Karyotype of male (MN43822) *Trinomys eliasi* (2n=58, FN=112) from Maricá, RJ. Pair ten shows a secondary constriction. Scale bars = 10μm.

Table 1. Taxa of the genus *Trinomys*, mitochondrial clades, diploid and fundamental numbers, and localities of specimens examined.

SPECIES	MITOCHONDRIAL CLADES	2n	FN	LOCALITY	REFERENCE
T. dimidiatus	Clade 1	60	116	Ubatuba-SP	Present study
T. dimidiatus	Clade 1	60	116	Rio Bonito-RJ	Present study
T. gratiosus	Clade 1	56	108	Venda Nova	ZANCHIN, 1988
T. g. bonafidei	Clade 1	56	108	Teresópolis-RJ	Present study
T. iheringi	Clade 1	61-65	116	4 localities-SP	YONENAGA-YASSUDA *et al.*, 1985
T. eliasi	Clade 2	58	112	Maricá-RJ	Present study
T. albispinus	Clade 3	60	116	Morro do Chapéu-BA	LEAL-MESQUITA *et al.*, 1992

DISCUSSION

As outlined in the introduction, our primary aim was to evaluate whether chromosomal morphology provides markers that contribute to the diagnosis of taxa in the genus *Trinomys*. The specimens analyzed were identified on the basis of craniodental, pelage, and bacular traits as, *T. g. bonafidei*, *T. eliasi* and *T. dimidiatus*, and it was demonstrated here that these taxa do differ in their diploid and fundamental numbers and, therefore, can be diagnosed on a chromosomal basis. The implications and relevance of these new data on chromosomal morphology for the taxonomy and systematics of *Trinomys* must be evaluated in the context of the implied relationships derived from the molecular taxonomic structure and of the limited information available on distribution records.

Trinomys dimidiatus is included in clade 1 of the molecular taxonomic structure (LARA & PATTON, 2000) and has so far been thought to be restricted in distribution to the State of Rio de Janeiro (MOOJEN, 1948). The specimens analyzed here from the locality of Ubatuba were identified on the basis of craniodental, pelage, and bacular traits as *T. dimidiatus*, extending the range of this species by at least 100km south into the State of São Paulo. *Trinomys dimidiatus* and *T. iheringi* mitochondrial haplotypes share a most recent common ancestor as indicated by the molecular phylogeny (LARA & PATTON, 2000). The normal complement of *T. dimidiatus* (2n=60 and FN=116) from the localities of Rio Bonito (Rio de Janeiro) and Ubatuba (São Paulo) is identical to that of *T. iheringi* described from the localities of Casa Grande, Ubatuba, and Iguape in the State of São Paulo (YONENAGA-YASSUDA *et al.*, 1985). The normal complements are therefore not useful as a marker to diagnose either taxon. On the other hand, the Y chromosome was shown here to be metacentric in *T. dimidiatus* whereas it is submetacentric in *T. iheringi* (YONENAGA-YASSUDA *et al.*, 1985). Furthermore, individuals of *T. iheringi* in the populations sampled so far always show variable numbers (from 1 to 5) of supernumerary chromosomes (YONENAGA-YASSUDA *et al.*, 1985). Thus in this case, the morphology of the Y submetacentric chromosome and the presence of supernumerary chromosomes are useful markers to differentially diagnose *T. dimidiatus* and *T. iheringi*.

The second taxon for which chromosomal data are provided here, *T. g. bonafidei*, is known only from the type locality at Fazenda Boa Fé and a few other nearby sites in the locality of Teresópolis, State of Rio de Janeiro. This taxon shares recency of common ancestry with mitochondrial haplotypes of several geographical populations of *T. g. gratiosus* (LARA & PATTON, 2000), and together with the sister taxa *T. dimidiatus* and *T. iheringi* comprise clade 1 of the molecular taxonomic structure (LARA & PATTON, 2000). *Trinomys g. bonafidei* and *T. dimidiatus* both occur in Teresópolis in the State of Rio de Janeiro, although apparently each taxon locally occurs at different altitudes and is associated with distinct plant communities (MOOJEN, 1948). Both taxa can be uniquely diagnosed on a chromosomal basis since *T. g. bonafidei* has a chromosomal complement of 2n=56 and FN=108 and the *T. dimidiatus* complement is 2n=60 and FN=116.

The third taxon sampled for chromosomal data is

T. eliasi from the type locality, which is included in clade 2 of the molecular taxonomic structure (LARA & PATTON, 2000). *Trinomys eliasi* was originally described from the coastal sand dunes in the locality of Maricá in the State of Rio de Janeiro (PESSÔA & REIS, 1993). Until recently, *T. eliasi* was known only from the type locality and this evidence might suggest that this species is strictly associated with coastal sand dunes. Nevertheless, *T. eliasi* was later found to occur inland in the locality of Silva Jardim in the State of Rio de Janeiro, where the habitat is lowland seasonal forest (specimens deposited in the Museu Nacional; L.M.PESSÔA, personal data). Both of the localities, Maricá and Silva Jardim, where *T. eliasi* is currently known to occur are close (ca.30km) to Rio Bonito where one of our samples of *T. dimidiatus* was collected. Again, both taxa can be diagnosed on the basis of the normal chromosomal complement, as *T. eliasi* has 2n=58 and FN=112 and *T. dimidiatus* has 2n=60 and FN=116.

Since Moojen's seminal publication, significant progress has been made towards the understanding of the taxonomy and systematics of spiny rats of eastern Brazil. New taxa have been described and new information has become available regarding cranial quantitative variation and bacular morphology for most taxa (PESSÔA & REIS, 1992a,b; PESSÔA, OLIVEIRA & REIS, 1992; PESSÔA & REIS, 1993; REIS & PESSÔA, 1995; ROCHA, 1995; LARA, PATTON & HINGST-ZAHER, 2002). In addition, molecular data have allowed the inference of phylogenetic relationships (LARA & PATTON, 2000). Chromosomal information was limited however to very few taxa. Chromosomal information is now available for *T. dimidiatus*, *T. gratiosus bonafidei*, *T. eliasi* (this study) and also for *T. gratiosus gratiosus* (ZANCHIN, 1988), *T. albispinus* (LEAL-MESQUITA *et al.*, 1992), *T. yonenagae* (LEAL-MESQUITA *et al.*, 1992), and *T. iheringi* (YONENAGA-YASSUDA *et al.*, 1985). Furthermore, chromosomal data for *T. moojeni* and *T. setosus* are being presented in this volume by CORRÊA *et al.* (2005).

Given the availability of detailed information on morphological variation, the data on chromosomal complements and the molecular taxonomic structure, attention must now be directed to the definition of distribution limits of each taxon. Unfortunately, knowledge of the geographic range and distribution limits of recognized taxa has not experienced much progress and many of taxa characterized or described by MOOJEN (1948), and those described after his review, are known only from the type locality and few studies have extended the distribution of known taxa (see PESSÔA *et al.*, 1993, and present study). Evidently, detailed knowledge and characterization of the geographic range and distribution limits of recognized natural units are of fundamental importance to understand the processes that generated the observed patterns of diversity. We hope that the data presented in the present paper will contribute to this endeavor.

ACKNOWLEDGEMENTS

The authors thank curators at the Museu Nacional - Rio de Janeiro for allowing access to specimens. Stella M. S. Franco kindly helped with the handling of specimens. We are also indebted to Stephen Hyslop for reviewing the English of the manuscript. This work was funded by grants from Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). IBAMA (02022002209/99-16) issued permits for the collection of specimens examined in this work.

LITERATURE CITED

CORRÊA, M.M.O.; LOPES, M.O.G.; CÂMARA, E.V.C.; OLIVEIRA, L.C. & PESSÔA, L.M., 2005. The karyotype of *Trinomys moojeni* Pessôa, Oliveira & Reis, 1992, and *Trinomys setosus elegans* (Lund, 1841) (Rodentia: Echimyidae), from Minas Gerais, eastern Brazil. **Arquivos do Museu Nacional**, Rio de Janeiro, **63**:169-174.

FORD, C.E. & HAMERTON, J.L., 1956. A colchicine hypotonic citrate squash sequence for mammalian chromosomes. **Stain Technology**, Louisville, **31**:247-251.

LARA, M.C.; PATTON, J.L. & SILVA, M.N.F., 1996. The simultaneous diversification of South American echimyid rodents (Hystricognathi) based on complete cytochrome *b* sequences. **Molecular Phylogenetics and Evolution**, New York, **5**:403-413.

LARA, M.C. & PATTON, J.L., 2000. Evolutionary diversification of spiny rats (genus *Trinomys*, Rodentia: Echimyidae) in the Atlantic forest of Brazil. **Zoological Journal of the Linnean Society,** London, **130**:661-686.

LARA, M.C.; PATTON, J.L. & HINGST-ZAHER, E., 2002. *Trinomys mirapitanga*, a new species of spiny rat (Rodentia: Echimyidae) from the Brazilian Atlantic Forest. **Zeitshrift für Säugetierkunde**, Jena, **67**:233-242.

LEAL-MESQUITA, E.R.; YONENAGA-YASSUDA, Y.; CHU, T.H. & ROCHA, P.L.B., 1992. Chromosomal characterization and comparative cytogenetic analysis of two species of *Proechimys* (Echimyidae, Rodentia) from the Caatinga domain of the State of Bahia, Brazil. **Caryologia**, Florence, **45** (2):197-212.

LEITE, Y.L.R. & PATTON, J.L., 2002. Evolution of South American spiny rats (Rodentia, Echimyidae): the star-phylogeny hypothesis revisited. **Molecular Phylogenetics and Evolution**, New York, **25**:455-464.

LEVAN, A.; FREDGA, K. & SANDBERG, A.A., 1964. Nomenclature for centromeric position on chromosomes. **Hereditas**, Lund, **52**:201-220.

MOOJEN, J., 1948. Speciation in the Brazilian spiny rats (genus *Proechimys*, family Echimyidae). **University of Kansas Publications of the Museum of Natural History**, Lawrence, **1**:301-406.

PESSÔA, L.M. & REIS, S.F., 1992a. An analysis of morphological discrimination between *Proechimys iheringi* and *Proechimys dimidiatus* (Rodentia: Echimyidae). **Zoologischer Anzeiger**, Jena, **228**:189-200.

PESSÔA, L.M. & REIS, S.F., 1992b. Bacular variation in the subgenus *Trinomys*, genus *Proechimys* (Rodentia: Echimyidae). **Zeitschrift für Säugetierkunde**, Jena, **57**:100-102.

PESSÔA, L.M.; OLIVEIRA, J.A. & REIS, S.F., 1992. A new species of spiny rat genus *Proechimys*, subgenus *Trinomys* (Rodentia: Echimyidae). **Zeitschrift für Säugetierkunde**, Jena, **57**:39-46.

PESSÔA, L.M. & REIS, S.F., 1993. A new subspecies of *Proechimys iheringi* Thomas from Rio de Janeiro (Rodentia: Echimyidae). **Zeitschrift für Säugetierkunde**, Jena, **58**:181-190.

PESSÔA, L.M.; REIS, S.F.; PASSAMANI, M. & MENDES, S., 1993. Notes on the distribution of *Proechimys iheringi denigratus*, *Proechimys iheringi paratus* and *Proechimys iheringi gratiosus* in eastern Brazil (Rodentia: Echimyidae). **Zoologischer Anzeiger**, Jena, **231**:21-23.

PESSÔA, L.M.; REIS, S.F. & PESSÔA, M.F., 1996. Bacular variation and systematics of *Proechimys iheringi*, subgenus *Trinomys* (Rodentia: Echimyidae). **Studies on Neotropical Fauna and Environment**, Lisse, **31**:129-132.

REIS, S.F. & PESSÔA, L.M., 1995. *Proechimys albispinus minor*, a new subspecies of spiny rat from the State of Bahia, northeastern Brazil (Rodentia: Echimyidae). **Zeitschrift für Säugetierkunde**, Jena, **60**:237-242.

ROCHA, P.L.B., 1995. *Proechimys yonenagae*, a new species of spiny rat (Rodentia: Echimyidae) from fossil sand dunes in the Brazilian Caatinga. **Mammalia**, Paris, **59**:537-549.

SIMPSON, G.G., 1961. **Principles of Animal Taxonomy**. New York: Columbia University Press. viii, 247p.

SOUZA, M.J. & YONENAGA-YASSUDA, Y., 1982. Chromosomal variability of sex chromosomes and NOR's in *Thrichomys apereoides* (Rodentia, Echimyidae). **Cytogenetics and Cell Genetics**, Basel, **33**:197-203.

YONENAGA-YASSUDA, Y.; SOUZA, M.J.; KASAHARA, S.; L'ABBATE, M. & CHU, H.T., 1985. Supernumerary system in *Proechimys iheringi iheringi* (Rodentia, Echimydae) from the State of São Paulo, Brazil. **Caryologia**, Florence, **38**:179-194.

ZANCHIN, N.I.T., 1988. **Estudos cromossômicos em orizominos e equimídeos da Mata Atlântica**. Porto Alegre. 162p. M.Sc. Dissertation, Universidade Federal do Rio Grande do Sul.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.169-174, jan./mar.2005
ISSN 0365-4508

THE KARYOTYPES OF *TRINOMYS MOOJENI* (PESSÔA, OLIVEIRA & REIS, 1992) AND *TRINOMYS SETOSUS ELEGANS* (LUND, 1841) (RODENTIA, ECHIMYIDAE) FROM MINAS GERAIS, EASTERN BRAZIL [1]

(With 2 figures)

MARGARET MARIA DE O. CORRÊA [2]
MARIA OLÍMPIA G. LOPES [3]
EDELTRUDES V. C. CÂMARA [3]
LEONARDO C. OLIVEIRA [3]
LEILA MARIA PESSÔA [2, 4]

ABSTRACT: Two new karyotypes of species in the genus *Trinomys* are described from specimens collected recently in Morro do Pilar and Santa Bárbara, Minas Gerais State (MG), Brazil. *Trinomys moojeni* from Morro do Pilar had 2n=56 and FN=106 and *T. setosus elegans* from Santa Bárbara had 2n=56 and FN=104. Besides the differences in FN, different morphologies in the sex chromosomes also had been detected. These results at chromosomal level corroborate findings from the mitochondrial genome that suggest that *T. s. elegans* belongs to a clade composed by *T. s. setosus* and *T. s. denigratus*. The chromosomal data corroborated the inclusion of *T. moojeni* in this clade, as previously suggested on the basis of cranial morphology evidence.

Key words: *Trinomys moojeni*, *Trinomys setosus elegans*, cytogenetic data, cranial and bacular characters, qualitative analysis, Minas Gerais.

RESUMO: Os cariótipos de *Trinomys moojeni* (Pessôa, Oliveira & Reis, 1992) e de *Trinomys setosus elegans* (Lund, 1841) (Rodentia, Echimyidae) de Minas Gerais, leste do Brasil.

Dois novos cariótipos são descritos para espécies do gênero *Trinomys* com base em coletas recentes nos municípios de Morro do Pilar e Santa Bárbara no Estado de Minas Gerais (MG). *Trinomys moojeni* de Morro do Pilar apresentou o cariótipo com número diplóide (2n) igual a 56 e número fundamental (NF) igual a 106 e *T. setosus elegans* de Santa Bárbara apresentou 2n=56 e NF=104. Além da diferença nos valores de NF, diferenças na morfologia cromossômica do par sexual também foram detectadas. Os resultados no nível cromossômico corroboram aqueles encontrados com base no genoma mitocondrial, que evidenciou que *T. s. elegans* pertence a um clado composto por *T. setosus setosus* e *T. s. denigratus*. Os dados cromossômicos corroboraram a inclusão de *T. moojeni* neste clado, como previamente sugerido com base em evidências da morfologia craniana.

Palavras-chave: *Trinomys moojeni*, *Trinomys setosus elegans*, dados citogenéticos, caracteres cranianos e baculares, análise qualitativa, Minas Gerais.

INTRODUCTION

Trinomys moojeni (Pessôa, Oliveira & Reis, 1992), was described on the basis of a series of seven individuals collected in August 1954 by Professor Cory T. Carvalho in Mata Dr. Daniel and Boca da Mata (Conceição do Mato Dentro, Minas Gerais, Brazil), during an expedition to the Serra do Cipó, Minas Gerais. This material was later deposited in the mammal collection of the Museu Nacional - Rio de Janeiro, and originally identified on the labels as "*Proechimys setosus*"(Desmarest, 1817).

When analyzing cranial and bacular morphology in *Trinomys* Thomas, 1921, PESSÔA & REIS (1992) found that the baculum was useful as a morphological marker for the species described in the genus. A detailed comparison of the cranial

[1] Submitted on June 14, 2004. Accepted on January 6, 2005.
[2] Universidade Federal do Rio de Janeiro, IB, Departamento de Zoologia, 21941-590, Rio de Janeiro, RJ, Brazil. E-mail: margaret@biologia.ufrj.br.
[3] Pontifícia Universidade Católica de Minas Gerais. Rua Dom José Gaspar, 500, Coração Eucarístico, 30535-610, Belo Horizonte, MG, Brazil.
[4] Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

and bacular morphology of the Serra do Cipó sample and of specimens of *Trinomys setosus elegans* (Lund, 1841) from Peti, MG, deposited at the Universidade Federal de Minas Gerais, enabled PESSÔA, OLIVEIRA & REIS (1992) to describe the sample as a new species, *T. moojeni*. Cranial and bacular structures together with pelage traits were used to distinguish *T. moojeni* from the other species within *Trinomys* then a subgenus of *Proechimys* Allen, 1899.

No further specimens of *T. moojeni* were found for half a century, until PASCHOAL *et al.* (2004) collected new individuals of this species during a field trip to Morro do Pilar, 20km from Conceição do Mato Dentro, near to the type locality of the species. These finds provided an opportunity to investigate the diploid number (2n) and fundamental number (FN) of *T. moojeni*.

Trinomys elegans was originally described as *Echimys elegans* Lund, 1841, from Lagoa Santa, Minas Gerais. MOOJEN (1948), in his standard taxonomic structure of *Proechimys*, considered *P. setosus* to be polytypic with two subspecies: *P. setosus setosus* and *P. setosus elegans*. In a recent study using mitochondrial haplotypes of individuals from Minas Gerais, LARA & PATTON (2000) kept *T. setosus* as polytypic and included a third subspecies, *T. s. denigratus* Moojen, 1948.

During a recent expedition to Santa Bárbara, located approximately 100km from Lagoa Santa, State of Minas Gerais, four *Trinomys* specimens were collected. Detailed observation of their pelage and cranial and bacular morphology led to their identification as *T. s. elegans*. These specimens were also studied cytogenetically in order to investigate their diploid and fundamental numbers and to describe their karyotype.

The objective here is to describe the karyotypes of *T. moojeni* and *T. s. elegans* from Morro do Pilar and Santa Bárbara, State of Minas Gerais. Specifically we want to investigate whether karyotype characters can be used to diagnose the two species and whether they allow these two species to be assigned to the clades within *Trinomys* recently defined on the basis of mitochondrial haplotypes and cranial morphology (LARA & PATTON, 2000).

MATERIAL AND METHODS

Two specimens of *Trinomys* collected in Morro do Pilar, Serra do Cipó, Minas Gerais (19°12'56"S-43°22'35"W, 622m) (PASCHOAL *et al.*, 2004) were compared with the type series of *T. moojeni* in the mammal collection of the Museu Nacional, Rio de Janeiro (MN), and were identified as belonging to the same species. The voucher material consists of one skull and one skull and skin, and is lodged in the mammal collection of the Museu de Ciências Naturais da PUC, Minas Gerais (specimen numbers MCN-M 971 and MCN-M 985, respectively). Four *Trinomys* specimens collected in Santa Bárbara (19°53'19"S-43°22'26"W, 721m) were diagnosed as *T. setosus elegans* on the basis of pelage, and cranial and bacular morphology, and are kept in the mammal collection of the Museu Nacional (specimen numbers MN 68152, MN 68153, MN 68154, MN 68155).

Cytogenetic analyses were performed on mitotic metaphase chromosomes from bone marrow of one male *T. moojeni* (MCN-M 985) and one male and two females *T. s. elegans* (MN 68152, 68153 and 68154, respectively), following FORD & HAMERTON (1956) with modifications. Chromosomes were stained with Giemsa and classified according to LEVAN, FREDGA & SANDBERG (1964). A total of 47 metaphase cells of *T. moojeni* and 62 of *T. s. elegans* were analyzed. Metacentric, submetacentric, and subtelocentric chromosomes are considered biarmed and acrocentric ones uniarmed.

RESULTS

Cytogenetic analyses of *T. moojeni* revealed a diploid number 2n=56 and fundamental number FN=106. This karyotype comprises 26 pairs of metacentric, submetacentric, and subtelocentric autosomes and one pair of acrocentric autosomes (pair 27). The X chromosome is a large submetacentric corresponding in size to pair 2. The Y chromosome is a medium-sized metacentric intermediate between pairs 15 and 16 (Fig.1).

Trinomys setosus elegans displayed 2n=56 and FN=104. This karyotype consists of 25 pairs of metacentric, submetacentric, and subtelocentric autosomes and two pairs of acrocentric autosomes (pairs 26 and 27). The X chromosome is a large acrocentric corresponding in size to the third pair. The Y chromosome is acrocentric and one of the smallest chromosomes in the set (Fig.2).

Fig.1- Karyotype of male of *Trinomys moojeni* (MCN-M 985) (2n=56, FN=106) from Morro do Pilar, MG. Scale bar = 10μm.

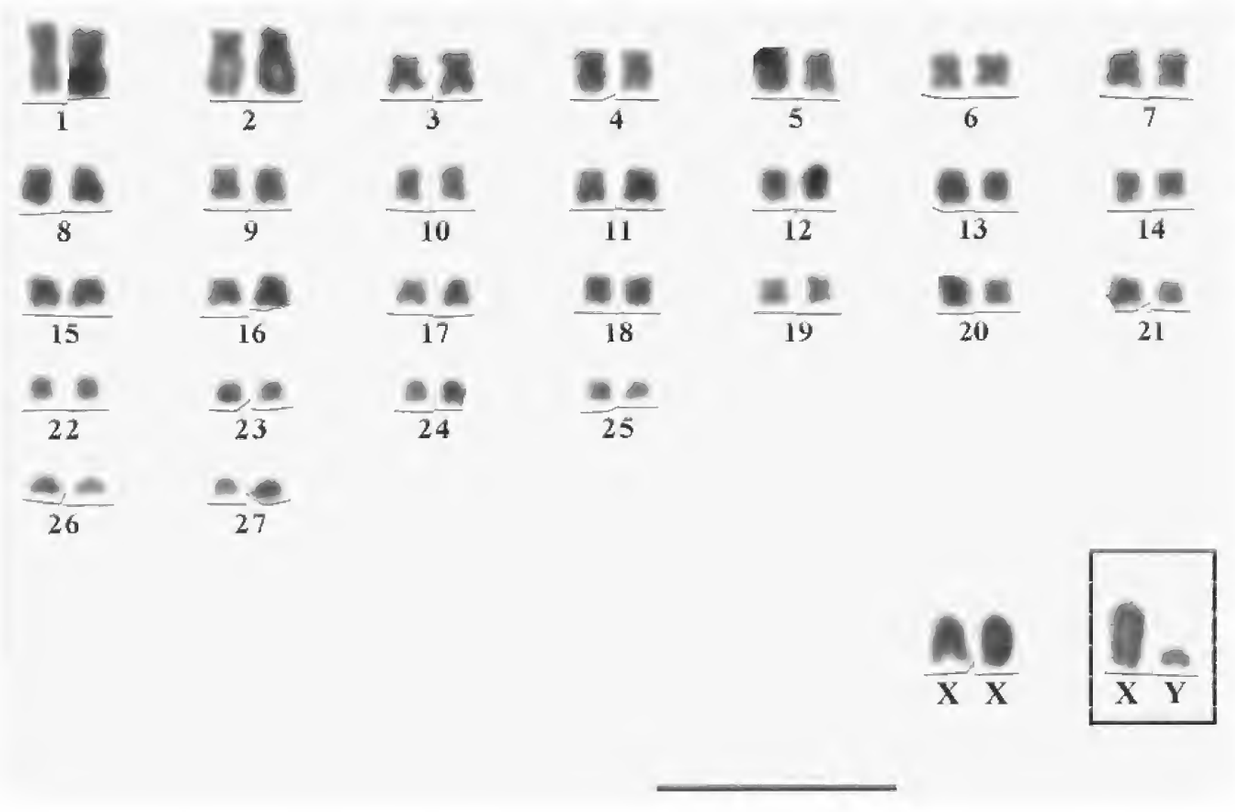

Fig.2- Karyotype of female of *Trinomys s. elegans* (MN 68153) (2n=56, FN=104) from Santa Bárbara, MG, and XY (inset) of a male specimen (MN 68152). Scale bar = 10μm.

Table 1. Cytogenetic data for taxa in the genus *Trinomys* and association with mitochondrial clades.

TAXA	MITOCHONDRIAL CLADES	2n	FN	M-SM	ST-A	X	Y	LOCALITY	REFERENCE
T. dimidiatus	Clade1	60	116	29	-	SM	M	Ubatuba SP	PESSÔA *et al.*, 2005
T. dimidiatus	Clade1	60	116	29	-	SM	M	Rio Bonito RJ	PESSÔA *et al.*, 2005
T. iheringi	Clade1	61-65	116	29	-	SM	SM	four localities SP	YONENAGA-YASSUDA *et al.*, 1985
T. g. gratiosus	Clade1	56	108	27	-	SM	-	Venda Nova ES	ZANCHIN, 1988
T. g. bonafidei	Clade1	56	108	27	-	SM	M	Teresópolis RJ	PESSÔA *et al.*, 2005
T. yonenagae	Clade2	54	104	26	-	A	M	Ibiraba BA	LEAL-MESQUITA *et al.*, 1992
T. eliasi	Clade2	58	112	28	-	SM	M	Maricá RJ	PESSÔA *et al.*, 2005
T. s. elegans	Clade 2	56	104	25	2	A	A	MG	Present study
T. moojeni	"Clade2"	56	96	21	6	SM	M	Morro do Pilar MG	Present study
T. albispinus	Clade3	60	116	29	-	SM	A	Morro do Chapéu BA	LEAL-MESQUITA *et al.*, 1992

(2n) diploid number, (FN) fundamental number, (X) X-chromosome, (Y) Y-chromosome, (M) metacentric, (SM) submetacentric, (ST) subtelocentric, (A) acrocentric.

DISCUSSION

THOMAS (1921) described *Trinomys* as a subgenus of *Proechimys* on the basis of the number of counterfolds in the upper molariform teeth: four in the subgenus *Proechimys* and three in the subgenus *Trinomys*. The subgenus *Proechimys* encompassed all species occurring in Central America, the Amazon Basin, and Central Brazil, as well as one species, *P. iheringi* Thomas, 1911, from the Atlantic forest in south-eastern Brazil (THOMAS, 1921). MOOJEN (1948) observed, however, that in all the forms allocated by Thomas to the subgenus *Proechimys*, except for *P. iheringi*, the main fold in the molariform teeth is short, whereas in the remaining forms this fold extends entirely across the occlusal surface of the tooth. MOOJEN (1948) used primarily this character to define each of the subgenera, and not the number of cheekteeth counterfolds as suggested by Thomas. He also claimed that the number of folds was variable at subspecific level in his standard taxonomic arrangement. According to MOOJEN's (1948) definition, the two subgenera (*Proechimys* and *Trinomys*) not only are morphologically differentiated but also occupy distinct geographic ranges. A recent study based on evidence from molecular sequences sampled from the mitochondrial genome indicated that the subgenus *Trinomys* as conceived by MOOJEN (1948) does not share a most recent common ancestor with *Proechimys*, suggesting that it should be granted generic status in its own right (LARA & PATTON, 2000). These authors based their taxonomic structure for *Trinomys* on the phylogenetic relationships of a haplotype lineage derived from 726 base pairs of the cytochrome-*b* gene. They recognized three major clades in this structure, encompassing the majority of the taxa recognized by MOOJEN (1948); only *Proechimys iheringi panema* Moojen, 1948, and *T. moojeni* were not sampled for molecular sequences in their study. Although they did not have sequence data for *T. moojeni*, LARA & PATTON (2000) suggested on the basis of cranial morphology that

it should be included in their clade 2, which also encompasses *T. s. setosus*, *T. s. elegans*, and *T. s. denigratus*.

Four other diploid numbers for the genus have been described in the literature and may be allocated to the following molecular clades: *T. yonenagae* (Rocha, 1995), from Ibiraba, Bahia (clade 2), with 2n=54 (FN=104); *T. albispinus* (Is. Geoffroy, 1838), from Morro do Chapéu, Bahia (clade 3), with 2n=60 (FN=116); *T. iheringi* from four localities in State of São Paulo (clade 1), with 2n=61-65 (due to the presence of 1 to 5 supernumerary chromosomes); and *T. gratiosus gratiosus* (Moojen, 1948) from Venda Nova, Espírito Santo (clade 1), with 2n=56 (FN=108) (LEAL-MESQUITA *et al.*, 1992; YONENAGA-YASSUDA *et al.*, 1985; ZANCHIN, 1988). Further diploid numbers are reported by PESSÔA *et al.* (2005). It can be seen from these data together with the details obtained in this study (Tab.1) that each taxon has some chromosomal character that may be used to diagnose it as a unit and differentiate it from the others.

The diploid numbers described here for *T. moojeni* and *T. s. elegans* in Minas Gerais State (2n=56) are identical, but the fundamental numbers (FN=106 and FN=104, respectively) and the morphology of sex chromosomes can be used to diagnose them. These two taxa share chromosomal characters, suggesting that they are more closely related to each other than to any other species in the genus. The results for *T. s. elegans* at the chromosomal level corroborate the findings from the mitochondrial genome, which place the taxon in clade 2 (LARA & PATTON, 2000). The chromosomal data also confirm that *T. moojeni* must be part of clade 2, as suggested by LARA & PATTON (2000) on the basis of cranial morphology.

ACKNOWLEDGEMENTS

We thank the curators for permission to study the type specimens and for their hospitality during visits to the Museu Nacional; Stella Maris Franco (Museu Nacional - Rio de Janeiro – MN), for help with specimens and information; Dr. Christopher J. Tribe (University Museum of Zoology, Cambridge) kindly revised a previous version of this manuscript and provided valuable comments. We are also grateful to the administration and staff of the Parque Nacional da Serra do Cipó for granting permission and providing support to study the small mammals in the reserve area. Fundação O Boticário de Proteção à Natureza and FIP/PUC-Minas (Fundo de Incentivo à Pesquisa) provided financial support. Work by the authors was funded by grants from the Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ-E-26/170.547/99). L.M.Pessôa was partially supported by a fellowship from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq-301386-927). A collecting licence was granted by the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA).

LITERATURE CITED

FORD, C.E. & HAMERTON, J.L., 1956. A colchicine hypotonic citrate squash sequence for mammalian chromosomes. **Stain Technology,** Louisville, **31**:247-251.

LARA, M.C. & PATTON, J.L., 2000. Evolutionary diversification of spiny rats (genus *Trinomys*, Rodentia: Echimyidae) in the Atlantic forest of Brazil. **Zoological Journal of the Linnean Society**, London, **130**:661-686.

LEAL-MESQUITA, E.R.; YONENAGA-YASSUDA, Y.; CHU, T.H. & ROCHA, P.L.B., 1992. Chromosomal characterization and comparative cytogenetic analysis of two species of *Proechimys* (Echimyidae, Rodentia) from the Caatinga domain of the State of Bahia, Brazil. **Caryologia**, Florence, **45**(2):197-212.

LEVAN, A.; FREDGA, K. & SANDBERG, A.A., 1964. Nomenclature for centromeric position on chromosomes. **Hereditas**, Lund, **52**:201-220.

MOOJEN, J., 1948. Speciation in Brazilian spiny rats (genus *Proechimys*, family Echimyidae). **University of Kansas Publications, Museum of Natural History**, Lawrence, **1**:301-401.

PASCHOAL, A.M.O.; SANTIAGO, F.L.; CASTILHO, M.V.; PERILLI, M.L.L.; CÂMARA, E.V.C. & OLIVEIRA, L.C., 2004. Novo registro de *Trinomys moojeni* (Rodentia: Echimyidae) no Parque Nacional da Serra do Cipó - MG. In: CONGRESSO BRASILEIRO DE ZOOLOGIA, 25., Brasília. **Resumos...**, Brasília: Universidade de Brasília, p.265.

PESSÔA, L.M.; CORRÊA, M.M.O.; BITTENCOURT, E. & REIS, S.F., 2005. Chromosomal characterization of taxa of the genus *Trinomys* Thomas, 1921, in the states of Rio de Janeiro and São Paulo (Rodentia: Echimyidae). **Arquivos do Museu Nacional**, Rio de Janeiro, **63**:161-168

PESSÔA, L.M.; OLIVEIRA, J.A. & REIS, S.F., 1992. A new species of spiny rat genus *Proechimys*, subgenus *Trinomys* (Rodentia: Echimyidae). **Zeitschrift für Säugetierkunde**, Jena, **57**:39-46.

PESSÔA, L.M. & REIS, S.F., 1992. Bacular variation in the subgenus *Trinomys*, genus *Proechimys* (Rodentia: Echimyidae). **Zeitschrift für Säugetierkunde**, Jena, **57**:100-102.

THOMAS, O., 1921. On the spiny rats of the *Proechimys* group from Southeastern Brazil. **Annals and Magazine of Natural History**, London, Series 9, **8**:140-143.

YONENAGA-YASSUDA, Y.; SOUZA, M.J.; KASAHARA, S.; L'ABBATE, M. & CHU, H.T., 1985. Supernumerary system in *Proechimys iheringi iheringi* (Rodentia, Echimyidae), from the State of São Paulo, Brazil. **Caryologia**, Florence, **38**:179-194.

ZANCHIN, N.I.T., 1988. **Estudos cromossômicos em orizominos e equimídeos da Mata Atlântica**. Porto Alegre. 162p. M.Sc. Dissertation, Universidade Federal do Rio Grande do Sul.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.175-181, jan./mar.2005
ISSN 0365-4508

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/UFRJ, 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 Minaçú 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, Mambaí, 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										
C. tener	3	2	66	66	31	1	SM	**	Fig.2a	(1,2, 3)
	3	9	66	68	30	2	SM	A	Fig.2b	(2, 4)
C. expulsus	4	5								
	2	10								
C. aff. expulsus	4	1	64	66	29	2	SM	**	Fig.2c	
Pampas Domain										
C. laucha	5	1	64	68	28	3	SM	**		(5)
Amazon Domain										
Calomys sp.	1	2	64	64	30	1	SM	A	Fig.2d	
C. callidus	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* (MUSSER & CARLETON 1993, EISENBERG & REDFORD 1999). In Ipamerí (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 (MUSSER & 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,

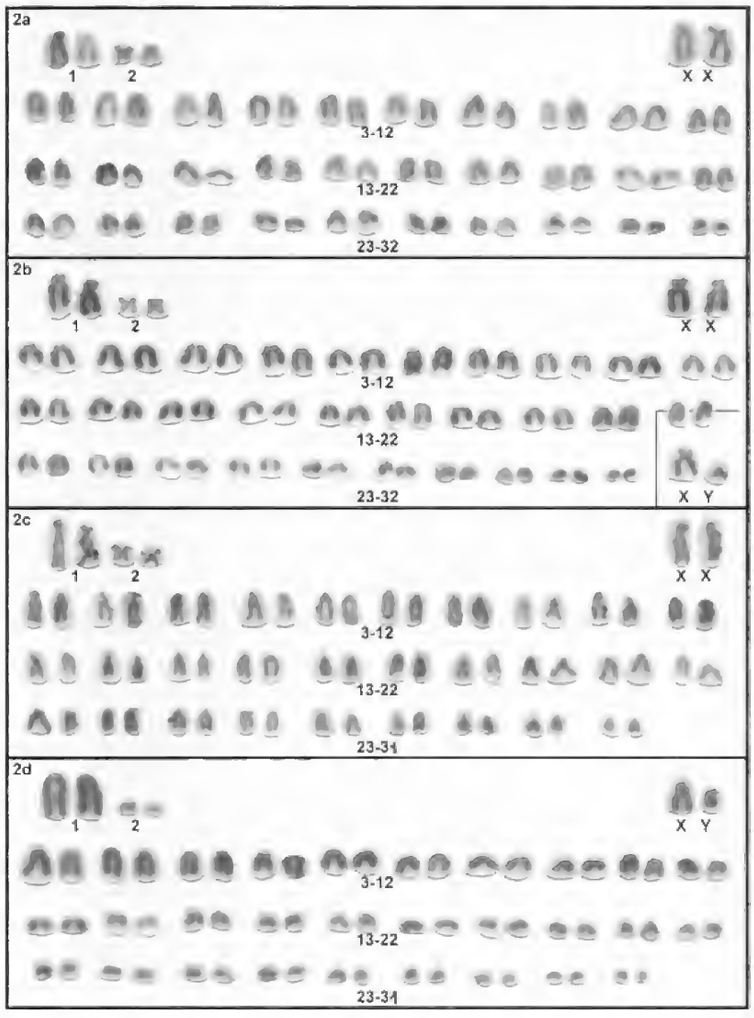

Fig.2- Karyotypes in conventional staining of a) *Calomys tener* (2n=66; FN_a=66), ♀ . b) *C. expulsus* (2n=66; FN_a=68), ♀ ; in the square the sex pair of a male. c) *C.* aff. *expulsus* (2n=64; FN_a=66), ♀ . d) *Calomys* sp. (2n=64; FN_a=64), ♂ .

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 *laucha-hummenlincki* 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°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 majors clades are found, one of them clustering *C. lepidus* + *C. musculinus* + *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. **Zeistschrift für Saügetierkunde**, 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.; PIANTANIDA, 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 musculinus* (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 karyotipyc 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*. **Zeistschrift für Saügetierkunde**, 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 Minaçú,13°31'S;48°13'W: *C. tener* (MN36276, MN36473); *C. expulsus* (MN36230, MN36255, MN36270, MN36275, MN36289, MN36360, MN36447, MN36508, MN37281); Ipamerí, Caldas Novas, and Corumbaíba, 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, Mambaí, 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)

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.183-190, jan./mar.2005
ISSN 0365-4508

KARYOLOGY OF LARGE SIZE BRAZILIAN SPECIES OF THE GENUS *OECOMYS* THOMAS, 1906 (RODENTIA, MURIDAE, SIGMODONTINAE) [1]

(With 4 figures)

ALFREDO LANGGUTH [2, 3]
VILNA MAIA [4]
MARGARETE S. MATTEVI [3, 5, 6]

ABSTRACT: Karyotypes in large size Brazilian *Oecomys* vary from 2n=58 to 2n=86. A new karyotype from Rio Jamari, 2n=82, FN=106, and a new locality in Pernambuco for the 2n=60, FN=62 karyotype are reported. A summary of karyological data on large size *Oecomys* available in the literature is used to discuss hypothesis on speciation and karyotype evolution in this *Oecomys* group.

Key words: Karyotypes, Brazilian *Oecomys* speciation, karyotype evolution.

RESUMO: O cariótipo em espécies brasileiras de grande tamanho do gênero *Oecomys* Thomas, 1906 (Rodentia, Muridae, Sigmodontinae)

O cariótipo em espécies brasileiras de *Oecomys* de grande tamanho varia de 2n=58 a 2n=86. Comunica-se um novo cariótipo do Rio Jamari, 2n=82, NF=106, e uma nova localidade em Pernambuco para o cariótipo de 2n=60, FN=62. Um resumo sobre a informação cariotípica disponível na literatura serve como base para formular uma hipótese sobre especiação e evolução cariotípica neste grupo.

Palavras-chave: Cariótipo, *Oecomys* brasileiros, especiação, evolução cariotípica.

INTRODUCTION

The genus *Oecomys* Thomas 1906 may be divided in two groups of species, lumped by the first and last reviser of the genus (HERSHKOVITZ, 1960) in two forms, the large size *Oecomys concolor* (Wagner, 1845) and the small size *Oecomys bicolor* (Tomes, 1860). The first karyotypes of a species of the *concolor* group were published by GARDNER & PATTON (1976) for *Oecomys superans* Thomas, 1911 from Balta, Rio Curanja, Peru, originally called *O. concolor* according to G. MUSSER in PATTON, SILVA & MALCOLM (2000). They also described a karyotype of a "true" *O. concolor* from Colombia, Villavicencio, 900km NW of the type locality (Tab.1). Later PATTON, SILVA & MALCOLM (2000) reported several karyotypes from populations at the Rio Juruá, revealing that up to four species of *Oecomys* may occur in sympatry (Tab.1). ANDRADES-MIRANDA *et al.* (2001) published other karyotypes from Goiás and from the Jamari river. More recently, ANDRADE & BONVICINO (2003) provided new cytogenetic data from the Rio Negro and from the Atlantic Forest (Tab.1).

This bulk of data showed that *Oecomys* is more diverse than suggested by HERSHKOVITZ (1960) and karyotypes are helping substantially in revealing such diversity.

We publish here for the first time a karyotype of *Oecomys bahiensis* Hershkovitz, 1960 from São Lourenço, Pernambuco, in Brazilian Northern Atlantic Forest, and also a karyotype of specimens of *Oecomys roberti* (Thomas, 1904) captured at the Rio Jamari in Rondônia State. We further discuss some issues on chromosome variability, morphology, and evolution in the group of large size species of *Oecomys*.

MATERIAL AND METHODS

The following specimens of *Oecomys* have been studied. They belong to the mammal collections of the Departamento de Sistemática e Ecologia,

[1] Submitted on August 2, 2004. Accepted on February 14, 2005.
[2] Universidade Federal da Paraíba, Departamento de Sistemática e Ecologia. Campus Universitário, 58059-900 João Pessoa, PB, Brasil.
[3] Bolsista do Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).
[4] Universidade Federal de Pernambuco, Departamento de Genética. Av. Professor Moraes Rego, Cidade Universitária, 50732-970, Recife, PE, Brasil.
[5] Universidade Luterana do Brasil, Curso de Pós-Graduação em Diagnóstico Genético-Molecular. Av. Farroupilha, 8001, Canoas, 92420-280, RS, Brasil.
[6] 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.

Universidade Federal da Paraíba (UFPB) and Naturhistorisches Museum Wien (NHM). Karyotyped animals are marked with (*)

Oecomys concolor – Rio Curicuriari, affluent of the right margin of the upper Rio Negro below São Gabriel da Cachoeira, State of Amazonas. NHM Inv. Nr. 482, holotype.

Oecomys bahiensis – Rancho Mineiro, 6km NE of São Lourenço da Mata, Km 12,5 of the road to Aldeia, Municipality of Camaragibe, State of Pernambuco: UFPB 4447*, UFPB 4449*, UFPB 5029*. Reserva Biológica de Saltinho, Rio Formoso, Pernambuco: UFPB 4450*.

Oecomys roberti – Rio Jamari at the Samuel Hydroelectric Dam, State of Rondônia, collected during flooding. We received a pregnant female which gave birth to 3 young on 5 Jan 1989, all were raised in the laboratory and killed (karyotyped) on 29 Aug 1989 (UFPB 5030*, UFPB 5031*, UFPB 5032*, UFPB 5033*). We also obtained other 4 adult specimens (UFPB 1258, UFPB 1260, UFPB 1261, UFPB 1263).

Table 1. Karyotypes in large size species of the genus *Oecomys*.

SPECIES	2n	FN	ONE- ARMED	BI-ARMED	LOCALITY	SOURCE
Oecomys sp.	72	90	25	10	Corumbá, MS	5
Oecomys sp.	86	98	35	7	Rio Juruá, AM	4
Oecomys bahiensis	60	62	27	2	São Lourenço da Mata, PE	2
Oecomys bahiensis	60	62	27	2	Saltinho, PE	2
Oecomys concolor	60	62	27	2	Brasília, DF	3
Oecomys concolor	60	62	27	2	Villavicencio, Meta, Colombia	1
Oecomys concolor	60	62	27	2	Sumidouro and Guapimirim. RJ	5
Oecomys concolor	60	62	27	2	Teresina de Goiás, GO	5
Oecomys concolor	60	62	27	2	Sete Barras and Capão Bonito, SP	5
Oecomys concolor	60	62	27	2	Guajará-Mirim, RO	6
Oecomys concolor	60	62	27	2	20 km NW de Colinas do Sul, GO	6
Oecomys concolor	60	62	27	2	Minaçú, GO	6
Oecomys concolor	60	62	27	2	Ipameri, Caldas Novas and Corumbaíba GO	6
Oecomys roberti	80	114	21	18	Rio Juruá, AM	4
Oecomys roberti	82	106	21	16	Rio Jamari, RO	2
Oecomys superans	80	108	24	15	Rio Curanja, Balta Ucayali, Peru	4
Oecomys superans	80	108	24	15	Rio Juruá, Penedo, AM	4
Oecomys superans	80	108	24	15	Lower Rio Negro, AM	5
Oecomys trinitatis	58	96	8	20	Rio Juruá, AM	4

(2n) diploid number; (FN) fundamental number. Brazilian States: (AM) Amazonas, (MS) Mato Grosso do Sul, (PE) Pernambuco, (DF) Distrito Federal, (RJ) Rio de Janeiro, (GO) Goiás, (SP) São Paulo, (RO) Rondônia. Sources: (1) GARDNER & PATTON (1976); (2) this paper; (3) SVARTMAN (1989); (4) PATTON, SILVA, & MALCOLM, (2000); (5) ANDRADE & BONVICINO (2003); (6) ANDRADES-MIRANDA *et al.* (2001). See figure 4.

The karyotypes were obtained from bone marrow cells according to the technique described by BAKER *et al.* (1982). C and G banding treatments were performed as described by SUMNER (1972) and SEABRIGHT (1971), NORs staining where obtained by the technique outlined by HOWELL & BLACK (1980).

RESULTS AND DISCUSSION

The karyotypes of *O. bahiensis* from São Lourenço da Mata in Pernambuco (Fig.1a) showed a 2n=60 and a FN=62 formed by one pair of large submetacentrics, 27 pairs of acrocentrics of decreasing size from large to small and one pair of small metacentrics. The sexual pair is formed by a large X chromosome and the Y is a large acrocentric, similar in size to the largest arm of the X chromosome. Constitutive heterochromatin (CH) was observed in the pericentromeric regions of all autosomes and in, at least, two pairs (17 and 23) is clearly present around the telemetric area. CH is spread in large parts of the short arm of the X chromosome and present as a positive band in the terminal third of its long arm. The whole Y appears CH positive (Fig.1b). Four to 7 nucleolar organizer regions were observed in 20 cells, all located in the short arms of acrocentric chromosomes (Fig.1c).

The karyotypes of *O. roberti* from Rio Jamari in Rondônia (UFPB 5033, Fig.2) showed a 2n=82 and a FN=106 formed by 27 pairs of acrocentrics or subtelocentric chromosomes gradually decreasing in size from large to medium and 13 pairs of metacentric or submetacentric chromosomes also gradually decreasing in size from medium to small. The sexual pair is formed by large X chromosomes. In the male specimen UFPB 5032 the Y is a small acrocentric.

The wide distribution of the 2n=60, FN=62 karyotype from Colombia to the Atlantic forest in Brazil (Tab.1, Fig.4) was not expected and raises questions about the co-specificity of specimens from Colombia and Pernambuco. Not expected was also that intensive collecting along the Juruá river (PATTON, SILVA & MALCOLM, 2000), not too far from Guajará-Mirim where ANDRADES-MIRANDA *et al.* (2001) reported the 2n=60, FN=62 karyotype, revealed four different species of *Oecomys* but none with the last referred chromosomes.

Up to now the karyotype of the true *O. concolor* of the type locality is unknown but *Oecomys* collected at the Rio Negro west but not too far away (ca. 450 km) of the type locality of *O. concolor* did not show the 2n=60, FN=62 chromosomes attributed to the species (ANDRADE & BONVICINO, 2003).

To identify Pernambuco specimens we compared them with HERSHKOVITZ's (1960) description of *O. concolor* and with a description of the holotype of this species made by Langguth in 1966 in the Natural History Museum of Vienna (Fig.3, skull; Tab.2). The holotype bears labels with a Nr. 12 (Sendung); a black ink Nr. 291; Natterer´s Nrs. 174 (67); and the inventory Nr. 482. The skull has a relatively short rostrum, 33.4% of total length, interorbital and postorbital regions with posteriorly diverging cristae continued with less marked temporal lines. The interparietal is large anteroposteriorly and the parietals strongly curved transversally. The frontal has a flat dorsal outline. The proximal end of nasals is depressed as well as the anterior end of frontals. The zygomatic plate is rounded in the antero-superior corner, and very slightly projected forward when seen from above thus configuring a shallow zygomatic notch. The incisive foramina, occupying 64% of diastema length, have convex lateral borders and are narrower anteriorly, reaching the anterior lamina of m^1. A long palate ends beyond m^3, with posterior palatal pits. The molars are as described for the genus by HERSHKOVITZ (1960). The connection between paracone and mesostyle and a paralofule are not conspicuous in m^1 but evident in m^2. First and second internal fold of m^{1-2} are confluent with corresponding primary folds. Anterior internal fold and anterior secondary fold coalesced, the last is isolated from the margin. At the procingulum of m_1 anterior primary fold, first secondary fold and first internal fold are also coalescent. Skull measurements of the holotype are given in table 2, they fall within the range of measurements given by HERSHKOVITZ (1960) for *O. concolor concolor*. Only the length of incisive foramen of the holotype is smaller.

The well-preserved skin of the holotype is dorsally rufous-brown and ventrally the pelage is white to the base. Sides are sharply defined from ventral coloration. The tail is longer than head and body length (tail length 125mm, head and body length 110mm both in the dry skin) and unicolored, covered with short brown hairs with no tuft at the end. The foot (c/u 26,5 and s/u 25,2 in the dry skin) is covered with short light colored hairs. The claws are medium sized and periungeal hairs are shorter than the claws. Ears (15mm dry) are covered with short, fine, and light colored hairs. The mystacial vibrissae are around 40mm long.

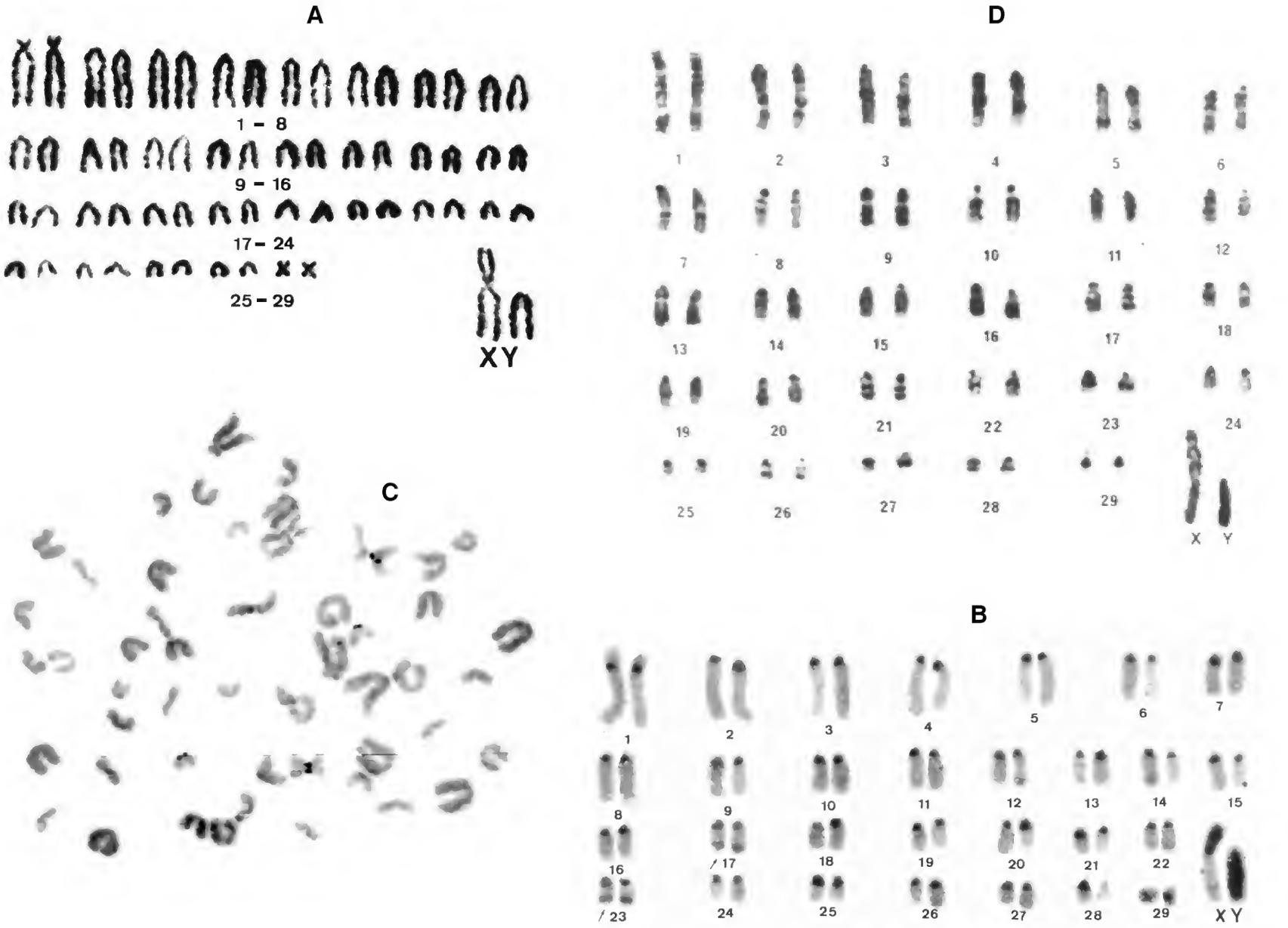

Fig.1- Karyotype of *Oecomys bahiensis* from São Lourenço da Mata, State of Pernambuco, male UFPB 4450. (A) Giemsa staining, (B) C banding, (C) NOR bands, (D) G banding.

Table 2. Measurements of selected specimens of *Oecomys*.

SPECIMEN #	SEX	HB	T	HF cu - su	E	SL	ZB	IF	LD	LR	MR	ZPW	IB
Oecomys concolor													
NHM Wien 482 holotype		124[3]	137[3]	cu 26	-	29,6	15,9	4,7	7,3	9,9	4,9	3,0	5,1
Oecomys bahiensis													
UFPB 4450	♂	103	100	-	-	27,3	14,5	4,7	6,1	9,8	5,2	2,7	4,9
UFPB 4449	♂	112	133	25 - 28	18	32,5	17,0	5,2	8,1	11,1	5,5	3,3	5,4
UFPB 4447	♂	-	-	-	-	32.8	17,4	5,4	7,9	11,1	4,9	3,4	5,5
UFPB5029	♀	-	-	-	-	28,9	16,1	4,8	7,3	-	4,8	3,2	5,6
holotype [2]	♂	140	145	27cu.	-	33,0	18,0	6,0	8,0	-	5,3	3,8	-
paratype [2]	-	130	150	28 cu.	-	36,6	16,7	5,9	7,9	-	5,3	3,4	-
Oecomys roberti													
Holotype [2]	♂	110	145	s/u 26,7	16	32,0	16,0	5,0	8,0	-	4,8	-	-
UFPB 5031	♀	143	136	25 - 27	16	34,6	17,9	5,8	9,2	12,3	5,2	3,1	5,9
UFPB 5032	♂	122	150	su.24 - cu25	16	33,2	16,5	4,6	8,5	11,6	4,7	3,1	6,2
UFPB 5033	♀	129	145	24 - 25	16	31,8	16,6	4,7	8,9	11,3	4,9	2,9	6,0
UFPB 5030	♀	124	139	23 - 24	15								
UFPB 1258	♀	100	170	24 - 26	14	32,3	16,9	5,2	8,2	11,3	4,9	3,2	5,7
UFPB 1261	-	-	-	-	-	-	-	-	-	-	-	-	-
UFPB 1263	-	-	-	-	-	31,6	15,2	4,3	8,3	11,6	4,7	3,2	4,6
UFPB 1260	♂	-	-	-	-	31,1	17,1	5,1	7,9	10,6	5,2	2,9	5,6
Oecomys superans													
holotype [2]	♀	150	199	su 31	17	37,3	18,7	6,3	-	-	6,2	-	-
Rio Juruá [4]	-	149	174	cu 33	-	33,7[1]	19,0	6,2	9,4	13,0	5,8	3,7	6,5

(HB) head and body length; (T) tail length, (HF) hind foot: s/u= without claw c/u= with claw, (E) ear height from notch, (SL) skull greatest length, (ZB) Zygomatic breadth, (IF) length of incisive foramina, (LD) length of diastema, (LR) length of rostrum, (MR) length of molar row, (ZPW) zygomatic plate width, (IB) interorbital breadth. Measurements taken according to LANGGUTH & BONVICINO (2002), (LR) according to PATTON, SILVA & MALCOLM (2000) and SL was taken to allow comparisons with holotype of *O. concolor*, and measured as greatest length with skull on a flat surface. (1) Condyloincisive length of a different, smaller, specimen; (2) mesurements from the original description; (3) Natterer´s measurements, (4) PATTON, SILVA & MALCOLM (2000).

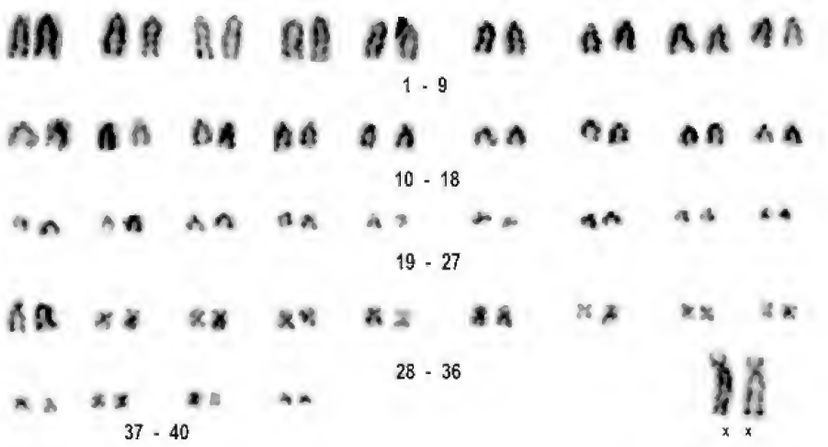

Fig.2- Karyotype of *Oecomys roberti* from Rio Jamari, State of Rondônia, female UFPB 5033. Giemsa staining.

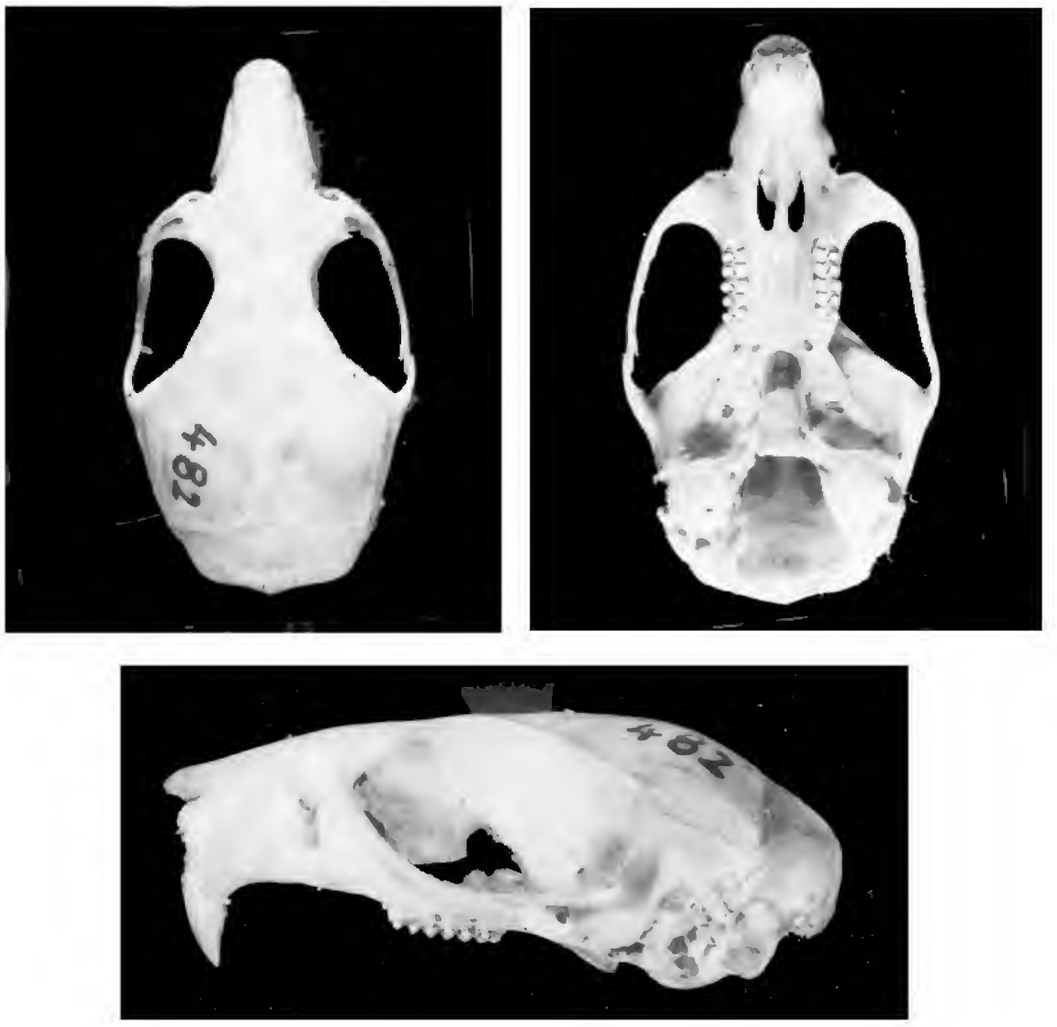

Fig.3- Dorsal, ventral, and lateral views of the skull of the holotype of *Oecomys concolor*.

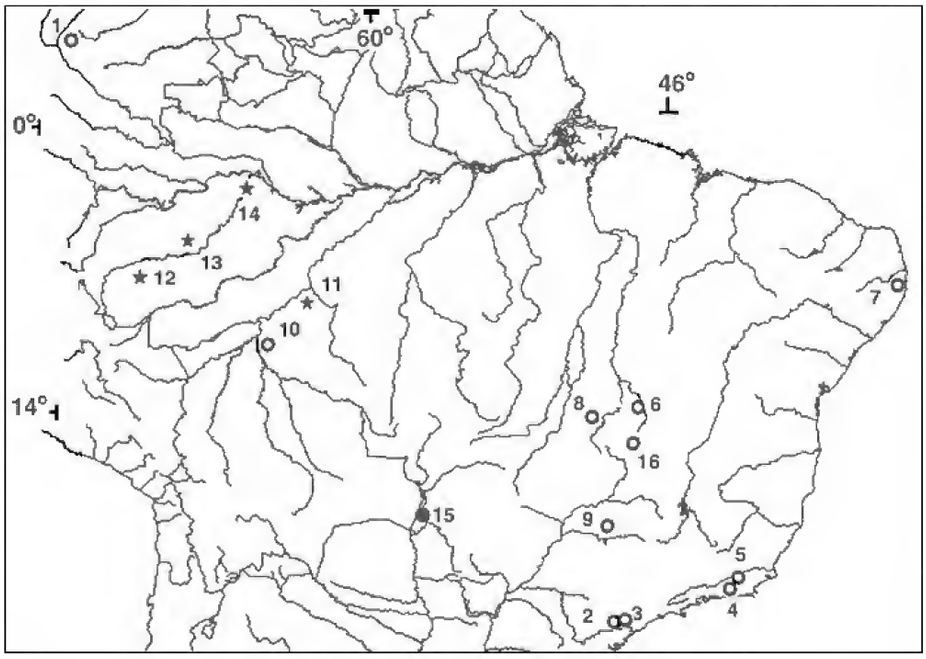

Fig.4- Localities where karyotyped specimens of some large species of *Oecomys* have been collected. (★) *Oecomys* group *concolor* 2n=60, FN=62. (○) *Oecomys roberti* 2n=80, FN=114; 2n=82, FN=106; (●) *Oecomys sp.* 2n=72, FN=90. Data from ANDRADE & BONVICINO (2003), ANDRADES-MIRANDA *et al.* (2001) and this paper.
(1) Villavicencio, Meta, Colombia; (2, 3) Sete Barras and Barra Grande, State of São Paulo; (4, 5) Sumidouro and Guapimirim, State of Rio de Janeiro; (6) Teresina de Goiás, State of Goiás; (7) São Lourenço da Mata, and Saltinho, State of Pernambuco; (8) 20km NW de Colinas do Sul and Minaçú, State of Goiás; (9) Ipameri, Caldas Novas and Corumbaíba, State of Goiás; (10) Guajará-Mirim, State of Rondônia; (11) Rio Jamari, State of Rondônia; (12) Sacado Rio Juruá, State of Amazonas; (13) Barro Vermelho, Rio Juruá, State of Amazonas; (14) Igarapé Arabidi, Rio Juruá, State of Amazonas; (15) Corumbá, State of Mato Grosso do Sul; (16) Brasília, Distrito Federal.

The karyotyped *Oecomys* specimens from Pernambuco have a long and dense dorsal fur, light brown colored with an orange wash, lighter on the sides, which are not well defined from belly. Venter is grayish with a light buffy wash the dark base of the hairs showing through. In the throat the hairs are white or light buffy to the base. The feet are well covered with light colored hairs.

The holotype of *O. concolor* and specimens from Pernambuco are both bright colored and have similar external and cranial measurements (Table II), but they differ in the pattern of ventral pelage color: the former is white and sharp defined from sides but the latter is not.

The ventral pattern in *Oecomys* from Pernambuco is similar to that found in Hershkovitz taxon *O. bahiensis* from São Lourenço, Pernambuco. Thus the specimens from Pernambuco could be co-specific with the animals sharing the same karyotype, reported from further south in the Atlantic Forest (Tab.1, Fig.4). The name *O. bahiensis* Hershkovitz 1960 is available and used here for the studied species from Pernambuco, because our specimens and those from the type-locality of *O. bahiensis* (HERSHKOVITZ, 1960) share important morphological characters, and are geographically close.

The other karyotype here reported is attributed to *Oecomys roberti*, based on characters of the pelage and size. Our specimens have underparts sharply defined from sides, covered with entirely white hairs. External and cranial measurements of specimens from Rio Jamari fall within the range given by HERSHKOVITZ (1960) and by PATTON, SILVA & MALCOLM (2000) for *O. roberti* (Tab.2). We believe that, in general, dorsally more dull colored specimens with white underparts sharply defined from sides and smaller size may be considered *O. roberti*. Large dull colored specimens with grayish belly are referred to *O. superans*.

In Corumbá, State of Mato Grosso do Sul (Fig.4) specimens that agree with HERSHKOVITZ (1960)

description of *O. roberti* have been reported with a new karyotype (ANDRADE & BONVICINO, 2003) (Tab.1). They have however a dark reddish dorsal color and grayish head not found in Bolivian *O. roberti* nor in *Oecomys marmorae* according to the descriptions of ANDERSON (1997). The holotype of the last species was, regrettably, fixed in alcohol so that the color of the specimen is biased. The specimen from Corumbá probably belongs to an undescribed species.

Further, PATTON, SILVA & MALCOLM (2000) reported another different karyotype (Tab.1) for specimens called *O. roberti* that also agree with Hershkovitz´s description of this species. Considering only the karyotypic characters they may be considered different biological species but according to the morphology they may belong to the same taxonomic species.

The collecting place at Rio Jamari is located nearly 1100km west of the type locality of *O. roberti*, but Rio Juruá, where a different karyotype (Tab.1) has been found is further 600km west (Fig.4). In summary, we find over a wide area a morphological species, *O. roberti*, with different karyotypes. Karyological differences are of such magnitude that isolating reproductive mechanisms may be involved. However, naming different species without clear-cut morphological distinctions is not recommendable.

Topotypes of *O. concolor, O. superans*, and *O. roberti* should be karyotyped. The picture that is emerging is similar to that found in *Oligoryzomys*. Several sibling karyological species with a variable pattern of color are described. Small statistical, cranial differences in size and proportions overlap with intrapopulational variation. Without cytogenetic information it's hard to recognize the different species.

An hypothesis to explain chromosome evolution in *Oecomys* suggests that the primitive karyotype may be 2n=60, FN=62 because it has the widest geographic distribution. The others may have originated from it by Robertsonian rearrangements such as pericentric inversions followed by central fissions. For instance, the 2n=82, FN=106 karyotype from Rio Jamari may have evolved from the ancestral form 2n=60, FN=62 by 44 pericentric inversions in uniarmed chromosomes followed by 16 fissions. A molecular phylogeny of the group accompanied by a detailed cytogenetic analysis may test this hypothesis.

ACKNOWLEDGEMENTS

We are grateful to ELETRONORTE for providing the specimens of *Oecomys roberti* and to Alexandre Percequillo for fruitful comments on the manuscript.

LITERATURE CITED

ANDERSON, S., 1997. Mammals of Bolivia, taxonomy and distribution. **Bulletin American Museum Natural History**, New York, **231**:1-652.

ANDRADE, A.F.B. & BONVICINO, C.R., 2003. A new karyological variant of *Oecomys* (Rodentia: Sigmodontinae) and its phylogenetic relationships based on molecular data. **Genome,** Ottawa, **46**:195-203.

ANDRADES-MIRANDA, J.; OLIVEIRA, L.F.B.; ZANCHIN, N.I.T. & MATTEVI, M.S., 2001. Chromosomal description of the rodent genera *Oecomys* and *Nectomys* from Brazil. **Acta Theriologica**, Warszawa, **46**:269-278.

BAKER, R.J.; HAIDUK, M.W.; ROBBINS, L.W.; CADENA, 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**. Pittsburgh: Special publication Series, Pymatuning Laboratory of Ecology, University of Pittsburgh. p.303-327.

GARDNER, A.L. & PATTON, J.L., 1976. Karyotypic variation in oryzomyine rodents (Cricetidae) with comments on chromosomal evolution in the Neotropical Cricetinae complex. **Occasional Papers Museum Zoology Louisiana State University**, Baton Rouge, **49**:1-48.

HERSHKOVITZ, P., 1960. Mammals of Northern Colombia, Preliminary report No. 8: arboreal rice rats, a systematic revision of the subgenus *Oecomys*, genus *Oryzomys*. **Proceedings United States National Museum,** Washington, **110**:535-568.

HOWELL, W.M. & BLACK, D.A., 1980. Controlled silver staining of nucleolus organizer regions with a protective colloidal developer: a 1-step method. **Experientia**, Basel, **36**:1014-1015.

PATTON, J.L.; SILVA, M.N.F. & MALCOLM, J.R., 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. **Bulletin American Museum Natural History**, New York, **244**:1-306.

SEABRIGHT, M., 1971. A rapid banding technique for human chromosomes. **Lancet**, London, **2**:971-972.

SUMNER, A.T., 1972. A simple technique for demonstrating centromeric heterocromatin. **Experimental Cell Research,** Stockholm, **75**:304-306.

SVARTMAN, M., 1989. **Levantamento cariotípico de roedores da região do Distrito Federal**. São Paulo. 217p. Ph.D. thesis, University of São Paulo.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, p.191-200, jan./mar.2005
ISSN 0365-4508

KARYOLOGIC AND MOLECULAR ANALYSIS OF *PROECHIMYS* ALLEN, 1899 (RODENTIA, ECHIMYIDAE) FROM THE AMAZONIAN REGION [1]

(With 3 figures)

CIBELE R. BONVICINO [2, 3, 4]
IVONE B. OTAZÚ [3, 5]
JÚLIO F. VILELA [3, 6]

ABSTRACT: Karyologic and molecular analyses were carried out in *Proechimys quadruplicatus* and two other *Proechimys* species from the northern bank of the Rio Negro, Brazil. Analyses of cyt*b* DNA sequence data and karyologic attributes partially sustained the *goeldii* species group. Molecular analyses grouped the two *Proechimys* sp. A haplotypes here sequenced with other specimens from the Amazonian region of Brazil and Venezuela, suggesting that they belonged to a single taxon. The three specimens of *Proechimys* sp. B also formed a monophyletic group. *Proechimys* sp. A, *Proechimys* sp. B, and *P. guyannensis* were grouped by karyologic and/or molecular data indicating that they are very similar one another and belong to the same species group, the *guyannensis* group. Phylogeographic analyses showed a high geographic structuration in the *Proechimys* sp. A population and the presence of a median vector between haplotypes of different rivers suggested that the large Amazonian rivers are barrier to these population.

Key words: Karyotype, phylogeny, *Proechimys*, Amazon, cytochrome *b*.

RESUMO: Análise cariológica e molecular de *Proechimys* Allen, 1899 (Rodentia, Echimyidae) da região Amazônica.

Análises cariológicas e moleculares foram realizadas em *Proechimys quadruplicatus* e duas outras espécies de *Proechimys* da margem norte do rio Negro, Brasil. Análises da seqüência de ADN do citocromo *b* e dos atributos cariológicos sustentam parcialmente o grupo de espécies *goeldii*. As análises moleculares agruparam os dois haplótipos de *Proechimys* sp. A aqui seqüenciados com outros espécimes da região Amazônica do Brasil e Venezuela sugerindo que eles pertençam ao mesmo táxon. Os três espécimes de *Proechimys* sp. B formam um grupo monofilético. *Proechimys* sp. A, *Proechimys* sp. B e *P. guyannensis* se agrupam pelos dados moleculares e/ou cariológicos indicando que eles são bastantes similares e pertencem ao mesmo grupo de espécies, o grupo *guyannenis*. A análise filogeográfica mostrou um padrão de estruturação geográfica forte nas populações de *Proechimys* sp. A, e a presença de vetores médios entre os haplótipos de diferentes rios, na análise de "median - joining", sugere que estes rios sejam barreiras para estas populações.

Palavras-chave: Cariótipo, filogenia, *Proechimys*, Amazonas, citocromo *b*.

INTRODUCTION

The genus *Proechimys* Allen, 1899 shows a drastic variation in diploid chromosome number, ranging from 2n=14 to 62 (BARROS, 1978; REIG & USECHE, 1976), and some authors have directly tied this diversity to speciation in the genus (REIG & USECHE, 1976). Moreover, karyologic data have also been valuable for a precise identification of *Proechimys* species (PATTON & GARDNER, 1972), which was the first paper to show that karyologic differences could be used to diagnose species and that each karyotypic form was morphologically unique. Conversely, morphologic analyses lead to controversial taxonomic

[1] Submitted on May 20, 2004. Accepted on January 27, 2005.
[2] Fundação Instituto Oswaldo Cruz, Departamento de Medicina Tropical, Laboratório de Biologia e Controle da Esquistossomose. Av. Brasil, 4365, Manguinhos, 21-45-900, Rio de Janeiro, RJ, Brasil.
[3] Instituto Nacional de Câncer, Divisão de Genética. Rua André Cavalcanti, 37, 4° andar, 20231-050, Rio de Janeiro, RJ, Brasil.
[4] Fellow of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).
[5] Hospital Universitário Clementino Fraga Filho/UFRJ. Ilha do Fundão, Rio de Janeiro, RJ, Brasil.
[6] Museu Nacional/UFRJ, Departamento de Vertebrados. Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil.

arrangements for the genus *Proechimys* as well as disparate criteria for defining subordinate taxa consequently to difficulties in identifying discrete morphological features. As postulated by THOMAS (1928), these rodents are characterised by an extensive morphological variability with overlapping morphological characters between different taxa. PATTON (1987), based on a morphological criterion, considered that *Proechimys sensu stricto* comprised nine species groups. Recently, another four *Proechimys* species, *P. kulinae*, *P. gardneri*, *P. pattoni*, and *P. echinothrix* have been described by DA SILVA (1998) and one species, *P. oris* Thomas, 1904, was considered junior synonym of *P. roberti* Thomas, 1901 (WEKSLER *et al.*, 2001).

In this paper we describe a new karyologic variant of *Proechimys quadruplicatus* Hershkovitz, 1948 and two new karyotypes of other two *Proechimys* species and comment on the role of karyology in species identification. We also analysed the phylogenetic relationships of these karyologic forms in respect to other *Proechimys* species using the mitochondrial gene cytochrome *b* (cytb) sequence data.

MATERIAL AND METHODS

Proechimys specimens were collected in eight Brazilian localities, in tributaries of the left bank of Rio Negro in the states of Amazonas (localities 1, 2, 3, 4 in Barcelos and localities 5, 6, 7 in Santa Isabel) and Roraima (locality 8, Fig.1). Additionally, sequences of species from locality 9 and 10, kindly provided by Dr. James L. Patton (JLP, University of California, Berkeley, USA), were used in molecular analyses. "Igarapé" refers to a small stream. Skins and skulls of CRB specimens are housed in the mammal collection of Museu Nacional - Rio de Janeiro (MN). The following acronyms refer to field numbers: (CRB) C.R.Bonvicino M.N.F. da Silva (MNFS), J.L.Patton (JLP), and A.L.Gardner (ALG). Acronyms U, AJ, and AY refer to accession numbers of GenBank.

Proechimys sp. A – State of Amazonas, Barcelos Municipality, (1) right bank of Rio Curuduri, Igarapé Tucunaré 00°09'89"N 63°30'49"W (♀ MN69019, 69020, 69022 69024, 53292, 69025, 69026, 69028, 63289; ♂ MN69017, all karyotyped); (2) right bank of Rio Curuduri, Igarapé

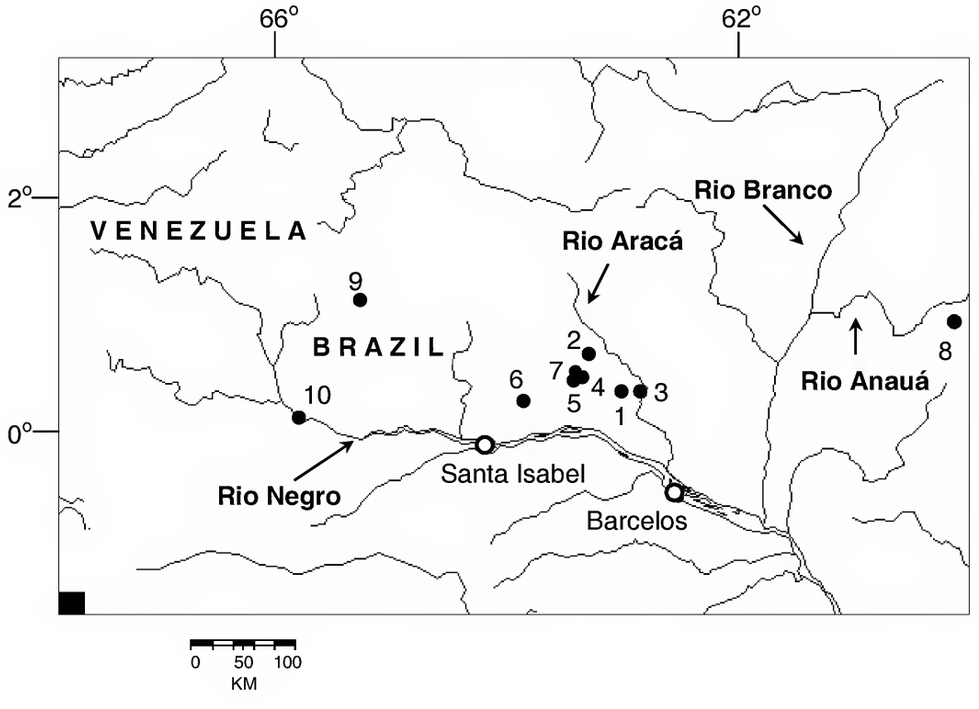

Fig.1- Localities of gather of *P. quadruplicatus* and *Proechimys* sp. A specimens analysed in this study. Brazil: State of Amazonas (1) Igarapé Tucunaré and (2) Igarapé Curudurizinho, tributaries of Rio Curuduri; (3) Igarapé do Bigorna, tributary of Rio Aracá; (5) Igarapé Ucuqui, (7) Igarapé Acuquaia and (4) Igarapé Japomeri, tributaries of Rio Padauari; (6) Igarapé Araújo, tributary of Rio Preto, (10) Comunidade Colina, São Gabriel da Cachoeira, right bank of Rio Tiquié; State of Rondônia (8) São João da Baliza. Venezuela: (9) Río Mawarinuma, Amazonas.

Curudurizinho 00°34'09"N 63°52'01"W (♀ MN69050-69052, ♂ MN69053, all karyotyped); (3) right bank of Rio Aracá, right bank of Igarapé do Limão, Igarapé do Bigorna 00°09'52"N 63°15'43"W (♀ MN69033,69034, 69038, 69040-69042, 69392, 69057, ♂ MN69032, 69035-69037, 69039, 69044, 69059 and CRB 1796, fifteen of which karyotyped, Cyt *b* sequence data from CRB1796, obtained by Dr. J.L.Patton, was used in molecular analyses); (4) left bank of Rio Padauari, Igarapé Japomeri 0°20'51"N 64°00'28"W (♀ MN69138), Santa Isabel Municipality, (5) left bank of Rio Padauari, Igarapé Ucuqui 00°18'50"N 64°01'40"W (♀ MN69001, 69004, 69008-69011, 69014, ♂ MN69005, 69012, 69015, 53291, 69017, all karyotyped), (6) left bank of Rio Preto, Igarapé Araújo 00°04'04"N 64°35'41"W (sex indetermined: MN69127, ♀ MN69124, 69128, 69131), (7) Rio Padauari, Igarapé Acuquaia 00°20'28"N 63°57'12"W (♀ MN69049, karyotyped).

P. quadruplicatus – State of Amazonas, Santa Isabel Municipality, (5) left bank of Rio Padauari, Igarapé Ucuqui 00°18'50"N 64°01'40"W (♀ MN69013, ♂ MN69003; CRB1483, all karyotyped; cyt*b* from CRB1483 and MN69007 was sequenced by us and used in molecular analyses).

Proechimys sp. B – State of Roraima, São João da Baliza Municipality, (8) UHE Alto Jatapú 00°57'01"N 59°54'40"W (♀ MN68174, 61642, ♂ MN61643, all karyotyped, cyt*b* sequences of this species were obtained by Dr. J.L.Patton, ♂ CRB635).

Chromosome preparations were obtained from bone marrow cultures in RPMI 1640, 20% foetal calf serum, colchicine (10^{-6} M) and ethidium bromide (5µg/ml) for two hours. This latter reagent is used to elongate the chromosomes (IKEUCHI, 1984). C- and G-banding were carried out as described by SUMNER (1972) and SEABRIGHT (1971) respectively.

DNA of specimens CRB1483 and MN69007 belonging to two *Proechimys* species was isolated from liver tissue fragments preserved in ethanol (Tab.1) following the procedures of SAMBROOK, FRITSCH & MANIATIS (1989). Cytochrome *b* DNA (ca. 472 bp) was amplified with primers MVZ 05 and MVZ 16 (SMITH & PATTON, 1993) and sequenced with an ABI Prism™ 377 automatic DNA sequencer. Sequences were manually aligned. NETWORK software (BANDELT, FOSTER & RÖHL, 1999; POSADA & CRANDALL, 2001) was used to analyze intraspecific phylogenies, and to evaluate the population structure and geographic distribution pattern of *Proechimys* sp. A. This analysis was carried out only with cyt*b* variable sites. Maximum parsimony trees were obtained through heuristic searches using the tree-bisection-reconnection branch-swapping algorithm in PAUP* 4.0b10 (SWOFFORD, 1999), with all sites equally weighted. Bootstrap values were calculated by heuristic search based on 1,000 replicates.

In addition to cyt*b* sequence data from specimens collected by us, sequence data were obtained in GenBank, WEKSLER *et al.* (2001) and PATTON, DA SILVA & MALCON (2000). The following specimens were used in molecular analyses: *P. quadruplicatus* (U35413, São Carlos do Rio Negro, AM, Venezuela, listed as *P. amphichoricus* (Moojen, 1948) by PATTON, DA SILVA & MALCON, 2000), *P. cuvieri* Petter, 1978 (U251402 from French Guiana), *P. guyannensis* E. Geoffroy, 1803 (AJ251395, AJ251396, AJ251397, AJ251398, AJ251399, AY206600, AY206601, AY206602 from French Guiana, listed as *P. cayennensis* (Desmarest, 1817, ICZN, 2002), *P. roberti* (LHE512, Rio Xingú, Brazil), *P. brevicauda* (Günther, 1877)(JLP 8271, Amazonas, Perú); *P. simonsi* Thomas, 1900 (JLP 15874 from Barro Vermelho 06°28'S 68°46'W, left bank of Rio Juruá, AM, Brazil); *P. steerei* Goldman, 1911 (JLP 15705 from Seringal Condor 06°45'S 70°51'W, left bank of Rio Juruá, AM, Brazil); *P. cuvieri* (U251402), *Proechimys* sp. A (INPA 2433, 2534 from Comunidade Colina, right bank of Rio Tiquié, São Gabriel da Cachoeira *ca.* 0°07'49"S 67°05'21"W, AM, Brazil; ALG 14242, 14255, 14282, 14297 from *ca.* 2km SE and in Neblina base camp, Río Mawarinuma *ca.* 01°11'N 66°25'W, Amazonas, Venezuela). *Mesomys hispidus* (Desmarest, 1817) (MNFS 436 from Rio Juruá, Amazonas, Brazil), *Trinomys gratiosus bonafidei* (Moojen, 1948)(AF194330) and *Trinomys gratiosus gratiosus* (Moojen, 1948) (AF194329) were used as outgroups in molecular analyses.

RESULTS

Karyotypic variation

Karyotypic analysis of three specimens of *P. quadruplicatus* showed 2n=28, FN=42. The autosome complement is composed of eight pairs of biarmed chromosomes (two large, five medium-sized and one small pair) and five acrocentric pairs (one medium sized and four small pairs). The X chromosome is a medium sized acrocentric and the Y chromosome is a small acrocentric (Fig.2A). A G-band karyotype is shown in figure 2D. C banding (not shown) showed pericentromeric heterocromatin in the sex

Table 1. Described karyotypes of the species of *Proechimys* here analysed.

TAXA	2n	FN	LOCALITY	SOURCE
GUYANNENSIS GROUP				
Proechimys sp.A	38	52	BR: AM, Barcelos and Santa Isabel	This study
Proechimys sp.B	46	50	BR: RR, São João da Baliza	This study
Proechimys sp.1	28	50-51	Peru: 44km de Pucalppa	ANISKIN (1994)
Proechimys sp.2	30	50	Peru: 39km of Iquitos, Aupauayo	ANISKIN (1994)
Proechimys sp.	44	52	BR: AM, Manaus	LEAL-MESQUITA (1991)
P. guyannensis	40	56	Venezuela	PATTON & GARDNER (1972)
P. guyannensis	40	54	French Guiana: Cayenne and Saul	REIG, TRAINER & BARROS (1979)
CUVIERI GROUP				
P. cuvieri	28	46	BR: AC and AM	MAIA & LANGGUTH (1993), PATTON, DA SILVA & MALCON (2000)
P. cuvieri	28	50	French Guyana: Cayenne; BR: AM	REIG, TRAINER & BARROS (1979), PATTON, DA SILVA & MALCON (2000)
GOELDII GROUP				
P. steerei	24	40-42	Peru: Dept Ucayali, Madre de Dios and Loreto; BR: AC and AM	REIG & USECHE (1976), PATTON & GARDNER (1972), GARDNER & EMMONS (1984), PATTON, DA SILVA & MALCON (2000)
P. goeldii	24	43-44	BR: PA; Peru, Dept Ucayali	PATTON, DA SILVA & MALCON (2000), ANISKIN (1994)
P. quadruplicatus (listed as *P.amphichoricus* -topotypes)	26	44	VEN: Territorio Federal Amazonas	REIG & USECHE (1976)
P. quadruplicatus	28	44	Ecuador: Limoncocha; Peru: Santiago	GARDNER & EMMONS (1984)
P. quadruplicatus	28	42	Peru, Amazonas; BR: AM	PATTON, DA SILVA & MALCON (2000), This study
LONGICAUDATUS GROUP				
P. brevicauda	28	48	Peru; BR: AC	GARDNER & EMMONS (1984), PATTON, DA SILVA & MALCON (2000)
P. aff. brevicauda	28	50-51	Peru: Dept Ucayali	ANISKIN (1994)
SIMONSI GROUP				
P. simonsi	32	58	Ecuador; S Peru; BR: AM	GARDNER & EMMONS (1984), PATTON, DA SILVA & MALCON (2000)
P. aff. simonsi	32	57-58	Peru: Ucayali and Loreto	ANISKIN (1994)

Species were grouped according to PATTON (1987). (VEN) Venezuela, (BR) Brazil, states: (AC) Acre, (AM) Amazonas, (PA) Pará, (RR) Roraima.

chromosomes, in five pairs of biarmed autosomes (numbers 1, 2, 3, 5, 6) and in an interstitial region in the mid part of the largest acrocentric pair (number 7). One medium sized metacentric pair (number 8) lacked pericentromeric heterochromatin, showing a heterochromatic region at the long arm telomere. In one specimen, a heterochromatic region in the long arm telomere of chromosome no. 1 was also observed.

Karyotypic analysis of 16 specimens of *Proechimys* sp. A showed 2n=38, FN=52 (Fig.2B). The autosome complement is composed by 8 pairs of biarmed chromosomes (three large metacentric, one medium-large sized metacentric and four small pairs) and ten pairs of acrocentric chromosomes. The X chromosome is a medium sized acrocentric and the Y chromosome is a small acrocentric. With conventional Giemsa staining both

members of pair number 5 showed a constriction at the distal region of the long arm. A G band karyotype of *Proechimys* sp. A is shown in figure 2E.

Karyologic analysis of three specimens of *Proechimys* sp. B showed 2n=46, FN=50 (Fig.2C). The autosome complement is composed by three small sized biarmed pairs and 19 acrocentric pairs varying gradually from large to small. The X chromosome is a medium sized acrocentric chromosome and the Y chromosome a small acrocentric. With conventional Giemsa staining both members of the largest submetacentric pair showed a constriction at the distal region of the long arm. C banding (not shown) revealed pericentromeric heterocromatin in the sex chromosomes, in three pairs of biarmed autosomes and all acrocentrics pairs, and in an interstitial region at the sub terminal region of the largest acrocentric pair.

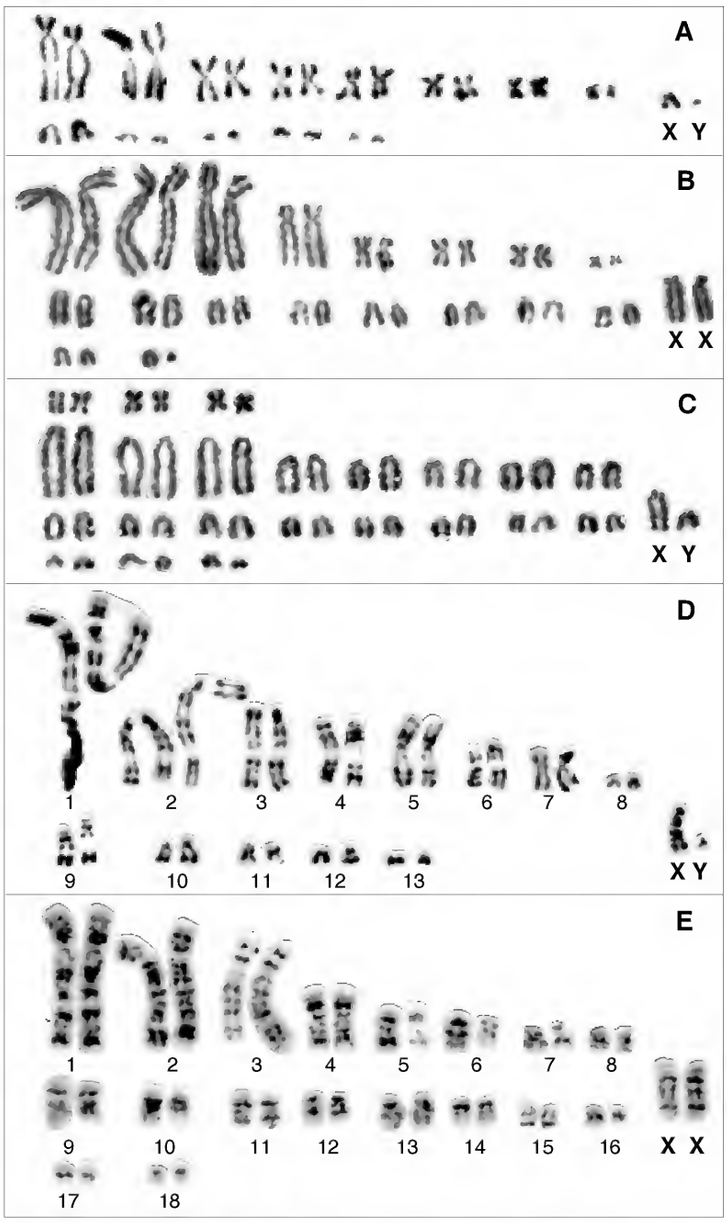

Fig.2- Conventional staining of (A) *P. quadruplicatus* with 2n=28, FN=42 (♂ MN69003), (B) *Proechimys* sp. A with 2n=38, FN=52 (♀ MN69042), (C) *Proechimys* sp. B with 2n=46, FN=50 (♂ CRB635), G - band karyotype of (D) *P. quadruplicatus* (♂ CRB 1483), and (E) *Proechimys* sp (♀ MN69020). X= X chromosome, Y= Y chromosome.

Molecular data

Cytochrome *b* data of specimens here sequenced were deposited in GenBank (GenBank 308435 and 308436). Inter-individual variation was observed in *Proechimys* sp. A, *Proechimys* sp. B, and *P. guyannensis*. Divergence levels between *Proechimys* sp. A (2n=38) and *Proechimys* sp. B (2n=46) are considerably greater (p-distance>0.04 in comparisons of any pair of haplotypes) than within either clade (0.03 or less). Divergence levels between *Proechimys* sp. A (2n=38) and *P. guyannensis* are slightly greater (p-distance>0.03 in comparisons of any pair of haplotypes) than within either clade (0.03 or less). Likewise, divergence levels between *Proechimys* sp. B (2n=46) and *P. guyannensis* are also slightly greater (p-distance>0.02 in comparisons of any pair of haplotypes) than within either clade (0.01 or less). Differences between inter-specific haplotypes were generally higher than 10%, except when comparing members of the same specie group (*sensu* PATTON, 1987). In such cases distances are normally greater than 4,0%.

Maximum parsimony (MP) analyses grouped all *Proechimys* species in one monophyletic clade and place *P. roberti* as the most basal offshoot (Fig.3A). *P. quadruplicatus*, *Proechimys* sp. A and *Proechimys* sp. B fall into three clearly defined molecular clades, each of which corresponds to one of the three karyotypes. The clades formed by *Proechimys* sp. A, *Proechimys* sp. B, and *P. guyannensis* haplotypes form a well supported group (94% bootstrap). The latter two are more closely related, however with a lower bootstrap support (68%). The Rio Tiquié *Proechimys* sp. A specimens are placed in a monophyletic clade with the others, with specimens of the same species supported by a bootstrap value of 99%.

Median-joining network analysis showed a more structured geographic pattern than maximum parsimony analyses for *Proechimys* sp. A since a median vector was postulated between haplotypes of each river (Fig. 3B).

DISCUSSION

Karyologic comparisons

The *Proechimys quadruplicatus* karyologic variant herein described is similar to all species of the *goeldii* species group (*sensu* PATTON, 1987, see Table 1). They share the same diploid and fundamental numbers with other specimens of *P. quadruplicatus* from Brazilian and Peruvian Amazon (PATTON, DA SILVA & MALCON, 2000). However, the karyotype herein analysed, despite sharing the same diploid number (2n=28) with *P. quadruplicatus* specimens from Ecuador and Santiago in Peru (Tab.1), differed from them in fundamental number and chromosome morphology. The *P. quadruplicatus* karyotype here described showed a medium-sized acrocentric pair that, in Peruvian specimens from Santiago, corresponded to a medium-sized metacentric pair. These results showed the need of further investigations to verify whether these karyologic variations are fixed or polymorphic. With G-band pattern, chromosome pairs numbers 1, 2, 3 and 4 of *P. quadruplicatus* here analysed were recognised as the respective homologues to chromosome pairs numbers 11, 1, 2 and 5 of the karyomorphotype 2n=24, FN=43-44. This karyological variant was tentatively identified as belonging to "*P. steeret*?" by ANISKIN (1994) and was referred to *P. goeldii* Thomas, 1905 by PATTON, DA SILVA & MALCON (2000). The chromosome complement of the *goeldii* species group (*sensu* PATTON, 1987) is characterised by diploid numbers varying from 24 to 28 with fundamental (autosome) numbers ranging from 40 to 44. This species group occurs in the Amazonian region of Peru, Ecuador, Venezuela, and Brazil.

The *Proechimys* sp. A karyotype (2n=38, FN=52) was also different from all other karytoypes previously described in *Proechimys* species. Karyologic data did not allow us to allocate this species to any of the described species groups defined in PATTON (1987) but morphologic traits suggested that this species belong to the *guyannensis* species group (*sensu* PATTON, 1987). Karyotypic comparisons with two species karyotyped by ANISKIN (1994) showed interspecific homologies between chromosome pairs 1, 2 and 3 of *Proechimys* sp. A and chromosome pairs 1, 10 and 11 of *Proechimys* sp.1 (2n=28, see table 1) and *Proechimys* sp.2 (2n=30, see Tab.1 and ANISKIN, 1994). These karyotypes also shared the same fundamental autosome number (FN=50). The 2n=46, FN=50 karyotype herein described in *Proechimys* sp. B specimens was very different from any other previously reported for *Proechimys* species due to its low ratio of biarmed: acrocentric pairs, resulting in unusual low number of autosome arms when compared to other *Proechimys* species (see Tab.1). Despite phylogenetically close related, based on the molecular analyses, the karyologic complement of *Proechimys* sp. B (2n=46, FN=50) differ from *P. guyannensis* (2n=40, FN=54) from French Guyana. The former showed only three biarmed pairs, whereas the latter showed eight biarmed pairs. To derive the *P. guyannensis* karyotype (from French

Guyana) from *Proechimys* sp. B karyotype we need three centric fusions and two inversion events. These karyologic data greatly suggested that these taxa belong to two evolutive lineages.

Proechimys quadruplicatus here analysed showed telomeric, pericentromeric, and interstitial heterochromatin. In the genus *Proechimys*, presence of pericentromeric heterochromatim in most autosomes was found to be widespread (ANISKIN, 1994; MAIA & LANGGUTH, 1993) contrary to scarce telomeric heterochromatin (BUENO & GOMEZ-LAVERDE, 1993; GOMEZ-LAVERDE, BUENO & CADENA, 1990). C-band variants in *P. quadruplicatus* were found to occur in the homozygote condition (both chromosomes with or without heterochromatin) probably due to a polymorphism, despite an apparent lack of heterozigotes.

Proechimys species are generally sympatric, but taxa belonging to the same species group (and sharing similar karyotypes) were not sympatric as we would expect in an allopatric model of chromosome speciation. Extreme variations in heterochromatin, diploid and fundamental numbers in *Proechimys* species pointed to the relevance of karyotypic rearrangements in speciation and to the usefulness of cytotaxonomic studies. Furthermore, groups formed by species sharing karyologic similarities are coincident with the one sharing morphologic similarities.

Molecular analyses

Estimates of inter-specific sequence divergence were generally high (Tab.2), however these values are particular for each *Proechimys* taxa.

The monophyly of the *goeldii* group (*sensu* PATTON, 1987) was supported by karyologic data but not by parsimony analyses. This result confirmed previous analyses based on a larger number of taxa and longer sequence fragments which did not support the monophyly of Patton's *goeldii* group (DA SILVA, 1998).

Proechimys sp. A specimens from different localities (Mawarinuma, Tiquié, Padauari, and Aracá rivers) formed a well supported clade in MP analyses (93% bootstrap values), indicating the monophyly of this group. *Proechimys* sp. B haplotypes also formed a monophyletic group, as expected to occur with specimens belonging to the same taxon. Specimens of *Proechimys* sp. A, *P. guyannensis* and *Proechimys* sp. B grouped in a well - supported clade (bootstrap value of 94%), indicating close phylogenetic affinities between these taxa. These results confirm the morphologic traits that suggested that *Proechimys* sp. A belong to *guyannensis* group (*sensu* PATTON, 1987). However, the *P. roberti* haplotype here analysed did not cluster with the remaining species of the *guyannensis* group.

The position of specimens from Rio Tiquié with respect to the other *Proechimys* sp. A specimens in the median joining analyses is coherent with geographic data, because the Rio Tiquié specimens are separated from the others by a wide water course, the Rio Negro (Fig.1). This analysis showed a high geographic structuration in the *Proechimys* sp. A population and the presence of a median vector between haplotypes of different rivers suggested that the large Amazonian rivers represent barriers to gene flow between these populations. However, isolation by distance cannot be ruled out in view that riverine effects affected only *P. echinothrix* but not other species like *P. stereei* and *P. simonsi* (MATOCQ, PATTON & DA SILVA, 2000).

MP analyses grouped *Proechimys* sp. A specimens from different localities; two of these specimens have the same G-banded chromosome complement and belonged to the same species, suggesting that this new and undescribed species has a wide distribution, with well geographically structured populations.

Morphologic comparisons

Comparisons of *Proechimys* sp. B with the illustration of incisive foramen (PATTON, 1987) and part of the ventral part of skull of topotypes of *Proechimys guyannensis arabupu* Moojen, 1948 (PATTON, 1987) showed that these taxa share similar morphology, suggesting that they belong to the same species. On the other hand, molecular and karyological data showed that *P. guyannensis* and *Proechimys* sp. B (=*P. g. arabupu*) are independent evolutive lineages. These morphological similarities suggested that the name *Proechimys arabupu*, whose type locality is Boa Vista, State of Roraima, is available to *Proechimys* sp. B populations.

Karyologic analysis grouped *Proechimys* sp. A with two other *Proechimys* species of Peru and molecular analyses grouped *Proechimys* sp. A, *Proechimys arabupu* (=*Proechimys* sp. B) and *P. guyannensis* suggesting that these species are very related, probably belonging to a single species group, the *guyannensis* group, as defined by PATTON (1987).

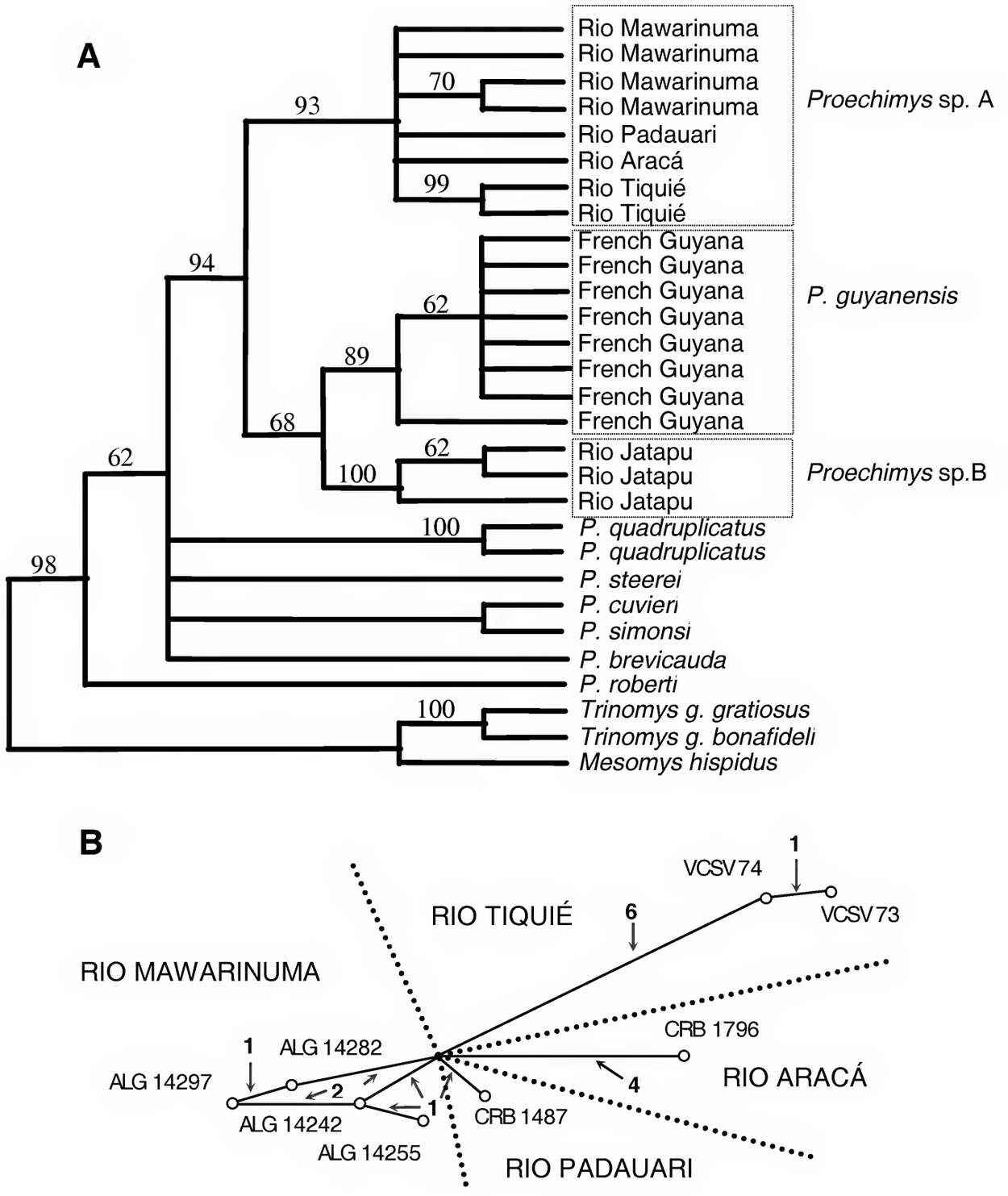

Fig.3- Molecular analyses showing phylogenetic relationships between *Proechimys* specimens: (A) Consensus parsimony tree (length=325, Consistency Index=0.529); (B) median-joining analysis. (○) haplotypes, (●) median vector, (→) number of nucleotide substitution.

Table 2. Distance p estimates between haplotypes. Numbers in bold are distance between specimens of the same species and locality, and shaded case are distance between specimens of the same taxon.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1.*Proechimys* sp.A																		Venezuela, Río Mawarinuma - ALG14242							
2. *Proechimys* sp.A	**.00**																	Venezuela, Río Mawarinuma - ALG14255							
3. *Proechimys* sp.A	**.01**	**.01**																Venezuela, Río Mawarinuma - ALG14282							
4. *Proechimys* sp.A	**.01**	**.01**	**.00**															Venezuela, Río Mawarinuma - ALG14297							
5. *Proechimys* sp.A	.01	.02	.02	.02														Brazil, rio Aracá, Ig. Bigorna- CRB1796							
6. *Proechimys* sp.A	.01	.01	.01	.01	.01													Brazil, Rio Padauari - CRB1487							
7. *Proechimys* sp.A	.02	.02	.02	.03	.03	.02												Brazil, Rio Tiquié - VCSV73							
8. *Proechimys* sp.A	.02	.02	.02	.02	.03	.02	**.00**											Brazil, Rio Tiquié - VCSV74							
9. *P. guyannensis*	.04	.04	.05	.05	.05	.05	.06	.06										French Guyana - AJ251399							
10. *P. guyannensis*	.04	.04	.05	.05	.05	.05	.06	.06	.00									French Guyana - AJ251395							
11. *P. guyannensis*	.04	.04	.05	.05	.05	.05	.06	.06	.00	.00								French Guyana - AJ251396							
12. *P. guyannensis*	.04	.04	.05	.05	.05	.05	.06	.06	.00	.00	.00							French Guyana - AJ251397							
13. *P. guyannensis*	.05	.05	.06	.06	.05	.06	.07	.06	.01	.01	.01	.01						French Guyana - AJ251398							
14. *P. guyannensis*	.04	.04	.05	.05	.05	.05	.06	.06	.00	.00	.00	.00	.01					French Guyana - AY206600							
15. *P. guyannensis*	.04	.04	.05	.05	.05	.05	.06	.06	.00	.00	.00	.00	.01	.00				French Guyana - AY206601							
16. *P. guyannensis*	.04	.04	.05	.05	.04	.05	.06	.05	.00	.00	.00	.00	.01	.00	.00			French Guyana - AY206602							
17. *Proechimys* sp.B	.06	.06	.07	.07	.07	.07	.05	.05	.04	.04	.04	.04	.05	.04	.04	.03				Brazil, Rio Jatapu - MN68174					
18. *Proechimys* sp.B	.06	.06	.06	.06	.07	.06	.05	.05	.03	.03	.03	.03	.04	.03	.03	.03	**.01**			Brazil, Rio Jatapu - MN61642					
19. *Proechimys* sp.B	.06	.06	.07	.06	.07	.06	.05	.05	.03	.03	.03	.03	.04	.03	.03	.03	**.01**	**.01**		Brazil, Rio Jatapu - MN61643					
20.*P. quadruplicatus*	.12	.12	.13	.13	.12	.12	.13	.12	.12	.12	.12	.12	.12	.12	.12	.11	.12	.12	.12						
21.*P. quadruplicatus*	.13	.13	.14	.14	.13	.13	.14	.13	.13	.13	.13	.13	.13	.13	.13	.12	.13	.12	.12	.02					
22. *P. steerei*	.11	.11	.12	.11	.11	.11	.13	.12	.09	.09	.09	.09	.10	.09	.09	.09	.10	.10	.10	.10	.10				
23. *P. cuvieri*	.11	.11	.12	.11	.12	.12	.13	.13	.11	.11	.11	.11	.12	.11	.11	.11	.12	.12	.12	.13	.14	.11			
24. *P. brevicauda*	.13	.13	.14	.13	.13	.13	.14	.14	.13	.13	.13	.13	.14	.13	.13	.13	.13	.13	.13	.12	.14	.12	.11		
25. *P. simonsi*	.11	.11	.11	.11	.12	.12	.13	.13	.12	.12	.12	.12	.13	.12	.12	.12	.13	.13	.13	.15	.15	.12	.13	.15	
26. *P. roberti*	.12	.12	.13	.12	.12	.12	.13	.13	.11	.11	.11	.11	.12	.11	.11	.11	.13	.129	.13	.13	.13	.11	.11	.14	.13

ACKNOWLEDGMENTS

We are grateful to P.S.D'Andrea, A.Junqueira, P.Albajar, and P.Borodin (IOC-FIOCRUZ), for helping in field expeditions; S.M.Franco (Museu Nacional - Rio de Janeiro), for helping with museum collection; H.N.Seuánez (CPQ-INCA), for reviewing the manuscript and to J.R.Coura (IOC-FIOCRUZ), for financial support received. To Dr. J.L.Patton (MVZ-Berkeley) and an anonymous referee, for valuable

suggestions in a previous version of this manuscript. Brazilian Institute of Environment and Natural Resources (IBAMA)) granted us licenses for collecting samples. Work supported by FIOCRUZ (Dept of Tropical Medicine), Fundação Rio-Zoo, Rio de Janeiro, CAPES, and CNPq (Brazil).

LITERATURE CITED

ANISKIN, U.M., 1994. Evolutionary cytogenetics of chinchillas of Peruvian Amazonia (Rodentia, Echimyidae). In: HAYKA, M. (Ed.) **Mammals of Peruvian Amazonia.** Hayka: Moscou. p.62-82.

BANDELT, H.J.; FOSTER, P. & RÖHL, A., 1999. Median-joining networks for inferring intraspecific phylogenies. **Molecular Biology and Evolution**, Oxford, **16**(1):37-48.

BARROS, R.M.S., 1978. **Variabilidade cromossômica em *Proechimys* e *Oryzomys* (Rodentia) do Amazonas**. São Paulo. PhD Thesis. Universidade de São Paulo.

BUENO, M.L. & GOMEZ-LAVERDE, M., 1993. Variación heterocromática en *Proechimys semispinosus* (Rodentia: Echimyidae) de la región pacífica Colombiana. **Caldasia**, Bogotá, **17**:333-340.

DA SILVA, M.N.F., 1998. Four new species of spiny rats of the genus *Proechimys* (Rodentia: Echymyidae) from the western Amazon of Brazil. **Proceedings of the Biological Society of Washington**, Washigton, **11**:436-471.

GARDNER, A.L. & EMMONS, L., 1984. Species group in *Proechimys* (Rodentia: Echimyidae) as indicated by karyology and bullar morphology. **Journal of Mammalogy**, Provo, **65**:10-25.

GOMEZ-LAVERDE, M.; BUENO, M.L. & CADENA, A., 1990. C. Poblaciones de ratas (*Proechimys semispinosus*) (Rodentia: Echimyidae). In: AGUIRRE, J. & RANGEL, O. (Eds.) **Biota y Ecosistema de Gorgona y Gorgonilla**. Bogotá: Fundo Fen Colombia, Editorial Presencia. p.244-251.

IKEUCHI, T., 1984. Inhibitory effect of ethidium bromide on mitotic chromosome condensation and its application to high resolution chromosome banding. **Cytogenetics and Cell Genetics**, Basel, **38**:35-61.

KUMAR, S.; TAMURA, K.; JAKOBSEN, I.B. & NEI, M., 1993. MEGA2: molecular evolutionary genetics analysis software. **Bioinformatics**, Oxford, **17**(12):1244-1245.

LEAL-MESQUITA, E.R.R.B.P., 1991. **Estudos citogenéticos em dez espécies de roedores brasileiros da família Echimyidae**, São Paulo. Ms. Dissertation. Universidade de São Paulo.

MAIA, V. & LANGGUTH A., 1993. Constitutive heterochromatin polymorphism and NORs in *Proechimys cuvieri* Petter, 1978. **Brazilian Journal of Genetics**, Rio Preto, **16**:145-154.

MATOCQ, M.D.; PATTON, J.L. & DA SILVA, M.N., 2000. Population genetic structure of two ecologically distinct Amazonian spiny rats: separating history and current ecology. **Evolution: International Journal of Organic Evolution**, Lawrence, **54**(4):1423-1432.

MOOJEN, J., 1948. Speciation in the Brazilian spiny rats (genus *Proechimys*, family Echimyidae). **University of Kansas Publications**, Lawrence, **1**:301-406.

PATTON, J.L., 1987. Species group of spiny rats, genus *Proechimys* (Rodentia, Echimyidae). **Fieldiana Zoology, ns**, Chicago, **39**:305-345.

PATTON, J.L. & GARDNER, A.L., 1972. Notes on systematics of *Proechimys* (Rodentia: Echimyidae), with emphasis on Peruvian forms. **Occasional Papers Museum Zoology, Louisiana State University**, Baton Rouge, **44**:1-30.

PATTON, J.L.; DA SILVA, M.N.F & MALCON, J.R., 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. **Bulletin American Museum of Natural History**, New York, **244**:1-306.

POSADA, D. & CRANDALL, K.A., 2001. Intraspecific gene genealogies: trees grafting into networks. **Trends in Ecology and Evolution**, Oxford, **16**(1):37-44.

REIG, O.A. & USECHE, M., 1976. Diversidad cariotípica y sistemática en poblaciones venezolanas de *Proechimys* (Rodentia, Echimyidae), con datos adicionales sobre poblaciones de Perú y Colombia. **Acta Científica Venezolana**, Caracas, **27**:132-140.

REIG, O.; TRAINER, M. & BARROS, M.A., 1979. Sur l'identification chromosomique de *Proechimys guyannensis* (E. Geoffroy, 1803) et de *Proechimys cuvieri* Petter, 1978 (Rodentia, Echimyidae). **Mammalia**, Paris, **43**:501-505.

SAMBROOK, J.; FRITSCH, E.F. & MANIATIS, T., 1989. **Molecular Cloning: A Laboratory Manual**. Cold Spring Harbor: Cold Spring Harbor Laboratory Press.

SEABRIGHT, M., 1971. A rapid banding technique for human chromosomes. **Lancet**, London and New York, **2**:971-972.

SUMNER, A.T., 1972. A simple technique for demonstrating centromeric heterochromatin. **Experimental Cell Research**, Bath, **75**:304-306.

SMITH, M.F. & PATTON, J.L., 1993. The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data for the akodontine tribe. **Biological Journal of Linnean Society**, London, **50**:149-177.

SWOFFORD, D.L., 1999. "**PAUP*: Phylogenetic Analysis Using Parsimony (and other methods), version 4.1**", Washington: Smithsonian Institution Press.

THOMAS, O., 1928. The Goldman-Thomas expedition to Peru. VII. The mammals of the Rio Ucayali. **Annals and Magazine of Natural History**, London, series 10, **2**:249-265.

WEKSLER, M.; BONVICINO, C.R.; OTAZÚ, I.B. & SILVA JR., J.S., 2001. The status of *Proechimys roberti* and *Proechimys oris* (Rodentia: Echimyidae) from Eastern Amazonia and Central Brazil. **Journal of Mammalogy**, Provo, **82**(1):109-122.

Arquivos do Museu Nacional, Rio de Janeiro, v.63, n.1, jan./mar.2005
ISSN 0365-4508

SUMÁRIO / CONTENTS

Depoimento: João Moojen de Oliveira - Pioneiro da Mastozoologia Brasileira.
C.A.FREITAS 5

João Moojen (1904-1985).
F.D.AVILA-PIRES 7

A coleção de mamíferos do Serviço Nacional de Peste no Museu Nacional, Rio de Janeiro, Brasil.
The collection of mammals of the National Plague Service in the Museu Nacional, Rio de Janeiro, Brazil.
J.A.OLIVEIRA & S.M.FRANCO 13

Mamíferos colecionados pelo Serviço de Estudos e Pesquisas sobre a Febre Amarela nos municípios de Ilhéus and Buerarema, Estado da Bahia, Brasil.
Mammals collected by the Yellow Fever Research Service in the municipalities of Ilhéus and Buerarema, State of Bahia, Brazil.
S.M.VAZ 21

Fatores ambientais e a reprodução de marsupiais e roedores no leste do Brasil.
Environmental factors and reproduction of eastern Brazilian marsupials and rodents.
R.CERQUEIRA 29

Intergradação de hábitats de pequenos mamíferos não-voadores na paisagem retalhada do bioma Cerrado.
Intergradation of habitats of non-volant small mammals in the patchy Cerrado landscape.
C.J.R.ALHO 41

Modelos de distribuição de *Zygodontomys brevicauda* (ALLEN & CHAPMAN, 1893) (Mammalia, Muridae) nas savanas de Roraima, norte do Brasil.
Models of the distribution of *Zygodontomys brevicauda* (ALLEN & CHAPMAN, 1893) (Mammalia, Muridae) in the savanas of Roraima, northern Brazil.
J.L.P.CORDEIRO & L.F.B.OLIVEIRA 49

Diferenciação morfométrica e notas sobre a distribuição de três espécies de *Akodon* (Muridae, Sigmodontinae, Akodontini) na área costeira atlântica do Brasil.
Morphometric differentiation and distributional notes of three species of *Akodon* (Muridae, Sigmodontinae, Akodontini) in the Atlantic coastal area of Brazil.
L.GEISE, D.A.MORAES & H.S.SILVA 63

Variação geográfica em caracteres cranianos quantitativos de *Kerodon rupestris* (Wied, 1820) (Rodentia, Caviidae).
Geographical variation in quantitative cranial characters of *Kerodon rupestris* (Wied, 1820) (Rodentia, Caviidae).
G.LESSA, P.R.GONÇALVES & L.M.PESSÔA 75

Novo gênero para *Loncheres grandis* Wagner, 1845, com comentários taxonômicos sobre outros equimídeos arborícolas (Rodentia, Echimyidae).
A new genus for *Loncheres grandis* Wagner, 1845, with taxonomic comments on other arboreal echimyids (Rodentia, Echimyidae) .
G.E.IACK-XIMENES , M.VIVO & A.R.PERCEQUILLO 89

Taxonomia dos camundongos-do-mato, gênero *Oligoryzomys* Bangs, 1900 (Rodentia, Sigmodontinae) do Cerrado Brasileiro, com a descrição de duas novas espécies.
Taxonomy of pigmy rice rats genus *Oligoryzomys* Bangs, 1900 (Rodentia, Sigmodontinae) of the Brazilian Cerrado, with description of two new species.
M.WEKSLER & C.R.BONVICINO 113

Uma nova espécie de *Rhipidomys* (Rodentia, Muroidea) do Nordeste brasileiro.
A new species of *Rhipidomys* (Rodentia, Muroidea) from North-eastern Brazil.
C.J.TRIBE 131

SUMÁRIO / CONTENTS

Novos dados sobre as relações filogenéticas de dois macacos gigantes extintos do Novo Mundo (Primates, Platyrrhini).
New insights on the phylogenetic relationships of the two giant extinct New World monkeys (Primates, Platyrrhini).
P.G.GUEDES & L.O.SALLES 147

Caracterização cromossômica de taxa do gênero *Trinomys* Thomas, 1921 (Rodentia, Echimyidae) nos Estados do Rio de Janeiro e São Paulo.
Chromosomal characterization of taxa of the genus *Trinomys* Thomas, 1921 (Rodentia, Echimyidae) in the states of Rio de Janeiro and São Paulo.
L.M.PESSÔA, M.M.O.CORRÊA, E.BITENCOURT & S.F.REIS 161

Os cariótipos de *Trinomys moojeni* (Pessôa, Oliveira & Reis, 1992) e de *Trinomys setosus elegans* (Lund, 1841) (Rodentia, Echimyidae) de Minas Gerais, leste do Brasil.
The karyotypes of *Trinomys moojeni* (Pessôa, Oliveira & Reis, 1992) and *Trinomys setosus elegans* (Lund, 1841) (Rodentia, Echimyidae) from Minas Gerais, eastern Brazil.
M.M.O.CORRÊA, M.O.G.LOPES, E.V.C.CÂMARA, L.C.OLIVEIRA & L.M.PESSÔA 169

Caracterização cromossômica de espécies brasileiras de *Calomys* Waterhouse, 1837 dos domínios Amazônico, do Cerrado e dos Pampas (Rodentia, Sigmodontinae).
Chromosomal characterization of Brazilian species of *Calomys* Waterhouse, 1837 from Amazon, Cerrado and Pampas domains (Rodentia, Sigmodontinae).
M.S.MATTEVI, T.HAAG, L.F.B.OLIVEIRA & A.R.LANGGUTH 175

O cariótipo em espécies brasileiras de grande tamanho do gênero *Oecomys* Thomas, 1906 (Rodentia, Muridae, Sigmodontinae).
Karyology of large size Brazilian species of the genus *Oecomys* Thomas, 1906 (Rodentia, Muridae, Sigmodontinae)..
A.R.LANGGUTH, V.MAIA & M.S.MATTEVI 183

Análise cariológica e molecular de *Proechimys* Allen, 1899 (Rodentia, Echimyidae) da região Amazônica.
Karyologic and molecular analysis of *Proechimys* Allen, 1899 (Rodentia, Echimyidae) from the Amazon region.
C.R.BONVICINO, I.B.OTAZÚ & J.F.VILELA 191

INSTRUCTIONS TO AUTHORS

The authors are totally responsible for the content of the texts

1 - The MUSEU NACIONAL/UFRJ publishes reports of original scientific research in the field of Natural and Anthropological Sciences in the following publications: *Arquivos do Museu Nacional* (ISSN 0365-4508); *Publicações Avulsas do Museu Nacional* (ISSN 0100-6304); *Relatório Anual do Museu Nacional* (ISSN 0557-0689); *Boletim do Museu Nacional, Nova Série – Antropologia* (ISSN 0080-3189), *Botânica* (ISSN 0080-3197), *Geologia* (ISSN 0080-3200) and *Zoologia* (ISSN 0080-312X); *Série Livros* (ISBN 85-7427). All are indexed in the following data base: Biological Abstracts, ISI - Thomson Scientific, Ulrich's International Periodicals Directory, Zoological Record, NISC Colorado, Periodica and C.A.B. International.

2- The manuscript must be submitted in three high-quality copies, printed on one side of A4 paper, double-spaced, font Times New Roman (12), together with an electronic version (Word for Windows) not formatted. The manuscripts can be submitted in Portuguese or English (for other languages consult the Editorial Board). All foreign expressions have to be italicized.

3- The text has to be preceded by the identification of the author (name, institutional affiliation, and complete address).

4- An abstract followed by the title and key works in both languages have to be provided in English and Portuguese.

5- All illustrations, designated in the text as figure (Fig.1, Fig.2, etc.), must have scale bars. Titles or captions must be typed apart. Illustrations should be digitalized.

6- All citations must indicate author and year of publication, with the author(s') last name(s) in upper case followed by the publications date of the cited document, separated by a comma and in brackets; i.e.: (PEREIRA, 1996).

7- The references must be presented at the end of the text in alphabetical order, as follows (adapted from the ABTN regulations):

Books/chapters in books:
LIMA, D.A., 1982. Present-day forest refuges in Northeastern Brazil. In: PRANCE, G.T. (Ed.) **Biological diversification in the tropics**. New York: Columbia University Press. p.245-251.

Periodicals:
MORA, O.A.; SIMÕES, M.J. & SASSO, W.S., 1987. Aspectos ultra-estruturais dos fibroblastos durante a regressão da cauda dos girinos. **Revista Brasileira de Biologia**, Rio de Janeiro, **47**(4):615-618, figs.1-2.

Papers published in scientific meetings:
VENTURA, P.E.C., 1985. Avifauna de Morro Azul do Tinguá, Miguel Pereira, Rio de Janeiro. In: CONGRESSO BRASILEIRO DE ZOOLOGIA, 12., Campinas. **Resumos...**, Campinas: Universidade Estadual de Campinas, p.273.

Documents obtained at the internet:
POMERANCE, R., 1999. **Coral mortality, and global climate change**. Available: <http://www.gov/topical/global/envinon/99031002.htm>. Captured on 18 abr. 1999.

8- A total of 50 (fifty) copies, per article, are offered free of charge for the author(s).

9- All correspondence and manuscripts must be sent to the following address:
Comissão de Publicações
Museu Nacional/UFRJ
Quinta da Boa Vista, São Cristóvão
20940-040 – Rio de Janeiro, RJ, Brasil
Tels.: (0xx21) 2568 1347 ramal 22
E-mail: <compubli@mn.ufrj.br>

INSTRUÇÕES PARA AUTORES

O conteúdo dos artigos é de inteira responsabilidade do(s) autor(es)

1- O MUSEU NACIONAL/UFRJ edita, nas áreas das Ciências Naturais e Antropológicas:

Arquivos do Museu Nacional (ISSN 0365-4508); *Publicações Avulsas do Museu Nacional* (ISSN 0100-6304); *Relatório Anual do Museu Nacional* (ISSN 0557-0689); *Boletim do Museu Nacional, Nova Série – Antropologia* (ISSN 0080-3189), *Botânica* (ISSN 0080-3197), *Geologia* (ISSN 0080-3200) e *Zoologia* (ISSN 0080-312X); *Série Livros* (ISBN 85-7427). Indexadas nas bases de dados: Biological Abstracts, ISI - Thomson Scientific, Ulrich's International Periodicals Directory, Zoological Record, NISC Colorado, Periodica e C.A.B. International.

2- Os originais devem ser apresentados em três vias, em papel A4, espaço duplo, em uma só face do papel, bem como em disquete no programa Word for Windows, em fonte Times New Roman (corpo 12), sem qualquer tipo de formatação. Os manuscritos podem ser encaminhados em português ou inglês (outro idioma ficará a critério da Comissão Editorial). Os termos estrangeiros no texto deverão ser grafados em itálico.

3- Os textos deverão ser precedidos de identificação do autor (nome e instituição de vínculo com endereço completo).

4- Deverão constar Resumo e Abstract, juntamente com título e palavras-chave em português e inglês.

5- As ilustrações, designadas no texto como figura (Fig.1, Fig.2, etc.), deverão conter escalas com as unidades abreviadas (legendas à parte). Digitalizadas e salvas individualmente (inclusive quando apresentadas em pranchas).

6- As citações no texto devem ser indicadas pelo sistema autor-data que compreende o sobrenome do(s) autor(es), em caixa alta, seguido do ano de publicação do documento, separado por vírgula e entre parêntese. Ex.: (PEREIRA, 1996).

7- As referências bibliográficas (adaptadas das normas da ABNT) deverão ser apresentadas no final do texto, em ordem alfabética única dos autores.

Livro:
LIMA, D.A., 1982. Present-day forest refuges in Northeastern Brazil. In: PRANCE, G.T. (Ed.) **Biological diversification in the tropics**. New York: Columbia University Press. p.245-251.

Periódico:
MORA, O.A., SIMÕES, M.J. & SASSO, W.S., 1987. Aspectos ultra-estruturais dos fibroblastos durante a regressão da cauda dos girinos. **Revista Brasileira de Biologia**, Rio de Janeiro, **47**(4):615-618, figs.1-2.

Trabalhos apresentados em encontros científicos:
VENTURA, P.E.C., 1985. Avifauna de Morro Azul do Tinguá, Miguel Pereira, Rio de Janeiro. In: CONGRESSO BRASILEIRO DE ZOOLOGIA, 12., Campinas. **Resumos...**, Campinas: Universidade Estadual de Campinas, p.273.

Documentos disponíveis na internet:
POMERANCE, R., 1999. **Coral mortality, and global climate change**. Disponível em: <http://www.gov/topical/global/envinon/99031002.htm>. Acesso em: 18 abr. 1999.

8- Serão fornecidos ao(s) autor(es) 50 (cinqüenta) exemplares por artigo.

9- A correspondência editorial e os artigos deverão ser enviados para:
Comissão de Publicações
Museu Nacional/UFRJ
Quinta da Boa Vista, São Cristóvão
20940-040 – Rio de Janeiro, RJ, Brasil
Tels.: (0xx21) 2568 1347 – ramal 22
E-mail: <compubli@mn.ufrj.br>

Associação Amigos do
Museu Nacional

www.samn.kit.net
amigos@mn.ufrj.br
2568-8262 - ramal: 203
2568-1347 - ramal: 26

A Associação Amigos do Museu Nacional (SAMN) é uma instituição sem fins lucrativos. Fundada em 13 de janeiro de 1937 por professores do Museu Nacional, em 23 de dezembro de 1966 foi reconhecida como de utilidade pública pela Lei Estadual n°1200.

Os objetivos da SAMN ligam-se ao enriquecimento da cultura nacional – incentivar o ensino das Ciências Naturais e Antropológicas através de visitas, cursos, concursos, etc.; enriquecer as coleções científicas do Museu Nacional; promover expedições científicas e atividades técnico-científicas no país; incentivar o respeito ao índio e a suas manifestações culturais, à natureza e à preservação de suas riquezas e, finalmente, promover atividades esportivas, recreativas e sociais.

A atual Diretoria da SAMN está trabalhando no sentido de revitalizar a Sociedade, objetivando, inclusive, maior integração com as escolas que visitam o Museu Nacional.

Com vistas a promover essa integração, está sendo lançada uma campanha de adesões, de caráter permanente. A filiação à SAMN poderá ser feita por fax (ficha de inscrição abaixo) ou on line (ficha de inscrição na homepage).

The Friends of the Brazilian National Museum (SAMN) is a non-profit institution. It was founded on January 13, 1937 and on December 23, 1966 it was recognized as an institution of public utility by State Law # 1200.

The objectives of SAMN are linked to the enrichment of the national culture – motivation of the teaching of Natural and Anthropological sciences through visits, courses, contests etc.; enrichment of the scientific collections of Museu Nacional; promotion of scientific expeditions and technical-scientific activities in the country; motivation of the respect to the Native and their culture, to Nature and the preservation of its wealth and, finally, promotion of sports, recreational and social activities.

The current Directory of SAMN works hard for the revitalization of the Society, also aiming at the integration with the many schools that visit the Museu Nacional.

The affiliation to SAMN can be made by fax (application form below) or online (application form on the homepage)

Endereço / Address
Quinta da Boa Vista, São Cristóvão, 20940-040, Rio de Janeiro, RJ, Brasil

NOME/NAME: .....

ENDEREÇO/ADDRESS: .....

..... CEP/CODE: .....

TEL/PHONE #: ..... CEL/MOBILE: .....

E-MAIL: ..... HOMEPAGE: .....

NASCIMENTO/BIRTH: ...../...../..... CPF/CNPJ/CGC: .....

ID/ÓRGÃO EXP.: .....

ATIVIDADES/ACTIVITIES: .....

.....

MUSEU NACIONAL
Universidade Federal do Rio de Janeiro
Quinta da Boa Vista, São Cristóvão
20940-040 – Rio de Janeiro, RJ, Brasil

Impresso na Gráfica da UFRJ