IGHOR ANTUNES ZAPPES

FILOGEOGRAFIA E CITOGENÉTICA DO GÊNERO Kerodon (CUVIER, 1825) (RODENTIA: CAVIIDAE)

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Biologia Animal, para obtenção do título de Magister Scientiae.

VIÇOSA
MINAS GERAIS - BRASIL
2014

Ficha catalográfica preparada pela Biblioteca Central da Universidade Federal de Viçosa - Câmpus Viçosa

T
Z35f
2014

Zappes, Ighor Antunes, 1986-
Filogeografia e citogenética do gênero Kerodon (Cuvier, 1825) (Rodentia: Caviidae) / Ighor Antunes Zappes. – Viçosa, MG, 2014.
viii, 45f. : il. (algumas color.) ; 29 cm.

Orientador: Gisele Mendes Lessa Del Giúdice.
Dissertação (mestrado) - Universidade Federal de Viçosa.
Inclui bibliografia.

1. Mocó. 2. Citogenética. 3. Filogeografia. I. Universidade Federal de Viçosa. Departamento de Biologia Animal. Programa de Pós-graduação em Biologia Animal. II. Título.

CDD 22. ed. 599.3592

IGHOR ANTUNES ZAPPES

FILOGEOGRAFIA E CITOGENÉTICA DO GÊNERO Kerodon (CUVIER, 1825) (RODENTIA: CAVIIDAE)

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Biologia Animal, para obtenção do título de Magister Scientiae.

APROVADA: 24 de Abril de 2014.

.

_____ _____

Dr. Erika Hingst-Zaher

Dr Jorge Abdala Dergam dos Santos
(Coorientador)

_____

Dr. Gisele Mendes Lessa Del Giúdice
(Orientadora)

Dedico este trabalho ao meu avô Valdevino, o primeiro cientista da família.

AGRADECIMENTOS

Agradeço a Deus por criar tudo.

Aos meus pais Hubsclender e Sarah por serem os melhores pais do mundo..

À minha irmã Camilah, por compartilhar as vivências da infância comigo.

Aos meus familiares próximos a mim, pelo suporte e orações.

À toda a dinastia da república “Um dia a casa cai”, pelos quase dez anos de farras.

À equipe de trabalho do laboratório Beagle, pela ajuda e ensinamentos.

À professora Gisele, por entender meu jeito de trabalhar e por dividir seu estudo dos mocós comigo.

Ao professor Jorge, por me abrigar em seu laboratório e me auxiliar com as pesquisas.

Aos membros da banca pela disponibilidade e correção do trabalho.

À Marina e ao Bisa pela ajuda nas discussões dos meus resultados.

Ao Udson por me ensinar as técnicas laboratoriais.

A Alexandre Portella e Fabiano Aguiar, pela companhia nas coletas e excelente mira no campo.

À FAPEMIG pela concessão da bolsa de fomento.

À Universidade Federal de Viçosa e a Pós-Graduação em Biologia Animal pela oportunidade de obter o grau de Magister Scientiae.

Muito Obrigado!

ÍNDICE

LISTA DE FIGURAS

INTRODUÇÃO GERAL

ARTIGO I

ARTIGO II

LISTA DE TABELAS

RESUMO

ZAPPES, Ighor Antunes, M.Sc., Universidade Federal de Viçosa, abril de 2014. **FILOGEOGRAFIA, HIBRIDIZAÇÃO E CITOGENÉTICA DO GÊNERO Kerodon (RODENTIA: CAVIIDAE).** Orientadora: Gisele Mendes Lessa Del Giúdice. Coorientador: Jorge Abdala Dergam dos Santos.

Entre os mamíferos dos biomas brasileiros, os roedores do gênero Kerodon (Wied 1820), ou mocó, são um dos táxons mais especializados. Uma de suas espécies, o Kerodon rupestris, um dos poucos mamíferos endêmicos do semiárido brasileiro, a caatinga, possui sua distribuição fragmentada devido à descontinuidade dos afloramentos rochosos onde eles vivem, e isso favorece uma variação intraespecífica entre suas populações. A outra espécie do gênero, K. acrobata, vive em uma pequena área do cerrado, entre os estados de Tocantins e Goiás. O objetivo deste trabalho foi a caracterização citogenética de uma fêmea de Kerodon acrobata e molecular das duas espécies de Kerodon. Foi caracterizado o cariótipo de uma fêmea de K. acrobata, utilizando coloração Giemsa, bandeamento NOR, bandeamento de heterocromatina e fluorescência com DAPI. O espécime mostrou o mesmo número diploide, número fundamental e morfologia cromossômica que Kerodon rupestris. Porém, as localizações de NOR e de heterocromatina indicaram padrões diferentes em relação a outros roedores, enfatizando a singularidade dessa espécie. O DNA foi extraído de tecido hepático das duas espécies e amplificações foram feitas para o gene nuclear Adh1-I2. Após sequenciamento, alinhamentos foram realizados com o ClustalW. A filogenia foi inferida usando os métodos Máxima Parcimônia e Máxima Verossimilhança usando o PAUP e Análise Bayesiana, com o MrBayes. Uma rede de haplótipo foi realizada com os programas DnaSP e Network. O gene nuclear mostrou dois grupos bem estruturados: o primeiro formado por K acrobata sem resolução interna, e o segundo que incluiu as populações de K rupestris e três sequências do chamado 'híbrido'. Os dados obtidos sugerem alta diferenciação citogenética e molecular entre K rupestris e K acrobata, indicando diferentes idades entre elas. O chamado 'híbrido' pode representar uma população altamente divergente dentro de K rupestris, como resultado dentro da dinâmica de expansão e retração pleistocênica da caatinga.

.

ABSTRACT

ZAPPES, Ighor Antunes, M.Sc., Universidade Federal de Viçosa, April of 2014. **FILOGEOGRAFIA, HIBRIDIZAÇÃO E CITOGENÉTICA DO GÊNERO Kerodon (RODENTIA: CAVIIDAE).** Adviser: Gisele Mendes Lessa Del Giúdice. Co-adviser: Jorge Abdala Dergam dos Santos.

Among mammals from Brazilian biomes, rodent of genus Kerodon (Wied 1820), or mocó, englobes one of the most specialist species and one of the few endemic mammals from Brazilian semiarid, or caatinga, Kerodon rupestris, and other species from semi-arid islands within the savannah, or cerrado, Kerodon acrobata. Their distribution is fragmented, due to discontinuous rock outcrops where these animals live. It suggests an intraspecific variation among their populations. Cranial and cytogenetic studies with K. rupestris had showed a separation in three groups: one in Minas Gerais state, other in Bahia and the last in Ceará. This study investigated genes from populations of Kerodon species, in order to make analysis to check inter and intra variation. A small group from another locality, probably a hybrid, was also analyzed. We first characterize the karyotype of a female from K. acrobata. Giemsa staining, nucleolar organizer region (NOR) banding, C-positive heterochromatin banding and DAPI fluorescence were used in N metaphases of a specimen collected in Asa Branca Farm, in Aurora do Tocantins municipality, Tocantins state, Brazil. K. acrobata showed the same diploid number, fundamental number and chromosome morphology as Kerodon rupestris. But its NOR location and heterochromatin distribution patterns indicated a unique cytogenetic profile when compared to its sister species, emphasizing the evolutionary uniqueness of this relatively new and unknown species. This record also extends the distribution of this species northward. We also extracted DNA from livers and amplifications were made for gene Adh1-I2. After sequencing, alignments were done with ClustalW software. Phylogeny was inferred using Maximum Parsimony and Maximum Likelihood methods using PAUP software. Bayesian Analysis was also made, using MrBayes software. One haplotype network was done with DnaSP and Network. All trees and network showed similar results. These relations agree with variation observed in previous studies, separating K. rupestris populations in several groups. K. acrobata was also split in other groups, and some results indicate that the hybrid population is in fact a K. rupestris group in speciation. A possible explanation for these partitions is the fact that rock outcrops fragmented geography from caatinga during Pleistocene and events of expansion/retraction of the habitat may have generated population isolation and differentiation.

1 INTRODUÇÃO GERAL

Na subordem Hystricognathi, uma das famílias mais vastamente distribuídas é a Caviidae (Gray, 1821). Ela contém três subfamílias: Dolichotinae (Pocock 1922) com um gênero: Dolichotis (Desmarest, 1820); Caviinae (Gray 1821) com três gêneros: Cavia (Pallas, 1766), Galea (Meyen 1831) e Microcavia (Gervais and Ameghino 1880); Hydrochoerinae (Gray 1825) com dois gêneros: Hydrochoerus (Linnaeus 1766) e Kerodon (Cuvier 1825). Alguns cientistas agrupam Hydrochoerus e Kerodon na antiga família Hydrochoeridae, devido à falta de dados fósseis na análise filogenética (DESCHAMPS et al. 2013). Porém a maior parte dos pesquisadores concorda com a recente criação da subfamília Hydrochoerinae desde 2002 (ROWE and HONEYCUTT 2002, WOOD and KILLPATRICK 2005, PÉREZ and POL 2012). Os caviídeos ocupam grande parte da América do Sul (MARES and OJEDA, 1982), porém sua ocupação na porção central do continente ainda não está clara, bem como sua filogenia, com poucos estudos feitos neste grupo. Um deles (REIS et al. 1988) mostrou uma relação mais próxima entre Galea e Kerodon,de acordo com sua ontogenia, enquanto outros relacionam Kerodon com Hydrochoerus (ROWE and HONEYCUTT 2002, PÉREZ and POL 2012). O gênero Kerodoncompreende duas espécies conhecidas: Kerodon rupestris (Wied 1820) eKerodon acrobata (Moojen et al 1997).

O Príncipe Wied visitou o Brasil entre os anos de 1815 e 1817. Após essa viagem dois livros sobre o assunto foram publicados na Alemanha e na França. Em 1940 uma edição em português foi editada como "Viagem ao Brasil – Maximiliano Príncipe de Wied Neuwied". Esse livro contém as anotações do Príncipe Wied desde seu desembarque no Rio de Janeiro até a ida à Bahia. Nos seus relatos, diz-se que, em 1816, ele fez uma incursão da cidade de Belmonte até Barra-da-Vereda. Passou alguns dias estudando a história natural da região. Em suas notas há a descrição de um mamífero similar a Cavia que não havia sido descrito ainda, conhecido como "mocó". Era um pequeno animal, como um coelho, que viva sob os afloramentos rochosos do Rio Pardo, e com uma carne saborosa. A cidade de Barra-da-Vereda já não existe mais, mas sua localização coincide com o município de Inhomirim, na Bahia. Quando Príncipe Wied descreveu formalmente a espécie como Cavia rupestris, disse que sua localidade-tipo estava entre tres rios: Rio Grande, em Belmonte (agora Rio Jequitinhonha), Rio Pardo e Rio São Francisco.

K rupestris vive entre afloramentos rochosos no semiárido brasileiro, a caatinga, e em pequenas porções limítrofes com o cerrado. Ele é encontrado do norte de Minas Gerais até o estado do Piauí (LACHER 1981, MARES and OREJA 1982, ALHO 1982). Pode ser

identificado por algumas características, como um grande focinho, orelhas de tamanho reduzido, garras curtas e arredondadas cobertas por pelos, dedos compridos, ausência de cauda e pelagem acastanhada (Figura 1). LESSA et al. (2005) mostraram, através de análises craniométricas, uma variação clinal entre suas populações, indicando uma possível separação entre elas. Havia inclusive em seu estudo uma discriminação total entre três destas populações no espaço multivariado de caracteres: uma em Minas Gerais, uma na Bahia e outra no Ceará, sugerindo a necessidade de pesquisas genéticas a fim de compreender o nível de separação intraespecífico.

Moojen et al. (2007) descreveram uma nova espécie de mocó, com o nome de Kerodon acrobata,com base em análises morfométricas. Àquela época, a recém descoberta espécie foi encontrada apenas em Goiás, na localidade-tipo do Rio São Mateus (MOOJEN et al. 1997). Os únicos indivíduos coletados datam de coleções dos anos 60, de habitats secos a oeste da Serra Geral de Goiás (MOOJEN et al. 1997). Recentemente nove espécimes foram coletados, expandindo a area de distribuição conhecida para o estado do Tocantins (BEZERRA et al., 2010). Seu nome, acrobata, se deve à sua habilidade de pular de um galho ao outro dos arbustos retorcidos do cerrado, alimentando-se de cactus e folhas (MOOJEN et al. 1997). BEZERRA et al. (2010) indicaram que a presença deste roedor está associada ao cerrado sensu stricto em florestas tropicais secas sazonais no domínio do cerrado.

Figura 1. Kerodon acrobata. Fêmea e filhote. Foto de Alexandre Portella.

REFERÊNCIAS BIBLIOGRÁFICAS

ALHO CJR. Brazilian rodents: their habitats and habits. In: MARES MA & GENOWAYS HH (Eds.) Mammalian Biology in South America. Pennsylvania, Spec Publ Pymatuning Lab Ecol. 1982.143-166.

BARTON NH. 2001. The role of hybridization in evolution. Mol. Ecol. 10:551-568.

BEZERRA AMR, BONVICINO CR, MENEZES AN and MARINHO-FILHO J. 2010. Endemic climbing cavy Kerodon acrobata (Rodentia: Caviidae: Hydrochoerinae) from dry forest patches in the Cerrado domain: new data on distribution,natural history, and morphology. Zootaxa. 2724: 29-36.

DESCHAMPS CMV, VUCETICH MG, MONTALVO CI and ZARATE MA. 2013. Capybaras (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the late MioceneePliocene sequences of South America. J. of South Amer Earth Sci. 48:145-158.

LARSEN PA, MARCHAN-RIVADENEIRA MR, and BAKER RJ. 2010. Natural hybridization generates mammalian lineage with species characteristics. Proc Natl Acad Sci USA, 107:11447-11452.

LESSA GM, GONÇALVES FR and PESSOA LM. 2005. Variação geográfica em caracteres cranianos quantitativos de Kerodon rupestris (WIED, 1820) (RODENTIA, CAVIIDAE). Arq Mus Nac. 63:75-88.

MALLET J. 2007.Hybrid speciation. Nature 446: 279–283.

MOOJEN J, LOCKS M and LANGGUTH A. 1997.A New Species of Kerodon, Cuvier, 1825 from the State of Goiás, Brazil (Mammalia, Rodentia, Caviidae).Bol Mus Nac. 377:1-10.

PÉREZ ME and POL D. 2012.Major Radiations in the Evolution of Caviid Rodents: Reconciling Fossils, Ghost Lineages, and Relaxed Molecular Clocks. PLoS ONE. 7:e48380.

ROWE DL and HONEYCUTT RL. 2002. Phylogenetic relationships, ecological correlates, and molecular evolution within the cavioidea (mammalia, rodentia). Mol Biol Evol. 19:263-77.

WOOD CA and KILPATRICK CW. Infraorder Hystricognathi Brandt, 1855. In: WILSON DE and REEDER DM (Eds.) Mammal Species of the World: A Taxonomic and Geographic Reference, third ed. Baltimore. Johns Hopkins University Press. 2005. 1538-1600.

LACHER TE. 1981. The comparative social behavior of Kerodon rupestris and Galea spixii and the evolution of behavior in the Caviidae. Bull Carnegie Mus Nat Hist. 17:1-71.

MARES MA and OREJA RA.Patterns of diversity and adaptation in South American hystricognath rodents. In: MARES MA and GENOWAYS HH (Eds.) Mammalian Biology in South America. Pennsylvania. Special Publication, Pymatuning Laboratory of Ecolog. 1982. 393-412.

TOSI AJ, MORALES JC and MELNICK DJ. 2002. Y-chromosome and mitochondrial markers in Macaca fascicularis indicate introgression with Indochinese M. mulatta and a biogeographic barrier in the Isthmus of Kra. Inter J Primatol. 23:161-178.

YONEKAWA H, MORIWAKI K, GOTOH O, MIYASHITA N, MATSUSHIMA Y, SHI LM, CHO WS, ZHEN XL and TAGASHIRA Y. 1988. Hybrid origin of Japanese mice "Mus musculus molossinus": evidence from restriction analysis of mitochondrial DNA. Mol Biol Evol. 5:63-78.

2 OBJETIVOS

2.1 OBJETIVOS GERAIS

Compreender o padrão de diferenciação das populações das duas espécies de Kerodon no Brasil, usando como base um intron nuclear (Adh1-I2). Descrever o cariótipo de Kerodon acrobata.

2.2 OBJETIVOS ESPECÍFICOS

I. Determinar o cariótipo, posicionamento de NORs, padrão de banda-C e DAPI de uma fêmea da espécie Kerodon acrobata.

II. Comparar os dados moleculares das espécies de Kerodon entre si, para melhor compreender a filogenia do gênero, integrando os resultados com a história geológica do semiárido brasileiro.

3 ARTIGO I

THE KARYOTYPE OF *Kerodon acrobata*, AN ENDEMIC RODENT OF BRAZILIAN CERRADO

Ighor Antunes Zappes, Alexandre Portella, Gisele Lessa

Laboratório de Sistemática Molecular – Beagle, Departamento de Biologia Animal, Universidade Federal de Viçosa, CEP 36570-000, Viçosa, Minas Gerais, Brasil.

INTRODUCTION

The suborder Hystricognathi, Caviidae (Gray, 1821) is one of the families with the widest distribution. There are three subfamilies, including Dolichotinae (Pocock, 1922) with one genus, Dolichotis (Desmarest, 1820); Caviinae (Gray 1821) with three genus: Galea (Meyen, 1831), Microcavia (Gervais and Ameghino, 1880) and Cavia (Pallas, 1766); and Hydrochoerinae (Gray, 1825) with two genus, Hydrochoerus (Brisson, 1762) and Kerodon (Cuvier, 1825). Kerodon was traditionally included within the subfamily Caviinae with guinea pigs and its relatives, but now it is placed as sister genus from Hydrochoerus within the Hydrochoerinae subfamily, according to new molecular studies by ROWE and HONEYCUTT (2002). This subfamily occupies a wide array of habitats. Hydrochoerus lives from forested riversides to open savannas and flooded areas of South America (GONZÁLEZ, 1995; MONES and OJASTI, 1986). Kerodon occupies dry forests of South America (MARES and OJEDA, 1982), but its phylogeny and occupation in central portion of this continent are uncertain. One of the few phylogenetic studies with caviideans (REIS et al., 1988) shows closer relation

between Galea and Kerodon, according to their ontogeny. The genus Kerodon has two species: Kerodon rupestris (Wied, 1820) and Kerodon acrobata (Moojen et al., 1997).

Prince Wied visited Brazil between 1815 and 1817. Two books were published by him, in German and French. In 1940 an edition in Portuguese was edited as "Viagem ao Brasil – Maximiliano Príncipe de Wied Neuwied". There, Prince Wied recorded notes since his arrival in Rio de Janeiro until Bahia. In Barra-da-Vereda, Minas Gerais state, he spent some days studying the natural history of the region. In his notes he included an undescribed mammal similar to Cavia, known as "mocó". It was described as a small rabbit-like animal that dwelled under rocks from Pardo River, and with a tasty meat. Newied named it as Cavia rupestris.

Kerodon rupestris lives in rock outcrops in Brazilian semiarid, the caatinga. It is found from northern Minas Gerais to Piauí (LACHER, 1981; MARES and OREJA, 1982; ALHO, 1982). Its meat is considered tasty by local communities, so the mocós are traditionally hunted with the use of "arremedo" (imitation of vocalization) and fire arms in rural areas (ALVES et al., 2009), which has probably driven some populations to extinction.

Only in 1997, Moojen and collaborators described a new species of mocó, Kerodon acrobata, based on qualitative and morphometric analyses. At that time, the species was found only in Goiás state, at its type locality in São Mateus River (MOOJEN et al., 1997). This species was studied just from type series of individuals collected in the 1960's in the states of Goiás and "probably" Tocantins, in dry habitats west of the Serra Geral de Goiás (MOOJEN et al.,1997). More recently nine individuals were collected in Goias (BEZERRA et al., 2010).

K. acrobata may be identified by some characters, like a very long muzzle, reduced size of ears, long mystacial vibrissae, short and blunt nails covered by hair, large digital pads, lack of tail, and gray-light brown agouti coarse pelage. The specific name, acrobata, is due to its ability to jump from one branch to another. It feeds on cacti and leaves (MOOJEN, et al., 1997). BEZERRA et al. (2010) studied nine new specimens of this species and indicated that the presence of this rodent is associated to the cerrado sensu stricto, in seasonally dry tropical forest patches in the northeastern Cerrado domain.

The K. acrobata chromosome composition is unknown. The aim of this study was to describe the karyological features of a K. acrobata female, including

chromosome formula, C-banding and NOR regions, and to compare them with K. rupestris.

MATERIAL AND METHODS

It is extremely difficult to capture K. acrobata specimens alive, but a new method proposed by Portella and Vieira (unpublished data) seems to be efficient enough to catch them. They used wire traps and casting nets ("tarrafas") hung in trees, and used leaves and vegetables as bait.

One female was collected using Portella and Vieira method (unpublished data), at the Asa Branca Farm, in the Aurora do Tocantins municipality, Tocantins state, Brazil (12°39'35.4" S / 46°28'04.4" W). It was collected in August 20, 2012. The specimen was transported to the Laboratório de Ecologia dos Vertebrados, Universidade de Brasília, Distrito Federal, Brazil, where it was dissected and then deposited in the mammal collection of the same institution, with the identification number 3276. After that, mitotic chromosomes were obtained from cell suspensions of the bone marrow of the femur, using the FORD and HAMERTON protocol (1956). Metaphase chromosomes were stained with Giems. Chromosome nucleolar organizer regions were detected with silver nitrate staining (HOWELL and BLACK, 1980) in order to see the nucleolar organizer regions (Ag-NOR). In addition, we used C-banding (SUMNER, 1972) and DAPI fluorescence (Kapuscinski, 1995) to check for heterochromatin and adenine-thymine-rich regions respectivelly. The chromosomes were measured using Image Pro Plus® and classified following LEVAN et al. (1964), in metacentric (m), sub-metacentric (sm), sub-telocentric (st) and telocentric (t).

RESULTS

The female specimen showed diploid number (2n) = 52 chromosomes and fundamental number (FN) = 92. Its karyotypic formula was 44m+8t (Figure 1. More than 50 Giemsa-stained, 20 Ag-NOR, 10 C-banded and 10 DAPI fluorescence metaphases were analyzed. Sex chromosomes were assumed as the largest of the complement. Ag-NOR were telomeric and detected in two pairs (Figure 2), identified as 10 and 21. In both pairs, NOR regions occurred in the long arms. Telomeric

heterochromatin was evident only in sexual chromosome pair, in the short arms, while the autosomes did not show this pattern (Figure 3). DAPI fluorescence also showed this pattern for heterochromatin, with adenine-thymine richness in sexual pair of chromosomes (Figure 4).

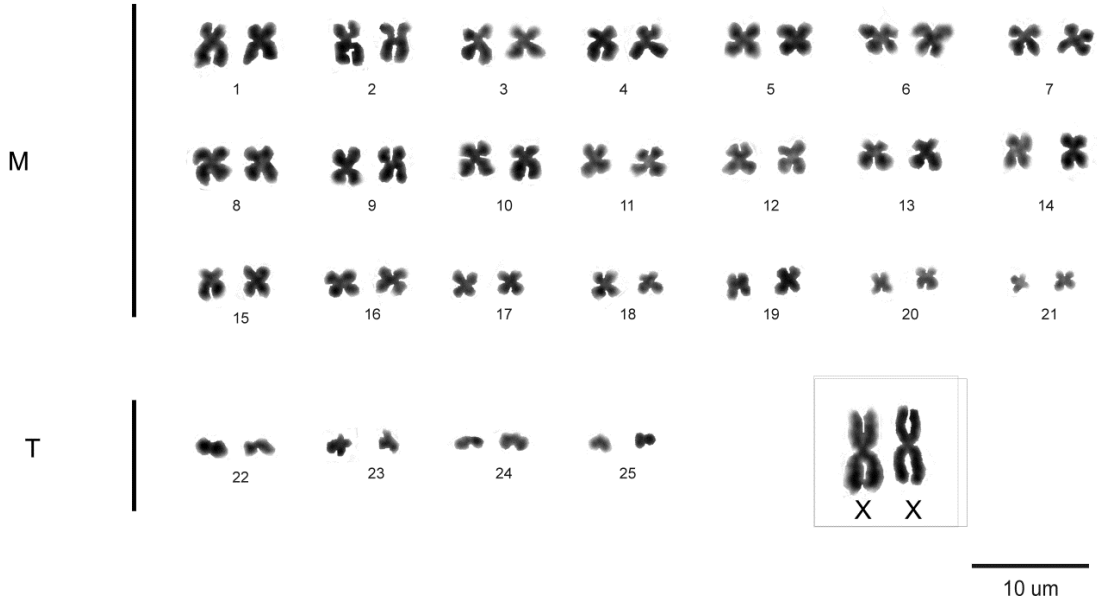


Figure 1.The karyotype of Kerodon rupestris from Aurora, Tocantins.Conventional staining (Giemsa).

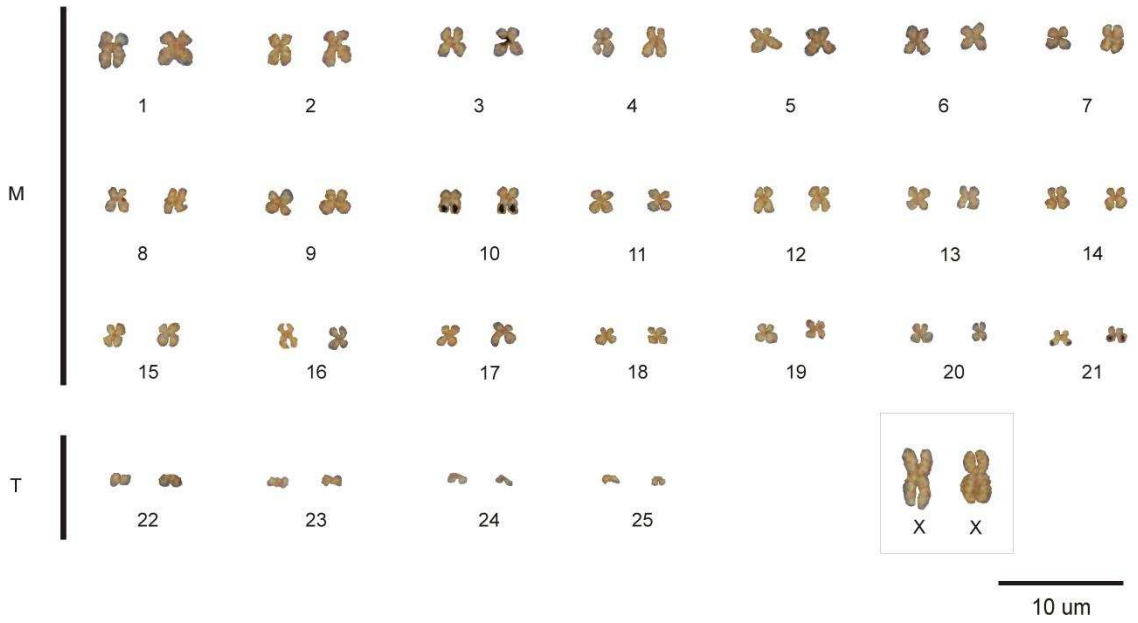


Figure 2.Ag-NOR banding marks in chromosome pairs 10 and 21 of Kerodon acrobata.

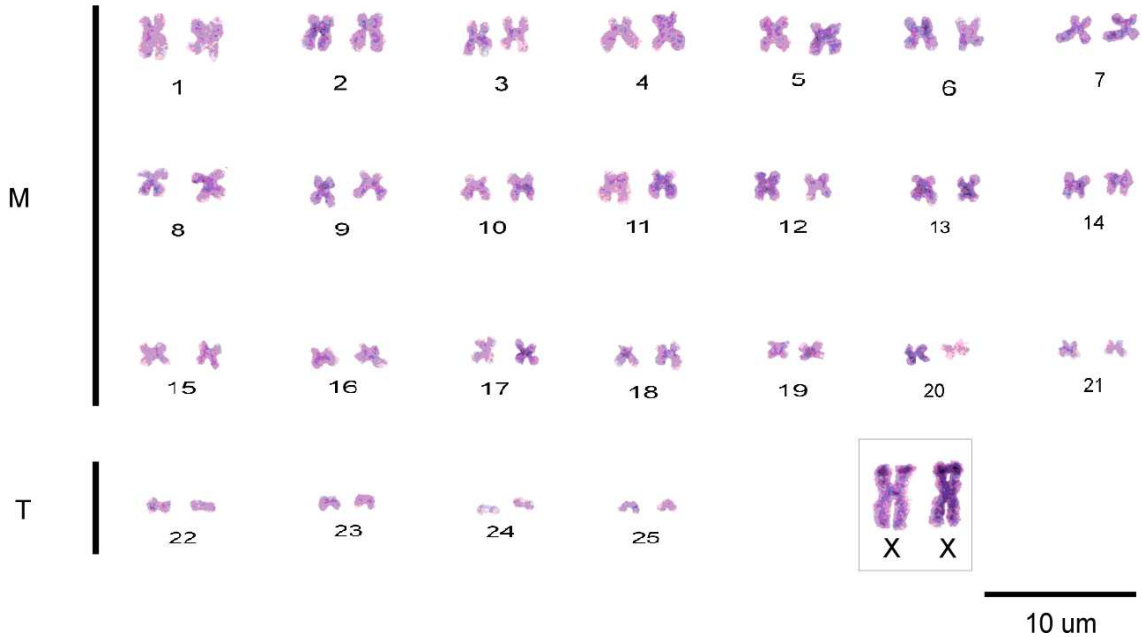


Figure 3.Heterochromatic blocks obtained with C-banding. Inset shows the sex chromosome pair of Kerodon acrobata.

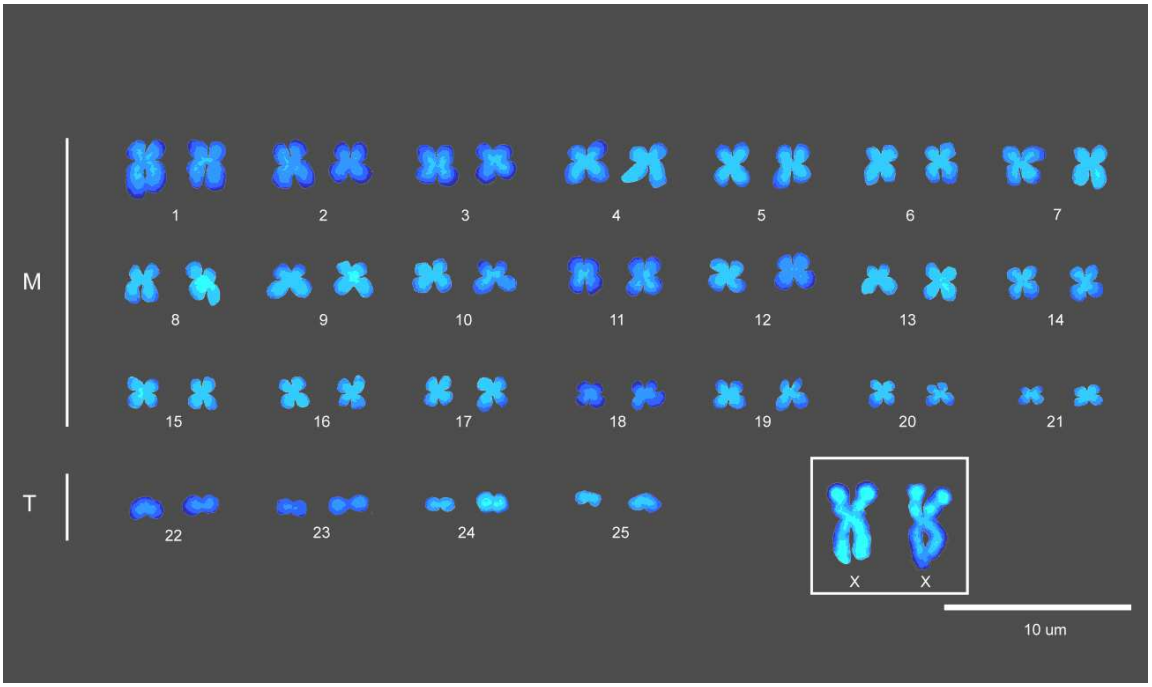


Figure4. Heterochromatic marks obtained by DAPI fluorescence in sexual chromosome pair of K. acrobata.

DISCUSSION

The sex chromosome pair was assumed to be the largest in the karyotype, as reported in K. rupestris (MAIA, 1984). The X chromosome of most placental mammals comprises around five percent of the genome, and it is rarely small and often biarmed in hystricognaths. In general X chromosomes of mammals have a highly conserved genetic content and a similar relative size representing about 5% of a haploid set, as was estimated by OHNO (1969). That seems to hld in the genus Kerodon.

The observed diploid number 2n = 52 with FN = 92 and the number of metacentric and telocentric chromosomes in K. acrobata are similar to K. rupestris (MAIA, 1984). This seems to be an apomorphy for the genus Kerodon, because all other Caviidae are 2n=64: Cavia (GAVA et al., 1998), Galea (MAIA, 1984), Dolichotis (WURSTLER et al. 1971) and Hydrochoerus (SAEZ 1971,CALDERA 2005). This karyotypical structure is an evidence for the monophyly of the genus. On the other hand, the presence of a metacentric sexual X chromosome pair as the largest of the

complement in Kerodon characterizes the group Hystricomorpha (WURSTLER et al. 1971).

LESSA et al. (2013) studied K. rupestris cytogenetics. NOR regions were observed on chromosome pairs 10 e 11. K. acrobata shows the same diploid number (2n=52), but banding patterns were distinct from K. rupestris. In K. acrobata NOR regions are present in pairs 10 and 21, and only the telomeric regions of the short arms of X chromosome are heterocromatic. Thus, these patterns are relevant for understanding the karyotypical evolution of this species.

NOR regions are usually present in two pairs of autosomes for the family Caviidae, as in Cavia (GAVA et al., 2012) and K. rupestris (LESSA et al., 2013). They differ however in one chromosome pair. Despite of being closely related species, some minor karyotype differences show distinct evolutionary histories among them. Such divergence is evident in structural terms, by differential expression of the NORs.

Karyological variation was studied in Cavia, Galea and Kerodon (MAIA, 1984). Their results indicate that 80% of their chromosomes are biarmed. The diploid and fundamental numbers for K. rupestris was 2n=52 and FN= 92. C-band results showed that all constitutive heterochromatin was in the X chromosome, differing from the pattern observed in Cavia and Galea (Maia, 1984). K. acrobata is even more different, showing a small and telomeric region in the sexual pair. bitelomeric heterochromatic markings are considered to be plesiomorphic within taxa(por referencia). The different pattern observed in K. acrobata suggests the occurrence of paracentromeric inversions in this species. In general, chromosomal rearrangements are involved in the processes of speciation (KING, 1993). Chromosomal inversions are crucial for the reproductive isolation of populations (STEFANSSON et al., 2005) and contribute to the speciation process (HOFFMANN and RIESEBERG, 2008). It is hypothesized that chromosomal rearrangements need to be fixed in a short period of time (ANISKIN et al., 2006), so they may create reproductive isolation between populations (AYALA and COLUZZI, 2005), because heterochromatic regions are regarded as the main contenders for the roleof stabilizing or destabilizing evolution (GRAPHODATSKY, 1989; HENNIG, 1999).

The occurrence of rodents in South America derives from two colonization events: the hystricognath, from the end of Eocene to the present (HUCHON and DOUZERY, 2001; ADKINS et al., 2003); and the sciurognath which entered the continent during the transition Miocene/Pliocene (EISENBERG and REDFORD, 1999).

REIG (1986) showed that the Caviidae originated in northeastern Brazil, followed by two diversifications, one in the south, and the other associated with the uplift of the Andes. Dolichotis and Kerodon probably derived first, while Cavia and Galea remained as sister groups later, during the Late Miocene, around 10 million years ago (DUNNUM and SALAZAR-BRAVO 2010). Climate change at the end of the Pleistocene introduced modifications in the dominant ecosystems in the inter-tropical Brazil, with the expansion of dry regions (AB'SABER 2003). Rain forests that once dominated Brazilian northeast scenario probably retracted form east to west within the continent, because of isolated islands of caatinga and cerrado, which exposed the rocky outcrops. This fact can be corroborated by studies with primate fossils that could only have lived in humid forests in the region, around 11000 years ago (VIVO, 1997). These cerrado islands which occurred in the states of Goiás and Tocantins, Brazil, may have isolated Kerodon populations, and that could have caused this differentiation in K. acrobata, making it endemic of that region of cerrado, through genetic drift or founding effect, according to THORPE (1983).

The unique cytogenetic features of K. acrobata, when compared to K. rupestris or other Caviidae from close related biogeographical units suggests that this species is a separate phylogenetic unit that faces extinction risks, also due to its small range area.

ACKNOWLEDGEMENTS

The authors would like to thank Dr. Emerson M. Vieira and the team of Laboratório de Ecologia de Vertebrados and Laboratório de Mamíferos (Universidade de Brasília) for support and help with the collect and deposition of the specimen. To professor Dr. Jorge Dergam and the team of Laboratório de Sistemática Molecular Beagle (Universidade Federal de Viçosa) for utilization of equipment, protocols and photographies used in this study. Work by the authors has been funded by grants from FAPEMIG, Universidade Federal de Viçosa, Universidade de Brasília, and from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

REFERENCES

AB'SABER AB. 2005. Os domínios de natureza no Brasil: potencialidades paisagísticas. 3rd ed. São Paulo. Ateliê Editorial, 160p.

ADKINS RM, WALTON AH and HONEYCUTT RL. 2003. Higher-level systematics of rodents and divergence time estimates based on two congruent nuclear genes. Molecular Phylogenet Evol. 26:409-420.

ALHO CJR. Brazilian rodents: their habitats and habits. In: MARES MA and GENOWAYS HH. Mammalian Biology in South America. Pennsylvania. Special Publication, Pymatuning Laboratory of Ecology. 1982. 143-166.

ALVES RRN,MENDONÇA LET, CONFESSOR MVA,VIEIRA WLS and LOPEZ LCS. 2009. Hunting strategies used in the semi - arid region of northeastern Brazil. J Ethnobiol Ethnomed. 5:12.

ANISKIN VM, BENAZZOU T, BILTUEVA L, DOBIGNY G, GRANJON L and VOLOBOUEV V. 2006. Unusually extensive karyotype reorganization in four congeneric Gerbillus species (Muridae: Gerbillinae). Cytogenet Genome Res. 112:131-140.

AYALA FJ and COLUZZI M. 2005. Chromosome speciation: humans, drosophila, and mosquitoes. Proceed Nat Acad Sci. 102:6535–6542.

BEZERRA AMR, BONVICINO CR, MENEZES AAN and MARINHO-FILHO J. 2010. Endemic climbing cavy Kerodon acrobata (Rodentia: Caviidae: Hydrochoerinae) from dry forest patches in the Cerrado domain: new data on distribution, natural history, and morphology. Zootaxa. 2724:29-36.

CALDERA T. 2005. Estudio citogenético (Bandeos C y NOR) em Hydrochoerus hydrocahaeris hydrochaeris e Hydrochoerus hydrocahaeris isthmius

(Hydrochoeridae) presentes en Venezuela. Sucre: Universidad de Oriente. 60 p. Tesis de Licenciatura en Biología.

DUNNUM J and SALAZAR-BRAVO J. 2010. Phylogeny, Evolution, and Systematics of the Galea musteloides complex (Rodentia: Caviidae). J Mammal. 91:243-259.

EISENBERG JF and REDFORD KH. 1999. Mammals of the Neotropics. Chicago. University of Chicago Press, 609 p.

GAVA A, FREITAS TRO and OLIMPIO J. 1998. A new karyotype for the genus Cavia from a southern island of Brazil (Rodentia – Caviidae).Gen Mol Biol. 21:77-80.

GAVA A, SANTOS MB and QUINTELA FM. 2012. A new karyotype for Cavia magna (Rodentia: Caviidae) from an estuarine island and C. aperea from adjacent mainland. Acta Theriol. 57:9-14.

GONZÁLEZ-JIMÉNEZ E. 1995. El capybara (Hydrochoerus hydrochaeris) – Estado actual de su producción, Estudio FAO Producción y Sanidad Animal 122.

GRAPHODATSKY AS. Conserved and variable elements of mammalian chromosomes. In: HALNAN CRE and GRAPHODATSKY AS. CytogenAnimals.Oxon. CAB International Press. 1989 95-123.

HENNIG W. 1999.Heterochromatin.Chromosoma. 108:1-9.

HOFFMANN AA and RIESEBERG LH. 2008. Revisiting the impact of inversions in evolution: from population genetic markers to drivers of adaptive shifts and speciation. Ann Rev Ecol Evol Syst. 39:21-42.

HOWELL WM and BLACK DA. 1980. Controlled silver staining of nucleolus organizer regions with a protective colloidal developer: a 1-step method. Experientia, 36:1014-1015.

HUCHON D and DOUZERY EJ. 2001. From the Old World to the New World: a molecular chronicle of the phylogeny and biogeography of hystricognath rodents. Mol Phylogenet Evol. 20:238-251.

KAPUSCINSKI J. 1995. DAPI: a DNA-specific fluorescent probe. Biotech Histochem. 70:220-233.

KING M. 1993. Chromosomal Speciation Revisited (Again). Species Evolution.The Role of Chromosome Change. Cambridge. Cambridge University Press, 360p.

LACHER TE. 1981. The comparative social behavior of Kerodon rupestris and Galea spixii and the evolution of behavior in the Caviidae. Bull Carn Mus Nat Hist. 17:1-71.

LESSA GM, CORRÊA MMO, PESSÔA LM and ZAPPES IA. 2013. Chromosomal differentiation in Kerodon rupestris (RODENTIA:CAVIIDAE) from the brazilian semi-arid region. Mast Neotrop. 20:399-405.

LESSA GML, GONÇALVES FR and PESSÔA LM. 2005.Variação geográfica em caracteres cranianos quantitativos de Kerodon rupestris (WIED, 1820) (RODENTIA, CAVIIDAE). Arq MusNac. 63:75-88.

LEVAN A, FREDGA K and SANDBERG AA. 1964. Nomenclature for centromeric position on chromosome. Hereditas. 1:201–220.

MAIA V. 1984.Karyotypes of three species of Caviinae (Rodentia, Caviidae).Experientia. 40:564-566.

MARES MA and OREJA RA.Patterns of diversity and adaptation in South American hystricognath rodents. In: MARES MA and GENOWAYS HH. Mammalian Biology in South America. Pennsylvania. Special Publication, Pymatuning Laboratory of Ecology. 1982 393-412.

MONES A and OJASTI J. 1986. Hydrochoerus hydrochaeris, Mammal Spec.264:1-7.

MOOJEN J, LOCKS M and LANGGUTH A. 1997.A new species of Kerodon Cuvier, 1825 from the state of Goiás, Brazil (Mammalia, Rodentia, Caviidae).BolMus Nac.377:1-10.

OHNO S. 1969. Evolution of sex chromosomes in mammals. Ann Rev Genet.3:496-524.

REIG OA. Diversity patterns and differentiation of highAndean rodents. In: Vuilleumier F and MONASTERIO M. High altitude tropical biogeography. Oxford.Oxford University Press. 1986:404-439.

REIS SF,DA-CRUZ JF and VON-ZUBEN CJ. 1988. Análise multivariada da evolução craniana em roedores caviíneos: convergências de trajetórias ontogenéticas. Rev Bras Gen. 11:633-641.

ROWE DL and HONEYCUTTRL. 2002. Phylogenetic Relationships, Ecological Correlates, and Molecular Evolution Within the Cavioidea (Mammalia, Rodentia). Mol Biol Evol. 19:263-277.

SAEZ F,DRETS SM and BRUM-ZORRILLA N. 1971. Karyotype of the "Carpincho" Hydrochaeris hydrochaeris uruguayensis (Rodentia Hydrocheridae). Experientia15:584-585.

STEFANSSON H, HELGASON A,THORLEIFSSON G, STEINTHORSDOTTIR V. and MASSON G. 2005.A common inversion under selection in Europeans.Nat Rev Genet. 37:129-137.

SUMNER AT. 1972. A simple technique for demonstrating centromeric heterocromatin. Exp Cell Res. 75:604-306.

THORPE RS.A review of numerical methods for recognising and analysing racial differentiation. In: FELSENSTEIN J. Numerical Taxonomy. New York and London. Springer Verlag. 1983 404-423.

VIVO M. 1997. Mammalian evidence of historical ecological change in the caatinga semiarid vegetation of Northeastern Brazil. JComp Biol. 2:65-73.

WURSTLER DH, SNAPPER JR and BENIRSCHKE K. 1971. Unusually large sex chromosomes: new methods of measuring and description of karyotypes of six rodents (Myomorpha and Hystricomorpha) and one lagomorph (Ochontonidae). Cytogenetics. 10:153-176.

4 ARTIGO II

PHYLOGEOGRAPHY IN GENUS Kerodon (CUVIER, 1825) (RODENTIA: CAVIIDAE) IN BRAZILIAN SEMIARID

Ighor Antunes Zappes, Alexandre Portella, Udson Santos, Gisele Lessa

Laboratório de Sistemática Molecular – Beagle, Departamento de Biologia Animal, Universidade Federal de Viçosa, CEP 36570-000, Viçosa, Minas Gerais, Brasil.

INTRODUCTION

In suborder Hystricognathi, one of the most vastly distributed families is Caviidae (Gray, 1821). It contains three subfamilies: Dolichotinae (Pocock 1922) with one genus, Dolichotis (Desmarest, 1820); Caviinae (Gray 1821) with three genus: Cavia (Pallas, 1766), Galea (Meyen 1831) and Microcavia (Gervais and Ameghino 1880); Hydrochoerinae (Gray 1825) with two genus: Hydrochoerus (Linnaeus 1766) and Kerodon (Cuvier 1825). Some scientists include Hydrochoerus and Kerodon in the family Hydrochoeridae, because of the lack of extinct data in the cladistic analysis (DESCHAMPS et al. 2013). However, most researchers agree with the existence of the subfamily Hydrochoerinae since 2002 (ROWE and HONEYCUTT 2002, WOOD and KILLPATRICK 2005, PÉREZ and POL 2012). Caviidae occupy great part of South America (MARES and OJEDA, 1982), but their presence in the central portion of this continent is not clear, as well as its phylogeny. Few studies have been conducted in this group. One of these studies (REIS et al. 1988) shows close relation between Galea and Kerodon, according to ontogeny, while others studies put Kerodon grouped with Hydrochoerus (ROWE and HONEYCUTT 2002, PÉREZ and POL 2012). Genus

Kerodon contains two known species: Kerodon rupestris (Wied 1820) and Kerodon acrobata (Moojen et al 1997).

K rupestris is the largest species of the genus and lives in rock outcrops in the Brazilian semiarid, the caatinga. It is found from northern Minas Gerais to the Piauí state (LACHER 1981, MARES and OREJA 1982, ALHO 1982). Based on cranial analysis, LESSA et al. (2005) showed a clinal variation among K. rupestris populations,indicating a possible separation among them. One population occurs in Minas Gerais state, a second one in Bahia state and another in Ceará state (Figure 1).

Moojen and collaborators described a new species of mocó, Kerodon acrobata, based on qualitative and morphometric analyses. At that time, the species was found only in Goiás state, at its type locality in São Mateus River (MOOJENet al. 1997). This species was studied just from type series of individuals collected in the 1960's in the states of Goiás and "probably" Tocantins, in dry habitats west of the Serra Geral de Goiás (MOOJENet al. 1997). More recently nine individuals were collected, expanding its distribution range to the state of Tocantins (BEZERRAet al., 2010). But K. acrobata was thought to be found only in Goiás state, at its type locality in the São Mateus River region, until this study. The specific name, acrobata, is due to its ability to jump from branch to branch. It feeds on cacti and leaves (MOOJEN et al. 1997). BEZERRAet al. (2010) indicated that the presence of this rodent is associated to the cerrado sensu stricto and seasonally dry tropical forest patches in the northeastern Cerrado domain.

MATERIALS AND METHODS

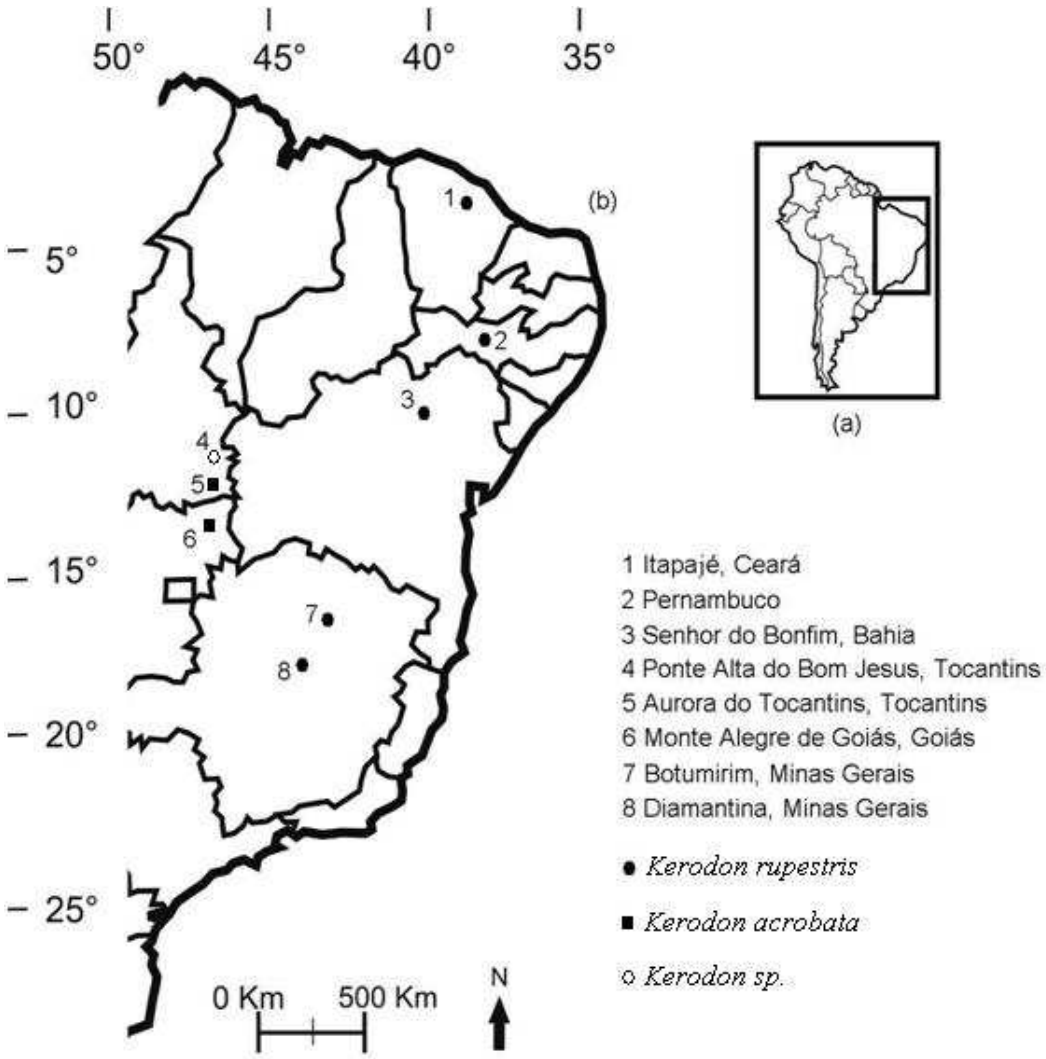
MOLECULAR ANALYSIS

Eight specimens of Kerodon were colected in central part of Brazil, in two bioma: caatinga and cerrado (Table I, Map I). collecting permission was issued by the Instituto Chico Mendes de Biodiversidade (ICMBio) (SISBIO13045-1) a G.M.L. Four of these especimens are deposited in the scientific collection of Museu de Zoologia João Moojen in UFV, Viçosa, Minas Gerais, Brazil (CM3983, CM3984, CM3985, CM4046),

and four of them are deposited in Museu de Zoologia da UnB, Brasília, Distrito Federal, Brazil (32, 76, 33, 08). Five more samples were kindly donated by the Universidade de Brasília; one more sample by Universidade Federal do Vale do São Francisco and six others by Museu Nacional, Rio de Janeiro, Brazil. The specimens were colected using an air gun with a 5.5mm pellet. The work was made under the authorization 001/2014 of the Comitê de Ética da Universidade Federal de Viçosa. Specimens were identified as Kerodon rupestris, Kerodon acrobata or Kerodon sp. (Figure 2). Kerodon sp. specimens were characterized by their unique fur color and they were collected outside both species ranges.

Table I Colected specimens of Kerodon, separated by species, number of individuals and localization (city, state).

Species	Number of Individuals		Localization
	Sex		
	♂	♀	
Kerodon rupestris	00	01	Parque Estadual do Biribiri, Diamantina, MG
	02	01	Botumirim, MG
	02	00	Senhor do Bonfim, BA
	00	01	Itapajé, CE
	00	01	Unidade de Conservação da Floresta Nacional de Negreiros, Serrita, Pernambuco
Kerodon acrobata	01	00	Fazenda São Domingos, Aurora do Tocantins, TO
	00	02	Fazenda Asa Branca, Aurora do Tocantins, TO
	00	05	Monte Alegre de Goiás, GO, Brazil
Kerodon sp.	02	02	Fazenda Triunfo, Ponte Alta do Bom Jesus, TO
Total	7	13	



603

604 Figure 1: South America map (a). Localization of the collected specimens in Brazil (b).

605

606

Figure 2 Species collected. Kerodon rupestris (a); Kerodon acrobata (b); Kerodon sp. (c). Photo by Tarcísio Duarte.

DNA EXTRACTION, PCR AND SEQUENCING

DNA was extracted from liver tissue and muscular tissue. The samples were conserved in ethanol 100%, according to BOYCE et al. (1989). Gene fragments from Adh1-I2 (558 pb fragment) were amplified with the primers EXONII-F (5'-GTAATCAAGTGCAAAGCRGCYYTRTGGGAG-3') and 2340 (5'-GACTTTATCACCTGGTTTYACWSAAGTCACCCC-3') (AMMAN et al. 2006) for the second one.

PCR reaction for Adh1-I2 was also made in a volume of 25µL [18.1 µL of H_20; 2.5 µL of buffer 10X (200 mM Tris-HCl pH 8,4, 500 mM KCl), 0.9 µL of $MgCl_2$ (25

mM), 0.25 µL of dNTPs (20 mM), 1.00 µL of each primer (10µM), 0,25 µL (2.5 U) of Taq polimerase (Phoneutria) and 1µL of DNA (100 ng/µl)], for each sample. The fragment was amplified in 30 cycles of 30 seconds at 95 ^{o}C, 30 seconds at 60 ^{o}C e one minute and half at 73 ^{o}C, with initial DNA denaturation at 95 ^{o}C for 10 minutes and final extension at 73 ^{o}C for 4 minutes.

Amplified products were run in a polyacrylamide gel, for one hour at 25 °C, and 100 volts (10-15 mA). Gel was revealed in silver nitrate to check the gene banding. All amplified products were purified with a salting (PEG 8000) (20% polyethyleneglycol, 2,5 M NaCl), and the sequencing was made in Macrogen framework, South Korea.

TREE AND NETWORK INFERENCES

After chromatograms checking, an alignment was made with the sequences using ClustalW software (THOMPSON et al. 1994), through MEGA program (TAMURA et al. 2007). 567 pb were used for Adh1-I2. For the trees inferred with Adh1-I2, a Xenomys nelsoni (Merriam, 1892) (Rodentia: Cricetidae) sequence was used, also from NCBI, together with an Oryzomys palustris (Harlan 1837) (Rodentia: Cricetidae), the only Adh1-I2 sequences found for rodents in NCBI.

Sequences were used for phylogenetic trees inference with PAUP (SWOFFORD, 2003) and MrBayes (RONQUIST & HUELSENBECK, 2003). Methods used were Maximum Parsimony (using TBR algorithm), Maximum Likelihood, with a thousand bootstrap repetitions and evolution models selected according to the information criterium of Akaike AIC, using ModelTest (POSADA & CRANDALL, 1998), and Bayesian Analysis using MrModelTest software 2.3 (NYLANDER, 2004). This last one was inferred for one million Markov Monte Carlo chains (MCMC), with one phylogenetic tree sampled each thousand generations. 25% of initial trees were discarded. Values bigger than 0,80 were considered well sustained in Bayesian Analysis, as well as 80 in Maximum Parsimony and Maximum Likelihood.

Haplotype networks are graphs created to ease the visualization of the sampled individuals, related to each other according to common features (in this case, common nucleotide sites), without the need for an outgroup. Within the network, haplotypes are

represented by nodes and the lines are the haplotype divergences. An haplotype network only makes sense with intraspecific data, analyzing small divergences in genetic material among individuals (GUIRALDELLI and ROCHA 2011). DnaSP software (LIBRADO & ROZAS, 2009) was used to check polymorphism levels inside populations, through nucleotide diversity (p) and haplotype diversity (h). Two haplotype networks were made with Networks software (FORSTER et al., 2000). Obtained groups and their divergences were compared with previous works, to analyze if there was corroboration about the differentiation in Kerodon.

Sequences in this work were deposited in GenBank. Sequences from other rodent species were also used (Table II and III).

678 Table II Sequences uploaded in GenBank from this work.

Species	Location	GenBank Access Number
Kerodon rupestris	Botumirim, Minas Gerais	XXXXX01
Kerodon rupestris	Botumirim, Minas Gerais	XXXXX02
Kerodon rupestris	Botumirim, Minas Gerais	XXXXX03
Kerodon rupestris	Diamantina. Minas Gerais	XXXXX04
Kerodon rupestris	Serrita, Pernambuco	XXXXX05
Kerodon rupestris	Senhor do Bonfim, Bahia	XXXXX06
Kerodon rupestris	Senhor do Bonfim, Bahia	XXXXX07
Kerodon acrobata	Aurora do Tocantins, Asa Branca, Tocantins	XXXXX08
Kerodon acrobata	Aurora do Tocantins, Asa Branca, Tocantins	XXXXX09
Kerodon acrobata	Aurora do Tocantins, São Domingos, Tocantins	XXXXX10
Kerodon acrobata	Monte Alegre de Goiás, Goiás	XXXXX11
Kerodon acrobata	Monte Alegre de Goiás, Goiás	XXXXX12
Kerodon acrobata	Monte Alegre de Goiás, Goiás	XXXXX13
Kerodon acrobata	Monte Alegre de Goiás, Goiás	XXXXX14
Kerodon acrobata	Monte Alegre de Goiás, Goiás	XXXXX15
Kerodon acrobata	Monte Alegre de Goiás, Goiás	XXXXX16
Kerodon sp.	Ponte Alta do Bom Jesus, Tocantins	XXXXX17
Kerodon sp.	Ponte Alta do Bom Jesus, Tocantins	XXXXX18
Kerodon sp.	Ponte Alta do Bom Jesus, Tocantins	XXXXX19

679

Table III Sequences obtained through GenBank.

Species	Location	GenBank Access Number
Xenomys nelsoni	Jalisco, Mexico	AY817628
Oryzomys palustris	Texas City, United States	DQ530614

RESULTS

GENE TREES

All trees had heterozygous sites, but in small number (18 in 567 for Adh1-I2), so alignments weren't a problem. For Adh1-I2 567 pairs of bases (bp) were aligned. Maximum Parsimony trees used evolution model HKY+G. Maximum Likelihood trees produced a counting of −lnL = 1509.60. Evolution model used was HKY. Bayesian analysis used evolution model GTR+G.

Values of posterior probability were usually higher than bootstrap values, but almost all bootstrap values were high as well. All trees showed a very similar pattern, but bayesian analysis had a better resolved topology than maximum parsimony and maximum likelihood.

The nuclear pattern (Adh1-I2) shows both species grouped in two well-defined clades. The clade with K. acrobata genes is unresolved at all. The clade with K. rupestris genes groups the population from Botumirim in one branch, Senhor do Bonfim in other branch, Kerodon sp. in another one (inside K. rupestris clade) and Diamantina and Itapajé not grouped (Figure 3).

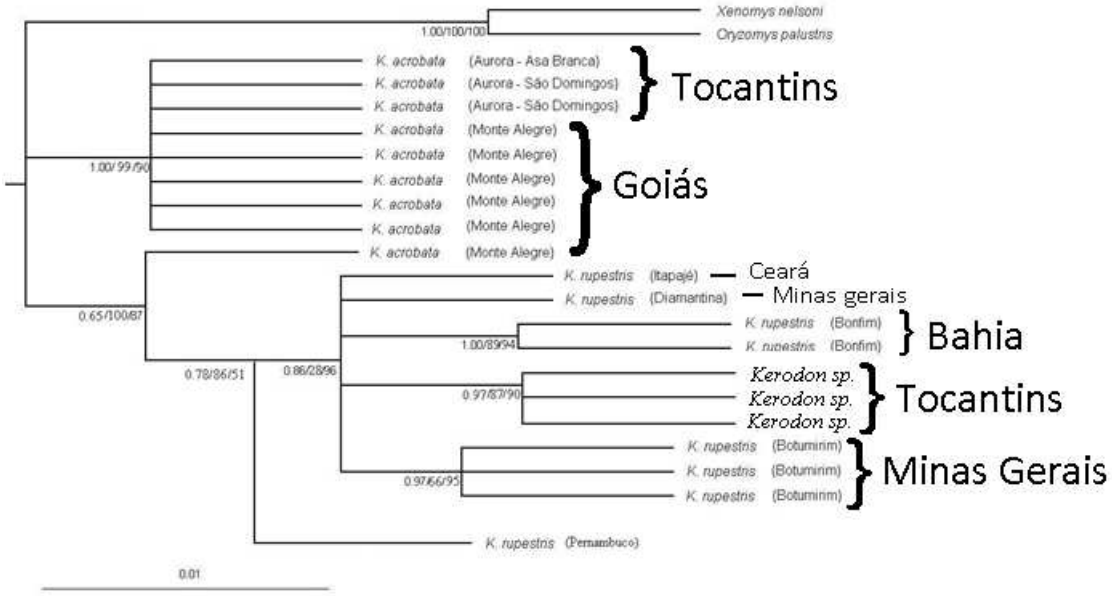


Figura 3 Phylogenetic hypothesis for Kerodon and its hybrids based on polimorphism of Adh1-I2 gene (nuclear DNA) with bayesian analysis, maximum likelihood and maximum parsimony. The bar represents molecular distance.

HAPLOTYPE NETWORK

The statistical analysis generated one haplotype networks for the genus Kerodon, using gene Adh1-I2. Haplotype diversity (Hd), nucleotide diversity (p) and haplotype quantity (h) were calculated for it: Hd=0,826 +- 0,00539, p=0,012 and h=9.

The inferred nesting design resulted in groups up to the 2-step hierarchical nesting level. Haplotypes represent the 0-step level in the network, which are nested into clades going from 1-step through 2-step (Figure 6). Clade I represents specimens of K rupestris from Botumirim (haplotypes c, d). Clade II grouped all other specimens of K. rupestris with the hybrids (haplotypes e, f, g, h, i). Clade III is the sum of I and II, and clade IV represents all individuals of K. acrobata (haplotypes a, b).

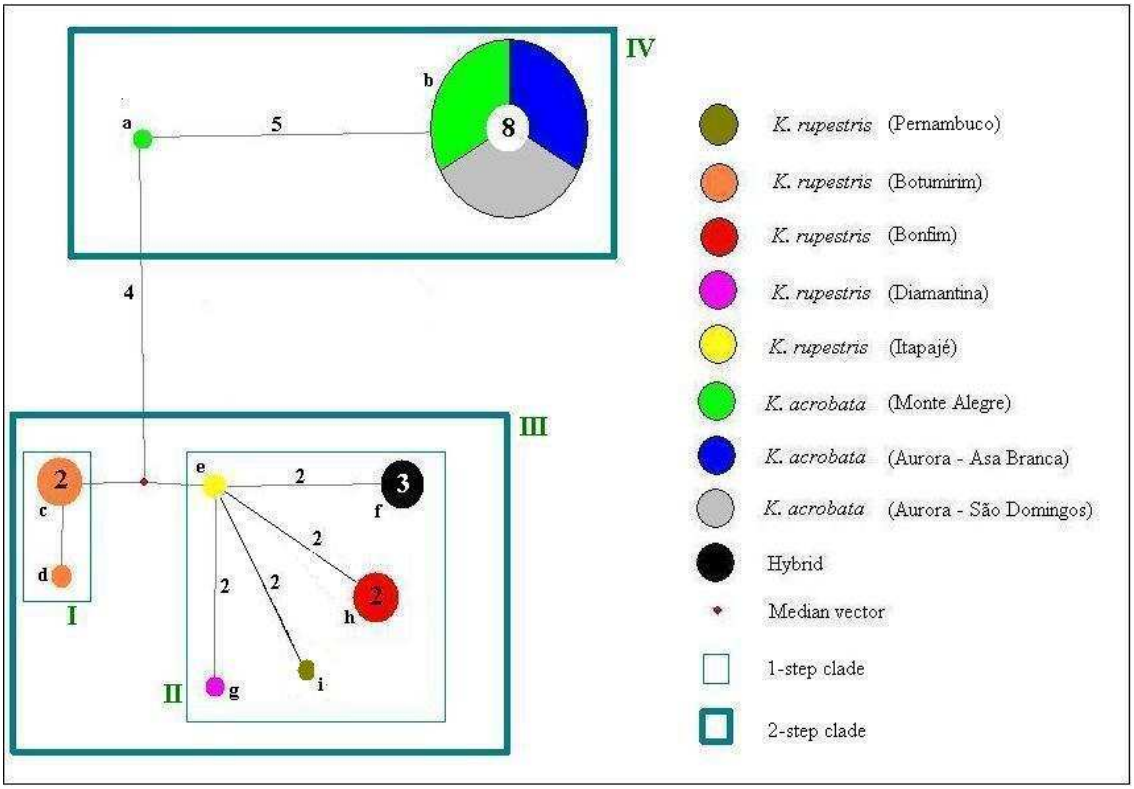


Figure 4 Haplotype network for the genus Kerodon, based on nuclear gene Adh1-I2. Haplotypes are represented by coloured circles according to the sample localities. The circle size is proportional to the number of sequences sharing a haplotype. Letters identify haplotypes. Numbers of individuals for each haplotype exceeding one are given inside the circles. Red dots represent unsampled haplotypes. Connective lines represent one mutational step. Numbers in the lines show the quantity of mutacional steps, if more than one. Clades with hierarchical nesting design superimposed are shown with rectangles.

DISCUSSION

Transition/transversion rate (1.48 for Adh1-I2) is close to other rodent analysis, like 2,1:1 for Adh1-I2 (LONGHOFER and BRADLEY 2006). Adh1-I2 was chosen as the nuclear gene because it is an intron, and intron markers are a great source of nuclear variability suitable for low-level phylogenetics, since their mutation rates are around three times the mutational rates in non-synonymous sites of exons, in mammals (HUGHES & YEAGER, 1997). They are relatively free from many of the functional constraints imposed on coding regions, resulting in phylogenetic markers which, in

vertebrates, usually show little base compositional bias, relatively low transition-transversion ratios, and minimal among-site rate heterogeneity (BIRKS and EDWARDS 2002; FUJITA et al. 2003). Introns have been used in several phylogenetic studies (HOWARTH and BAUM 2002, WEIBEL and MOORE 2002, ENGSTROM et al., 2004, PONS et al. 2004). Most of their nucleotide positions are adaptively neutral and generally are evolving faster than those in exons, having potential to analyze closed related species or even populations (PRYCHITKO and MOORE 2000, BALLARDet al. 2002), which is the case of the present work. For Bayesian Analysis trees, posterior probability values were high enough in most of branches. The same happens to most bootstrap values in Maximum Likelihood and Maximum Parsimony trees. All inferences in this work showed a similar pattern for the genus Kerodon. The separation between species K. rupestris and K. acrobata are well established, corroborating Moojen et al. (1997).

For the K. rupestris clade, the gene analysis showed a very clear divergence among populations. In nuclear trees, a branch containing the population from Botumirim and another one with the population from Senhor do Bonfim were well-supported. The inferences could not show the relations between individuals from Itapajé and Diamatina. A molecular clock would be useful to light this question, but the lack of fossil data and the extremely recent possible calibration point (less then two million years ago) make the estimative unreliable (NORMAN and ASHLEY 2000).

The individual from Pernambuco is apart from the other populations. This could indicate that the dispersion of K. rupestris started from that area, and expanded its range to the entire caatinga. In haplotype network, the K. rupestris population from Botumirim represented clade I, while all the others were grouped in clade II. That indicates that the populations from the northern part of caatinga are closer to each other than to the population from southern caatinga. LESSA et al. (2005) studied 319 individuals from seven K. rupestris populations, using cranial measures as parameters. With a multivariate state method, populations were separated in three caatinga areas: South (Minas Gerais state), North (Ceará state) and Center (Bahia state). A north-south clinal pattern was also observed in cranial size. Cranial size variation seems to follow a similar pattern in rodent species that occur in caatinga. LOPES (2005) obtained a similar result with the rodent Wiedomys pyrrhorhinos (Wied 1817). Cranial size of this rodent gets smaller when latitude decreases. (LESSA et al. 2013) compared cytogenetic

analysis from congruent populations of the present study. It was showed that the fundamental number (FN) varies in K. rupestris. Minas Gerais groups has FN=94, while others has FN=92. This variation may be explained by the occurrence of a pericentric invertion or a translocation on an autosome pair in the Minas Gerais group. The division of K. rupestris in the groups presented by these previous studies is corroborated by the present study, with the exception of the specimen from Diamantina, which did not group with the Botumirim population in order to establish a single group of Minas Gerais state. This probably happens because both localities are within the Serra do Espinhaço, an ancient Brazilian mountain chain that goes from Minas Gerais to Bahia, and has distinct environments and complex landscape structure (AB'SABER 1977), which may have caused the isolation of Kerodon rupestris populations.

The caatinga ("white forest", in tupi language) is a complex bioma composed by xerophytic semiarid forest, located in northeastern of Brazil and north of the state of Minas Gerais (LEAL et al. 2005), formed since the Neogene (PRADO 2003, QUEIROZ 2006). Its area has been estimated around 750000-850000 Km^2. the region is a flattened depression composed by sandstone dated from Cretaceous, in a basement of Pre-Cambrian crystalline rock (AB'SABER 1977). The caatinga is one of the 37 world major wilderness areas (AGUIAR et al. 2002), according to a list that shows areas that cover more than 10000 Km^2 with more than 70% of its natural vegetation intact.

Mammalian fauna in caatinga is relatively poor. Studies show a richness of less than one hundred species (WILLIG and MARES 1984), whereas other study indicates 143 mammal species (OLIVEIRA et al. 2003). Major part of them hasn't great adaptations for the arid climate of the region, which means that they are probably a subset of the fauna of Brazilian savanna (the cerrado), that arrived in caatinga during wetter times in Pleistocene (MARES et al. 1985). K. rupestris populations, however, seem to be remaining groups from autochthonous lineages from early caatinga (Oliveira et al. 2005), because no fossil was found in calcareous caves outside the Brazilian semiarid, between Late Pleistocene and Upper Holocene (SALLES et al. 1999), when modern vegetation was established there. So, the mocó is probably one of few endemic mammals from caatinga. It is possible that other endemic species occurred in caatinga, but their distribution was probably restricted and they didn't survive to the period of forest expansion that obliterated the caatinga (MARES et al. 1985). K. rupestris is,

today, a well spread species in caatinga, and that may have been crucial for its survival in those times.

For K. rupestris, changes in Brazilian caatinga may have caused this differentiation among populations. Modern caatinga rose recently. Arid region suffered retractions in the past (MARES et al. 1985). Pollen studies also show that, during Pleistocene/Holocene transition, the region housed a tropical forest (DE OLIVEIRA et al. 1999, BEHLING et al. 2000). But, with the last landscape drying due to climate changes in Late Holocene (around 11000 years ago), the vegetation started to dry up, approaching the current pattern (SOUZA et al.2005). At that time, Brazilian inter-tropical forests retracted from east to west, giving space to growing "caatinga's islands". This growth exposed the local rock outcrops (where mocós live). However, northern parts of caatinga are defined as "subdesertic semiarid", while southern parts are "moderate semiarid" (AB'SÁBER 1977). So, Minas Gerais outcrops are located in more humid and greener landscapes, while northern outcrops are located in warmer environments. These different regions made distinct habitats along caatinga, creating environmental pressures that could explain K. rupestris variations.

Within the K. acrobata clade, nuclear analysis could not recover the divergence among populations. The topology showed a grouping among individuals from Asa Branca farm and Monte Alegre de Goiás, with the specimen from São Domingos farm further related. Haplotype networks followed the same pattern. K. acrobata lives in a very small area in Brazilian cerrado. Until today, it was only know in the northeastern of Goias state (BEZERRA et al. 2010). In the present work we expanded the distribution of K. acrobata to southeastern Tocantins, in Asa Branca farm and São Domingos farm, Aurora do Tocantins. This locality presents typical cerrado vegetation (cerrado sensu stricto, a dense arboreal savannah) with limestone outcrops, ca. 468 m altitude. All records of K. acrobata (including this one) indicate an endemism for the species in enclaves of seasonally dry tropical forests (STDF) in the cerrado of Northeastern Goias and southeastern Tocantins. These forests are typically found in the caatinga, with enclaves in cerrado domain (relicts of the maximum extension of these forests during the last glacial maximum of the Pleistocene Arc (PRADO&GIBBS 1993). That was a dry-cool period, around 18,000 years ago, with contraction of humid forest and great expansion of STDFs (PENNINGTON et al. 2000). At that time, species that lived on the semi-arid expanded their ranges. But when the glacial maximum

ended, humid forests rose in size, turning the previous expansion of semi-arid into small islands of STDFs embedded in what would become the present savannah, or cerrado, according to botanical studies (AB'SABER 1977). So, these dry islands out of caatinga became refuge areas for some species of the caatinga. In central Brazil, SDTFs cover more than 15% of the two million hectares of the cerrado dominium, being fragmented and forming a seasonal corridor of fragments (FELFILI2003). K. rupestris is a well spread species in the caatinga, while K. acrobata occurs only in a small area in STDFs of the cerrado. Some of K. rupestris populations probably reached STDF areas during their extension in the last glacial maximum, becoming isolated later, during the retraction of these areas. So, K acrobata is possibly one of these populations, being an example of how expansion/vicariance can cause speciation in a short period of time. There are lots of examples of mammal endemism in small SDTFs. Lepus flavigularis, Spermophilus annulatus, Neotoma phenax, Peromyscus perfulvus are mammals species from small SDTFs in western Mexico (CEBALLOS and RODRÍGUEZ 1993); Marmosaxerophila is found only in a SDTF in Venezuela. Ctenomysfochi and Ctenomyspundit are from very small Chaco areas of SDTFs (REDFORD and EISENBERG 1992). These are all examples of mammals with low mass, poor dispersion and short generation times. These features indicate that these speciation events happened due to habitat fragmentation and isolation during the Pleistocene (CEBALLOS and GARCIA 1995).

All the possible hybrid specimens were collected in Ponte Alta do Bom Jesus, a city located at least 85 Km northern of all locations where K. acrobata was collected, beyond its range of distribution. The lack of proximity between hybrids and K. acrobata indicates that, they are probably an isolated lineage from the northern populations of K. rupestris, just as K. acrobata, due to the isolation of SDTFs in the border of caatinga in the end of the last ice-age (PRADO&GIBBS 1993; CEBALLOS and GARCIA 1995).So, this group may not be a hybrid between Kerodon species, but a K. rupestris population in speciation process due to its small area of occurrence and no connection to other similar areas, with no connection to the populations of K. acrobata, since there are not any cord of this species in Ponte Alta do Bom Jesus, or even north of Aurora do Tocantins.

Two mountain ranges probably isolate the caatinga area and the cerrado, affecting distribution patterns of both species. They are called Serra Geral de Goiás and

Serra Geral do Tocantins. These geographic elements are dated from the Mesozoic Era, being a natural barrier since before the emergence of the mammals. These chains make a ruptured landscape in the transition caatinga/cerrado, with high scarps and cliffs that can achieve more than 100 meters high (VILLELA and NOGUEIRA 2011). It possibly would block the expansion of K. rupestris during the rising of the SDTFs in Pleistocene. However, during the Cenozoic Era, the climate changes at the end of Paleogene and beginning of Neogene, such as modern tectonics and erosion caused by cycles of dry-humid weather, promoted the so called Tertiary breaks (ALMEIDA 1967). These rifts were more evident between two baselines, the Mangabeiras and the Chapadão Baiano Ocidental. At that place, very close to the present area of occurrence for K acrobata and the possible hybrids, the first K. rupestris may have crossed the barrier and colonized this new habitat. However, this dispersion was limited to that area, because the discontinuities in these mountain ranges are rare (VILLELA and NOGUEIRA 2011). This can be the reason why we cannot find other Kerodon species like K. acrobata, or even other populations like the one from Ponte Alta de Bom Jesus. It is possible that other SDTFs hosted more of these populations, but if they did, these groups no longer exist, due to high isolation levels and small geographic ranges, with possible low population densities, and these factors are crucial for the extinction of an animal populations (PIMM 1991, GASTON 1994).

CONCLUSION

K. rupestris is a fragmented species in Brazilian semiarid. Molecular analysis agreed with morphometric studies. Results suggest a variation among three groups along caatinga. Mocós from southern part of this biome are apart from the others, in nuclear portions of their DNA, which corroborates previous studies that concluded that this population from Minas Gerais state has biggest cranial measures and a distinct fundamental number in its karyotype. Pernambuco sample indicate that the species may have started its expansion in that locality.

K. acrobata is probably a species that rose from a population of K. rupestris during the expansion/retraction events in semi-arid during the Pleistocene. Its populations are diverging from each other in the north-south direction.

The subset of possible hybrids between Kerodon species is probably actually a population of K. rupestris, which is in differentiation process, in an isolated area apart from both species.

The events of caatinga progressive expansion and posterior retraction during Pleistocene and climate variations along this biome seem to be responsible for differentiation in populations of this single genus of Brazilian mammal species in the Brazilian semiarid, Kerodon.

ACKNOWLEDGMENTS

Thanks to Professor Jorge Abdala Dergam dos Santos for his assistance in final works; to Museu de Zoologia João Moojen da UFV and Laboratório de Sistemática Molecular Beagle for providing biologic and laboratory material; to Museu de Zoologia UnB, for providing some samples; to Rebeca Mascarenha Fonseca Barreto, for the donation of samples from Pernambuco.

REFERENCES

AB'SÁBER AN 1977. Os domínios de natureza no Brasil: potencialidades paisagísticas. São Paulo: Ateliê Editorial, 160p.

AGUIAR J, LACHER T and SILVA JMC. The Caatinga. In: GIL PR (Ed.) Wilderness – Earth's Last Wild Places. Cidade do Mexico. CEMEX. 2002. 174-181

ALHO CJR. Brazilian rodents: their habitats and habits. In: MARES MA & GENOWAYS HH (Eds.) Mammalian Biology in South America. Pennsylvania, Spec Publ Pymatuning Lab Ecol. 1982. 143-166.

ALMEIDA F.F.M. 1967. Origem e Evolução da Plataforma Brasileira. Rio de Janeiro, DGM, DNPM. Boletim n. 241, 36p.

AMMAN BR, HANSON JD, LONGHFER LK, HOOFER SR and BRADLEY RD. 2006. Intron 2 (Adh1-I2) of the alcohol dehydrogenase gene: a potential nuclear DNA phylogenetic marker for mammals. Occ Pap Mus Tex Tech Univ. 256:1-16.

BALLARD JW, CHERNOFF B and AVISE JC. 2002. Divergence of mitochondrial DNA is not corroborated by nuclear DNA, morphology, or behavior in Drosophila simulans. Evolution. 56:527-545.

BARTON NH. 2001. The role of hybridization in evolution. Mol. Ecol. 10:551-568.

BEHLING H, ARZ HW, PÄTZOLD J and WEFER G. 2000. Late quaternary vegetation and climate dynamics in northeastern Brazil, inferences from marine core GeoB. Quaternary Sci Rev. 19:981-994.

BEZERRA AMR, BONVICINO CR, MENEZES AN and MARINHO-FILHO J. 2010. Endemic climbing cavy Kerodon acrobata (Rodentia: Caviidae: Hydrochoerinae) from dry forest patches in the Cerrado domain: new data on distribution,natural history, and morphology. Zootaxa. 2724: 29-36.

BIRKS SM and EDWARDS SV. 2002. A phylogeny of megapodes (Aves: Magepodidae) based on nuclear and mitochondrial DNA sequences. Mol Phylogenet Evol. 23:408-421.

BOYCE TM, ZWICK ME and AQUADRO CF. 1989. Mitochondrial DNA in the bark weevils: size, structure and heteroplasmy. Genetics. 123:825-836.

CEBALLOS G and GARCIA A. 1995. Conserving Neotropical biodiversity: the role of dry forests in Western Mexico. Conserv Biol. 9:1349-1353.

CEBALLOS G and RODRIGUEZ P. Diversidad y conservación de los mamíferos de México: II. Patrones de endemicidad. In: MEDELLIN RA and CEBALLOS G (Eds.) Avances en el estudio de los mamíferos de México. Mexico. Asociación Mexicana de Mastozoología, A. C. 1993. 87-108.

DE OLIVEIRA PE, BARRETO AMF and SUGUIO K. 1999. Late Pleistocene/Holocene climatic and vegetational history of the Brazilian caatinga: the fossil dunes of the middle São Francisco river. Palaeogeogr Palaeocl. 152:319-337.

DESCHAMPS CMV, VUCETICH MG, MONTALVO CI and ZARATE MA. 2013. Capybaras (Rodentia, Hydrochoeridae, Hydrochoerinae) and their bearing in the calibration of the late MioceneePliocene sequences of South America. J. of South Amer Earth Sci. 48:145-158.

ENGSTROM TN, SHAFFER HB and MCCORD WP. 2002. Phylogenetic diversity of endangered and critically endangered southeast Asian softshell turtles (Trionychidae: Chitra). Biol Conserv. 104:173-179.

FELFILI JM. Fragmentos de florestas estacionais do Brasil Central: diagnóstico e proposta de corredores ecológicos. In: COSTA RBC (ed.). Fragmentação florestal e alternativas de desenvolvimento rural na região Centro-Oeste. UCDB. Campo Grande. 2003. 139-160.

FITCH WM and MARGOLIASH E. 1967. Construction of phylogenetic trees. Science. 55:279-284.

FORSTER P, BANDELT HJ and ROHL A. NETWORK 3.1.1.0. Software free available at: www.fluxus-engineering.com. Fluxus Technology Ltd., Cambridge. 2000.

FUJITA MK, ENGSTROM TN, STARKEY DE and SHAFFER HB. 2003. Turtle phylogeny: insights from a novel nuclear intron. Mol Phylogenet Evol. 31:1031-1040.

GASTON KJ. Rarity. London. Chapman & Hall. 1994.

GUIRALDELLI RHG and ROCHA RLA. 2011. Adaptative unification of graphs applied to haplotype networks. Rev. IEEE Am. Lat. 9:950-955.

HOWARTH DG and BAUM DA. 2002. Phylogenetic utility of a nuclear intron from nitrate reductase for the study of closely related plant species. Mol Phylogenet.Evol. 23:525-528.

HUGHES AL and YEAGER M. 1997. Comparative Evolutionary Rates of Introns and Exons in Murine Rodents. J Mol Evol. 45:125-130.

LACHER TE. 1979. Rates of growth in Kerodon rupestris and an assessment of its potencial as a domesticated food source. Pap. Avul. Zool. 33:67-76.

LACHER TE. 1981. The comparative social behavior of Kerodon rupestris and Galea spixii and the evolution of behavior in the Caviidae. Bull Carnegie Mus Nat Hist. 17:1-71.

LARSEN PA, MARCHAN-RIVADENEIRA MR, and BAKER RJ. 2010. Natural hybridization generates mammalian lineage with species characteristics. Proc Natl Acad Sci USA, 107:11447-11452.

LEAL IR, TABARELLI M and SILVA JMC 2003. Ecologia e Conservação da Caatinga. João Pessoa. Editora Universitária, 807p.

LESSA GM, CORRÊA MMO, PESSÔA LM and ZAPPES IA. 2013. Chromosomal differentiation in Kerodon rupestris (RODENTIA:CAVIIDAE) from the brazilian semi-arid region. Mast Neotrop. 20:399-405.

LESSA GM, GONÇALVES FR and PESSOA LM. 2005. Variação geográfica em caracteres cranianos quantitativos de Kerodon rupestris (WIED, 1820) (RODENTIA, CAVIIDAE). Arq Mus Nac. 63:75-88.

LIBRADO P and ROZAS J. 2009. DnaSP v5: A software for comprehensive analysis of DNA polymorphism data. Bioinformatics. 25:1451-1452.

LONGHOFER LK and BRADLEY RD. 2006. Molecular systematic of the genus Neotoma based ond DNA sequences from intron 2 of the alcohol dehydrogenase gene. J Mammal. 87:961-970.

LOPES, MOG. Análise da variação craniométrica em Wiedomys pyrrhorhinos (Wied, 1817) (Rodentia: Muridae). 2005. vii, 31 f. Dissertação (Mestrado) - Pontifícia Universidade Católica de Minas Gerais, Programa de Pós-Graduação em Zoologia de Vertebrados.

MALLET J. 2007. Hybrid speciation. Nature 446: 279–283.

MARES MA and OREJA RA. Patterns of diversity and adaptation in South American hystricognath rodents. In: MARES MA and GENOWAYS HH (Eds.) Mammalian Biology in South America. Pennsylvania. Special Publication, Pymatuning Laboratory of Ecolog. 1982. 393-412.

MARES MA, WILLIG MR and LACHER TE. 1985. The Brazilian caatinga in southamerican zoogeography: tropical mammals in a dry region. J Biogeogr. 12:57-69.

MIYAKI CY, RUSSO CAM and PEREIRA SL. Reconstrução filogenética. Introdução e o método da máxima parcimônia. In: MATIOLI RS (ed.) Biologia Molecular e Evolução. Ribeirão Preto. Editora Holos. 2001. 97-129.

MOOJEN J, LOCKS M and LANGGUTH A. 1997. A New Species of Kerodon, Cuvier, 1825 from the State of Goiás, Brazil (Mam-malia, Rodentia, Caviidae). Bol Mus Nac. 377:1-10.

NABHOLTZ B, GLÉMIN S and GALTIER N. 2008. Strong Variations of Mitochondrial Mutation Rate across Mammals—the Longevity Hypothesis. Mol Biol Evol. 5:120-130.

NORMAN JE and ASHLEY MV. 2000. Phylogenetics of Perissodactyla and Tests of the Molecular Clock. J Mol Evol. 50:11-21.

NYLANDER JAA. 2004. MrModeltest v2. Program Distributed by the Author. Evolutionary Biology Centre, Uppsala University.

OLIVEIRA JA, GONÇALVES PR and BONVICINO CR. Mamíferos da Caatinga. In: Ecologia e conservação da Caatinga (editado por Leal I.R.; Tabarelli M. and Silva J.M.C.), Recife. Editora Universitária da UFPE. 2005 275-302.

PENNINGTON RT, PRADO DE and PENDRY CA. 2000. Neotropical seasonally dry forests and Quaternary vegetation changes.J Biogeog. 27:261-273.

PÉREZ ME and POL D. 2012.Major Radiations in the Evolution of Caviid Rodents: Reconciling Fossils, Ghost Lineages, and Relaxed Molecular Clocks. PLoS ONE. 7:e48380.

PETTIGREW JD. 1994. Flying DNA. Curr. Biol. 4:277-280.

PIMM SL. The balance of nature? Chicago. University of ChicagoPress.1991.

PONS J, BARRACLOUGH TG, THEODORIDES K, CARDOSO A and VOGLER AP. 2004. Using exon and intron sequences of the gene Mp20 to resolve basal relationships in Cicindela (Coleoptera: Cicindelidae). Syst Biol. 53:554-570.

PRADO D. As caatingas da América do Sul. In: LEAL IR, TABARELLI M and SILVA JMC (Eds.) Ecologia e conservação da Caatinga. Recife. Editora Universitária da Universidade Federal de Pernambuco. 2003. 3-73.

PRADO D and GIBBS PE. 1993. Patterns of species distributions in the dry seasonal forests of South America. Annals Missouri Bot Gard. 80:902-927.

PRYCHITKO TM and MOORE WS. 2000. Comparative evolution of the mitochondrial cytochrome b gene and nuclear b-fibrinogen intron 7 in woodpeckers. Mol Biol Evol. 17:1101-1111.

QUEIROZ LP. 2006. The Brazilian Caatinga: Phytogeographical patterns inferred from distribution data of the Leguminosae. In: PENNINGTON RT, LEWIS GP and RATTER J (Eds.) Neotropical Savannas and Dry Forests: Plant Diversity,

Biogeography, and Conservation. Oxford, Taylor & Francis C.R.C. Press. 2006. 113-149.

REDFORD KH and EISENBERG JG 1992. Mammals of the Neotropics. The Southern Cone. Chile, Argentina, Uruguay, Paraguay. Illinois. University os Chicago Pres, 440p.

REIS SF, DA-CRUZ JF and VON-ZUBEN CJ. 1988. Análise multivariada da evoluão craniana em roedores caviíneos: convergências de trajetórias ontogenéticas. Rev Bras Genet. 11:633-641.

RONQUIST F and HUELSENBECK JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinf. 12:1572-1574.

ROWE DL and HONEYCUTT RL. 2002. Phylogenetic relationships, ecological correlates, and molecular evolution within the cavioidea (Mammalia, Rodentia). Mol Biol Evol. 19:263-77.

SALLES LO, CARVALHO GS, WESKLER M, SICURO FS, ABREU F, CAMARDELLA AR, GUEDES PG, AVILLA LS, ABRANTES EAL, SAHATE V and COSTA ISA. 1999. Fauna de mamíferos do quaternário de Serra da Mesa. Publ Avul Mus Nac. 78:1-15.

SMITH MF and PATTON JL. 1993. The diversification of South American murid rodents: Evidence from mitochondrial DNA sequence data for the Akodontine tribe. Biol J Linn Soc Lond. 50:149-177.

SOUZA CRG, SUGUIO K, OLIVEIRA AMS and OLIVEIRA PE 2005. Quaternário do Brasil. Ribeirão Preto. Holos Editora, 380p.

SWOFFORD DL. 2003. PAUP*- A computer program for phylogenetic Inference using Maximum Parsimony (* and other methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

1137 TAMURA K, DUDLEY J, NEI M and KUMAR S. 2007. MEGA4: molecular
1138 evolutionary genetics analysis (MEGA) software version. 4.0. Mol Biol Evol. 24:
1139 1596-1599.
1140
1141 TASSE J. 1986. Maternal and paternal care in the rock cavy, Kerodon rupestris, a
1142 South American hystricomorph rodent. Zoo Biol. 5:27-43.
1143
1144 THOMPSON JD, HIGGINS DG and GIBSON TJ. 1994. CLUSTAL W: improving the
1145 sensitivity of progressive multiple sequence alignment through sequence weighting,
1146 positions-specific gap penalties and weight matrix choice. Nucleic Acid. 22:4673-
1147 4680.
1148
1149 TOSI AJ, MORALES JC and MELNICK DJ. 2002. Y-chromosome and mitochondrial
1150 markers in Macaca fascicularis indicate introgression with Indochinese M. mulatta
1151 and a biogeographic barrier in the Isthmus of Kra. Inter J Primatol. 23:161-178.
1152
1153 VILLELA FNJ and NOGUEIRA C. 2011. Geologia e geomorfologia da estação
1154 ecológica Serra Geral do Tocantins. Biota Neotrop. 11:217-230.
1155
1156 WEIBEL AC and MOORE WS. 2002. A test of a mitochondrial gene-based phylogeny
1157 of woodpeckers (Genus Picoides) using an independent nuclear gene, B-fibrinogen
1158 intron 7. Molec Phylogenet Evol. 22:247-257.
1159
1160 WILLIG MR and MARES MA. 1984. Mammals from the caatinga: an updated list and
1161 summary of recent research. Rev Brasil Biol. 49:361-367.
1162
1163 WOODS CA and KILPATRICK CW. Infraorder Hystricognathi Brandt, 1855. In:
1164 WILSON DE and REEDER DM (Eds.) Mammal Species of the World: A
1165 Taxonomic and Geographic Reference, third ed. Baltimore. Johns Hopkins
1166 University Press. 2005. 1538-1600.
1167
1168 YONEKAWA H, MORIWAKI K, GOTOH O, MIYASHITA N, MATSUSHIMA Y,
1169 SHI LM, CHO WS, ZHEN XL and TAGASHIRA Y. 1988. Hybrid origin of

1170 Japanese mice "Mus musculus molossinus": evidence from restriction analysis of
1171 mitochondrial DNA. Mol Biol Evol. 5:63-78.
1172

5 CONCLUSÕES GERAIS

As características citogenéticas únicas de Kerodon acrobata, quando comparadas com Kerodon rupestris ou outro cavídeo de unidades biogeográficas únicas, sugeres que essa espécie é uma unidade biogeográfica única, que enfrenta riscos de extinção devido à sua pequena área de distribuição.

Kerodon rupestris é uma espécie fragmentada do semiárido brasileiro. Análises moleculares concordam com os estudos morfométricos. Os resultados sugerem uma variação entre três grupos da Caatinga. Os mocós da parte sul do bioma estão separados dos outros, de acordo com porções nucleares de seu DNA. Isto corrobora esudos anteriores que concluíram que a população de Minas Gerais tem tamanho cranial maior e número fundamental distinto no seu cariótipo. A amostra de Pernambuco indica que a espécie iniciou sua expansão naquela região..

Kerodon acrobata provavelmente surgiu de uma população de Kerodon rupestris durante os eventos de expansão/retração da Caatinga no Pleistoceno. O subrupo encontrado em Tocantins na verdade é uma população de Kerodon rupestris em processo de diferenciação, em uma área isolada de ambas as espécies.

Os eventos climáticos ocorridos na Caatinga no Pleistoceno parecem ser os responsáveis pela história evolutiva deste gênero de roedores do Brasil.