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Revisão taxonômica e filogenômica de *Saimiri* Voigt, 1831 (Primates, Cebidae)

Belém, 2019

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Tese de doutorado apresentada ao Programa de Pós-Graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do título de Doutora em Zoologia.

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Orientador: Prof. Dr. José de Sousa e Silva Júnior

Co-orientadora: Jessica W. Lynch, Ph.D

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Profa. Dra. Ana Lúcia Costa Prudente, Museu Paraense Emílio Goeldi

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Ao meu filho João Gabriel e à minha família

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Sumário

Taxonomic review and phylogenomics of *Saimiri* Voigt, 1831 (Primates; Cebidae)

ABSTRACT

Squirrel monkeys (genus *Saimiri* Voigt, 1831) are small Neotropical primates (650-1200g). They are widely distributed in the Amazon Basin and have two taxa that occur in Central America. Although it is a frequentely used group in biomedical research, there is still a great divergence in the number of recognized species, ranging from 2 to 12 taxa. Recently several papers have been published using mitochondrial DNA to understand the origin and diversification of *Saimiri*, as well as the relationship between species. However, even after these publications, diversity and intra-generic relationship still present divergences, with no cogruence between morphological and genetic data. The present study aimed to propose a phylogenetic hypothesis for *Saimiri* from the *double digest* restriction-site associated DNA sequencing (ddRADseq), as well as to review *Saimiri*, defining the species that make up the genus, as well as its distribution. This thesis is divided into three chapters. In the first, "Phylogenomics of Amazon squirrel monkeys (*Saimiri*; Primates; Cebidae)", we use 44 tissue samples and 6 blood samples to obtain ddRADseq molecular phylogeny through Maximum Likelihood analysis and a time-calibrated tree from BEAST. We verified the relationship between the studied populations with the Bayesian cluster analysis of STRUCTURE. Our results recovered the monophyly between the Gothic and Roman groups, our trees recovered ten lineages within *Saimiri* of the Amazon Basin. In addition, we confirm that intra-generic diversification is recent and has occurred in the Pleistocene epoch. In the second chapter, "How many squirrel monkey (*Saimiri* Voigt, 1831) species are there? A morphological diagnosis and refined mapping of geographical distribution", we analyzed 887 specimens of all currently recognized species and 18 types, representing almost the entire geographic distribution of the group, we also included the phylogenomic data obtained in the first chapter. Our results support the existence of two morphological groups (Gothic and Roman) and the recognition of thirteen species with one new species. For each of them are presented synonymy, type material, type locality, diagnosis, variation, comparison with other species, distribution, remarks, conservation status and specimens examined. In the third chapter, "New records of *Saimiri collinsi* Osgood, 1916 (Cebidae, Primates), with comments on habitat use and conservation", we indicate the expansion of geographic distribution of the Collins' squirrel monkey (*Saimiri collinsi*), to a transition area between Amazon and Cerrado. We also indicated the need for monitoring of these populations due to the intense anthropic action in the region that reduced the habitat of the species in most of Maranhão and northern Tocantins.

Keywords: phylogeny, squirrel monkeys, geographic distribution.

Revisão taxonômica e filogenômica de *Saimiri* Voigt, 1831 (Primates; Cebidae)

RESUMO

Os macacos-de-cheiro (gênero *Saimiri* Voigt, 1831) são primatas neotropicais de pequeno porte (650-1200g), amplamente distribuídos na Bacia Amazônica, além de dois *taxa* que ocorrem na América Central. Existe grande divergência em relação ao número de espécies reconhecidas, podendo variar de 2 a 12 *taxa*. Recentemente diversos trabalhos foram publicados utilizando DNA mitocondrial visando entender a origem e diversificação de *Saimiri*, bem como o relacionamento entre as espécies. Entretanto, mesmo após estas publicações a diversidade e o relacionamento intra genérico ainda apresenta divergências, não havendo cogruência entre os dados morfológicos e genéticos. O presente estudo teve como objetivo propor uma hipótese filogenética para *Saimiri* através de parte do genoma (*double digest* restriction-site associated DNA sequencing - ddRADseq), assim como revisar taxonomia do genêro e sua distribuição. Esta tese está dividida em três capítulos. No primeiro, "Phylogenomics of Amazon squirrel monkeys (*Saimiri*; Primates; Cebidae)", foram analisadas 44 amostras de tecido e seis de sangue para obtenção de uma filogenia molecular de parte do genoma (ddRADseq) através da análise de Máxima Verossimilhança e de uma árvore datada através do BEAST. Verificou-se a estrutura entre as populações estudadas através do STRUCTURE. Recuperou-se a monofilia recíproca entre o grupo Gótico e Romano. Além disso, as árvores recuperaram dez linhagens dentro de *Saimiri* da Bacia Amazônica, confirmando que a diversificação intra-genérica é recente, tendo ocorrido no Pleistoceno. No segundo capítulo, "How many squirrel monkey (*Saimiri* Voigt, 1831) species are there? A morphological diagnosis and refined mapping of geographical distribution", foram analisados 887 espécimes de todas as espécies atualmente reconhecidas, incluindo 18 espécimes tipos. Foi verificada a congruência entre os resultados de análises morfológicas com a filogenia obtida no primeiro capítulo. Os resultados apoiam a existência de dois grupos morfológicos (Romano e Gótico) e o reconhecimento de 13 espécies, sendo uma espécie nova. Para cada uma delas são apresentados sinonímia, material tipo, localidade tipo, diagnose, variação, comparação com outras espécies, distribuição, comentários, status de conservação e material examinado. No terceiro capítulo, "New records of *Saimiri collinsi* Osgood, 1916 (Cebidae, Primates), with comments on habitat use and conservation", a distribuição geográfica da espécie *Saimiri collinsi*, foi ampliada para uma área de transição entre Amazônia e Cerrado, indicando também a necessidade de monitoramento dessas populações devido à intensa ação antrópica na região que reduziu o habitat da espécie na maior parte do Maranhão e no norte do Tocantins.

Palavras-chave: filogenia, macaco-de-cheiro, distribuição geográfica.

INTRODUÇÃO GERAL

A ordem Primates é bastante diversificada na região Neotropical, sendo o terceiro grupo com maior número de espécies no Brasil (Paglia et al. 2012). Entre os diferentes biomas no país, este grupo é mais diverso na Amazônia. Nos últimos anos várias espécies de primatas foram descritas para a região (p. e. Defler et al. 2010, Gualda-Barros et al. 2012, Dalponte et al. 2014, Marsh 2014, Boubli et al. 2019, Costa Araújo et al. 2019), indicando que o conhecimento a respeito deste grupo ainda apresenta lacunas, com relação à diversidade, biogeografia, comportamento e nicho ecológico.

Entre os primatas do Novo Mundo, a família Cebidae é composta por três subfamílias: Cebinae, Callitrichinae e Aotinae (Perez et al. 2012, Schneider e Sampaio 2015). Na primeira estão inclusos os gêneros *Cebus*, *Sapajus* e *Saimiri*. O monofiletismo destes três gêneros tem sido amplamente reconhecido (Harada et al. 1995, Springer et al. 2012). A divergência entre *Saimiri* e os outros dois gêneros ocorreu há cerca de 13.8-15.5 milhões de anos (Chiou et al. 2011, Springer et al. 2012). Entre as características morfológicas compartilhadas pelos Cebinae é possível destacar a face curta, molares largos, dimorfismo sexual nos caninos, osso nasal estreito, caixa craniana arredondada com cérebro relativamente grande e sistema digestivo curto (Rylands et al. 2013).

De acordo com Hershkovitz (1984) e Thorington (1985), o gênero *Saimiri* apresenta distribuição geográfica disjunta distribuindo-se no norte da América do Sul e parte da América Central. Na América do Sul, ocorre em toda a Bacia Amazônica, desde o leste dos Andes na Colômbia, Peru e norte da Bolívia até o limite leste da Amazônia no Brasil, incluindo partes da Venezuela, Guiana, Suriname e Guiana Francesa. O limite sudeste ainda não é conhecido. É possível que esteja presente em toda a área de floresta amazônica e também na região ecotonal que marca o limite entre os biomas Amazônia e Cerrado como observado por Mercês et al. (2018) em relação ao limite leste do gênero, nos estados do Maranhão e Tocantins. O contingente populacional que ocorre de forma disjunta na América Central inclui dois táxons que se distribuem em partes do Panamá e Costa Rica (Hershkovitz 1984, Thorington 1985, Figura 1). De acordo com a compilação de Rylands et al. (2013) são considerados válidos 11 *taxa*: *Saimiri boliviensis boliviensis, S. b. peruviensis, S. cassiquiarensis cassiquiarensis, S. c. albigena, S. macrodon, S. oerstedii oerstedii, S. o. citrinellus, S. sciureus sciureus, S. s. collinsi, S. ustus* e *S. vanzolinii*.

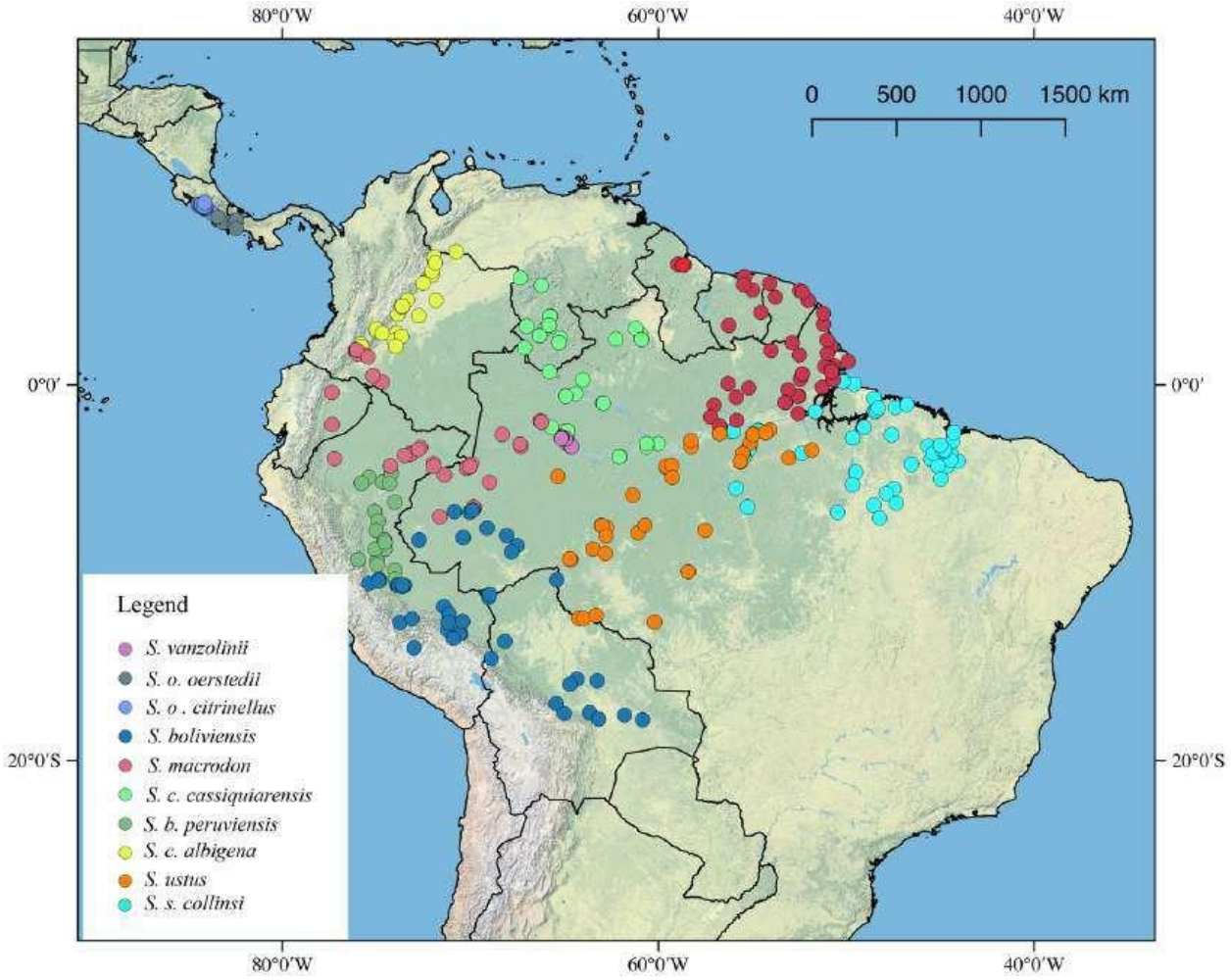

Figura 1. Mapa de distribuição de *Saimiri* com registros de museus e da literatura, considerando os táxons listados por Rylands et al. (2013).

Os macacos-de-cheiro (*Saimiri* spp.) são animais de pequeno porte, pesando em média cerca de 800g (650-1200g). Podem ser identificados no nível de gênero por apresentar a pele da região circumbucal melânica e um arco bem definido na região acima dos olhos (Hershkovitz 1984, Figura 2). Possuem cauda não preênsil com pincel caudal na extremidade. São primatas insetívoros/frugívoros (Mitchell 1990, Boinski et al. 2003, Stone 2007). Stone (2007) observou que em locais com baixa densidade de árvores frutíferas, *Saimiri collinsi* pode se alimentar dos frutos da palmeira (*Attalea maripa*), em especial durante o período de seca. Os macacos-de-cheiro passam a maior parte do seu tempo em florestas secundárias ou matas de igapó, sendo escassos ou ausentes em florestas de terra firme com pouco sub-bosque (Boinski et al. 2003, Stone 2007).

Figura 2. Espécime de *Saimiri oerstedii citrinellus.* Foto: W. de Paula.

Todos os táxons de *Saimiri* apresentam dimorfismo sexual na idade adulta (Hershkovitz 1984, Silva Júnior 1992, Muniz 2005, Goldschmidt et al. 2009). Os machos são mais pesados e maiores que as fêmeas nas medidas corporais e cranianas (Hershkovitz 1984, Silva Júnior 1992, Muniz 2005). No período reprodutivo, apresentam uma "condição de engorda", quando se tornam mais ativos e agressivos. Esta condição é considerada uma característica única deste gênero (DuMond e Hutchinson 1967, Baldwin e Baldwin 1981, Hershkovitz 1984, Baldwin 1985, Stone 2014). Os machos apresentam menor variação intraespecífica na coloração da pelagem dorsal do que as fêmeas, as quais apresentam melanismo em algumas regiões, especialmente na área pré-auricular, que pode se estender à área central da cabeça (Muniz 2005, Goldschmidt et al. 2009). Com relação à dentição, os machos apresentam os caninos bastante desenvolvidos e sulcados, enquanto as fêmeas possuem caninos menores e sem sulcos (Silva Júnior 1992, Muniz 2005), permitindo a fácil identificação do sexo de espécimes adultos através de análise qualitativa do crânio.

O padrão de dominância entre machos e fêmeas nas espécies de macaco-de-cheiro pode variar. Em *S. sciureus* o macho apresenta comportamento dominante em relação às fêmeas (Boinski et al. 2005). Em *S. collinsi* e *S. boliviensis* as fêmeas são dominantes em relação aos machos (Mitchell et al. 1991, Izar et al. 2009). Já na espécie da América Central (*S. oerstedii*) a dominância entre machos e fêmeas é igualitária (Boinski 1994, Blair e Melnick 2012).

TAXONOMIA DE *Saimiri*

O gênero *Saimiri* foi proposto por Voigt em 1831. Este autor designou *Simia sciurea* Linnaeus, 1758 como a espécie tipo do gênero. MacLean (1964) dividiu o gênero em dois grupos ("Gótico" e

"Romano"). Segundo Hershkovitz (1984), estas diferenças morfológicas seriam congruentes com dados comportamentais e imunológicos. Visando testar a monofilia destes grupos utilizando genes mitocondriais, Lynch Alfaro et al. (2015) observaram que as espécies do grupo Romano e Gótico não formaram agrupamentos monofiléticos.

Os autores que revisaram o gênero *Saimiri* divergiram consideravelmente em seus arranjos taxonômicos, a maioria reconhecendo a existência de subespécies. Elliot (1913) reconheceu seis espécies e duas subespécies. Cabrera (1958) considerou válidos seis táxons, todas subespécies de *S. sciureus*. No arranjo de Hershkovitz (1984, 1987), quatro espécies e 10 subespécies foram reconhecidas. Thorington (1985) considerou válidas duas espécies com 4 subespécies (Tabela 1). Costello et al. (1993) propuseram que duas espécies fossem reconhecidas, *S. oerstedii* para América Central e *S. sciureus* para América do Sul.

Groves (2001) seguiu a taxonomia proposta por Hershkovitz (1984, 1987), com algumas modificações. Groves (2001) restituiu o status de espécie plena a *S. vanzolinii*, mas invalidou *S. pluvialis* e *S. jaburuensis*, reduzindo-os a sinônimos de *S. boliviensis*. Posteriormente, diversas compilações e listas foram publicadas. Groves (2005) considerou válidas cinco espécies (*S. boliviensis. S. oerstedii, S. sciureus, S. ustus* e *S. vanzolinii*). Rylands e Mittermeier (2009) seguiram estritamente o arranjo de Groves (2005). Na lista de Paglia et al. (2012) foi reconhecida a existência de sete táxons com ocorrência no Brasil, todos alocados na categoria da espécie (*S. boliviensis, S. cassiquiarensis, S. collinsi, S. macrodon, S. sciureus, S. ustus* e *S. vanzolinii*). Na compilação de Rylands et al. (2013) foram consideradas sete espécies válidas com 11 subespécies, a subespécie *S. s. albigena* sendo realocada para *S. cassiquiarensis* e a subespécie *S. ustus collinsi* foi realocada para *S. sciureus*.

Tabela 1. Arranjos taxonômicos propostos por diversos autores que revisaram o gênero *Saimiri*, incluindo a compilação mais recente (Rylands et al. 2013).

Elliot (1913)	Cabrera (1958)	Hershkovitz (1984, 1987)	Thorington (1985)	Groves (2005)	Rylands et al. (2013)
		Grupo Romano			
Saimiri boliviensis	*Saimiri boliviensis boliviensis*	*Saimiri boliviensis boliviensis*	*Saimiri sciureus boliviensis*	*Saimiri boliviensis*	*Saimiri boliviensis boliviensis*
	Saimiri sciureus nigriceps				
		Saimiri boliviensis jaburuensis			
		Saimiri boliviensis pluvialis			
		Saimiri boliviensis peruviensis			*Saimiri boliviensis peruviensis*
		Saimiri boliviensis vanzolinii		*Saimiri vanzolinii*	*Saimiri vanzolinii*
		Grupo Gótico			
Saimiri sciureus	*Saimiri sciureus sciureus*	*Saimiri sciureus sciureus*	*Saimiri sciureus sciureus*	*Saimiri sciureus*	*Saimiri sciureus sciureus*
	Saimiri sciureus collinsi				*Saimiri sciureus collinsi*
Saimiri macrodon	*Saimiri sciureus macrodon*	*Saimiri sciureus macrodon*			*Saimiri macrodon*
Saimiri cassiquiarensis		*Saimiri sciureus cassiquiarensis*	*Saimiri sciureus cassiquiarensis*		*Saimiri cassiquiarensis cassiquiarensis*
		Saimiri sciureus albigena			*Saimiri cassiquiarensis albigena*
		Saimiri oerstedii citrinellus			*Saimiri oerstedii citrinellus*
Saimiri oerstedii		*Saimiri oerstedii oerstedii*	*Saimiri sciureus oerstedii*	*Saimiri oerstedii*	*Saimiri oerstedii oerstedii*
Saimiri ustus	*Saimiri sciureus ustus*	*Saimiri ustus*		*Saimiri ustus*	*Saimiri ustus*
Saimiri madeirae			*Saimiri madeirae*		

Os trabalhos de Carretero-Pinzon et al. (2009) e Lavergne et al. (2010) resultaram nas primeiras propostas de mudança taxonômica desde 2005. Carretero-Pinzon et al. (2009) sugeriram duas classificações, a elevação taxonômica de *S. c. albigena, S. c. cassiquiarensis* e *S. macrodon* para a categoria da espécie ou a realocação de *S. s. albigena* para *S. cassiquiarensis*. Por sua vez, Lavergne et al. (2010) sugeriram a revalidação da subespécie *S. s. collinsi*, realocando-a para *S. ustus* (*S. u. collinsi*). Além disso, Lavergne et al. (2010) propuseram que as subespécies *S. s. albigena, S. s. cassiquiarensis* e *S. s. macrodon* também fossem realocadas para *S. ustus* (*S. u. albigena, S. u. cassiquiarensis* e *S. u. macrodon*). Chiou et al. (2011) observaram que Lavergne et al. (2010) haviam realocado incorretamente as subespécies *S. s. albigena, S. s. cassiquiarensis* e *S. s. macrodon* para *Saimiri ustus*. Considerando o Princípio da Prioridade (Artigo 23) do Código Internacional de Nomenclatura Zoológica, Chiou et al. (2011) constataram que o nome *Simia sciurea cassiquiarensis* Lesson, 1840 tem prioridade em relação a *Saimiri ustus* I. Geoffroy, 1843. Posteriormente, Mercês et al. (2015) elevaram *S. s. collinsi* a espécie plena, usando dados genéticos e morfológicos.

Ruiz Garcia et al. (2015) sugeriram a existência de apenas uma ou poucas espécies de *Saimiri*. Estes autores propuseram mudanças taxonômicas utilizando o conceito biológico de espécie e sugeriram a seguinte classificação para *Saimiri*: *S. oerstedii* (com duas subespécies – *S. o. oerstedii* e *S. o. citrinellus*), *S. sciureus* com duas subespécies (*S. s. boliviensis* com duas linhagens e *S. s. sciureus* com 12 linhagens) e *S. vanzolinii*. Outra possibilidade considerada por Ruiz-Garcia et al. (2015) seria *S. sciureus* incluir três subespécies: *S. s. boliviensis* (2 linhagens), *S. s. sciureus* (2 linhagens) e *S. s. cassiquiarensis* (10 linhagens). Por sua vez, Lynch Alfaro et al. (2015) não propuseram nenhuma modificação taxonômica definitiva. Apenas sugeriram um arranjo provisório que estava relacionado aos clados recuperados na filogenia: *S. sciureus*, S. *oerstedii* (*S. o. oerstedii* e *S. o. citrinellus*), S. *collinsi*, *S. ustus* (A, B, e C), *S. boliviensis*, *S. cassiquiarensis* (*S. c. cassiquiarensis*, *S. c. albigena*, *S. c. macrodon* A, *S. c. macrodon* B, e *S. c. macrodon* C) e *S. vanzolinii*.

FILOGENIA E HISTÓRIA EVOLUTIVA

Ao analisar as informações disponíveis na literatura a respeito da filogenia de *Saimiri* (Boinski e Cropp 1999, Cropp e Boinski 2000, Carretero-Pinzón et al. 2009, Lavergne et al. 2010, Chiou et al. 2011, Lynch Alfaro et al. 2015, Mercês et al. 2015, Ruiz-Garcia et al. 2015), é possível constatar que quase 90% dos dados disponíveis são de genes mitocondriais. Portanto, a maior parte da história evolutiva conhecida do gênero é aquela associada à herança materna. Além disso, alguns trabalhos utilizaram amostras limitadas ou de espécimes de cativeiro (e. g. Lavergne et al. 2010). Considerando

a história taxonômica do grupo, o uso de espécimes de cativeiro pode enviesar os dados, devido à identificação incorreta ou hibridização.

Boinski e Cropp (1999) consideraram *S. sciureus* como espécie irmã de *S. oerstedii* com base em informações sobre comportamento, morfologia e mtDNA (*D-loop*). Por sua vez, *S. boliviensis* ficou em outro clado da árvore. Posteriormente, após nova análise molecular incluindo dois genes mitocondriais e dois genes nucleares, Cropp e Boinski (2000) obtiveram resultados diferentes em diferentes análises para a relação entre *S. sciureus, S. oerstedii* e *S. ustus*. A espécie *S. boliviensis* não foi incluída nas análises. Os tempos de divergência entre os clados obtidos com os diferentes conjuntos de genes também foram incongruentes. A diversificação intra-genérica foi datada em cerca de 4 a 6,4 milhões de anos atrás com base nos dados mitocondriais, enquanto os dados de genes nucleares indicaram uma diversificação mais recente, ocorrida há cerca de 1,2 a 1,8 m. a. a.

No estudo molecular de Lavergne et al. (2010) com o gene mitocondrial Citocromo *b,* o complexo de espécies *Saimiri sciureus* foi recuperado como parafilético. Este incluía *S. s. albigena, S. s. cassiquiarensis, S. s. collinsi, S. s. macrodon* e *S. s. sciureus*. A subespécie *S. s. sciureus* foi recuperada como irmã de *S. oerstedii,* enquanto as subespécies *S. s. albigena, S. s. cassiquiarensis* e *S. s. macrodon* formaram outro clado. As populações do arquipélago do Marajó (PA) foram reconhecidas como um táxon válido, considerado por Lavergne et al. (2010) como uma subespécie de *S. ustus* (*S. u. collinsi*). O clado O clado formado por *S. b. boliviensis* + *S. b. peruviensis* agrupou-se com *S. sciureus* + *S. oerstedii*. Estes autores sugeriram que a diversificação das espécies do gênero começou a ocorrer no Plioceno (2,4 a 6,6 m. a. a.), e teria se originado no oeste da Amazônia. Entretanto, os rios parecem não ter exercido um papel importante na diversificação do gênero ao longo de sua história evolutiva, pois não representam barreiras para este grupo (Lavergne et al. 2010).

Utilizando o genoma mitocondrial, Chiou et al. (2011) encontraram uma relação mais próxima entre *S. s. macrodon* e *S. s. sciureus* + *S. oerstedii*. Os táxons irmãos *S. b. boliviensis* e *S. b. peruviensis* ficaram isoladas em outro clado da árvore (Figura 3). Entretanto, esta topologia pode sofrer alterações, pois na análise de Chiou et al. (2011) não foram incluídos todos os *taxa* de *Saimiri*. A diversificação obtida através do genoma mitocondrial foi estimada em 1,5 milhões de anos atrás com a análise do BEAST e 1,1 m.a.a com a análise do multidivtime. Portanto, diferentemente da proposta de Lavegne et al. (2010), os resultados obtidos por Chiou et al. (2011) indicaram que a diversificação do gênero ocorreu mais recentemente, durante o Pleistoceno. Consequentemente, as mudanças climáticas e os refúgios do Pleistoceno podem ter tido um papel muito mais importante na diversificação do grupo, se comparado com outros primatas neotropicais.

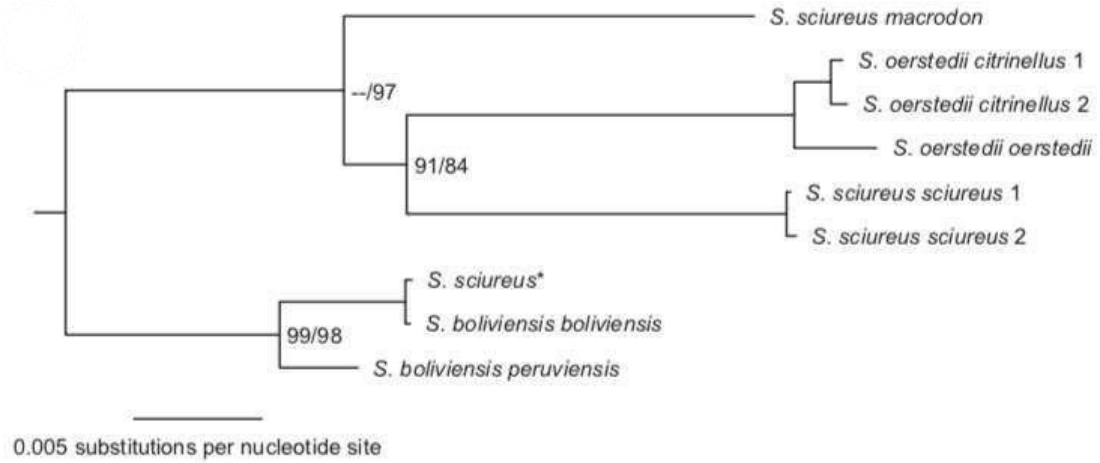

Figura 3. Árvore filogenética obtida partir do genoma mitocondrial de *Saimiri* com os valores de máxima verossimilhança e probabilidade posterior, respectivamente (Retirado de Chiou et al. 2011).

Na análise molecular (*D-loop e Cytb*), morfológica e morfométrica realizada por Mercês et al. (2015) foi observada a presença duas espécies válidas dentro de *Saimiri sciureus sciureus*. De acordo com a filogenia obtida, *S. s. collinsi* e *S. s. sciureus* não são irmãs. A primeira é irmã de *S. macrodon,* e a segunda de *S. oerstedii*, uma das espécies que ocorrem na América Central. Assim, o complexo de espécies *S. sciureus* foi considerado parafilético. Além de elevarem *S. collinsi* ao status de espécie plena, Mercês et al. (2015) observaram que esta não faz parte do complexo *S. sciureus*.

Ruiz-Garcia et al. (2015), utilizando dois genes mitocondriais (Citocromo oxidase subunidades I e II), recuperaram *S. macrodon* e *S. ustus* como grupos polifiléticos, *S. sciureus* como parafilético, e *S. collinsi* como espécie irmã de *S. vanzolinii*. Por sua vez, *S. cassiquiarensis* e *S. oerstedii* foram recuperadas como monofiléticas, sendo *S. oerstedii* irmã das demais espécies de *Saimiri*.

Lynch Alfaro et al. (2015), utilizando genes mitocondriais (Citocromo *b* e *D-loop*) e uma amostragem mais abrangente que a disponível na literatura, encontraram algumas congruências e incongruências com as filogenias disponíveis até então. Estes autores não observaram diferenciação entre *S. b. boliviensis* e *S. b. peruviensis*. A espécie "Romana" *S. vanzolinii* não foi recuperada como irmã de *S. boliviensis* (Figura 4). Os táxons *S. macrodon* e *S. ustus* foram recuperados como parafiléticos. *Saimiri sciureus* e *S. collinsi* foram recuperados como agrupamentos taxonômicos distintos, tal como observado por Mercês et al. (2015).

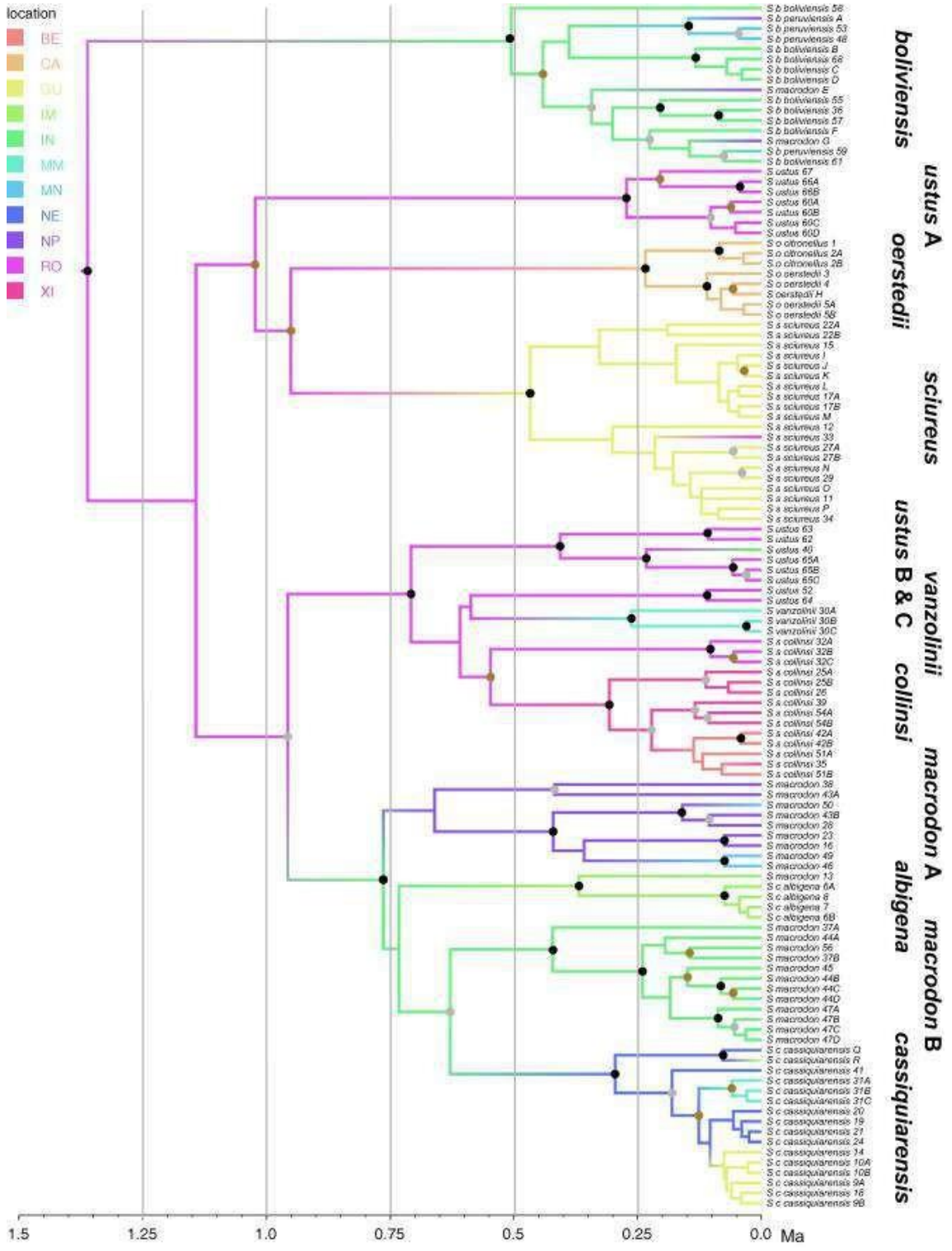

Figura 4. Árvore filogeográfica do BEAST obtida por Lynch Alfaro et al. (2015) através dos genes mitocondriais D-loop e Cytb para *Saimiri*. Os círculos pretos significam nós com probabilidade posterior de 1; círculos cinza com pp de 0,9-0,99; círculos marrons com pp de 0,70 a 0,89. Os demais nós da árvore têm probabilidade posterior menor que 0,70 (retirado de Lynch Alfaro et al. 2015).

Considerando as filogenias obtidas em todos esses trabalhos, observa-se que a única relação congruente entre os resultados da maioria foi aquela entre *S. oerstedii* e *S. sciureus*. Também ficou claro que existe uma relação pouco esclarecida entre os táxons *S. albigena*, *S. cassiquiarensis* e *S. macrodon*. Nos trabalhos mais recentes, *S. macrodon* e *S. ustus* foram recuperados como polifiléticos.

Sendo assim, é possível constatar que até o momento não existe consenso a respeito das relações intra-genéricas. Com o objetivo de tentar elucidar as relações entre as espécies de *Saimiri* na Bacia Amazônica e, consequentemente, sua evolução na região, no presente estudo foi utilizada uma metodologia inédita para o grupo, o sequenciamento de nova geração associado à metodologia *double digest* Restriction-site Associated DNA Sequencing (ddRADseq).

SEQUENCIAMENTO DE NOVA GERAÇÃO (NSG) E *DOUBLE DIGEST* RESTRICTION SITE-ASSOCIATED DNA SEQUENCING (ddRADseq)

Nos últimos anos o sequenciamento de nova geração (NSG) tem se mostrado como uma ferramenta mais barata e eficiente. Esta técnica permite o sequenciamento de milhares de pares de bases de marcadores independentes de uma só vez, quando comparada com a técnica tradicional de Sanger (McCormak et al. 2013). Entretanto, outros desafios surgem com a disponibilidade do genoma de um indivíduo, entre estes: como reduzir esse genoma tornando possível inferir filogenias com esses dados e como obter fragmentos ortólogos entre estes indivíduos.

Nesse contexto, uma das ferramentas que vêm sendo utilizadas para diversos grupos taxonômicos, desde invertebrados até plantas e mamíferos, é o *double digest* RAD sequence (DaCosta e Sorenson 2016, de Oca et al. 2017, Byrne 2017, Silva et al. 2018, Boubli et al. 2018, 2019, Valencia et al. 2018, Costa Araújo et al. 2019). Nesta metodologia o DNA do individuo é digerido por duas enzimas de restrição, que possuem precisão que permite selecionar o tamanho dos fragmentos (Peterson et al. 2012). Com esta ferramenta é possível reduzir a complexidade do genoma, fazendo subamostras e selecionando apenas sítios específicos ao longo do genoma através das enzimas de restrição. Recentemente Valencia et al. (2018) propuseram um procotolo de ddRADseq para primatas neotropicais. Neste estudo os pesquisadores indicam quais as enzimas de restrição maximizam a recuperação de locus e também indicam a influencia de diferentes *pipelines* e *clustering thresholds* para a identificação de loci homólogos.

O projeto aqui executado constituiu um esforço para compreender as relações de parentesco entre as espécies do gênero *Saimiri* e revisar o status taxonômico das espécies reconhecidas para o grupo, além de atualizar as informações sobre distribuição geográfica, utilizando dados de ddRad-Seq em combinação com a tecnologia de sequenciamento de nova geração. Além disso, a inclusão da análise morfológica de espécimes de coleções científicas brasileiras e norte americanas, bem como a análise de material tipo de todos os nomes disponíveis na literatura possibilitou uma apreciação mais abrangente do grupo, permitindo uma classificação taxonômica congruente com a evolução das linhagens de *Saimiri*.

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Capítulo 1

Phylogenomics of Amazonian squirrel monkeys (*Saimiri*: Primates, Cebidae)

O Capítulo 1 desta tese foi elaborado e formatado conforme normas de publicação cientifica da Revista Molecular Phylogenetics and Evolution, as quais se encontram no Anexo 1

Title Page

Phylogenomics of Amazonian squirrel monkeys (*Saimiri*: Primates, Cebidae)

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ABSTRACT

Phylogeny relationship among squirrel monkeys (genus *Saimiri*) is still poorly resolved. Morphology-based taxonomies range from two to 12 taxa, while molecular phylogenies recovered 17 different lineages. The last species account lists 11 taxa: *Saimiri boliviensis boliviensis*, *S. boliviensis peruviensis*, *S. vanzolinii*, *S. oerstedii oerstedii*, *S. oerstedii citrinellus*, *S. sciureus sciureus*, *S. sciureus collinsi*, *S. cassiquiarensis cassiquiarensis*, *S. cassiquiarensis albigena*, *S. macrodon* and *S. ustus*. Here we gather the first phylogenomic dataset for *Saimiri* using *double digest* restriction-site associated DNA sequencing (ddRadseq) to construct a phylogeny for Amazon squirrel monkeys. All the phylogenomic analysis strongly support the division of the genus in two main clades, the Gothic and Roman arch groups, and provided strong support for ten lineages. Our Bayesian clustering analyses revealed a third lineage in *Saimiri ustus* clade. Our time-calibrated tree confirmed that the diversification within *Saimiri* occurred during the Pleistocene.

Keywords: ddRadseq, neotropical primates, time tree

1. INTRODUCTION

The relationship between squirrel monkeys (*Saimiri* Voigt, 1831) and their sister group, the capuchin monkeys (genera *Cebus* and *Sapajus*), has been well-established using both mitochondrial and nuclear genomic data (Chiou et al., 2011; Springer et al., 2012). According to Chiou et al. (2011) squirrel monkeys and capuchin monkeys diverged at about 13.8 million years ago (12.1-16.1 Ma 95% HPD).

However, intrageneric relationships are still poorly resolved in *Saimiri*, with substantial discordance between morphological and molecular (mitochondrial) studies (e. g. Hershkovitz, 1984; Thorington, 1985; Lavergne et al., 2010; Lynch Alfaro et al., 2015; Ruiz Garcia et al., 2015).

Squirrel monkeys occur throughout the Amazon Basin, with a distribution spanning from east of the Andes in Colombia to the transition zone between the Amazon and Cerrado in Maranhão state, Brazil. The woodlands of Bolivia form the southern limit to their distribution, while their northern limit is the Orinoco River in Venezuela, extending eastwards along the Atlantic Ocean in the Guianas. Two Central American taxa, disjunct from the Amazonian distribution, inhabit lowland rain forest in Costa Rica and Panama (Hershkovitz, 1984; Thorington, 1985; Mercês et al., 2018). Hershkovitz (1984) and Thorington (1985) each revised the genus, and the most recent taxonomic review is by Groves (2005); these three reviews diverge significantly both in terms of which taxa are considered valid, and how many species and subspecies of *Saimiri* are recognized. Hershkovitz (1984), who based his review on external characters, chromosome number, geographic distribution and behavioral information, argued that the genus should be divided in two species groups, the Roman and Gothic, based in MacLean (1964). According to Hershkovitz (1984) the Gothic group is characterized by an arching band of whitish hairs above the eyes, that contrasts with the crown color with bushy tail pencil, while the Roman group the forehead is like the crown, with a narrow arching band above the eyes and presents thin tail pencil. Hershkovitz (1984) considered nine taxa to be valid: *S. boliviensis boliviensis, S. b. peruviensis, S. sciureus sciureus, S. s. albigena, S. s. cassiquiarensis, S. s. macrodon, S. oerstedii oerstedii, S. o. citrinellus,* and *S. ustus*. Subsequently, Hershkovitz (1987) recognized more three subspecies of *S. boliviensis* (*S. b. pluvialis*, *S. b. jaburuensis,* and *S. b. vanzolinii*). In contrast Thorington (1985) considered only two species to be valid: one monotypic (*S. madeirae*), and another, *S. sciureus*, with four subspecies (*S. sciureus sciureus*, *S. s. boliviensis*, *S. s. cassiquiarensis*, and *S. s. oerstedii*).

Groves (2005) was the last taxonomic review of the genus and considered five species as valid with no subspecies, recognizing *Saimiri vanzolinii* as a full species. The species account of Rylands et al. (2013) resurrects part of the proposal by Groves (2001); they considered seven species with 11 subspecies (*S. boliviensis boliviensis*, *S. b. peruviensis, S. vanzolinii; S. cassiquiarensis cassiquiarensis*, *S. c. albigena*, *S. macrodon, S. oerstedii oerstedii*, *S. o. citrinellus*, *S. sciureus sciureus*, *S. s. collinsi*, and *S. ustus*). They modified Groves' (2001) proposal by separating *S. cassiquiarensis* and *S. macrodon* as distinct species from *S. sciureus* and classifying *S. s. albigena* as a subspecies of *S. cassiquiarensis* (rather than *S. sciureus*). They also considered the subspecies *S. s. collinsi* to be valid.

A mitogenomic appraisal by Chiou et al. (2011) recovered two main clades concordant with Hershkovitz' (1984) morphological hypothesis: one comprised of the Roman group (*S. b. boliviensis*

and *S. b. peruviensis*) and the other made up of the Gothic group (*S. macrodon* (*S. s. sciureus* (*S. o. oerstedii + S. o. citrinellus*)). Phylogenetic relationships recovered in other recent molecular studies based on mitochondrial loci, however, are substantially discordant from morphological evidence. In the molecular phylogeny by Lavergne et al. (2010), which was based on one mitochondrial locus (cytochrome *b*), the Roman group clade (*S. b. boliviensis* and *S. b. peruviensis*) was recovered as sister to some members of the Gothic *S. sciureus* clade (terminal taxa: *macrodon, albigena, cassiquiarensis*). *Saimiri s. sciureus* was recovered as paraphyletic and Lavergne et al. (2010) proposed the revalidation of *S. ustus collinsi*. The molecular phylogeny of Lynch Alfaro et al. (2015) included all taxa considered as valid by Rylands et al. (2013); *S. macrodon* and *S. ustus* were each recovered as paraphyletic and *S. vanzolinii* was not recovered as sister to *boliviensis* group despite Roman morphology. A molecular phylogeny based in two other mitochondrial loci (COI and COII) recovered *S. macrodon* and *S. ustus* as polyphyletic (Ruiz Garcia et al., 2015). Ruiz Garcia et al. (2015) proposed that *Saimiri* should include three species: *S. sciureus, S. vanzolinii* and *S. oerstedii*. Considering all molecular phylogenetic evidence to date, the only pattern consistently recovered is the sister relationship between *S. oerstedii* and *S. sciureus*, while the relationships among all other taxa remain uncertain or unknown. One of the few studies that included nuclear genes, Springer et al. (2012) recovered the following relationship among *Saimiri* species (*S. boliviensis* (*S. ustus* (*S. sciureus* (*S. oerstedii*))). However, one of the limitations of this study is that they were using captive specimens' sample and just one sample per species. The differences of topology across these studies could be a result of incomplete lineage sorting, introgression/hybridization or sex-biased migration. Since migration among squirrel monkeys population is sex-biased (Mitchell et al., 1991; Boinski et al., 2002; Blair and Melnick, 2012) where males or females can disperse depending on the sex, the population relationship based in mtDNA (maternal inheritance) will not necessarily correspond to population relationship based in nuclear DNA.

Divergence dating estimates among *Saimiri* taxa are incongruent across previously published studies. Lavergne et al. (2010) estimated a Pliocene divergence at ~ 4.3 Ma (2.4-6.6 Ma 95% HPD), while other studies estimated the initial divergence at ~ 1 to 1.5 Ma [1.5 Ma (1.1-2.9 Ma 95% HPD) using BEAST, or 1.10 Ma (0.72-1.88 Ma 95% HPD) using multidivtime (Chiou et al., 2011); 1.36 Ma (1.1-1.91 Ma 95% HPD) (Lynch Alfaro et al., 2015)]. Springer et al. (2012) estimated the Pleistocene divergence within *Saimiri* at ~1.75 Ma (1.06-2.88 Ma 95% HPD), while Perelman et al. (2012) estimates an early divergence for the genus at ~ 2.24 (1.05-3.73).

Recently, with the decreasing of the cost to generate genomic data, made this tool available to the study of phylogeny and population genetics of many taxa. One of these methods is the *double digest* restriction-site associated DNA sequencing (ddRADseq), this methodology generates reduced representation libraries of complete genomes. ddRADseq methodology uses two restriction enzymes

to digest genomic DNA into several DNA fragments. These fragments are size selected to reduce the number of fragments to be sequenced (Peterson et al. 2012), resulting in libraries that represents a subset of homologous loci from across the genome. Valencia et al. (2018) developed a protocol to use ddRADseq across the entire radiation of New World monkeys. They verified that this tool is suitable for phylogenetic studies in diverse taxonomic levels and evolutionary time scales.

To elucidate the phylogenetic relationships between *Saimiri* taxa in the Amazon basin and their evolutionary history in the region, we used *double digest* restriction-site associated DNA sequencing (Peterson et al., 2012) to generate a genome-wide molecular dataset for *Saimiri* taxa. Our ddRADseq data matrices were subsequently employed to infer phylogenetic relationships among squirrel monkey lineages and to assess genetic structuring. Our phylogenetic results were then assessed for congruence with evidence from mitochondrial markers and morphology. Recently, phylogenomics approaches have provided new insights into Neotropical primate diversity and evolution (Byrne, 2017; Boubli et al., 2018, 2019; Lima et al., 2018; Silva et al., 2018; Valencia et al., 2018; Costa Araújo et al., 2019). The present study constructs the first phylogeny for squirrel monkeys that utilizes genome-wide nuclear markers to analyze genetic relationships across taxa using morphologically identified samples of known geographic origin.

2. MATERIAL AND METHODS

2.1. Taxon sampling and DNA extraction

A total of 44 fresh tissue samples were collected from museum voucher specimens and six blood samples from live wild individuals in the field (Table 1, Fig. 1). The live individuals were captured by F. P. Paim with Tomahawk traps in trapping stations. The trapping methodology is described in detail in Paim and Rabelo (2015) with information on ethical considerations and authorization numbers from Brazilian authorities. Tissue samples were obtained from the following institutions: Museu Paraense Emílio Goeldi (MPEG), Belém, Pará state, Brazil, Universidade Federal do Pará (UFPA), Belém, Pará state, Brazil, Instituto de Desenvolvimento Sustentável Mamirauá (IDSM), Tefé, Amazonas state, Brazil, Universidade Federal do Mato Grosso (UFMT), Cuiabá, Mato Grosso state, Brazil, Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá (IEPA), Macapá, Amapá state, Brazil, and University of California (UCLA), Los Angeles, California, United States.

DNA was extracted from blood and muscle tissues using the Qiagen DNeasy Blood & Tissue Kit according to the manufacturer's protocol. After extraction we quantified DNA with a Qubit 2.0 Fluorometer.

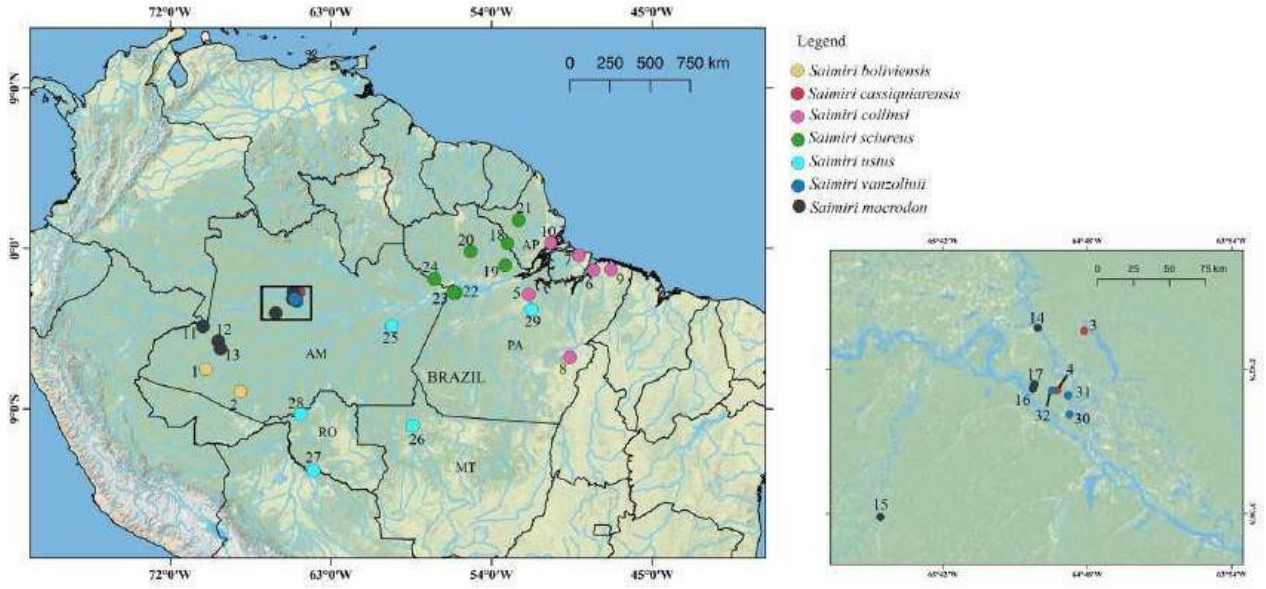

Fig. 1. Map showing the sampled localities for *Saimiri*. The map numbers correspond to the sample numbers in Table 1. Species names are based on Rylands et al. (2013) and Mercês et al. (2015). The inset square represents the location of the smaller map which provides details for sampled localities at Solimões-Japurá interfluvium. Acronyms: AM: Amazonas; AP: Amapá; MT: Mato Grosso; PA: Pará.

Table 1. Map number, List of samples, coordinates and voucher number.

Map ID	Species	Latitude	Longitude	Voucher number	Institution
1	*Saimiri boliviensis*	-6.77	-70.01	FES056	IDSM
2	*Saimiri boliviensis*	-8.02	-68.07	RS050	MPEG
3a	*Saimiri cassiquiarensis*	-2.46	-64.82	LB719	UFPA
3b	*Saimiri cassiquiarensis*	-2.46	-64.82	LB735	UFPA
3c	*Saimiri cassiquiarensis*	-2.46	-64.82	LB738	UFPA
4a	*Saimiri cassiquiarensis*	-2.83	-64.99	SC4.2	IDSM
4b	*Saimiri cassiquiarensis*	-2.83	-64.99	SC4.4	IDSM
5a	*Saimiri collinsi*	-2.58	-51.92	LB463	UFPA
5b	*Saimiri collinsi*	-2.58	-51.92	LB459	UFPA
5c	*Saimiri collinsi*	-2.58	-51.92	LB389	UFPA
6	*Saimiri collinsi*	-1.21	-48.29	MIC01	MPEG
7a	*Saimiri collinsi*	-0.40	-49.11	MAR05	MPEG
7b	*Saimiri collinsi*	-0.40	-49.11	MAR04	MPEG
8	*Saimiri collinsi*	-6.1	-49.60	LB603	UFPA
9	*Saimiri collinsi*	-1.18	-47.31	AF4	UCLA
10a	*Saimiri collinsi*	0.32	-47.31	LB561	UFPA
10b	*Saimiri collinsi*	0.32	-47.31	LB560	UFPA
11a	*Saimiri collinsi*	-2.47	-56.01	LB801	UFPA
11b	*Saimiri collinsi*	-2.47	-56.01	LB796	UFPA
11c	*Saimiri collinsi*	-2.47	-56.01	LB798	UFPA
12	*Saimiri collinsi*	-2.48	-56.16	LB806	UFPA
13a	*Saimiri collinsi*	-1.71	-57.21	CN30	MPEG
13b	*Saimiri collinsi*	-1.71	-57.21	CN15	MPEG
14a	*Saimiri macrodon*	-4.37	-50.69	LB125	UFPA
14b	*Saimiri macrodon*	-4.37	-70.17	LB128	UFPA
14c	*Saimiri macrodon*	-4.37	-70.17	LB127	UFPA
15a	*Saimiri macrodon*	-5.2	-69.31	RDSC03	MPEG
15b	*Saimiri macrodon*	-5.2	-69.31	RDSC27	MPEG
16a	*Saimiri macrodon*	-5.63	-69.18	RDSC30	MPEG
16b	*Saimiri macrodon*	-5.63	-69.18	RDSC47	MPEG

Map ID	Species	Latitude	Longitude	Voucher number	Institution
17a	*Saimiri macrodon*	-2.44	-65.11	LB791	UFPA
17b	*Saimiri macrodon*	-2.44	-65.11	LB762	UFPA
18	*Saimiri macrodon*	-3.62	-66.09	BJ002	IDSM
19	*Saimiri macrodon*	-2.82	-65.14	SM9.2	IDSM
20	*Saimiri macrodon*	-2.79	-65.13	SV15.1	IDSM
21a	*Saimiri sciureus*	0.28	-53.11	AP124	IEPA
21b	*Saimiri sciureus*	0.28	-53.11	AP104	IEPA
22a	*Saimiri sciureus*	-0.94	-53.24	CN276	MPEG
22b	*Saimiri sciureus*	-0.94	-53.24	CN243	MPEG
23	*Saimiri sciureus*	-0.16	-55.18	CN297	MPEG
24	*Saimiri sciureus*	1.59	-52.49	AP221	IEPA
25	*Saimiri ustus*	-4.34	-59.59	L556	UFPA
26a	*Saimiri ustus*	-9.95	-58.41	MSN147	UFMT
26b	*Saimiri ustus*	-9.95	-58.41	MSN144	UFMT
27	*Saimiri ustus*	-12.44	-63.97	RGB02	MPEG
28	*Saimiri ustus*	-9.29	-64.71	JIR9791	MPEG
29	*Saimiri ustus*	-3.41	-51.75	LB468	UFPA
30	*Saimiri vanzolinii*	-2.97	-64.91	LB727	UFPA
31	*Saimiri vanzolinii*	-2.86	-64.92	SV6.2	IDSM
32	*Saimiri vanzolinii*	-2.83	-65.02	SV1.4	IDSM
-	*Sapajus robustus*			robustus	UCLA

2.2. ddRADseq library preparation and sequencing

After normalization, a total of 100 ng of genomic DNA for each sample was sent for ddRAD library preparation with the SphI-MluCl enzyme pair, size selected to focus on fragments of 300±30 bp [at the Genome Sequencing Facility at the University of Texas, San Antonio (GSAF)]. With this size selection window, we estimated that we could generate sufficient coverage (6x) for a genotyping set of ~100,000 ddRAD loci by targeting a total of 2–4 million reads per sample. Subsequently the samples were sequenced on one lane of HiSeqX (400 million reads, for a target of 4 million 2x150 bp PE reads per sample), an Illumina platform, by Novogene (USA). Our protocol and pipelines were modified from Valencia' et al. (2018) protocol.

2.3. Quality control

Raw reads were quality checked with FASTQC (Andrews, 2010). We used the bbmap tool bbduk.sh to trim any adapter sequence present at the 3' end of the reads using a kmer length of 22 with a maximum of 3 mismatches, discarding any reads smaller than 30 bp, with the "tbo" and "tpe" options. We used the bbmap tools bbduk.sh and reformat.sh to remove phiX contamination and to reverify pairing, respectively. We trimmed the 3' end of reads to remove bases with quality score less than 20 with the bbmap tool bbduk.sh.

We demultiplexed the sequence reads per sample in iPyRAD, allowing for no barcode mismatches. We used the program Cutadapt (Martin, 2010) to remove restriction enzyme recognition

sites from the 5' end of reads with an error rate of 0.25, remove any remaining P5 and P7 adapter sequences from the 5' end, trim bases with a quality score less than 20 from the 5' end, and remove all reads with more than 5% Ns and reads now smaller than 30 bp. After this step, we merged forward and reverse reads in VSEARCH (Rognes et al., 2016), using a minimum length of 30 bp for the entire merged sequence, a minimum of 20 bp for the length of overlap between the reads, and a maximum of four mismatched bases in the overlap region (this step was performed outside iPyRAD).

We performed reference-based assembly to generate ddRADseq data matrices and SNPs calling in iPyRAD (Eaton and Overcast, 2016) using the *Callithrix jacchus* reference genome from GenBank (accession number GCA_000004665.1). We filtered for quality/length and merged the forward and reverse reads outside iPyRAD as described above so we continued directly to within-sample clustering (Step 3 of the iPyRAD pipeline). We used a clustering threshold of 90% and set the following parameters: minimum depth of 6X, a maximum of 6 Ns and 8 Hs in consensus reads, a max of 30 SNPs and 8 indels per locus, and maximum shared Hs as a proportion at 0.5.

2.4. Phylogenomic analyses and divergence dating analyses

All phylogenetic analyses (RAxML and Bayesian) were run on the CIPRES Science Gateway v 3.3 server (Miller et al., 2010). Our Maximum Likelihood analysis was conducted using RAxML v. 8.2.10 (Stamatakis, 2014) with the GTR + G (gamma) substitution model and 1,000 bootstrap replicates integrated with 200 searches for the optimal tree for our "main" dataset.

Phylogeny and diversification times were jointly estimated under an uncorrelated lognormal relaxed clock model in the program BEAST v. 1.8.4 (Drummond et al., 2012) for the "time" dataset. A Yule speciation process and the GTR + G substitution model were used, and the ucld.mean prior was set to an exponential distribution (mean=0.05). To obtain the posterior distribution of the estimated divergence times, one calibration point on the root node (capuchin monkey/squirrel monkey divergence) was implemented with a lognormal distribution to set hard minimum and soft maximum bounds. A minimum age of 12.5 Ma was used based on the fossil *Neosaimiri* Stirton, 1951 based in Hartwig and Meldrum (2002) and a soft maximum bound was set at 26 Ma based on the fossil *Branisella boliviana* Hoffstetter, 1969, from the Deseadan fauna of La Salla (McFadden, 1990; see Byrne et al., 2016). The log standard deviation (= 0.8) and log mean (= 1.287) were set such that 95% of the prior distribution falls before the maximum age to create the soft maximum bound.

We conducted two replicate runs of 100 million MCMC generations, sampling every 10,000 generations. We visualized the sampling distributions of each run with Tracer v. 1.6 to evaluate convergence and effective sample size after a burn-in of 10%. Independent runs were combined with the first 10% of samples of the posterior distribution discarded as burn-in using LogCombiner v. 1.8.4 and the maximum credibility tree with mean heights was generated in TreeAnnotator v. 1.8.4. and

trees are visualized in FigTree v. 1.4.4. For detail of each dataset, number of samples, number of loci, parsimony informative sites and data set usage check Table 2.

Table 2. Summary of the final ddRADseq datasets, including number of loci, parsimony informative sites (PIS) and dataset usage.

Dataset	No. samples	No. loci	Pis (bp)	Usage
main	48	5794	9873	Parallel Structure
Struc1_17	17	1605	1692	Parallel Structure
Struc2_21	21	1957	1279	Parallel Structure
Struc3_6	6	2967	717	Parallel Structure
main	48	5794	9873	RaxML
time	10	12847	6580	BEAST

2.5. Bayesian clustering analyses

To better understand the structure of squirrel monkey genetic diversity from our genomic data in the context of previous taxonomic classification and phylogenetic results, we conducted population structure analyses. The model-based Bayesian clustering method in ParallelStructure v. 3.3.4 (Besnier and Glover, 2013), which is an R-based implementation of the program Structure (Pritchard et al., 2000), allows for the assessment of the degree of gene flow across clades. We used the admixture model and no putative origins specified for individuals. For each dataset, 10 runs at each value of K were performed with a burn-in of 100,000 steps and MCMC length of 500,000 steps. We ran the analyses for four datasets: the first included all the clades retrieved in molecular analyses (dataset= "main"; K=1-14), and the other three were subsampled datasets within the *S. sciureus* clade (dataset=Struc2_21; K=1-6), the *S. macrodon* clade (dataset=Struc1_17; K=1-5), and the *S. ustus* clade (dataset=Struc3_6; K=1-6).

We identified the most likely number of clusters for each dataset, with an initial assessment using LnP(D). If several K values had similar LnP(D) scores, the assignment of the additional clusters was evaluated to check if they were informative or assigned equally to the putative populations. We implemented the ad hoc statistic delta K (Evanno et al., 2005) in the program STRUCTURE HARVESTER (Earl and vonHoldt, 2012) to detect the most appropriate number of clusters, in particular for the subsampled datasets. The Evanno method chooses the optimum number of clusters based on the second order rate of change in the log probability of data between successive K values, however, when there is strong hierarchical structure it often returns only the top level of stratification (Evanno et al., 2005). For the full dataset, it is likely that delta K will strongly detect the major axes of structure representing deeper divergences within *Saimiri*, possibly obscuring finer structure within or even among species, and resulting in a smaller value (e.g., three) than expected (eight or above) for the optimum number of clusters using this method. STRUCTURE HARVESTER (Earl and

vonHoldt, 2012) was used to examine LnP(D) and delta K for each possible number of clusters (K) for each dataset. The program CLUMPP (Jakobsson and Rosenberg, 2007) was used to combine and average individual assignments probabilities across all replicates, and the combined data was visualized with DISTRUCT 1.1 (Rosenberg, 2004).

3. RESULTS

3.1. ddRADseq data assembly

The ddRADseq samples had an average of 9 million raw reads (Table 3), which were subsequently quality filtered and cluster into an average of 97K quality filtered reads per sample. We clustered into an average of 789148 stacks (90% of clustering threshold), with a mean depth of around 5.9X and subsequent filtered average of 3533 loci. The "main" dataset contained 5797 ddRADseq loci, while the other datasets contained between 1695 and 12847 loci. The heterozygosity varies significantly among *Saimiri* taxa (0.00056-0.0055, mean = 0.018). S*aimiri macrodon* (clade 2) and *S. collinsi* (clade 2) individuals are the most polymorphic, while *S. boliviensis* and *S. collinsi* (clade 1) are the least.

Table 3. Summary of the ddRadseq data assembly (90% clustering threshold): sequencing information per sample. [2] Heterozygosity measured as the proportion of called sites.

Species	**Sample ID**	**Reads**	**Reads passed**	**Clusters**	**Avg. Depth**	**Cons. Loci**	**No. Sites**	**H^2**
S. boliviensis	FES056	1416829	60896	286002	4.89	717	20228866	0.00086
S. boliviensis	RS050	6589825	57799	335159	2.92	813	8945411	0.00056
S. cassiquiarensis	LB719	1235377	31454	344492	4.92	1192	20070968	0.00072
S. cassiquiarensis	LB735	10963885	104088	1134229	4.74	3933	19143916	0.00125
S. cassiquiarensis	LB738	8852072	96790	869333	5.38	4865	22286007	0.00197
S. cassiquiarensis	SC4.2	4723641	94187	456923	13.77	5083	12795797	0.00187
S. cassiquiarensis	SC4.4	4389803	93728	416111	7.41	5086	19485342	0.00158
S. collinsi	AF4	11509231	128437	457706	17.26	1834	27336098	0.00119
S. collinsi	CN15	25287365	170694	1178386	12.34	4536	36299180	0.00522
S. collinsi	CN30	5396707	94342	731608	3.23	4995	12653653	0.00087
S. collinsi	LB389	3010863	81239	514108	4.85	2913	19068332	0.00189
S. collinsi	LB459	15122893	162118	1040340	4.27	4412	18033139	0.00069
S. collinsi	LB463	6723397	109504	720889	8.39	2413	35364835	0.00331
S. collinsi	LB560	2777039	47805	531993	6.69	2152	18448861	0.00113
S. collinsi	LB561	1356705	34694	319584	2.66	1781	10794964	0.00087
S. collinsi	LB603	9239567	96103	1061069	2.81	5214	7855265	0.00086
S. collinsi	LB796	9768125	91287	1228375	3	5084	9488273	0.00163
S. collinsi	LB798	13405714	91801	1815885	4.33	5008	18830606	0.00114
S. collinsi	LB801	5204030	116852	526239	3.88	3200	18797133	0.0012
S. collinsi	LB806	8716914	91705	1048071	6.99	5100	26022550	0.00219
S. collinsi	MAR04	7355502	83363	1033428	4.76	5062	19269714	0.00111
S. collinsi	MAR05	4821078	82718	672469	4	4006	17717634	0.00071
S. collinsi	MIC01	36110844	210925	1876837	4.67	4436	18143184	0.0006

Species	Sample ID	Reads	Reads passed	Clusters	Avg. Depth	Cons. Loci	No. Sites	H^2
S. macrodon	SV15.1	7446569	112480	506184	4.75	5145	34430491	0.00553
S. macrodon	BJ002	28986768	190810	1707575	8.19	4442	41025900	0.00423
S. macrodon	LB125	28587364	199714	1617309	2.84	4430	11095607	0.00087
S. macrodon	LB127	6625126	77496	1102722	8.73	4690	42893784	0.00407
S. macrodon	LB128	6915175	87718	857206	3.23	4498	16627156	0.00189
S. macrodon	LB762	2870684	54153	634417	6.37	2809	20685902	0.00144
S. macrodon	LB791	1602309	41782	381894	2.79	1915	12162371	0.0016
S. macrodon	RDSC03	3308181	70196	631578	3.94	3909	15261108	0.00116
S. macrodon	RDSC27	5285276	93452	654183	3.42	3852	15497945	0.00188
S. macrodon	RDSC30	1194419	31679	348268	5.44	1324	20509560	0.00185
S. macrodon	RDSC47	1643819	44649	383271	2.51	2134	7293232	0.00171
S. macrodon	SM9.2	6024597	105539	543810	7.58	5202	19463469	0.00164
S. sciureus	AP104	1828553	60414	363768	3.83	887	13626130	0.00164
S. sciureus	AP124	11079743	145278	852739	7.97	3965	31969293	0.00336
S. sciureus	AP221	18585390	164251	1130784	9.34	4482	35506971	0.00429
S. sciureus	CN243	9887530	145425	889626	5.31	2800	32571880	0.00193
S. sciureus	CN276	12083616	147638	907206	2.09	4212	2282392	0.00116
S. sciureus	CN297	2155387	56221	465476	8	2462	32341192	0.00335
S. ustus	JIR9791	1542612	48981	413861	4.08	1420	13322362	0.00231
S. ustus	LB556	3542124	87485	385810	4.43	4750	16918656	0.00076
S. ustus	MSN145	48408050	221031	1858737	8.9	4082	44887626	0.00368
S. ustus	MSN147	3424920	70188	567881	11.67	4179	46414967	0.00364
S. ustus	LB468	3709941	76140	564758	5.04	2931	24390715	0.00161
S. ustus	RGB02	1255023	39059	322781	3.05	1113	10094234	0.00176
S. vanzolinii	LB727	6466707	89889	841024	2.55	4461	7239354	0.00129
S. vanzolinii	SV1.4	14716485	164764	580386	7.97	4258	22032961	0.00156
S. vanzolinii	SV6.2	8727451	114853	687674	10.48	4734	23457993	0.00179

3.2. Phylogenetic inferences

We generated two phylogenetic trees using the concatenated ddRADseq data matrices; maximum likelihood tree was inferred for the "main" dataset, and the phylogeny and diversification times were jointly estimated for the "time" data set using BEAST.

We recovered the same topology for ML (Fig. 2) and Bayesian analyses. The phylogeny inferred from ddRADseq divided *Saimiri* into two major clades (corresponding to the Roman and Gothic arch groups based on morphology) and four subclades. All clades and subclades were highly supported with bootstrap values higher than 95 and posterior probability of 1. The Roman group clade was composed of *S. boliviensis* and *S. vanzolinii*.

The Gothic group clade was composed of four main lineages (here called *S. ustus* clade, *S. cassiquiarensis*, *S. macrodon* clade, *S. sciureus* clade). The *S. ustus* clade compromising the bare-eared squirrel monkeys is the earliest diverging Gothic lineage and was composed of *S. ustus* 1 and

S. ustus 2. The second group among Gothic lineage was the tufted-eared group. *Saimiri cassiquiarensis* diverged early, while *S. macrodon* (composed of two lineages, *S. macrodon* 1 and *S. macrodon* 2) was sister to the *S. sciureus* clade (Eastern Amazon clade). Within the *S. sciureus* clade, we recovered *S. collinsi* as paraphyletic, with some *S. sciureus* specimens forming sister to *S. collinsi* to the exclusion of remaining *S. collinsi* samples (referred to as *S. collinsi* 2).

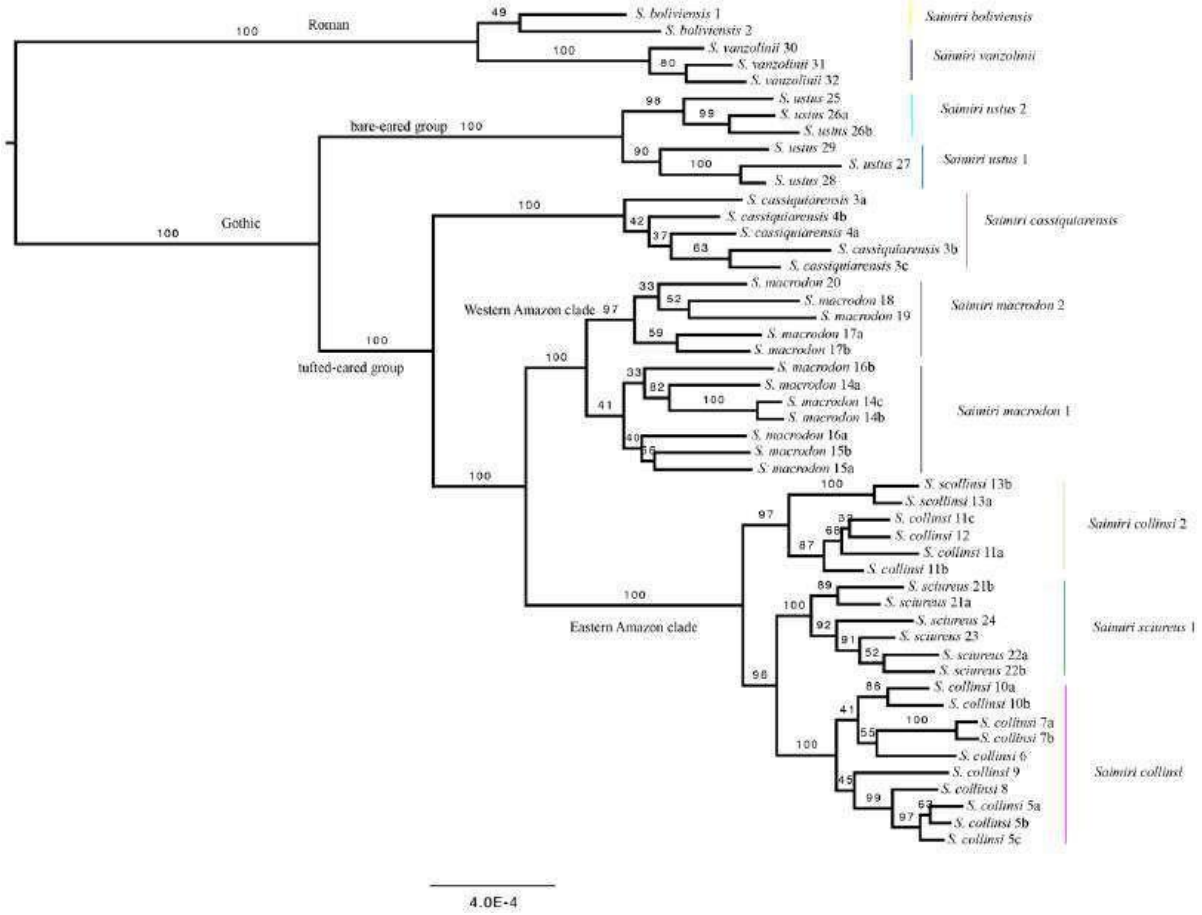

Fig. 2. Maximum likelihood tree inferred with the ddRADseq "main" dataset. Numbers at each node represent percentages from bootstrap value. Sample numbers correspond to those in Table 1 and Fig. 1.

2.1. Bayesian clustering analyses

Bayesian cluster analyses were performed using four datasets of ddRADseq: main with all *Saimiri* taxa (6484 SNPs), struc2_21 with *S. sciureus* clade (6603 SNPs), strc3_6 with *S. ustus* clade (3795 SNPs), and struc1_17 with *S. macrodon* clade (4585 SNPs).

The first structure dataset analyzed was "main". Mean likelihood increased with each added cluster from K=1 to K=6 (Fig. 3a). When K=6 is assumed *S. boliviensis* and *S. vanzolinii* formed a cluster, all the samples are assigned together in one single cluster, *S. cassiquiarensis* was recovered its own cluster, all samples of *S. macrodon* were recovered in one cluster, and the last cluster is formed by *S. collinsi* and *S. sciureus* samples (Fig 3.b). *Saimiri cassiquiarensis* individuals shares some ancestry with *S. macrodon*.

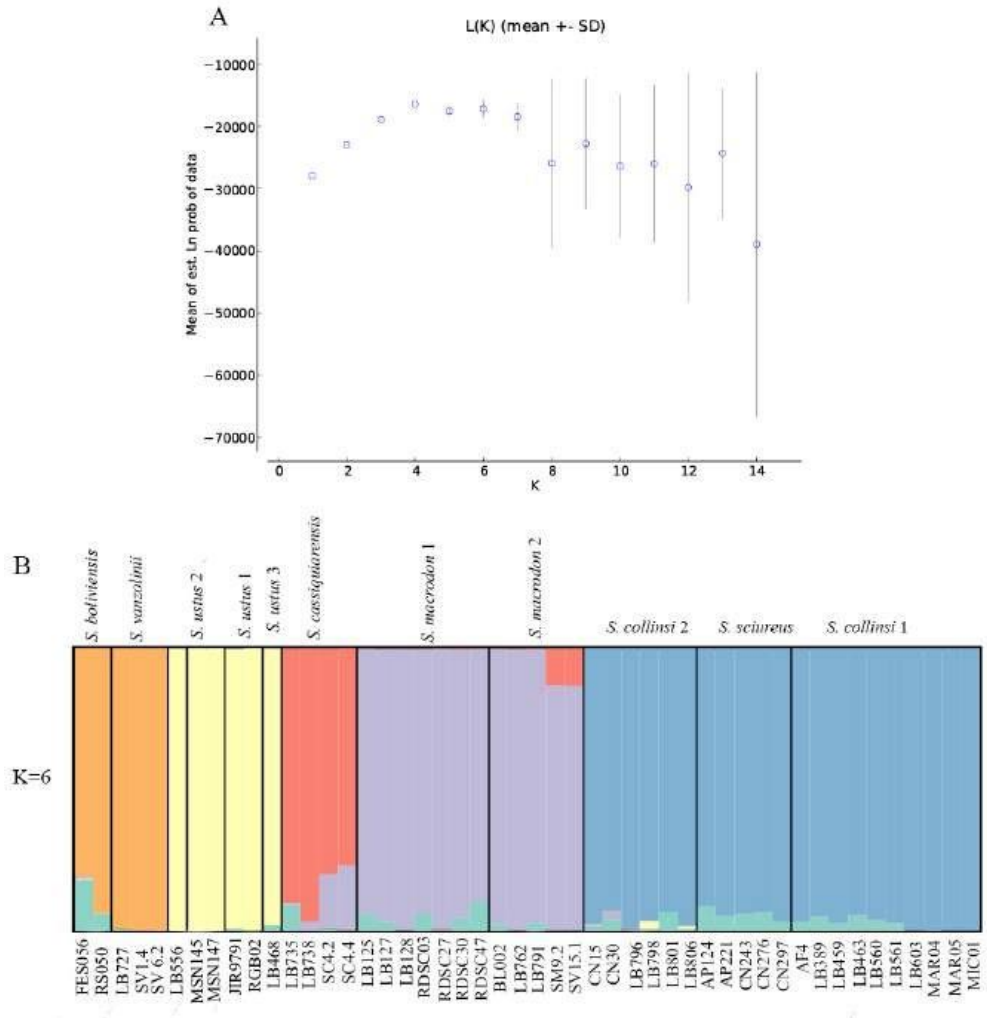

Fig. 3. (A) Mean likelihood [LnP(D) ± SD]. (B) Genetic structure of *Saimiri* populations inferred from "main" dataset using Bayesian cluster analyses for K = 6. Samples ID are shown.

We tested the number of clusters for the Eastern Amazon clade (*S. sciureus* clade), with the dataset "Struc2_21". Mean likelihood remained stable until K=4 and decreased after that (Fig. 4a), while the Evanno deltaK method selected K=2 (Fig. 4b). When K=2 is assumed, one genetic cluster correspond to *S. collinsi* 1, and the other corresponds to *S. collinsi* 2 + *S. sciureus* (Fig. 4c). Two individuals of *S. sciureus* showed some ancestry with *S. collinsi* 1. In our phylogeny *S. collinsi* 2 appeared as sister to *S. sciureus* + *S. collinsi* 1. While in this analysis, we recovered *S. collinsi* 2 and *S. sciureus* as a single unit. It is unclear if this topology is result of true phylogenetic signal or incomplete lineage sorting/introgressive hybridization.

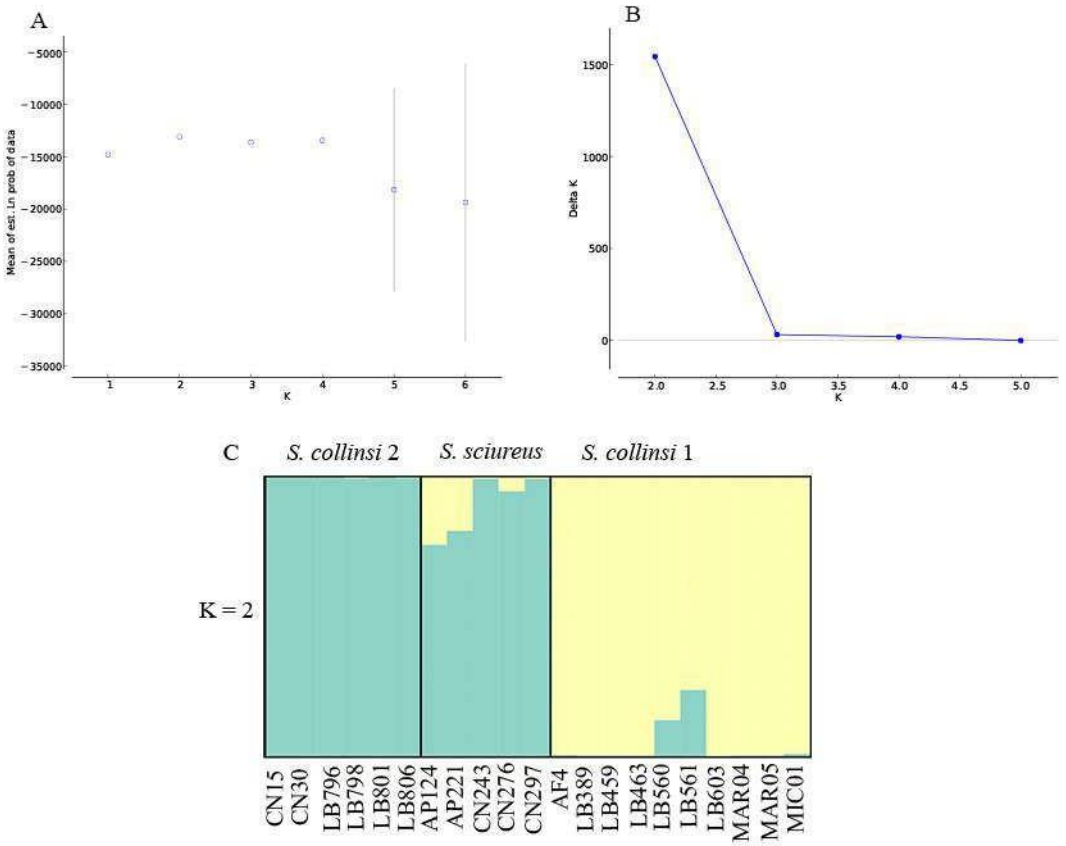

Fig. 4. (A) Mean likelihood [LnP(D) ± SD]. (B) deltaK calculated for the "Struct2_21" dataset using ParallelStructure from 5 independent runs for each value of K from 1 to 6. (C) Genetic structure of the Eastern Amazon clade inferred from "Struct2_21" dataset using Bayesian cluster analyses for K = 2. Samples ID are shown.

For the dataset "Struc3_6" with bare-eared clade (*S. ustus* clade), the mean likelihood remained stable until K=4 clusters (Fig. 5a), after that it decreased, while the Evanno method deltaK selected K=3. Assuming K=3, one cluster correspond to Rondonia specimens (*S. ustus* 1), the other to *S. ustus* 2 (Madeira River and Mato Grosso populations) and the third corresponded to *S. ustus* 3 (Xingu River population). In our maximum likelihood tree *S. ustus* 1 and *S. ustus* 3 appeared as sister clades.

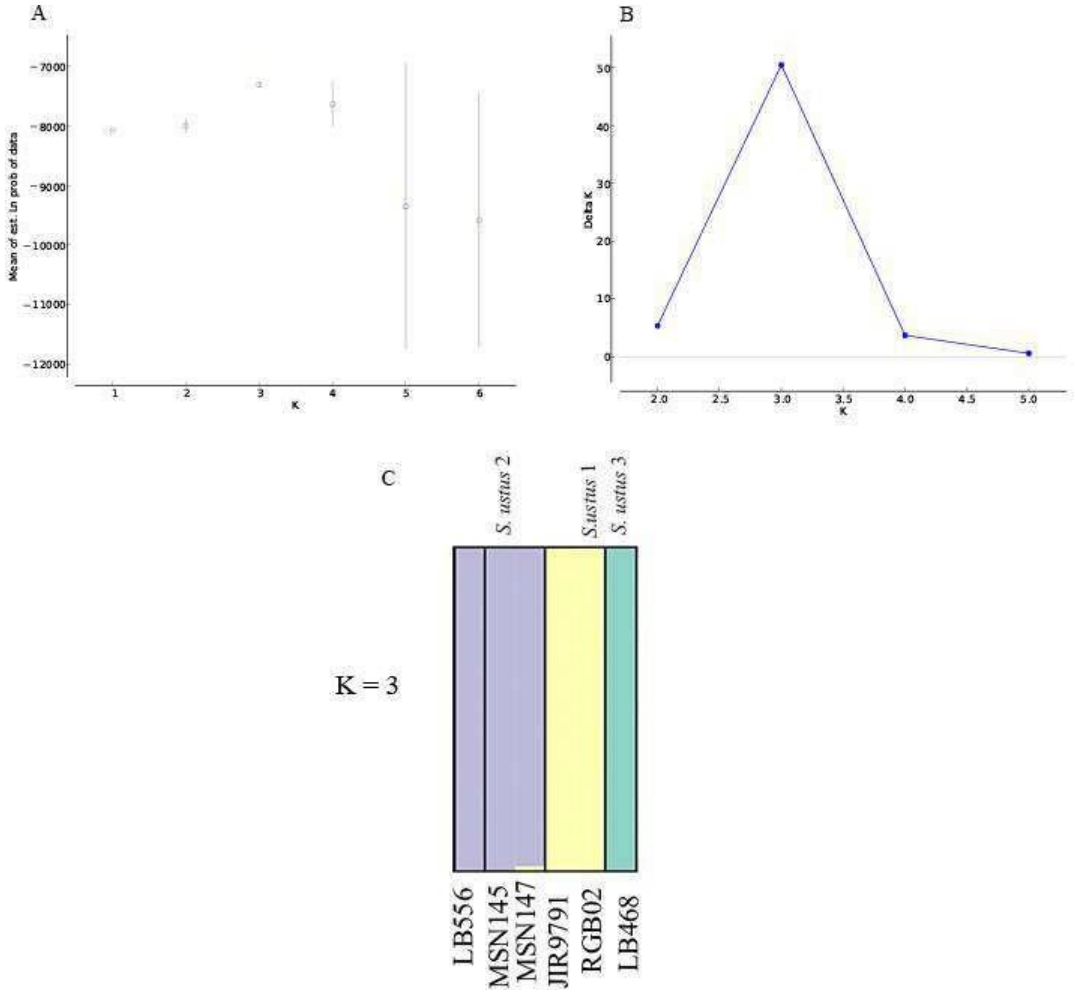

Fig. 5. (A) Mean likelihood [LnP(D) ± SD]. (B) deltaK calculated for the "Struct3_6" dataset using ParallelStructure from 5 independent runs for each value of K from 1 to 6. (C) Genetic structure of the bare-eared clade inferred from "Struct3_6" dataset using Bayesian cluster analyses for K = 3. Samples ID are shown.

For the third dataset "Struc1_17" we tested the sub clusters for Western Amazon squirrel monkeys (*Saimiri macrodon* clade). The mean likelihood remained stable until K = 3 and after it decreased (Fig. 6a). The deltaK Evanno method selected K = 2 (Fig. 6b), if we assumed K = 2, one cluster corresponded to *S. macrodon* 1, a population located at Western Amazon and the second *S. macrodon* 2 that occurs between Solimões-Japurá rivers, with some specimens in both banks of Juruá River. Some individuals of *S. macrodon* 2 presented ancestry with *S. macrodon* 1 (Fig. 6c).

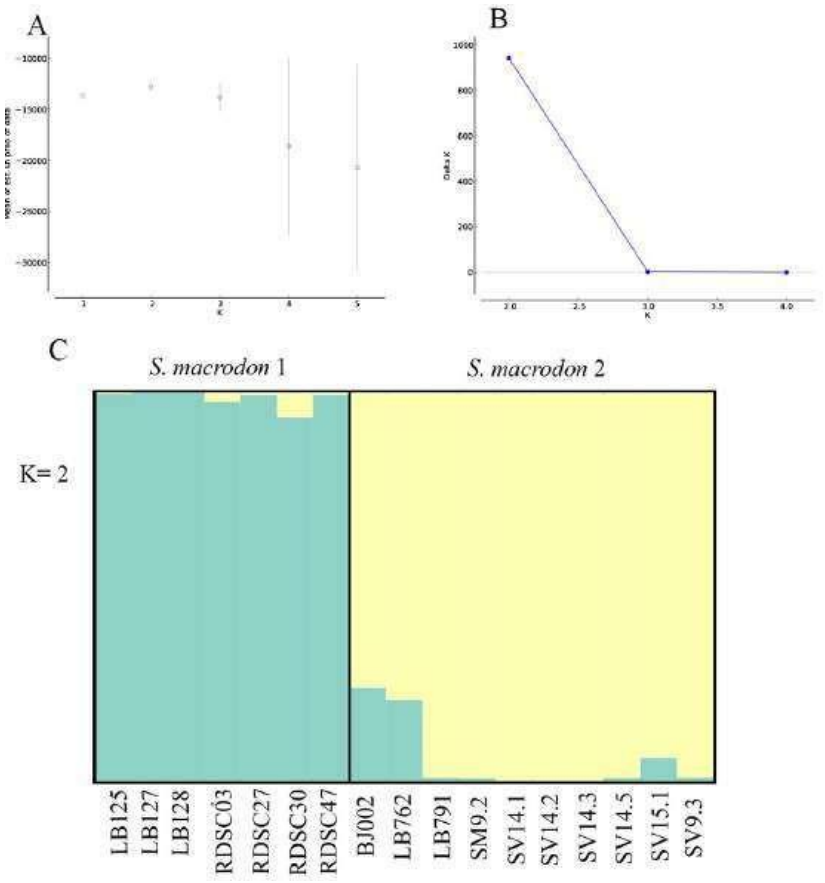

Fig. 6. (A) Mean likelihood [LnP(D) ± SD]. (B) deltaK calculated for the "Struct1_17" dataset using ParallelStructure from 5 independent runs for each value of K from 1 to 5. (C) Genetic structure of the *Saimiri macrodon* clade inferred from "Struct1_17" dataset using Bayesian cluster analyses for K = 2 Samples ID are shown.

2.2. Divergence time analysis

The most recent common ancestor of the extant *Saimiri* taxa is estimated to have diverged in the Miocene (15.1 Ma: 95% HPD 12.7-20.7). The estimated divergence time for the split between Gothic and Roman lineages was at 1.74 Ma (95% HPD = 0.97-3.13; Fig. 7), while the divergence of the *S. ustus* lineage from tufted-eared squirrel monkeys was at 1.07 Ma (95% HPD = 0.62-1.92). For detail in the time estimated divergence among clades see Table 4. For this analysis we had to extract *Saimiri boliviensis* from the "time" dataset, due to the high rate of missing data, if compared to the other samples (for details see Table 2).

Table 4. Mean ages and upper and lower 95% HPD for splits and clades within the genus *Saimiri*.

Splits or clades	**Mean age (Ma)**	**Lower 95% HPD**	**Upper 95% HPD**
S. vanzolinii vs. all other *Saimiri*	1.74	0.97	3.13
S. ustus + tufted ear *Saimiri*	1. 07	0.62	1.92
S. cassiquiarensis + (*S. macrodon* clade + *S. sciureus* clade)	0.89	0.48	1.52
S. macrodon clade + *S. sciureus* clade	0.64	0.37	1.15
S. macrodon radiation	0.43	0.18	0.78
S. ustus radiation	0.22	0.10	0.47
S. collinsi 2 + (*S. collinsi* 1 + *S. sciureus*)	0.34	0.18	0.62
S. collinsi 2 + *S. sciureus*	0.24	0.12	0.46

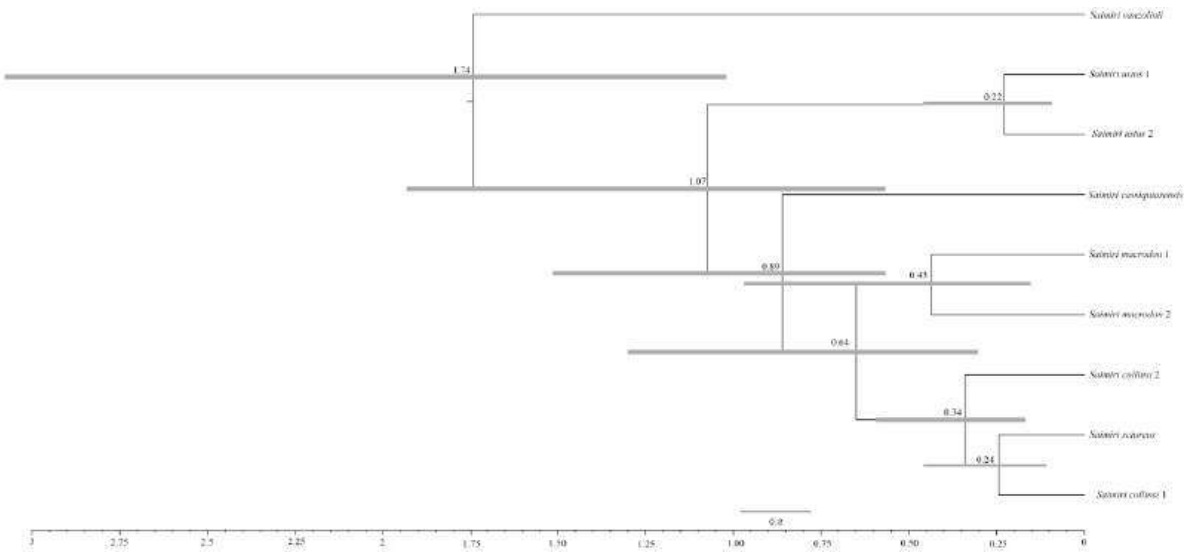

Fig. 7. A time-calibrated phylogeny for *Saimiri* inferred with ddRADseq "time" dataset. All received full support (PP=1.0). Gray bars represented 95% highest posterior density (HPD) intervals.

3. DISCUSSION

The topology of our phylogenetic tree was largely concordant with mitogenomic analysis (Chiou et al., 2011) and nuclear phylogeny (Springer et al., 2012). However, we recovered more distinct clades and did not find the species paraphyly observed in previous phylogenetic analyses that were restricted to mitochondrial loci (Lynch Alfaro et al., 2015; Ruiz Garcia et al., 2015). *Saimiri boliviensis* was recovered as sister to *S. vanzolinii*, in the Roman clade, matching the species grouping proposed by Hershkovitz (1984) based on morphology and behavior. The first species occurs from Bolivia to northwestern Brazil in the states of Acre and Amazonas, and the second is endemic to the Reserva de Desenvolvimento Sustentável Mamirauá, located in the Solimões-Japurá interfluvium, in Amazonas state, Brazil. Our study and the morphological assessment (Mercês et al., in preparation) are discordant with previous mitochondrial phylogenetic analyses in which *S. vanzolinii* was retrieved as

sister to *S. ustus* (Lynch Alfaro et al., 2015), or as sister to *S. collinsi* (Ruiz Garcia et al., 2015). Lynch Alfaro et al. (2015) considered that the Roman morphology of *S. vanzolinii* was a convergence, as the species did not group with the other Roman species (*S. b. boliviensis* and *S. b. peruviensis*). The incongruence between nuclear and mitochondrial signals could be evidence of incomplete lineage sorting and/or past or present introgression and/or sex-biased dispersal, as seen in other recent rapid primate diversifications, such as the macaque radiation (Tosi et al., 2003) and the baboon radiation (Rogers et al., 2019; Zinner et al., 2009).

The second major clade (Gothic) of squirrel monkeys is widespread in Amazon Basin and all species presented a more similar morphology, with the exception of the *S. ustus* clade, that can be easily be differentiated by the absence of tufted in the ears. The bare-eared squirrel monkey (*Saimiri ustus*) was previously retrieved as a paraphyletic species (Lynch Alfaro et al., 2015), one lineage *S. ustus* A (correspond to our *S. ustus* 1) was retrieved as sister to Central American and Guianan squirrel monkeys, while the other *S. ustus* B (our *S. ustus* 2**)** lineage was sister to *S. collinsi* + *S. vanzolinii*, here we recovered these clades as reciprocally monophyletic. Our population structure analysis indicated a third population, here called as *S. ustus* 3. As we only had one sample of this population, we considered that further investigation with more samples is necessary to understand the distribution and genetic structure of this group. The monophyly of *S. ustus* 1 + *S. ustus* 2 corroborate the morphology shared among the species and geographical distribution, which collectively occurs from the right bank of the Purus River to the left bank of the Xingu River, including Rondonia state and the northwest of Mato Grosso state in Brazil (Fig. 8).

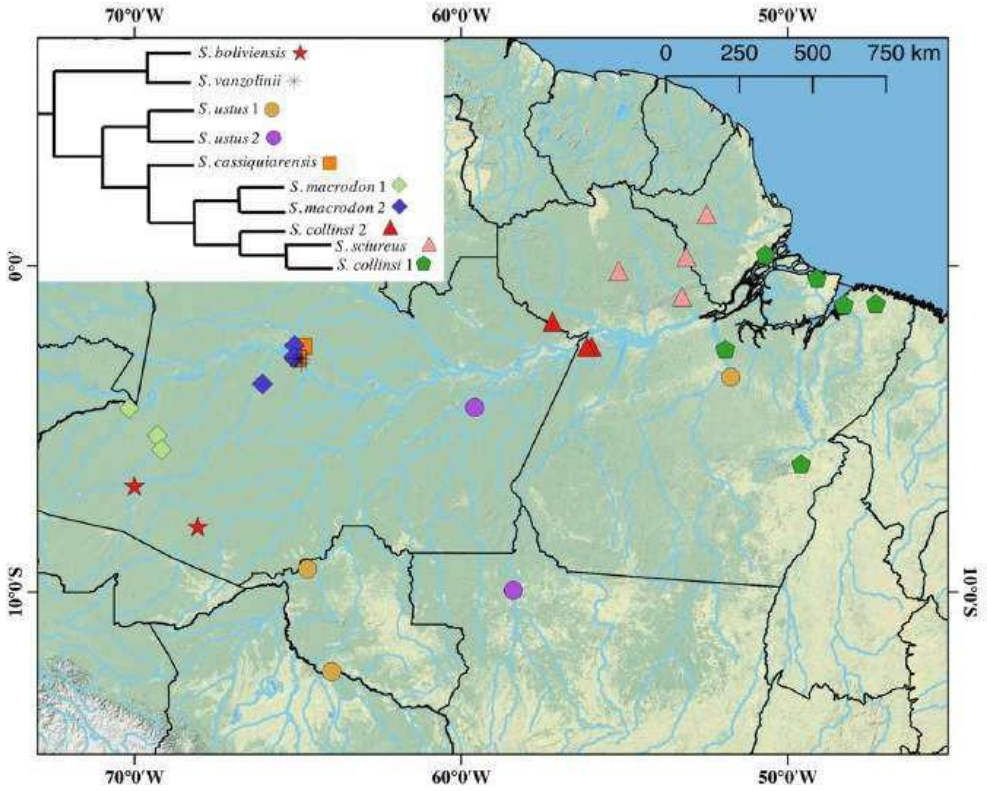

Fig. 8. Collecting localities of specimens included in molecular analyses, and corresponding clade structure found in the ddRadseq phylogeny, with taxon names associated with them (tree to the left).

Some authors considered tufted-eared squirrel monkeys as synonymous of *S. sciureus* (Thorington, 1985; Groves, 2005), due to their morphological resemblance. The monophyly of the tufted-eared squirrel monkeys recovered here agrees with their morphology, and in previous studies this group was paraphyletic (Lavergne et al., 2010; Lynch Alfaro et al., 2015; Ruiz Garcia et al., 2015). Elsewhere *S. cassiquiarensis* was recovered as closely related to *S. albigena* and *S. macrodon*, but our results here position *S. cassiquiarensis* as sister to *S. macrodon* lineage + *S. sciureus* lineage. Our Bayesian cluster analyses revealed evidence for admixture between *S. cassiquiarensis* and *S. macrodon*, which may help clarify previously phylogenetic relationships. As Lynch Alfaro et al. (2015) that recovered *S. cassiquiarensis* as sister to *S. macrodon* B, a clade that was distributed in Inambari center of endemism. We did not sample *S. albigena* in this study.

Paim et al. (2013) observed that three species of *Saimiri* occur within Reserva de Desenvolvimento Sustentável Mamirauá (RDSM), one of which they identified as *S. sciureus macrodon* (*sensu* Hershkovitz, 1984). Though *S. macrodon* morphology at RDSM differs from the specimens from Ecuador, Colombia and adjacent areas in Brazil, they referred to this different phenotype in Mamirauá Reserve as *Saimiri sciureus macrodon* 2 (Paim et al., 2013). One of the *S. macrodon* lineages in our phylogeny corresponds to the specimens from Mamirauá and adjacent areas. Costello et al. (1993) considered this phenotype to be a result of hybridization between *S. madeirae* (= *S. ustus*) and other *Saimiri* species. However, our Bayesian cluster analyses do not reveal evidence for hybridization between those two species. *Saimiri macrodon* 1 occurs in the west of Brazilian Amazon and *S. macrodon* 2 occurs in the Solimões-Japurá interfluvium, with some specimen in the both banks of lower Juruá River.

The Eastern Amazonian *S. sciureus* clade, which includes *S. sciureus* and *S. collinsi* 1 as sister taxa, as well as a third clade that we provisionally refer to as *S. collinsi* 2. In four phylogenetic studies with mitochondrial loci (Lavergne et al., 2010; Lynch Alfaro et al., 2015; Mercês et al., 2015; Ruiz Garcia et al., 2015), *S. sciureus* and *S. collinsi* never appeared as sister taxa, rather *Saimiri sciureus* was always retrieved as sister to *S. oerstedii* (Boinski and Cropp, 1999; Cropp and Boinski, 2000; Lavergne et al., 2010; Chiou et al., 2011; Springer et al., 2012; Lynch Alfaro et al., 2015; Mercês et al., 2015; Ruiz Garcia et al., 2015). However, these results may not reflect the relationship among *S. sciureus* and *S. oerstedii*. As we did not have access to samples of *S. oerstedii*, our results do not take into account the whole diversification history of *Saimiri*, so further investigation is necessary to elucidate the position of *S. oerstedii* in a genome-wide *Saimiri* tree. In terms of the lineage '*S. collinsi* 2', the specimens in this clade are all found quite near to the Amazon River. Mercês et al. (2015) had already identified through morphological and mitochondrial loci analyses that the specimens from

this region represent a complex evolutionary situation. Specimens that had the morphology and haplotypes of *S. collinsi* were found on the "wrong" side of the Amazon River and vice versa. *Saimiri collinsi* 2 was retrieved in their phylogeny as sister to *S. collinsi* 1, while in the present study *S. collinsi* 2 was recovered as sister to *S. collinsi* 1 + *S. sciureus*. Mercês et al. (2015) argued that this region presented unique water dynamics that might facilitate the crossing or passive transport of primates. Further field studies and sampling across the distribution is required to access the relationship between these lineages.

Our BEAST analysis estimated the age for diversification of modern squirrel monkeys at ~1.74 Ma. This is comparable to previous studies, that estimated divergence age in the crown of *Saimiri* at 1.75 Ma (95% HPD = 1.06-2.88) using 69 nuclear and ten mitochondrial loci (Springer et al., 2012), at 1.5 Ma (95% HPD = 1.12-190) using a BEAST analysis with mitogenomic data (Chiou et al., 2011) and at 1.36 (95% HPD = 1.1-1.91) using mitochondrial loci (Lynch Alfaro et al., 2015). In other words, the diversification within *Saimiri* genus occurred during the Pleistocene, which was confirmed by other genetic studies with squirrel monkeys. The speciation of squirrel monkeys is more recent than other Neotropical primates, including titi monkeys (Byrne et al., 2016) and gracile capuchin monkeys (Boubli et al., 2012). Even the sister species of *Cebuella* (Boubli et al., 2018) present an older divergence (2.24, 95% HPD = 1.70-2.96), around the Pliocene/Pleistocene boundary.

Considering the time frame diversification in squirrel monkeys, the Pleistocene climate changes seems to have played an important role in the intraspecific diversity within *Saimiri*. While in trumpeters (*Psophia*) the diversification happened before major glacial cycles (Ribas et al., 2012), for *Saimiri* most of the events for Gothic group occurred during the three major glacial maxima. The Pleistocene climate fluctuations promoted changes in the forest structure and composition (Wang et al., 2017). These changes might have affected *Saimiri* diversification, due to its ecological requirements. Paim et al. (2018) had already observed that differences among habitats are related to differences in habitat use of *Saimiri.* These changes in forest structure might have been one of the drivers to *Saimiri* diversification.

4. CONCLUSION

The genome-wide data generated with ddRADseq data matrices represents a massive increase compared to previous phylogenies multilocus-based published. Our data was one of largest molecular datasets generated for New World monkeys, and the largest for squirrel monkeys (*Saimiri*).

Our phylogenomic data provide strong support for two major clades within *Saimiri,* the Gothic and Roman species groups. This is concordant with mitogenomic data (Chiou et al., 2011) and nuclear genes (Springer et al., 2012). In our BEAST analysis, the median estimated age for the *Saimiri* crown

was similar to studies with mitogenomic and nuclear evidence, well within the Pleistocene epoch (Chiou et al., 2011; Springer et al., 2012).

Altogether, our phylogeny based in genome-wide ddRADseq data was not congruent with mitochondrial loci phylogenies (Lavergne et al., 2010; Lynch Alfaro et al., 2015; Ruiz Garcia et al., 2015). Our ddRAD phylogeny distinguished 10 lineages, the Roman group with two (*S. boliviensis* and *S. vanzolinii*) and the Gothic group with eight (*S. cassiquiarensis, S. macrodon* 1, *S. macrodon* 2, *S. ustus* 1, *S. ustus* 2, *S. sciureus*, *S. collinsi* 1 and *S. collinsi* 2). Our results provided new information of the relationship among *Saimiri*, and suggested gene flow between species that needs further investigation. The Bayesian structure analyses recovered a third group in *S. ustus* clade and did not separate *S. collinsi* 2 and *S. sciureus*, which highlights the necessity of increasing the sampling in several areas of Amazon.

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Capítulo 2

How many squirrel monkey (*Saimiri* Voigt, 1831) species are there? A morphological diagnosis and refined mapping of geographical distribution

O Capítulo 2 desta tese foi elaborado e formatado conforme normas de publicação científica da Zoological Journal of Linnean Society as quais se encontram no Anexo 2.

Title Page

How many squirrel monkey (*Saimiri* Voigt, 1831) species are there? A morphological diagnosis and refined mapping of geographical distribution

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Running title: Diversity and distribution in *Saimiri*

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ABSTRACT

Squirrel monkeys (*Saimiri*) occur in the Amazonian rainforest in South America and in the Central American coastal lowlands. There is no consensus for the taxonomy and evolutionary relationships within this group, with some morphospecies recovered as non-monophyletic in genetic studies. Using a multidisciplinary approach (morphology, morphometry, and phylogenomics) the aim of this work is to clarify the taxonomy of *Saimiri*. We examined 887 squirrel monkey specimens, including 18 type specimens, housed in scientific collections. We verified the congruence between our morphological, and cranio-dental measurements with the phylogeny. Our results provided evidence supporting the recognition of thirteen species (*Saimiri sciureus*, *S. cassiquiarensis*, *S. albigena*, *S. oerstedii*, *S. citrinellus*, *S. macrodon*, *Saimiri* sp.n., *S. madeirae*, *S. ustus*, *S. collinsi*, *S. vanzolinii*, *S. boliviensis* and *S. peruviensis*). We provide information on the type material, type locality, emended diagnosis, comparison among the species, information about geographic distribution, remarks for each taxon conservation status and specimens examined. We elevate three taxa to the species category, revalidate one species, designate a neotype for *S. cassiquiarensis* and identify a new species.
Keywords: Diversity – neotropical primates – taxonomy – Cebidae

INTRODUCTION

According to Hershkovitz (1984) the squirrel monkeys (genus *Saimiri* Voigt, 1831) are small primates (650-1200g) within Cebidae, found throughout the Amazon Basin and in a disjunct distribution in Central America (Costa Rica and Panama). In Amazonia squirrel monkeys are found north and south

of the Amazonas River and in the following countries: Bolivia, Peru, Ecuador, Colombia, Brazil, Venezuela, Guyana, French Guiana and Suriname (Hershkovitz, 1984).

The first three names associated with squirrel monkeys were described by Linnaeus (1758) in the genus *Simia*. Not all subsequent species have been described in these genera (*Simia*, *Cebus*, *Callithrix*, *Chrysothryx*, *Saimiris*). According to Cabrera (1958) the most recent ones have been described in the current genus, *Saimiri*. Voigt (1831) proposed the genus *Saimiri* with *Simia sciurea* Linnaeus, 1758 as type-species. Groves (2001) revealed that this type was actually a *Saimiri boliviensis* specimen but did not propose any changes to resolve this issue.

The number of *Saimiri* taxa increased considerably during the XXth century, reaching up to 26 taxa. Many of these were described based on individual or sexual variation and now most of them are synonyms (e. g. Lönnberg, 1940). Elliot (1913) reviewed all the taxa published until that time as part of *Saimiri* and concluded that the following were valid species: *Saimiri boliviensis, S. cassiquiarensis, S. macrodon, S. madeirae, S. oerstedii, S. ustus*, and *S. sciureus*. Cabrera (1958) listed six taxa, but all as subspecies of *Saimiri sciureus.* Hill (1960) recognized five species (*S. boliviensis, S. madeirae, S. oerstedii, S. sciureus* and *S. ustus*) with 11 subspecies.

Hershkovitz (1984) published a taxonomic arrangement for *Saimiri*. In this article, he described a new subspecies, *Saimiri boliviensis peruviensis* and considered four species valid with a total of nine subspecies. One year later, Thorington (1985) published another taxonomic review recognizing five squirrel monkey taxa, including two species and five subspecies (Table 1). These two reviews differ in the taxonomic status and species groups under which each taxon was kept. Thorington (1985) is one of the few authors that considered *S. madeirae* as a valid species. Ayres (1985) named a newly discovered species *Saimiri vanzolinii*. Subsequently, Hershkovitz (1987a) recognized more three subspecies of *S. boliviensis* (*S. b. pluvialis*, *S. b. jaburuensis* and *S. b. vanzolinii*). The taxonomic arrangement proposed by Hershkovitz (1984, 1987a) was widely followed by subsequent authors over the next 17 years. Groves (2001) kept almost the same arrangement as Hershkovitz (1984, 1987a), only changing the status of *S. vanzolinii* from subspecies of *S. boliviensis* to species, and regarding *S. b. pluvialis* and *S. b. jaburuensis* as synonyms of *S. boliviensis*. Meanwhile, Groves (2005) only considered valid five species with no subspecies. There has been some research on the validity of *S. vanzolinii* (Groves, 2001; Silva-Júnior & Queiroz, 2008) and *S. oerstedii* (Boinski & Cropp 1999; Cropp & Boinski, 2000; Groves, 2001, 2005; Rylands *et al*., 2006), with general agreement that both species are valid.

Rylands *et al*. (2013) updated the status of some species, elevating *S. cassiquiarensis* and *S. macrodon* to species level, and revalidating *S. ustus collinsi*, as proposed by Lavergne *et al*. (2010), but as a subspecies of *S. sciureus*. Lavergne *et al*. (2010) considered that the subspecies *S. s. albigena, S. s. cassiquiarensis*, and *S. s. macrodon* should be reallocated to *S. ustus* (*S. u. albigena*, *S. u.*

cassiquiarensis, *S. u. collinsi* and *S. u. macrodon*). Chiou *et al*. (2011) argued that Lavergne *et al*. (2010) had incorrectly reallocated these species because according to the Priority Principle (Article 23) of the International Code of Zoological Nomenclature (ICZN), *Simia sciurea cassiquiarensis* Lesson, 1840 has priority over *Saimiri ustus* I. Geoffroy, 1843. Rylands *et al*. (2013) also considered results from Lavergne *et al*. (2010) and data from Carretero-Pinzon *et al*. (2009) to reallocate *S. s. albigena* as a subspecies of *S. cassiquiarensis*.

Table 1. Taxonomic arrangements proposed by three authors who reviewed the *Saimiri* genus, including the most recent compilation (Rylands *et al*., 2013).

Hershkovitz (1984, 1987a)	**Thorington (1985)**	**Groves (2005)**	**Rylands *et al*. (2013)**
Roman group			
Saimiri boliviensis boliviensis	*Saimiri sciureus boliviensis*	*Saimiri boliviensis*	*Saimiri boliviensis boliviensis*
Saimiri boliviensis peruviensis			*Saimiri boliviensis peruviensis*
Saimiri boliviensis vanzolinii		*Saimiri vanzolinii*	*Saimiri vanzolinii*
Saimiri boliviensis jaburuensis			
Saimiri boliviensis pluvialis			
Gothic group			
Saimiri sciureus sciureus	*Saimiri sciureus sciureus*	*Saimiri sciureus*	*Saimiri sciureus sciureus*
			Saimiri sciureus collinsi
Saimiri sciureus macrodon			*Saimiri macrodon*
Saimiri sciureus cassiquiarensis	*Saimiri sciureus cassiquiarensis*		*Saimiri cassiquiarensis cassiquiarensis*
Saimiri sciureus albigena			*Saimiri cassiquiarensis albigena*
Saimiri oerstedii citrinellus			*Saimiri oerstedii citrinellus*
Saimiri oerstedii oerstedii	*Saimiri sciureus oerstedii*	*Saimiri oerstedii*	*Saimiri oerstedii oerstedii*
Saimiri ustus		*Saimiri ustus*	*Saimiri ustus*
	Saimiri madeirae		

Mercês *et al*. (2015), using a multi-pronged approach with morphological, cranio-dental metric and mitochondrial genetic evidence, were able to confirm the divergence between *S. sciureus* and *S. collinsi* and updated the species' distribution, taxonomic status and morphological differences. In molecular phylogenetic studies based on mitochondrial DNA, neither of the two species, *S. ustus* or *S. macrodon*, were recovered as monophyletic clades (Lynch Alfaro *et al*., 2015; Ruiz-Garcia *et al*., 2015). Lynch Alfaro *et al*. (2015) argued that further research was necessary with more data, including nuclear DNA, for a better understanding of *Saimiri* lineages. Ruiz Garcia *et al*. (2015), utilizing the biological species concept, proposed a new classification that recognized only three squirrel monkey species (*S. oerstedii*, *S. vanzolinii* and *S. sciureus*).

It is clear that the identification and delimitation of species and subspecies are serious issues for *Saimiri* systematics and that species relationships have not been resolved despite new molecular studies. In order to clarify *Saimiri* taxonomy, our goals are: (1) to characterize and define each taxon using morphology, morphometry and phylogenomic data, and to describe individual and sexual variation within each taxon; (2) to define species geographical distribution; and (3) to provide a synonymy and identify valid names for the recognized taxa.

METHODS

Samples and collections

We obtained quantitative and qualitative morphological data from skins and skulls of *Saimiri* specimens (n= 887) housed in the following collections: American Museum of Natural History, New York, USA (AMNH), Field Museum of Natural History, Chicago, USA (FMNH), Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Macapá, Brazil (IEPA), Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, Brazil (IDSM), Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MN), Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG), Museu de Zoologia José Hidasi, Porto Nacional, Brazil (MZJH), Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), and Natural History Museum of Los Angeles County, Los Angeles, USA (LACM). We also examined photographs from specimens deposited in Naturhistoriska Riksmuseet, Stockholm, Sweden (NRM), Muséum National D'Histoire Naturelle, Paris, France (MNHN), Natural History Museum of Denmark, Denmark (ZMUC), Natural History Museum of London, London, United Kingdom (BMNH), and Zoologisches Museum Berlin (= Museum für Naturkunde – ZMB), Berlin, Germany. A list of analyzed specimens is provided within each species description.

Geographic data

The geographic records (Figure 1) confirm that *Saimiri* occurs in the Amazon basin (Bolivia, Peru, Ecuador, Colombia, Brazil, Venezuela, Guyana, French Guiana and Suriname) as well as in Central America (Costa Rica and Panama). A total of 314 localities were represented by the examined specimens. Geographic distribution data for each taxon were assessed utilizing the collection locations obtained from specimen labels. Coordinates were obtained directly from the labels and from published gazetteers (Hershkovitz, 1984, 1987a, 1987b; Paynter Jr., 1982, 1992; Stephens & Traylor Jr., 1983; Stephens *et al*., 1985; Paynter Jr. & Traylor Jr., 1991; Paynter Jr. *et al*., 1997) or online databases (Global gazetteer 2.3; Geonames). In some cases, the exact locality was not available or not found in the methodologies employed, so we used the coordinates of the nearest county.

Figure 1. Localities (dots) of the *Saimiri* specimens examined in this study.

Morphological and morphometric analyses

All specimens were analyzed qualitatively and quantitatively for external and cranial features regardless of the previous attributed name of the taxon. We analyzed 13 qualitative traits, based on previous studies (Hershkovitz, 1984; Paim *et al*., 2013; Mercês *et al*., 2015): 1. Tuft in the ears; 2. Arch format; 3. Hair color in the central crown area; 4. Hair coloration on the nape of the neck; 5. Hair coloration in the shoulders; 6. Hair coloration in the back; 7. Coloration of the forearms; 8. Coloration of the hands; 9. Coloration of the shin; 10. Coloration of the feet; 11. Chest coloration; 12. Pre-auricular patch (sideburns – females); 13. Tail pencil. The traits were grouped through the congruence among each trait, after that we verified the existence of geographical patterns.

For quantitative characters we obtained 11 measurements from cranial and dental features, following Thorington (1985), Paim *et al*. (2013) and Mercês *et al*. (2015) using the nomenclature from Hershkovitz (1977): Braincase width (BW); zygomatic width (ZIG); canine length (CAL); width across upper canines (AUC); length of the upper molar series (UML); basion vertex distance (BVD); total length (TL) – greatest length of skull; palate width (PW); across upper molars (AUM); mandibular length (ML); length of the lower molar series (LLM). Measurements were taken with digital calipers to the nearest 0.01 mm, always on the right side of the cranium, unless there was damage in that region. We used only young adults and adults in our analyses. We considered young adults to be those specimens in which the third molars or canines have not completely emerged, and adults those with completed permanent dentition, following the classification by Thorington (1985). The Kolmogorov-Smirnov test was applied to all craniodental variables. As *Saimiri* shows sexual dimorphism (Hershkovitz, 1984; Muniz, 2005), we performed Hotelling T^2 test to check which variables were sexual dimorphic. After these results, we decided to run the Discriminant Function Analysis separated by sex.

The Discriminant Function Analysis (DFA) tries to assess how much it is possible to separate two or more groups of individuals (Manly, 2008). We performed DFA to investigate if the clades retrieved through a molecular phylogenomic analysis of *Saimiri* (Mercês *et al*., in preparation), could be distinguished based on craniodental morphometry. We tested for craniodental distinction between the Roman vs. Gothic arched groups, a defining morphological axis of variation within the genus. We also analyzed data for the species that were not included in our phylogenomic tree (*S. boliviensis peruviensis, S. oerstedii, S. albigena*), to test the degree of their craniodental differentiation from the other morphospecies. All statistical analyses were performed with Statistica 13 software.

Phylogenomic analyses

In our phylogenomic study (Mercês *et al*., in preparation) we sampled genomes from all Brazilian Amazon squirrel monkey taxa. For the other taxa (*S. b. peruviensis, S. c. albigena, S. o. oerstedii* and *S. o. citrinellus*), we did not have access to genetic material, so we utilized information available in the literature (Carretero-Pinzon *et al*., 2009; Chiou *et al*., 2011; Blair & Melnick, 2012; Perelman *et al*., 2012; Springer *et al*., 2012; Blair *et al*., 2013; Lynch Alfaro *et al*., 2015; Ruiz Garcia *et al*., 2015).

A total of 50 samples of *Saimiri* were collected, this included 44 fresh muscle from museum voucher specimens (Table 2), and blood extractions from 6 live individuals in the field. *Sapajus robustus* was included as outgroup. Details of the capture of live specimens are provided in Paim & Rabelo (2015). We utilize the *double digest* restriction site-associated DNA sequencing (ddRADseq).

Details of DNA extraction, library preparation for ddRADseq, sequencing, quality control check and phylogenetic analyses are available in Mercês *et al*. (in preparation). Here we presented the maximum likelihood tree to support our morphological data.

Table 2. List of samples, locality data and voucher number of the genomic specimens from Mercês *et al*. in preparation.

Species	**Locality**	**Latitude**	**Longitude**	**Voucher number**
Saimiri boliviensis	Brazil, Amazonas, Eirunepé	-6.77	-70.01	FES056
Saimiri boliviensis	Brazil, Amazonas, National Forest of Purus	-8.02	-68.07	RS050
Saimiri cassiquiarensis	Brazil, Amazonas, Maraã	-2.46	-64.82	LB719, LB735, LB738
Saimiri cassiquiarensis	Brazil, Amazonas, Jarauá	-2.83	-64.99	SC4.2, SC 4.4
Saimiri collinsi	Brazil, Pará, Senador José Porfírio	-2.58	-51.92	LB463, LB459, LB389
Saimiri collinsi	Brazil, Pará, Santa Barbara do Pará	-1.21	-48.29	MIC01
Saimiri collinsi	Brazil, Pará, Ilha de São Geraldo	-0.40	-49.11	MAR05, MAR04
Saimiri collinsi	Brazil, Pará, Curionópolis	-6.10	-49.60	LB603
Saimiri collinsi	Brazil, Pará, Peixe-Boi	-1.18	-47.31	AF4
Saimiri collinsi	Brazil, Amapá, Itaubal	0.32	-50.69	LB561, LB560
Saimiri collinsi	Brazil, Pará, Juruti	-2.48	-56.16	LB806
Saimiri collinsi	Belém, Pará, Juruti, acampamento Barroso	-2.47	-56.01	LB796, LB798, LB801
Saimiri collinsi	Brazil, Pará, Faro	-1.71	-57.21	CN30, CN15
Saimiri macrodon	Brazil, Amazonas, Jutaí, comunidade Pirarucu	-5.63	-69.18	RDSC30, RDSC47
Saimiri macrodon	Brazil, Amazonas, Uarini	-2.44	-65.11	LB791, LB762
Saimiri sp. n.	Brazil, Amazonas, Juruá	-3.62	-66.09	BJ002
Saimiri sp. n.	Brazil, Amazonas, Jarauá	-2.82	-65.14	SM9.2
Saimiri sp. n.	Brazil, Amazonas, Horizonte	-2.79	-65.13	SV15.1
Saimiri sciureus	Brazil, Amapá, Iratapuru River	0.28	-53.11	AP124, AP104
Saimiri sciureus	Brazil, Pará, Almeirim	-0.94	-53.24	CN276, CN243
Saimiri sciureus	Brazil, Pará, Alenquer	-0.16	-55.18	CN297
Saimiri sciureus	Brazil, Amapá, Tumucumaque	1.59	-52.49	AP221
Saimiri madeirae	Brazil, Amazonas, Borba	-4.34	-59.59	L556
Saimiri madeirae	Brazil, Mato Grosso, Contriguaçu	-9.95	-58.41	MSN147, MSN145
Saimiri ustus	Brazil, Rondonia, São Francisco do Guaporé	-12.44	-63.97	RGB02
Saimiri ustus	Brazil, Rondonia, Porto Velho	-9.29	-64.71	JIR9791
Saimiri ustus	Brazil, Pará, Vitória do Xingu	-3.41	-51.75	LB468
Saimiri vanzolinii	Brazil, Amazonas, Uarini	-2.97	-64.91	LB727
Saimiri vanzolinii	Brazil, Amazonas, Jarauá	-2.86	-64.92	SV6.2
Saimiri vanzolinii	Brazil, Amazonas, Jarauá	-2.83	-65.02	SV1.4
Sapajus robustus	-			robustus

Criteria used for the recognition of *Saimiri* species

In the present study, the *Saimiri* species were recognized based on the Phylogenetic Species Concept (PSC). According to Cracraft (1983, 1989) and Aleixo (2007), PSC defines species as "the smallest diagnostic group of individuals where there is a pattern of ancestry and offspring, which together become basal diagnostic units". Aleixo (2007) observed that, in a pragmatic perspective, "if two groups of individuals can be diagnosed from one another by any characters or even a single character, they should be treated as distinct species, since reciprocal diagnosis can only have been acquired through independent evolutionary histories, reflected in a phylogeny across distinct terminal branches". Thus, differentiated and evolutionarily independent, but closely related, populations should be considered as full species (Aleixo 2007, 2009).

The results of the present study were obtained from four sources of biological information, each containing a set of characters. Our study considers previous mtDNA evidence (Lynch Alfaro *et al.*, 2015), along with new genomic data (Mercês *et al*., in preparation), external morphology, and cranio-dental morphometry. The criterion used here for the recognition of the *Saimiri* species was the congruence of the results obtained between at least two of these sources.

RESULTS AND DISCUSSION

External morphology

We observed two main morphological groups, the Roman arch group and the Gothic arch group, corroborating results from Hershkovitz (1984), Boinski & Cropp (1999) and Chiou *et al*. (2011). The Roman group presents a forehead with the same coloration as the crown, with the arch above the eyes with roman shape, and the tail pencil is thin. It includes three species: *Saimiri vanzolinii*, *S. boliviensis* and *S. peruviensis*. We divided the Gothic group in two morphological and geographical groups, the gothic arch and the more acute gothic arch, both present bushy tail pencils. The first can be recognized by a whitish arch band over the eyes and occurs in Amazon. In the second, the arch band over the eyes is more pronounced and progresses higher onto the forehead and occurs in Central America. We also separated the Gothic group in bare-eared squirrel monkeys (compromises two morphospecies *S. ustus* and *S. madeirae*) and tufted-eared squirrel monkeys (compromises *S. albigena*, *S. cassiquiarensis*, *S. macrodon*, *Saimiri* sp.n., *S. collinsi* and *S. sciureus*).

Each of the morpho groups recognized can be identified through a set of traits that we list on Table 3.

The trait that present the most intra and inter species variation among females was the preauricular patch. In *S. collinsi* and *S. sciureus* the darkening it is restricted to the sideburns and can present some blacking in the arch above the eyes and in the temporal area (vs. in males the crown of *S. collinsi* is entirely grayish with yellow and in *S. sciureus* is gray with little yellow, in both species

the sideburns is whitish). In the bare-eared species (*S. ustus* and *S. madeirae*), generally the pre-auricular patch it is much more evident and darker and can present a dark area around the crown, forming a ring (vs. in males in both species the pre-auricular patch is whitish and the crown is entirely bluish gray in *S. madeirae* and bluish-orange in *S. ustus*). Females of *Saimiri citrinellus* also present this darkening in the arch and in sideburns, while males present agouti grayish crown. In *Saimiri oerstedii* it is possible to observe the black sideburns, as a continuous darkening from the crown to the sideburns, while in males the sideburns is whitish. For details of the differences between species see Species Account.

Table 3. Summarizes the main diagnostic traits in external morphology between the species of *Saimiri*.

Species	TRAITS												
	Hair tufts on the ears	**Arch format**	**Hair color on central crown**	**Hair color on the nape of the neck**	**Hair color on the shoulders**	**Hair color on the back**	**Color of the forearms**	**Color of the hands**	**Color of the shin**	**Color of the feet**	**Chest color**	**Pre-auricular patch (females)**	**Tail pencil**
Saimiri vanzolinii	Present	Roman	Blackish	Blackish	Grayish	Blackish	Golden-yellow	Golden-yellow	Dark gray	Golden-yellow	Burnt yellow	Present	Thin
Saimiri boliviensis	Present	Roman	Blackish	Blackish	Yellowish	Grayish with yellow	Golden-yellow	Golden-yellow	Yellowish	Golden-yellow	Yellowish	Present	Thin
Saimiri peruviensis	Present	Roman	Agouti	Agouti	Grayish	Dark chestnut	Golden-yellow	Golden-yellow	Grayish	Golden-yellow	Yellowish	Present	Thin
Saimiri sciureus	Present	Gothic	Gray with little yellow	Gray with little yellow	Grayish	Reddish chestnut	Bright yellow	Bright yellow	Grayish	Bright yellow	Whitish	Present	Bushy
Saimiri cassiquiarensis	Present	Gothic	Yellowish (tawny)	Yellowish/Whitish	Grayish	Brighter reddish	Orange	Orange	Grizzled gray	Orange	Whitish	Present	Bushy
Saimiri albigena	Present	Gothic	Grayish	Grayish	Grayish	Chestnut	Grizzled gray	Grizzled gray	Grayish	Grizzled gray	Whitish	Present	Bushy
Saimiri oerstedii	Present	Acute Gothic	Blackish	Orange	Yellowish	Orange	Orange	Orange	Yellowish	Orange	Orangish	Present	Bushy
Saimiri citrinellus	Present	Acute Gothic	Agouti Grayish	Bright orange	Grayish	Orange	Grayish	Orange	Grayish	Grizzled gray	Whitish	Present	Bushy
Saimiri macrodon	Present	Gothic	Grayish olivaceous	Grayish olivaceous	Grayish	Chestnut with orange	Yellowy orange	Yellowy orange	Grayish	Yellowy orange	Whitish	Present	Bushy
Saimiri sp. n.	Present	Gothic	Grayish	Grayish	Grayish	Grizzled -gray speckled with yellow	Grizzled gray	Grizzled gray	Grizzled gray	Grizzled gray	Whitish	Present	Bushy
Saimiri madeirae	Absent	Gothic	Bluish-gray	Orange speckled with black	Grayish	Orange speckled with black	Grayish	Orange	Grayish	Orange	Whitish	Present	Bushy
Saimiri ustus	Absent	Gothic	Bluish-orange	Orange	Grayish	Golden speckled with black	Burnt yellow-orange	Burnt yellow-orange	Grayish	Burnt yellow-orange	Whitish	Present	Bushy
Saimiri collinsi	Present	Gothic	Grayish with yellow	Grayish with yellow	Grayish	Chestnut	Dark tawny	Dark tawny	Grayish	Dark tawny	Whitish	Present	Bushy

Morphometrics

Statistical analyses were based on groups we recovered in morphological analyses. The descriptive statistics of the skulls (mean, standard deviation, minimum and maximum value and number of specimens per group) are available in Table 4. We tested each of the eleven variables for sexual dimorphism; seven presented sexual dimorphism (ZIG, CAL, AUC, BVD, TL, ML AND LLM). For DFA we included only those specimens for which both skull and skin were available, in order to test if the pelage morpho groups also separate in cranial morpho space.

We also separated the DFA into two different data sets, one that included all the groups retrieved from our morphological analyses and another that only included the groups for which we had phylogenomic data (Mercês *et al*., in preparation). *Saimiri citrinellus, S. vanzolinii* (for both male and female datasets), and *S. albigena* (for female data set) could not be analyzed statistically, due to the low number of specimens available.

A total of 188 male specimens were included in the morphology group data set, and 10 morphospecies were analyzed (*S. boliviensis, S. peruviensis, S. cassiquiarensis, S. albigena, S. collinsi, S. macrodon, S. sciureus, S. oerstedii, S. ustus* and *S. madeirae*). Ten of the twelve variables had statistical significance in the separation of all species analyzed (Wilk's Lambda = 0.20, $p<0.05$). The first function was responsible for 35.39% of the total variance, explained by the variables total length (TL), zygomatic breadth (ZIG) and mandibular length (ML) (Figure 2). The second function was responsible for 28.63% of the total variance, explained by the variables basion-vertex distance (BVD), braincase width (BW) and across upper molars (AUM).

For females 129 specimens were analyzed included five morphospecies (*S. collinsi, S. macrodon, S. madeirae, S. ustus* and *S. sciureus*). Seven (BW, ZIG, AUC, TL, PW, AUM, ALC) of the twelve variables had statistical significance in the separation of the morphospecies (Wilk's Lambda = 0.14; $p<0.05$). The first function was responsible for 50.35% of the total variance, explained by the variables TL, ZIG and BW. The second function was responsible for 27.5% of the variance, explained by ALC, PW and AUC. DFA for female *Saimiri* is found in Figures S1, S2, S3 and S4 in the Supplementary Material.

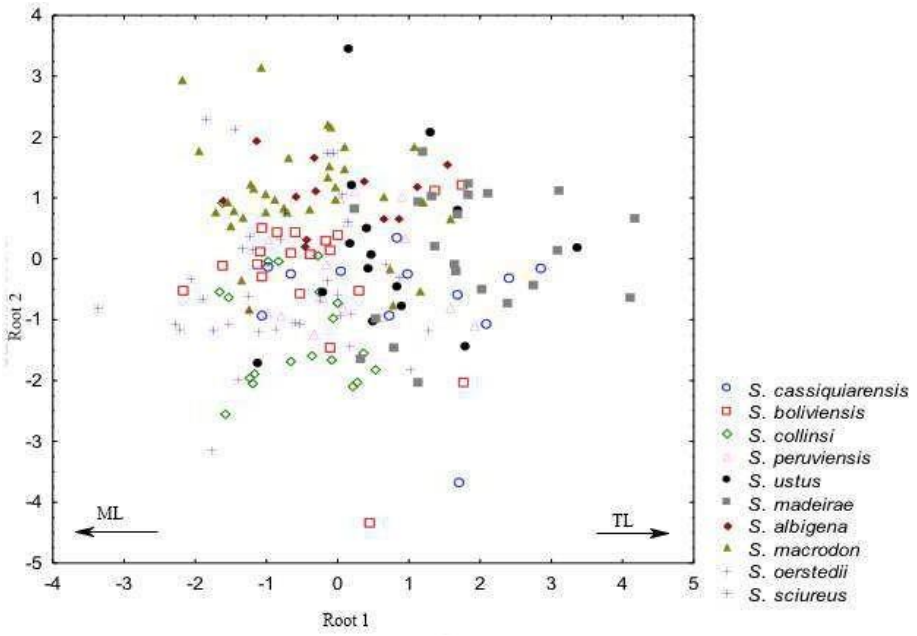

Figure 2. Discriminant function analyses of male for cranio-dental measurements for *Saimiri* based on phylogenomic and morphospecies groups.

Roman vs Gothic arch groups

We tested the separation in cranio-dental measurements between Roman and Gothic squirrel monkeys taxa using discriminant function analyses; the DFA showed statistical significance for separation of Roman and Gothic species, in both male and female analyses (Wilk's Lambda = 0.92; $p<0.05$, Figure 3). For males two variables were responsible for the separation of the two groups: braincase width (BW) and canine length (CAL) (Figure 3), while for females the two variables responsible for the separation were BW and zygomatic breadth (ZIG).

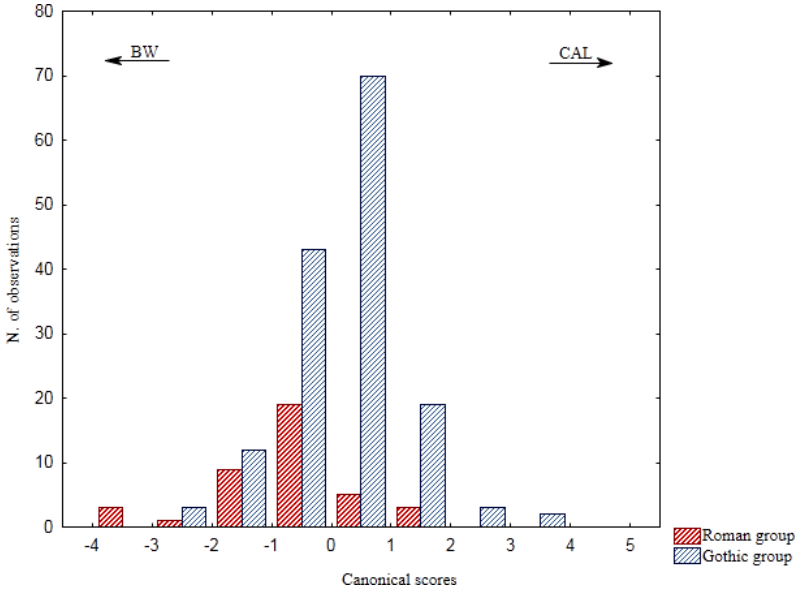

Figure 3. Discriminant function analyses for cranio-dental measurements for *Saimiri* males separated by gothic and roman group.

Gothic Group

Within the Gothic group, we tested for the differences in cranio-dental variables in the morphospecies based on phylogenomic clades recovered in Mercês *et al*. (in preparation). The first was the bare-eared squirrel monkeys, the morphospecies *S. ustus* and *S. madeirae*. While the results did not show a difference between *S. ustus* and *S. madeirae*, the p value bordered on significance (p=0.07). This non-significant result might be a result of low discriminatory power in the analysis due to the small number of specimens available for the analysis.

The second group compared was the tufted-eared squirrel monkeys clade including *Saimiri cassiquiarensis*, *S. macrodon* 1, *S. macrodon* 2, *S. sciureus*, *S. collinsi* and *S. oerstedii* (groups retrieved from phylogenomic data). We did not include *S. collinsi* 2 and S. *macrodon* 2, due to the low number of specimens available. Seven variables (BW, ZIG, BVD, TL, PW, AUM, ML) were responsible for the separation of the morphospecies of the clade in males (Figure 4). The variables basion-vertex distance (BVD) and palate width were (PW) responsible for 64% of the variance. For females the most important distinguishing variables were zygomatic breadth (ZIG) and palate width (PW).

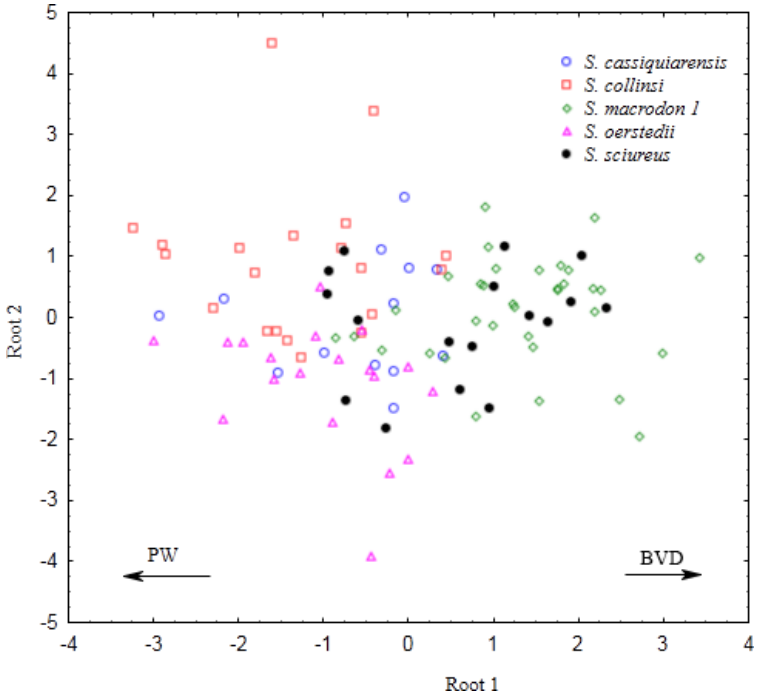

Figure 4. Discriminant function analyses for cranio-dental measurements of males for tufted-eared squirrel monkeys.

Roman Group

Within the Roman arch group, we were only able to test the cranio-dental differences between the two morphospecies *S. b. boliviensis* and S. *b. peruviensis*, due to the low number of specimens available for *S. vanzolinii*. The separation of *S. b. boliviensis* and *S. b. peruviensis* was statistically significant (Wilk's Lambda = 0.55; p<0.05, Figure 5). For males four variables were responsible for the separation of the morphospecies (BW, CAL, AUC, BVD). The two most important variables were

across upper canines (AUC) and braincase width (BW). For females the variable responsible for the separation was braincase width (BW).

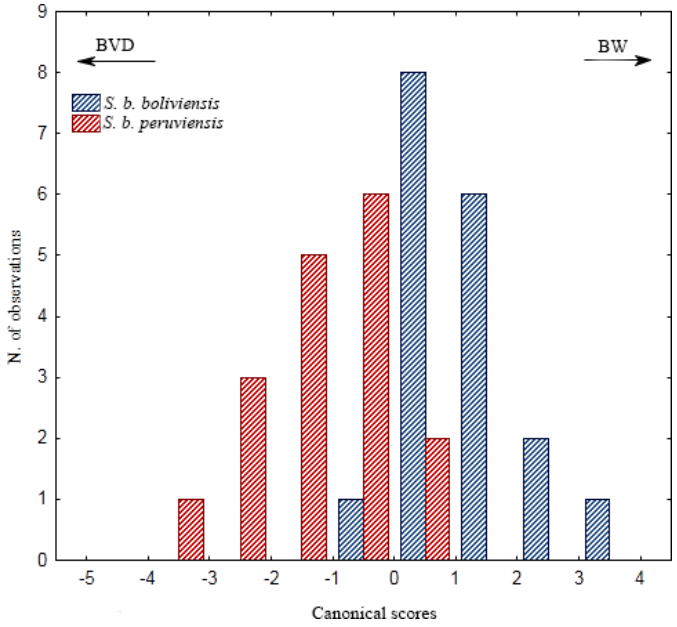

Figure 5. Discriminant function analyses for cranio-dental measurements for males of *S. b. boliviensis* and *S. b. peruviensis.*

Table 4. Cranial measurements (in millimeters) for the *Saimiri* species. SD = variable that present sexual dimorphism in test-t analysis.

Variables	*Saimiri albigena*		*Saimiri boliviensis*		*Saimiri cassiquiarensis*		*Saimiri citrinellus***		*Saimiri collinsi*		*Saimiri macrodon*		*Saimiri madeirae*		*Saimiri sciureus*		*Saimiri ustus***		*Saimiri oerstedii*		*Saimiri peruviensis*		*Saimiri vanzolinii*	
Sex	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
BW	35.60 ± 1.07	36.20 ± 1.36	35.78 ± 1.42	35.28 ± 1.04	34.64 ± 1.52	34.16 ± 1.73	34.60 ± 1.65	36.05	35.08* ± 1.34	34.38* ± 1.60	35.74 ± 1.55	35.19± 1.06	33.93 ± 1.19	33.78 ± 1.11	35.88 ± 1.43	35.86 ± 1.03	36.85 ± 0.96	37.12 ± 0.65	35.03 ± 1.05	34.81 ± 0.72	35.47 ± 1.28	35.26 ± 1.27	34.48 ± 0.67	35.06 ± 1.62
	32.94 - 37.47 (17)	34.01 - 37.76 (6)	33.07 - 38.91 (24)	33.28-38.46 (33)	31.17-37.12 (16)	31.65-36.78 (8)	33.62 - 36.52 (3)	36.05 (1)	32.88 - 38.09 (32)	31.34-38.15 (48)	33.02-38.62 (49)	33.27-36.95 (33)	31.91-36.31 (27)	32.09-36.52 (20)	32.15 - 38.68 (44)	33.48-37.77 (24)	35.41-38.65 (10)	36.37-37.57 (3)	32.78-36.83 (26)	33.69-35.66 (9)	33.28-38.61 (18)	33.32-38.75 (13)	33.8 - 35.4 (7)	33.3-36.5 (3)
ZIG (SD)	41.16 ± 2.58	37.41 ± 2.24	40.37 ± 2.63	37.25 ± 1.88	39.47 ± 2.55	35.86 ± 2.18	41.87 ± 2.53	36.93 ± 0.16	38.38 ± 1.75	34.72 ± 1.26	40.15± 2.60	37.37 ± 1.63	41.97 ± 1.77	37.39 ± 0.96	40.17 ± 2.81	36.11 ± 1.40	43.62 ± 0.91	39.11 ± 0.10	38.89 ± 2.98	36.32 ± 1.04	39.16 ± 2.68	36.78 ± 1.34	39.03 ± 1.95	35.3 ± 1.27
	36.77 -44.7 (13)	33.77 - 40.04 (7)	34.89 - 44.55 (23)	33.7-40.43 (33)	35.4-43.61 (16)	32.46-38.54 (10)	38.96 - 43.61 (3)	36.81-37.05 (2)	35.51 - 42.04 (32)	31.93-37.46 (36)	34.85-44.15 (40)	33.58-41.86 (32)	38.46-45.65 (26)	35.97-39.04 (21)	34.65 - 44.44 (41)	33.47-38.37 (21)	42.44-44.65 (7)	39.04-39.19 (2)	34.27-44.13 (23)	34.07-38.21 (11)	34.54-44.12 (17)	34.66-39.56 (13)	36.3 - 42.2 (7)	33.9-36.4 (3)
CAL (SD)	9.18 ± 0.75	5.68 ± 0.39	8.72 ± 1.30	5.58 ± 0.52	8.82 ± 0.76	5.62 ± 0.60	8.97 ± 0.14	5.61 ± 0.04	8.94 ± 0.85	5.22 ± 0.90	8.96 ± 0.94	5.84 ± 0.59	8.98 ± 0.91	5.75 ± 0.52	8.95 ± 0.88	5.42 ± 0.64	10.26 ± 0.78	5.60 ± 0.17	8.37 ± 1.01	5.62 ± 0.43	8.43 ± 1.07	5.29 ± 0.45	7.91 ± 1.5	4.06 ± 0.91
	7.62-10.39 (17)	5.14-6.37 (7)	4.93-11.52 (28)	4.68-6.38 (35)	7.74-10.54 (18)	4.6-7.03 (12)	8.87-9.07 (2)	5.58-5.65 (2)	7.51-10.81 (37)	3.02-7.1 (51)	6.28 - 11.1 (45)	4.71 - 7.52 (34)	7.03-11.18 (29)	4.86 - 7.06 (22)	7.14-10.62 (49)	3.21-6.33 (24)	9.18 - 11.83 (10)	5.47-5.84 (4)	5.22-10.45 (30)	4.0-6.35 (16)	5.68 - 9.98 (18)	4.6-6.39 (13)	4.3-9.9 (16)	2.5-4.7 (5)
AUC (SD)	18.28 ± 1.03	16.06 ±1.04	18.06 ± 1.14	15.50 ± 0.91	17.5 ± 1.25	15.25 ± 1.26	18.09 ± 0.71	14.41 ± 1.30	17.82 ± 0.89	14.72 ± 0.65	18.67 ± 1.05	16.17 ± 0.75	18.27 ± 0.94	15.67 ± 0.49	18.16 ± 1.09	15.45 ± 0.82	19.61 ± 0.60	16.49 ± 0.33	17.29 ± 0.74	15.33 ± 0.51	17.31 ±1.26	15.10 ± 0.76	-	-
	16.41 - 19.76 (17)	14.93 - 18.24 (7)	15.66 - 20.31 (25)	13.67-17.79 (34)	15.51-19.52 (19)	13.22-17.44 (12)	17.29 - 18.67 (3)	13.49-15.34 (2)	15.81 - 20.33 (38)	13.5-16.21 (50)	16.6 - 20.86 (46)	14.64-18.15 (34)	16.06-20.27 (30)	14.56-16.49 (22)	16.05 - 20.83 (49)	14.38-17.96 (25)	18.70-20.37 (8)	16.26-16.73 (2)	15.06-18.46 (30)	14.38-15.96 (14)	14.46-19.29 (18)	13.98-16.44 (12)	-	-
UML	12.50 ± 0.45	12.41 ± 0.32	12.12 ± 0.48	11.90 ± 0.44	11.88 ± 0.74	11.76 ± 0.58	12.03 ± 0.39	11.69 ± 0.36	11.96* ± 0.53	11.44* ± 0.56	12.52 ± 0.57	12.34 ± 0.40	12.16 ± 0.45	12.05 ± 0.37	12.24 ± 0.48	12.02 ± 0.48	12.68 ± 0.31	12.35 ± 0.62	11.55 ± 0.43	11.28 ± 0.48	11.66 ± 0.50	11.57 ± 0.48	-	-
	11.48 - 13.52 (17)	11.93 - 12.85 (7)	10.8-13.23 (27)	10.53-12.59 (35)	10.46-12.92 (19)	10.67-12.43 (9)	11.58 - 12.28 (3)	11.44-11.95 (2)	10.33 -12.8 (38)	10.22-12.9 (51)	11.43-14.02 (48)	11.23-13.18 (33)	11.13-12.98 (29)	11.41-12.58 (22)	11.48 - 13.34 (50)	11.1-12.87 (25)	11.99-12.98 (10)	11.72-13.12 (4)	10.78-13.07 (29)	10.39-11.9 (12)	10.94-12.52 (17)	10.22-12.13 (13)	-	-

Variables	*Saimiri albigena*		*Saimiri boliviensis*		*Saimiri cassiquiarensis*		*Saimiri citrinellus***		*Saimiri collinsi*		*Saimiri macrodon*		*Saimiri madeirae*		*Saimiri sciureus*		*Saimiri ustus***		*Saimiri oerstedii*		*Saimiri peruviensis*		*Saimiri vanzolinii*	
BVD (SD)	35.46 ± 0.94	32.43 ± 1.21	34.48 ± 1.03	33.10 ± 1.07	33.73 ***± 0.76	32.84*** ± 1.40	34.14 ± 0.60	-	33.08 ± 1.17	31.66 ± 1.08	35.45 ± 1.66	33.58 ± 1.09	34.32 ± 1.17	32.83 ± 0.92	34.76 ± 1.39	33.35 ± 1.08	36.52 ± 1.19	33.84 ± 0.70	33.70 ± 0.73	31.91 ± 0.74	34.47 ± 1.13	33.19 ± 0.95	-	-
	33.27 - 37.02 (16)	32.42 - 36.07 (7)	32.25 - 36.47 (21)	30.74-35.21 (32)	32.11-35 (16)	31.05-35.08 (7)	33.8-34.84 (3)	-	31.08 - 36.32 (29)	29.3-34.26 (39)	32-39.1 (48)	32.04-35.85 (33)	32.2-36.86 (28)	31.37-34.62 (19)	31.54 - 37.93 (41)	31.44-35.35 (22)	34.43-38.2 (8)	32.87-34.48 (4)	32.06-35.25 (27)	31.14-33.61 (9)	32.82-36.56 (18)	31.76-35.07 (12)	-	-
TL (SD)	65.59 ± 1.75	63.48 ± 2.23	64.44 ± 2.07	61.19 ± 2.16	63.4 ±2.92	60.32 ± 3.02	63.1 ± 0.79	60.17 ± 1.66	62.30 ± 2.42	57.96 ±2.47	65.76 ± 2.02	62.98 ± 1.71	65.28 ± 2.19	62.53 ± 1.33	64.48 ± 2.42	61.52 ± 2.08	68.50 ± 1.08	66.01 ± 1.04	62.13 ± 1.27	59.50 ± 0.95	63.49 ± 1.75	61.02 ± 1.42	62.7*** ± 1.51	60.7 ± 1.8
	61.58 - 68.42 (17)	60.97 -66.9 (7)	60.26 - 68.33 (27)	56.69-65.4 (34)	57-96-66.81 (17)	55.59-64.96 (10)	62.2-63.7 (3)	59-61.35 (2)	56.81 - 67.08 (35)	54.4-62.23 (44)	59.7 - 69.83 (49)	60.14-67.78 (34)	58.95-68.13 (29)	59.9 - 65.49 (22)	58.93 - 69.75 (48)	57.71-64.32 (24)	66.35-69.88 (9)	65.29-67.21 (3)	59.83-64.44 (29)	57.6-61.04 (12)	60-66.59 (18)	58.51-63.1 (13)	60.39-65.1 (7)	58.9-62.5 (3)
PW	12.07 * ± 0.49	11.53 * ± 0.60	11.87 * ± 0.63	11.44* ± 0.66	11.88 ± 0.86	11.32 ± 0.63	12.65 ± 0.16	11.37 ± 0.82	12.01 * ± 0.75	11.36* ± 0.58	12.21* ± 0.65	11.84* ± 0.74	12.29* ± 0.57	11.99* ± 0.51	12.19 ± 0.56	12.06 ± 0.95	13.12 ± 0.30	12.52	11.96 ± 0.46	11.79 ± 0.51	11.66 ± 0.58	11.56 ± 0.70	-	-
	11.18 - 12.68 (16)	10.49 - 12.47 (7)	10.59 - 13.23 (24)	9.74-12.7 (32)	9.74-13.4 (19)	10.31-12.11 (11)	12.46 - 12.77 (3)	10.79-11.96 (2)	10.79 - 13.38 (38)	10.17-12.91 (48)	11-13.78 (45)	10.08-13.9 (34)	10.79-13.28 (30)	10.82-13.16 (22)	11.05 - 13.28 (48)	10.24-14.12 (25)	12.69-13.78 (9)	12.52 (1)	10.8-13.09 (30)	10.63-12.71 (12)	10.53-12.39 (18)	10.45-12.78 (11)	-	-
AUM	19.12 ± 0.64	18.66 ± 0.81	18.80 * ± 0.59	18.38* ± 0.71	18.16 ± 1.08	17.52 ± 0.97	18.67 ± 0.33	17.58 ± 0.77	17.99 * ± 0.55	17.33* ± 0.58	19.05* ±0.77	18.69* ± 0.63	18.75 ± 0.82	18.61 ±0.49	18.68 ± 0.67	18.38 ± 0.65	19.69 ± 0.20	18.69	18.03 ± 0.57	17.78 ± 0.57	18.3 ± 0.81	18.13 ± 0.59	-	-
	17.67 - 20.35 (15)	17.62 - 20.07 (7)	17.92 - 20.01 (25)	17.11-19.83 (32)	15.54-19.42 (17)	15.87-19.28 (9)	18.31 - 18.97 (3)	17.03-18.13 (2)	16.98 - 19.67 (38)	16.3-18.82 (48)	17.83-20.99 (45)	17.6 - 20.02 (32)	16.46-20.04 (28)	17.6 - 19.54 (22)	17.62 - 20.19 (49)	17.16-19.98 (25)	19.42-20.04 (9)	18.69 (1)	17.19-19.81 (29)	16.46-18.75 (11)	16.96-19.93 (18)	17.32-19.33 (11)	-	-
ML (SD)	36.46 ± 1.86	34.58 ± 0.99	36.19 ± 1.94	32.66 ± 1.62	34.79 ± 1.91	32.24 ± 1.80	35.45 ± 0.78	32.77 ±0.53	35.05 ± 1.29	31.91 ± 1.23	36.92 ± 1.96	34.06 ± 1.19	36.38 ± 1.57	33.80 ± 1.21	36.21 ± 1.73	33.16 ± 1.36	38.34 ± 0.85	34.70 ± 0.66	34.64 ± 1.39	32.23 ± 0.88	34.90 ± 1.80	32.35 ± 1.44	33.00 ± 1.47	30 ± 0.45
	32.42 - 39.42 (17)	33.42 - 36.24 (6)	32.29 - 39.86 (25)	29.41-35.67 (32)	31.74-37.05 (19)	29.91-35.21 (10)	34.56 - 36.02 (3)	32.39-33.15 (2)	32.25 - 37.84 (37)	29.39-34.48 (50)	32.36-40.83 (47)	31.6 - 36.69 (34)	32.98-39.03 (29)	31.8 - 37.22 (22)	32.23 - 38.89 (47)	30.53-35.6 (22)	37.33-39.92 (9)	34.02-35.45 (4)	31.96-37.45 (29)	30.29-33.82 (14)	31.77-37.32 (18)	30.22-34.9 (12)	31.44-35 (7)	29.6-30.5 (3)
LLM (SD)	15.21 ***	15. 16**	14.63 ± 1.11	14.26 ± 0.59	14.52 ± 0.81	13.26 ± 0.86	14.98 ±0.07	14.03 ± 0.61	14.41 ± 0.63	13.54 ± 0.73	15.14 ± 0.85	14.44 ± 0.66	14.75 ± 0.66	14.2 ± 0.58	15.06 ± 0.6	14.36 ± 0.66	15.4 ± 0.37	14.28 ± 0.50	14.50 ± 0.49	13.66 ± 0.60	14.27***	13.84 ± 0.69	-	-

Variables	*Saimiri albigena*		*Saimiri boliviensis*		*Saimiri cassiquiarensis*		*Saimiri citrinellus***		*Saimiri collinsi*		*Saimiri macrodon*		*Saimiri madeirae*		*Saimiri sciureus*		*Saimiri ustus***		*Saimiri oerstedii*		*Saimiri peruviensis*		*Saimiri vanzolinii*	
	± 0.40	* ± 0.77																			±0.94			
	14.05 - 15.75 (17)	14.24 - 16.33 (6)	11.09 - 15.92 (26)	12.84-15.26 (33)	13.01-15.86 (19)	11.38-14.44 (11)	14.91 - 15.06 (3)	13.6-14.47 (2)	12.89-15.4 (38)	12.12-14.92 (52)	12.41-16.84 (47)	12.46-16.13 (34)	13.27-16.26 (30)	13.16-15.59 (22)	13.57 - 16.32 (47)	12.51-15.36 (22)	14.94-16.07 (9)	13.82-14.97 (4)	13.43-15.39 (29)	12.8-14.48 (14)	13.09-16.14 (18)	12.82-14.85 (12)	-	-

All measurements are mean ± standard deviation/ minimum-maximum (N). *presented sexual dimorphism; ** due to the low number of specimens it was not possible to test the sexual dimorphism in cranial measurements; *** did not present sexual dimorphism.

BW: Braincase width - euryon to euryon; ZIG: Zygomatic breadth; CAL: Canine length; AUC: Across upper canines; UML: Length of upper molars; BVD: Basion-vertex distance; TL: Total length of skull - from prosthion to opistocranium; PW: Palate width; AUM: Across upper molars; ML: Mandibular length; ALC: Length of lower molar series.

Genomics

As another line of evidence to support our morpho-species arrangement, we included one maximum likelihood ddRADseq tree from Mercês *et al*. (in preparation). The tree analysis recovered two main clades, the Roman group (*S. boliviensis* and *S. vanzolinii*) and the Gothic group with four main subclades: (i) *S. ustus*, *S. madeirae*, (ii) *S. cassiquiarensis*, (iii) *S. macrodon* 1, *S. macrodon* 2 and (iv) *S. collinsi* 2, *S. sciureus* + *S. collinsi* 1. That we were able to separate in bare-eared and the tufted-eared squirrel monkeys. These four groups are supported with bootstrap values of 100.

These results corroborate mitogenomic data of Chiou *et al*. (2011), where they recovered *Saimiri* divided in two main clades, the Gothic and Roman group, but differs in topology from other analyses with mitochondrial loci (Lavergne *et al*., 2010; Lynch Alfaro *et al*., 2015; Ruiz Garcia *et al*., 2015).

In previous study with *Saimiri* mitochondrial loci *S. ustus* was retrieved as paraphyletic/polyphyletic (Lynch Alfaro *et al*., 2015; Ruiz Garcia *et al*., 2015). The other clade that was considered non-monophyletic in previous studies was *S. macrodon* and always related to *S. c. cassiquiarensis* and *S. c. albigena*, here we recovered two lineages inside of *S. macrodon*, provisionally called *S. macrodon* 1 and *S. macrodon* 2 and sister to the subclade (iv) *S. collinsi* 2 + (*S. collinsi* 1 + *S. sciureus*). The results from phylogenomic data differs from previous studies (Lavergne *et al*., 2010; Lynch Alfaro *et al*., 2015; Mercês *et al*., 2015; Ruiz Garcia *et al*., 2015) that found *S. collinsi* and *S. sciureus* were not closely related species. For more details in phylogenomic results see Mercês *et al.* (in preparation).

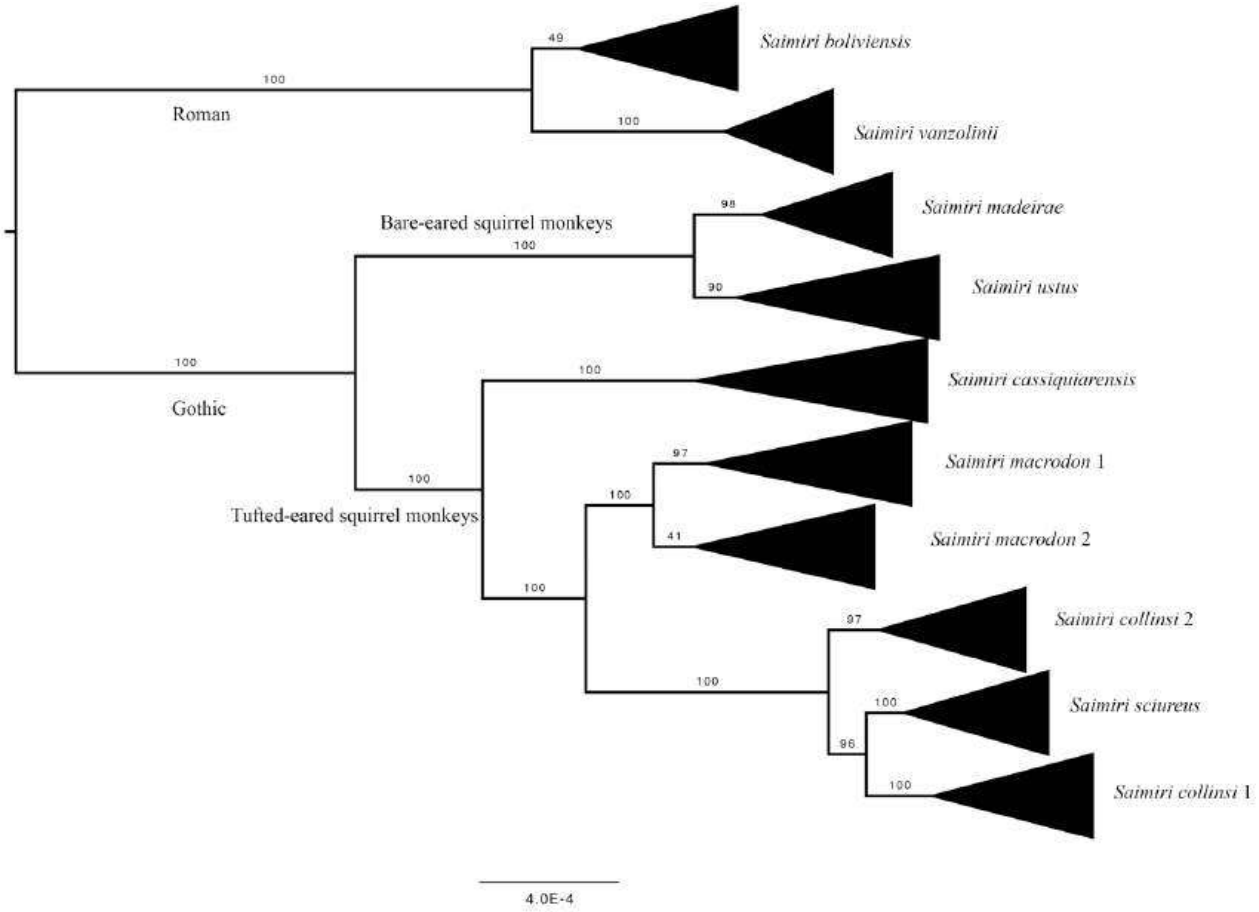

Figure 6. Phylogenomic tree obtained through maximum likelihood inference ddRadseq from *Saimiri* species (modified from Mercês *et al*., in preparation), the branches were collapsed to represent the clades of interest. The node support value is given on each branch.

Species account

The congruence between the geographically patterned results of the morphological data and the clades defined by the phylogenomic analysis allow us to recognize the two monophyletic species groups defined by Hershkovitz (1984) and thirteen species within *Saimiri*, including a new one previously identified as *Saimiri macrodon* 2. Another clade identified through the phylogenomic analysis (*Saimiri collinsi* 2) cannot yet be diagnosed for morphospecies on the samples available at this time. The first species group, Gothic, is composed of *Saimiri sciureus*, *S. cassiquiarensis*, *S. albigena*, *S. oerstedii*, *S. citrinellus*, *S. macrodon*, *S. madeirae*, *S. ustus*, *S. collinsi*, and *Saimiri* sp. n. The second species group, Roman, is composed of *S. vanzolinii*, *S. boliviensis*, and *S. peruviensis*. Hershkovitz (1984) had observed congruences among structural morphology, behavior and physiology related to these species' groups.

In this section we provide a general external description of *Saimiri* and offer a taxonomic history of the genus. Then, we list an account for each species of *Saimiri*, including synonyms, type material, type locality, emended diagnosis, variation, comparisons, geographic distribution, remarks, conservation status and specimens examined.

Table 4 summarizes the main diagnostic traits in external morphology between the species of *Saimiri*. Synonymies were mainly based in Cabrera (1958) and Hershkovitz (1984).

***Saimiri* Voigt, 1831**

Simia Linnaeus, 1758: 25 (part).

Cebus Erxleben, 1777: 51 (part).

Sapajus Kerr, 1792: 79 (part).

Callithrix Geoffroy, 1812: 114 (part).

Saguinus Lesson, 1827: 56 (part).

Saimiri Voigt, 1831: 95; *Simia sciurea* Linnaeus, 1758 type species by monotypy.

Type species: *Simia sciurea* Linnaeus, 1758 type species by monotypy.

Content: two species groups (Gothic and Roman) and thirteen species (*Saimiri sciureus, S. cassiquiarensis, S. oerstedii, S. citrinellus, S. macrodon, S. madeirae, S. ustus, S. collinsi, S. vanzolinii, S. boliviensis, S. peruviensis*, and *Saimiri* sp.n.)

Description: *Saimiri* are small sized primates (weight 800-1200 g), tail non-prehensile with tuft at the tip; head rounded with skull elongate, braincase large prolonged posteriorly, the face is relatively flat and is covered with short whitish hair. Muzzle region is pigmented. The ears are large and can be covered with a tuft, except in *S. ustus* and *S. madeirae* that have naked ears.

The color of the crown varies from blue-grayish or bright yellow to blackish. The arch above the eyes can present three shapes: roman, gothic or acute gothic. The hands can be grizzled gray to orange or golden yellow. The back varies from grayish with yellow, chestnut or orange to blackish. The tail pencil can be bushy or thin.

Saimiri presents sexual dimorphism. Males are larger and heavier than females. Males have a "fatted" condition during the mating season, were they gain weight (DuMond & Hutchinson, 1967). Males also present bigger and longer canines and more robust zygomatic arches (Hershkovitz, 1984). Adult females can present black sideburns (preauricular patch) that can extend until the crown area (Hershkovitz, 1984; Goldschmidt *et al*., 2009).

Saimiri can be divided in two main groups Gothic and Roman. These two groups are supported by phylogenomic, morphological and morphometric data. Here we present the species separated in these two groups: The Gothic species group is composed of ten species: *Saimiri sciureus, S. cassiquiarensis, S. albigena, S. oerstedii, S. citrinellus, S. macrodon, Saimiri* sp. n, *S. madeirae, S. ustus* and *S. collinsi.* The Roman species group is composed of three species: *Saimiri vanzolinii, S. boliviensis,* and *S. peruviensis*.

***Saimiri sciureus* (Linnaeus, 1758)**

Simia apedia Linnaeus, 1758: 25. Type locality: "Indiis". *Nomen oblitum*

Simia morta Linnaeus, 1758: 29. Illustration of Seba, Thes. i. p. 52, pl. xxxin.fig. 1, 1734. Type locality: "America". *Nomen dubium*

Simia sciurea Linnaeus, 1758: 29; original description (see below for type locality). *Nomen protectum*

Sapajou saimiri Lacépède 1803: 147. Based on "*Le saimiri*" plate of Buffon (1767:67, pl.51) from French Guiana.

Lemur leucopsis, Herman, 1804: 10; no type locality given.

Saimiri sciureus Elliot, 1913: 310; corrected gender agreement.

Type material: Linnaeus (1758) based the name *Simia sciurea* in the reference: "Mus[eum]. Ad[olph]. Fr[idericianu].1. P. 3." With no information about the collector or the date.

Type locality: "Indiis". Tate (1939) mentioned that if not previously restricted he proposed to limit the type locality to "Kartabo, British Guiana".

Emended diagnosis: Gothic arch above the eyes; ears tufted; crown gray with little yellow; bright yellow in the extremities of forearms extends from the hands up to the elbows (Figure 7); back reddish chestnut; bright yellow in the extremities of hindlimbs extends from the feet up to the heels; throat and chest whitish; tail pencil bushy.

Figure 7. *Saimiri sciureus* (FMNH 46174) from Guyana.

Variation: Presents sexual dimorphism in the preauricular patch (sideburns) with dark sideburns, usually restricted to area in front of the ears in females.

Comparison: Saimiri sciureus can be distinguished from *S. collinsi* by the coloration of the crown (grayish with little yellow vs. grayish with yellow), back (reddish chestnut vs. chestnut), and forearms (bright yellow vs. dark tawny). *Saimiri sciureus* differs from *S. macrodon* by the coloration of crown (grayish with little yellow vs. grayish olivaceous), back (reddish chestnut vs. orange chestnut), and limbs (bright yellow vs. yellowy orange).

Distribution: *Saimiri sciureus* occurs from Guyana, French Guiana and Suriname south to the north bank of the Amazonas River in Amapá, Pará and Amazonas states of Brazil (Figure 8). The western limit is the left bank of Negro and Branco rivers. The northeastern limit is the Atlantic Ocean (Mercês *et al*., 2018).

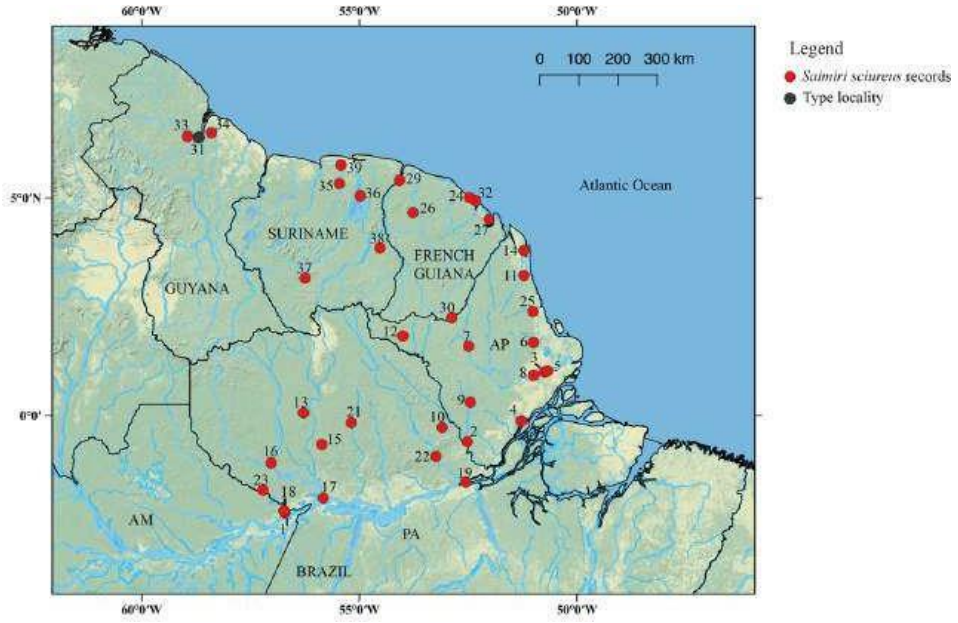

Figure 8. Geographic distribution of the specimens of *Saimiri sciureus* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality. Acronyms AM: Amazonas; AP: Amapá; PA: Pará.

Remarks: the name *Simia apedia* Linnaeus (1758) can be considered as a *nomen oblitum* (forgotten name) under the Articles 23.9.1.1. and 23.9.1.2 of International Code of Zoological Nomenclature (ICZN). Thomas (1911) attempted to identify Linnaeus types. He mentions that *Simia apedia* was "not determinable from description" and if the specimens still exist, they must be identified. Later, Fooden (1966) was able to analyze *Simia apedia* specimen, however only the skull remains preserved; it was identified as a squirrel monkey. Even, after it was identified as a squirrel monkey the senior synonym was not used as a valid name. The other senior synonym is *Simia morta*, which could be identified as a squirrel monkey through Seba's illustration. However, it was not possible to identify at the species level, and as such is considered as a *nomen dubium*. Thomas (1911) comments that *Simia morta* had a blackish head, which is not consistent with Guyana specimens. Groves (2001) after analyzing syntypes from the Swedish Museum of Natural History collection, identified *Simia sciurea* as a "Roman" type with a black crown. However, he did not resolve this issue, because the name still has a material type specimen that does not correspond to the named species' morphology. We have been in contact with researchers from the Swedish Museum of Natural History, and they are sending a proposal to ICZN to designate a neotype for *Saimiri sciureus* (Gendry A., personal communication). This proposal will resolve the problem with the type material associated with the name *Simia sciurea*.

Status: Least Concern (IUCN, 2015).

Specimens examined (n=106): BRAZIL – *Amapá*, Cachoeira de Santo Antônio (MPEG 21817-19), cidade do Amapá (MPEG 1196-98, 1200, 1202, 8482), Fazenda Nova (MPEG 1204), Iracema, Aporema River (MPEG 1218-19), Itaubal (Macacoari), Fazenda Lago Novo (MPEG 24027, 24029, IEPA 7), Itaubal (Macacoari), Fazenda Veja (MPEG 24028, IEPA 37-39), Macapá (MPEG 1265); left bank of Jari River (MPEG 21962-64, 21970), Mazagão, Vila Nova River (MPEG 659, 666), Mazagão, igarapé Novo, left bank of Iratapuru River (MPEG 1538-39); Mazagão, Branco River, right bank of Maracá River (MPEG 1902), PARNA Montanhas do Tumucumaque, Anacui River (IEPA 1306); PARNA Montanhas do Tumucumaque, Araguari River (IEPA 1460), Posto DNERu, Tracajatuba River (MZUSP 19709-10); REBIO Pirituba Lake (IEPA 3563), RDS Iratapuru River, Cupixi River (IEPA 1299, 2855), RDS Iratapuru River, igarapé Baliza (IEPA 2853-54), Vila Nova River (MPEG 662), Tracajatuba River (MN 20543, 20560, 20562-66), Vila Velha de Caciporé, Oiapoque (MPEG 2288, 2290-99, MN 20592); *Pará*, Alenquer, ESEC Grão-Pará (MPEG 39857-58), Almeirim, right bank of Paru do Leste River, FLOTA Paru (CN* 243-44, 276); Almeirim, Paru do Leste River, Uchizal (MN 23533-35), Lago Paru, Trombetas River (MZUSP 19135, 19141), Óbidos, ESEC Grão-Pará (CN* 297); GUYANA – Cuyuni-Mazaruni (AMNH 42323, 48117), Cuyuni-Mazaruni, Kartabo Point (AMNH 41948, 42851-52, 42877, 64095-96), Georgetown (FMNH 17761, 18553), East Demerara- West Coast Berbice, Essequibo River (FMNH 46169-74); SURINAME - *Brokopondo* (FMNH 95478-79), Saramacca (FMNH 95490), *Nickerie* (FMNH 93240-93243), Nickiere, Wilhelmina (FMNH 95491), Saramacca, Le Poule (FMNH 95480-95489). [Syntypes of *S. sciureus*]: NRM 532007, NRM532006, NRM532005. *CN = Calha Norte Project specimens are housed at Museu Paraense Emílio Goeldi (MPEG).

***Saimiri cassiquiarensis* (Lesson, 1840)**

Simia sciurea cassiquiarensis Lesson, 1840: 160; original description (see below for type locality).

Saimiris lunulatus I. Geoffroy, 1843: 1152. Type locality: "de l'Orénoque".

Chrysothrix nigrivittata Wagner, 1846:135. Type locality: "Ega am Solimoes". *Nomen dubium.*

Saimiri sciurea codajazensis Lönnberg,1940: 3. Type locality "Codajaz, state of Amazonas, Rio Solimões".

Type material: Lesson (1840) and I. Geoffroy (1843) used the Humboldt (1811) description to name *Simia sciurea cassiquiarensis* and *Saimiris lunulatus*, respectively. Therefore, there is no type material associated with *Simia sciurea cassiquiarensis*, only the original description of Humboldt (1811). Wagner (1846) described *Chrysothrix nigrivittata* based in three specimens brought from Éga (=Tefé) by J.B. von Spix. Later, Lönnberg (1940) named the species *Saimiri sciurea codajazensis*, which is the only synonymy that has type material associated with the name. Hershkovitz (1984) designated Wagner' (1855) illustration of *Chrysothrix nigrivitatta* as the lectotype of *S.*

cassiquiarensis. However, as it was not a syntype of *S. cassiquiarensis*, under the Article 74.2 of ICZN this illustration does not have lectotype status. Hershkovitz (1984) commented that the holotype of *C. nigrivittata* is probably at Zoologische Staatssammlung München (ZSM); however, we have been in contact with ZSM and the others where Wagner worked (e. g. Natural History Museum, Vienna) and we were not able to find these specimens to confirm the real identity of *Chrysothrix nigrivittata*. Kraft (1983) presents a list of Spix type specimens available at ZSM, but he does not mention the Wagner specimens. To resolve this issue, our decision was to designate a neotype for *Saimiri cassiquiarensis*, as there was no specimen related to the original description by Humboldt (1811), and the designation by Hershkovitz (1984) of lectotype was not appropriate. As a suitable neotype, we propose the specimen 78483 in the collection of American Museum of Natural History in New York. This specimen is an adult male collected on March 25, 1929 from mouth of Ocamo River, Venezuela by the Ollala Brothers, comprising skull and open skin (Figure 9), both in good condition.

Figure 9 . Dorsal and ventral view of the neotype of *Saimiri cassiquiarensis* (AMNH 78483), scale bar = 25 mm.

Type locality: "la Guiane espagnole [=Venezuela], sur les bords de l'Orénoque, du Cassiquiare", Venezuela.

Emended diagnosis: Gothic arch above the eyes; ears with tuft; crown yellowish tawny; nape yellow/whitish; hands and forearms orange; feet orange; back brighter reddish; throat and chest whitish; tail pencil bushy.

Variation: *Saimiri cassiquiarensis* females may present a dark patch in the preauricular region.

Comparison: *Saimiri cassiquiarensis* can be distinguished of *S. sciureus* by the coloration of the crown (yellowish vs. gray with little yellow), back (brighter reddish vs. reddish chestnut), and limbs (orange vs. bright yellow).

Distribution: *Saimiri cassiquiarensis* occurs in northern South America in Colombia, Venezuela and Brazil. The western limit of the species is the Guayabero River and Apaporis River in Colombia. The southern limit is Solimões/Japurá rivers in Brazil. The northern limit is the Orinoco River (Venezuela) and the eastern limit is Negro and Branco rivers (Brazil). According to Paim *et al*. (2013), in the Solimões/Japurá region at Mamirauá Reserve of Sustainable Development the species crosses the Japurá River (see detail in Figure 10).

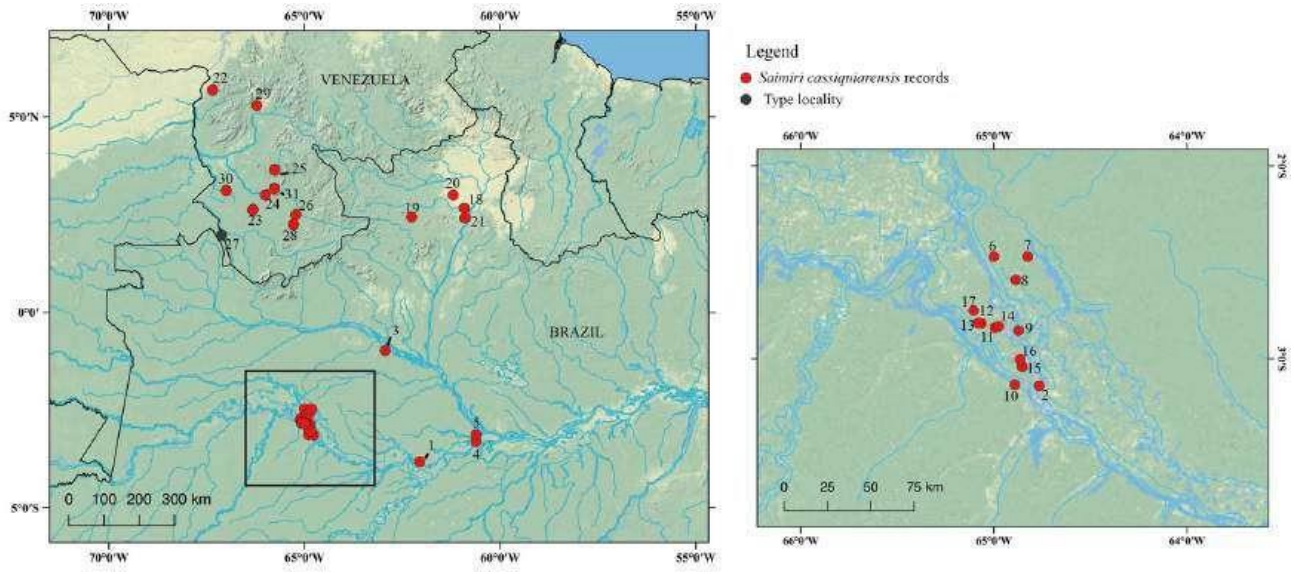

Figure 10. Geographic distribution of the specimens of *Saimiri cassiquiarensis* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality. The inset square represents the location of the small map which shows sampled localities at Solimões-Japurá interfluve.

Remarks: Humboldt (1811) described the specimen *Simia sciurea* (cassiquiarensis). However, this name was considered as unavailable according to the Article 11.5.2. (ICZN). Only Lesson (1840) publication made this name available as *Simia sciurea cassiquiarensis* Lesson, 1840. Hershkovitz (1984) and Thorington (1985) considered *S. cassiquiarensis* as subspecies of *S. sciureus*. Rylands *et al*. (2013) using the information from Carretero-Pinzón *et al*. (2009) phylogeny classified this taxon as distinct from *S. sciureus*. Here we considered *Saimiri cassiquiarensis* a valid species.

Status: Least Concern (IUCN, 2015).

Specimens examined (n=57): BRAZIL – *Amazonas*, Alvarães (IDSM-MASTO 1220, 1222-24, MPEG 39885, 39887), Codajás (FMNH 50873, MPEG 8912, NRM 620991 [syntype of *S. codajazensis*]), Mata do Engenho, Codajás (MN 23709-10, 23712, 24284), Japurá river (MZUSP 19008), Manacapuru (MZUSP 9961, MN 23715), Maraã (MPEG 36611, 36618, 36620, 36639-43, 366647), Paraná do Manacabi (MZUSP 17546, 17548), Parauari (MZUSP 9009-11), Paraná do Jarauá (MZUSP 17554, 17556), Uarini (MPEG 39878-81, *Roraima*, Apiaú (MZUSP 23927), Bonfim

(MZUSP 23931), Colonia do Apiaú, Mucajaí River (MPEG 21872), Rio Branco, Conceição (FMNH 20002, 20003), Mucajaí River (MPEG 2382, MZUSP 9673, 19708); COLOMBIA – Santander, Cimitarra, near San Fernando (AMNH 76872, 76873), Guaviare, Vaupés River (AMNH 78586); VENEZUELA – Amazonas, Atapabo, Mount Duida (AMNH 76863, 76871, 76918, 76920), Amazonas, Atures, Ocamo River (AMNH 78482, 78483 [neotype], 78485), Casiquiare River, El Merey (AMNH 78484, 78486), Casiquiare, 15 miles above Capibara (AMNH 77550), Casiquire River, El Merey.

***Saimiri albigena* (Pusch, 1941)**

Cebus sciureus albigena Pusch, 1941: 212; original description (see below for type locality).

Saimiri sciureus albigena Hershkovitz, 1984: 196.

Saimiri cassiquiarensis albigena Carretero-Pinzón *et al*. 2009: 5.

Type material: The holotype is an adult male with skin and skull (ZMB 33951;Figure 11). The specimen is housed at Museum für Naturkunde, Berlin, Germany, was collected by Hermano Apolinar-Marian.

Type locality: "Medina N5, W73", Colombia.

Figure 11. Dorsal and ventral view of the holotype of *Saimiri albigena* (ZMB 33951) provided by the staff of Museum für Naturkunde.

Emended diagnosis: Gothic arch above the eyes; ears with tuft; crown, neck and shoulders greyish; forelimbs grizzled gray with some yellow in the fingers but the upper part of the hands grizzled gray; back chestnut; hindlimbs grayish; feet grizzled gray; throat and chest whitish.

Variation: Females presented brownish coloration limited to in the front of the ears (sideburns).

Comparison: *Saimiri albigena* can be distinguished from *S. cassiquiarensis* by six traits: color of the crown (grayish vs. yellowish), nape color (grayish vs. yellowish/whitish), coloration of the back (chestnut vs. brighter reddish), color of the forearms (grizzled gray vs. orange), color of the hands

(grizzled gray vs. orange) and color of the feet (grizzled gray vs. orange). *Saimiri albigena* differs from *S. macrodon* by the coloration of the back (chestnut vs. chestnut with orange), forearms (grizzled gray vs. yellowy orange), hands (grizzled gray vs. yellowy orange), and feet (grizzled gray vs. yellowy orange).

Distribution: *Saimiri albigena* is the South American species with the northernmost geographical distribution (Figure 12). It occurs in the central region of Colombia, being limited to the west by the Andes and to the south by the Guayabero River. The eastern boundary is still poorly defined in the open vegetation areas of the departments of Boyacá and Arauca. According to Carretero-Pinzón *et al*. (2013) and Rylands *et al*. (2013), the species also occurs in a small area situated in the eastern part of the mountains of the Eastern Cordillera and Llanos orientales, from the north of the departments of Boyacá and Arauca, and south of the Guaviare River.

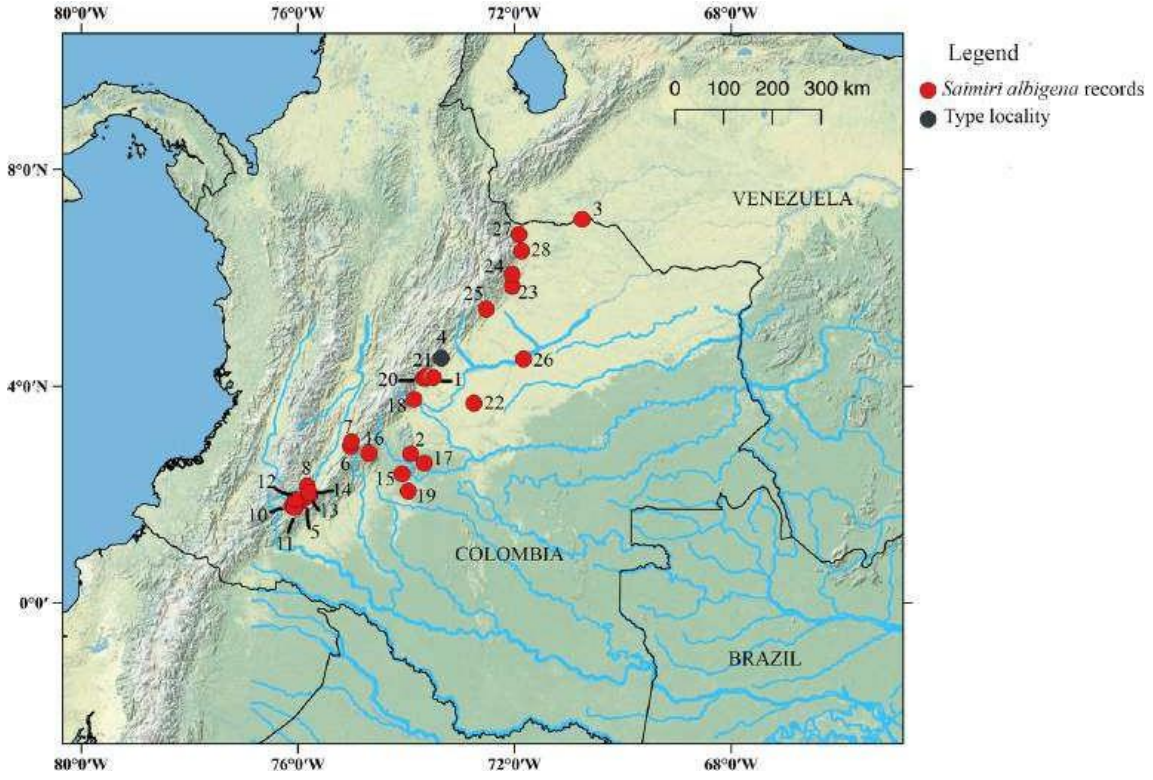

Figure 12. Geographic distribution of the specimens of *Saimiri albigena* studied and from literature (Carretero-Pinzon *et al*., 2013). Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality.

Remarks: *Saimiri sciureus albigena* was considered valid by Hershkovitz (1984) as a subspecies of *Saimiri sciureus*. Carretero-Pinzón *et al*. (2009) using cytochrome b data observed that *S. s. albigena* was more closely related to *S. s. cassiquiarensis* then to *S. sciureus*. Carretero-Pinzón *et al*. (2009) proposed that *S. s. albigena* should be reclassified as a subspecies of *S. cassiquiarensis* and not of *S. sciureus*, due to their phylogenetic relationship. The other possibility of classification that they suggested was that *S. c. albigena* should be classified as full species. Rylands *et al*. (2013) followed the subspecies proposal of Carretero-Pinzón *et al*. (2009) and classified the taxon as *Saimiri*

cassiquiarensis albigena. After analyzing all the molecular data available in the literature (Carretero-Pinzón *et al.*, 2009; Lavergne *et al*., 2010; Carretero-Pinzón *et al*., 2013; Rylands *et al*., 2013; Lynch Alfaro *et al*., 2015; Ruiz Garcia *et al*., 2015) and based on our morphological analysis, we propose that *S. c. albigena* should be treated as a separate species from *S. cassiquiarensis*, so here it is considered a full species.

Status: Vulnerable (IUCN, 2015).

Specimens examined (n=34): COLOMBIA – *Arauca* (FMNH 140251); *Guaviare*: Lower Guayabero River, Cerro Las Pinturas (FMNH 88239-88240); *Meta*: Cabuyaro, Puerto Barrigon (AMNH 37352-37354); Villavicencio (AMNH 63938, 136206, 136214-126216, 142230-142231); Villavicencio, 7km NE of the airport (AMNH 207932); Restrepo, El Caibe (AMNH 129414), Restrepo (AMNH 136206); Villavicencio, San Juan de Arama, Los Micos (FMNH 87821-87831, 87836); Villavicencio, La Macarena Parque, Guapaya River (FMNH 87834-87835); Villavicencio, La Macarena Parque, Yerley River (FMNH 87832-87833); *Vichada*, Territorio Faunistico del Tuparro (FMNH 140252); Medina (ZMB 33951 [holotype of *S. albigena*]).

***Saimiri oerstedii* (Reinhardt, 1872)**

Chrysothrix örstedii Reinhardt, 1872: 157; original description (see below for type locality).

Saimiri oerstedi Elliot, 1913: 316; incorrect subsequent spelling.

Saimiri oerstedi Hill, 1960: 302; incorrect subsequent spelling.

Saimiri oerstedi Hershkovitz, 1984: 197; incorrect subsequent spelling.

Saimiri oerstedti Groves, 2001: 157; incorrect subsequent spelling.

Saimiri oerstedii Groves, 2005: 138; correct spelling.

Type material: Adult male, mounted skin with skull number ZMUC-CN48 (Figure 13). Housed at the Natural History Museum of Denmark collected by A. S. Örsted.

Type locality: “David I Chiriqui”, Panamá.

Figure 13. Lateral view of the holotype of *Saimiri oerstedii* (ZMUC-CN48), photograph provided by Natural History Museum of Denmark, scale bar = 50 mm.

Emended Diagnosis: Acute gothic arch; ears with tuft; crown blackish; back orange; forelimbs orange up to the elbows; hindlimbs orange up to the knees; throat whitish; chest orangish; tail pencil bushy.

Variation: Presents sexual dimorphism in the preauricular patch (sideburns). Adult females present black sideburns that separate the white face from the white fur in the ears.

Comparison: *Saimiri oerstedii* can be distinguished from *Saimiri citrinellus* by the coloration of the crown (black vs. grizzled gray), coloration of the forelimbs (orange vs. gray), and the coloration of the chest (orangish vs. whitish). *Saimiri oerstedii* and *S. citrinellus* can be distinguished from all other species of *Saimiri* by the arch forming an acute angle on the forehead, in the arch above the eyes, higher than in all other species and by the pure orange coloration of the back.

Distribution: *Saimiri oerstedii* occurs from Pacific coast of southern Costa Rica (Puntarenas Province) and southwestern Panama (Chiriquí Province), from the south bank of the River Grande de Terrabá to the mouth of the Fonseca River and the Archipelago of the Golfo de Chiriquí; in Panama elevations from sea level to 500 m (Rylands *et al.*, 2013; Figure 14).

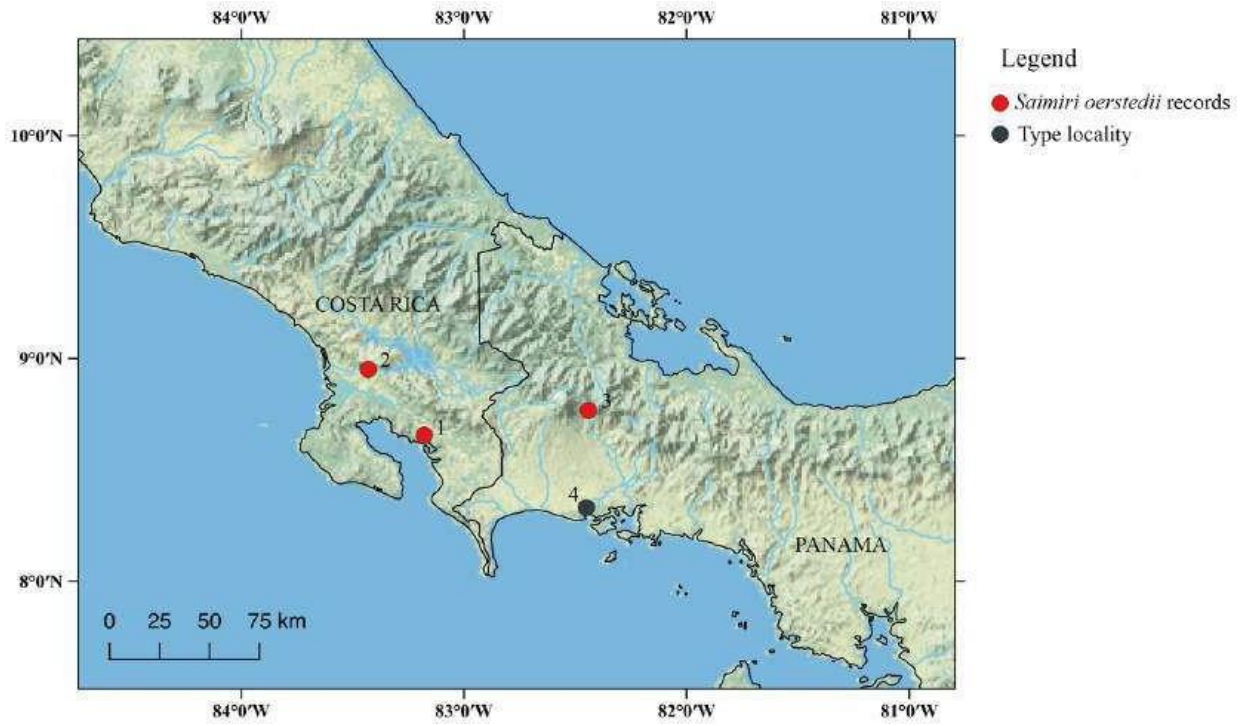

Figure 14. Geographic distribution of the specimens of *Saimiri oerstedii* studied and from literature (Blair *et al*., 2013). Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality.

Remarks: The original spelling of the species name by Reinhardt was *Chrysothrix örstedii*, nevertheless the ICZN does not accept any diacritic or mark in the name of species (Article 32.5) and this mark had to be removed, and the letter "e" inserted in publications before 1985 (Article 32.5.2). Taking this into account, the correct spelling is *Chrysothrix oerstedii*. In the Hershkovitz (1984) review it is misspelled (*Saimiri oerstedi*) and misspelled differently in Groves (2001): *Saimiri oerstedti*.

Status: Vulnerable (IUCN, 2015).

Specimens examined (n= 70): PANAMÁ – *Chiriqui*, Boqueron (AMNH 26935-48, 26951-64, 26966-67, 26970-80, 26982-86, 26989-92)-, David (ZMUC-CN48 [holotype of *S. oerstedii*]), Boqueron, Boquete (FMNH 14196-14201); COSTA RICA – *Puntarenas*, Palmar (AMNH 139290-139304), El Pozo de Terrabá (FMNH 44858).

***Saimiri citrinellus* Thomas, 1904**

Saimiri oerstedi citrinellus Thomas, 1904: 250; original description (see below for type locality).

Type material: Adult male (skin and skull). BMNH 1904.4.2.7.2 deposited at Natural History Museum in London, UK. Collected by C. F. Underwood in 1902.

Type locality: "Pozo Azul, Pirris", Costa Rica.

Emended diagnosis: Acute gothic arch; ears with tuft; crown agouti grayish; forelimbs grayish; hands orange; in the hindlimbs the toes present some orange, but the upper part of the feet is grizzled gray; back orange; throat and chest whitish (Figure 15); tail pencil bushy.

Figure 15. Dorsal and ventral view of a topotype of *Saimiri citrinellus* (FMNH 124542) from Pozo Azul, Costa Rica.

Variation: Females presents darkening in the preauricular patch, which can extend until the arch above the eyes and with some dark hair scattered on the crown.

Comparison: Saimiri citrinellus can be distinguished from *Saimiri oerstedii* by the coloration of the crown (grizzled gray vs. black), forelimbs (gray vs. orange), and the chest (whitish vs. orangish). *Saimiri citrinellus* and *S. oerstedii* differs from all other species of *Saimiri* by the arch above the eyes forming an acute angle higher than in all other species and by the pure orange coloration of the back.

Distribution: *Saimiri citrinellus* occurs in the west of Costa Rica along the Pacific coast in Puntarenas Province (elevations up to 500 m). Northeast limit is marked by the Tulín River, in the north by Herradura Mountains and Dota Mountains, and the southern limit by the north bank of the River Grande de Terrabá (Figure 16). Its populations are entirely fragmented (Rylands *et al*., 2013).

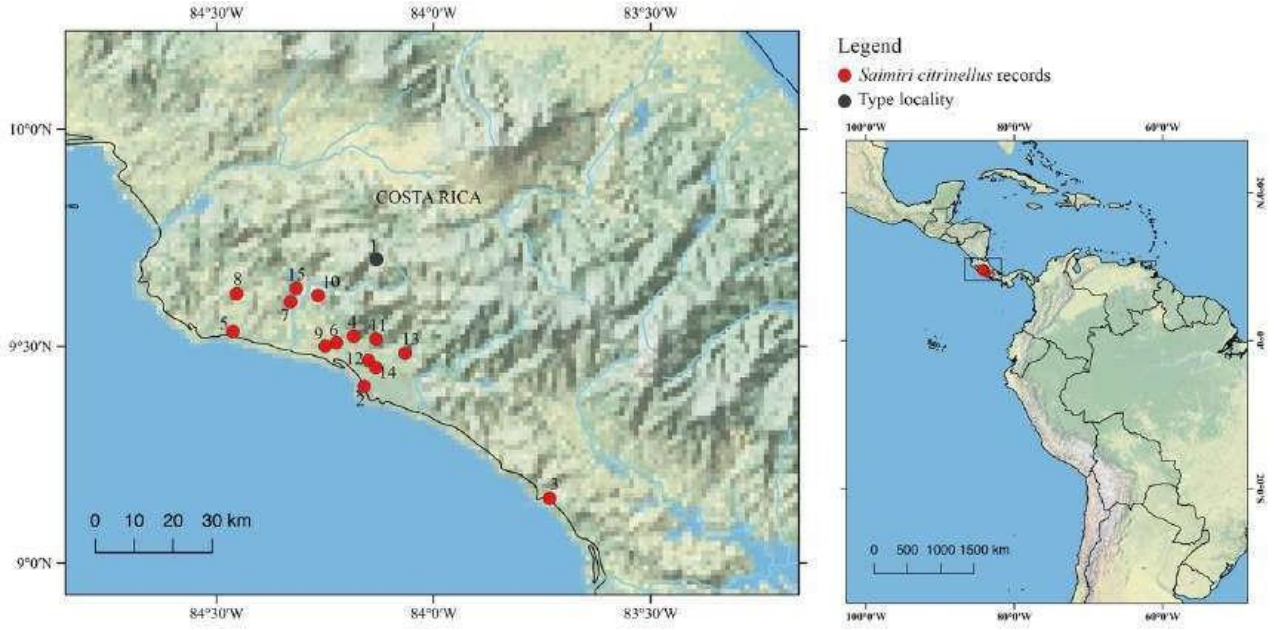

Figure 16. Geographic distribution of the specimens of *Saimiri citrinellus* studied and from literature (Sierra *et al*., 2003; Blair *et al*., 2013). Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality.

Remarks: *Saimiri citrinellus* was considered a valid subspecies of *Saimiri oerstedii* by Hill (1960) and Hershkovitz (1984). Groves (2005) classified it as synonym of *Saimiri oerstedii*. Thorington (1985) considered as a synonym of *S. sciureus*. Blair *et al*. (2013) proposed that this taxon should be treated as an evolutionarily significant unit (ESU) without changing the species status. After analyzing the results from Cropp & Boinski (2000), Chiou *et al*. (2011), Blair & Melnick (2012) and Blair *et al*. (2013), and our morphological data we determined that there is enough evidence to consider *S. oerstedii* and *S. citrinellus* as separate species. These species distributions are separated by the River Grande de Terrabá. They display different behaviors in terms of sex-biased dispersal patterns (Blair *et al*., 2013), and different external morphology (our data). For both mitogenomic (Chiou *et al*., 2011) and nuclear genes (Cropp & Boinski, 2000) they appear as reciprocally monophyletic clades.

Status: Endangered (IUCN, 2015).

Specimens examined (n=7): COSTA RICA – *Parrita*, Pozo Azul (AMNH 19212-19216); *Guanacaste*, Pirris River (FMNH 12542); Pozo Azul, Pirris (BMNH 4.2.7.2 [holotype of *S. citrinellus*]).

***Saimiri macrodon* Elliot, 1907**

Saimiri macrodon Elliot, 1907: 190; original description (see below for type locality).

Saimiri caquetensis Allen, 1916: 87. Type locality: "Florencia, altitude 1000 feet, Caquetá, Colombia".

Saimiri sciurea petrina Thomas, 1927: 364. Type locality: "Yurac Yacu, San Martin, Peru".

Saimiri madeirae juruana Lönnberg, 1940: 7. Type locality: Lönnberg does not provide one single type locality, some specimens were collected at "João Pessoa, Rio Juruá", and some at "Igarapé do Gordão, Rio Juruá".

Type material: Adult male with skin and skull, collected by C. Buckley. Housed at Natural History Museum of London, U.K, number BMNH 1880.5.6.15.

Type locality: "Copataza River, Ecuador".

Emended diagnosis: Gothic arch above the eyes, ears with tufted; crown, neck and shoulders grey;; forelimbs burnt yellow from the hands until the elbows; back chestnut; hindlimbs gray; feet burnt yellow until the ankles; throat and chest fur whitish; tail pencil bushy (Figure 17).

Variation: *Saimiri macrodon* presents geographic variation. Specimens from Caquetá, Colombia (LACM 27320) a more grayish inside area of the forearm than the specimens from Loreto, Peru (AMNH 268245), which presents a more yellowish inside of the forearm. Regarding sexual variation, in females the preauricular patch is black and extends above the ears forming a ring on the back of the crown.

Comparison: Saimiri macrodon can be distinguished from *S. sciureus* by the coloration of the crown (grayish olivaceous vs. gray with little yellow) and coloration of the limbs (yellowy orange vs. bright yellow*). Saimiri macrodon* differs from *S. albigena* by the coloration of the limbs (yellowy orange vs. grizzled gray) and coloration of the back (chestnut with orange vs. chestnut). Can be distinguished from *S. cassiquiarensis* by the coloration of the crown (grayish olivaceous vs. yellowish), coloration of the limbs (orange vs. yellowy orange) and coloration of nape of the neck (grayish vs. whitish).

Figure 17 . Dorsal and ventral view of *Saimiri macrodon* (AMNH 268245) from Loreto, Peru.

Distribution: Saimiri macrodon occurs in Ecuador, Colombia, Peru and Brazil. In eastern Ecuador (east of the Andes) to southwestern Colombia (up to the Apaporis River), northeastern Peru (north of the Marañón River) to the western Brazilian Amazon, between Japurá and Juruá rivers (Figure 18).

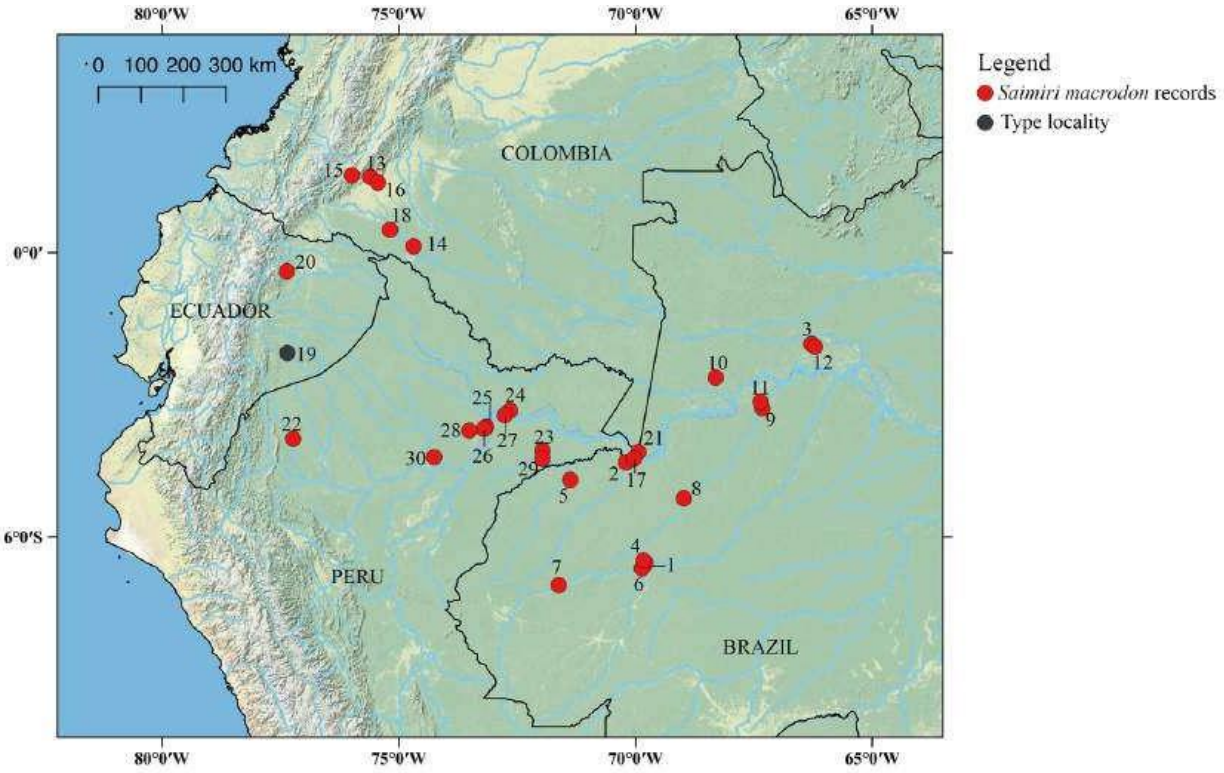

Figure 18. Geographic distribution of the specimens of *Saimiri macrodon* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality.

Remarks: Hershkovitz (1984) and Groves (2001) classified *S. macrodon* as a subspecies of *S. sciureus*, while Thorington (1985) and Groves (2005) considered this taxon as synonymous of *S. sciureus*. Carretero-Pinzón *et al*. (2009) based in cytochrome *b* sequences considered that *S. macrodon* should be classified as full species status considering the Phylogenetic Species Concept. Rylands *et al*. (2013) considered the Ecuadorian squirrel monkey as a valid species, separated from *S. cassiquiarensis*. Ruiz-Garcia *et al*. (2015) classified it as a lineage of *S. sciureus*.

Status: Least Concern (IUCN, 2015).

Specimens examined (n=106)*:* BRAZIL – *Amazonas*, Altamira (MPEG 22976), Atalaia do Norte (MPEG 30757-60), Auati-Paraná (IDSM AP001), ESEC Jutaí-Solimões (IDSM JT 036, 034), Estirão do Equador (MPEG 1091), Igarapé do Gordão, Juruá River (MZUSP 4801, NRM 602196 [syntype of *S. m. juruana*]), Ipixuna (MPEG 22991), Jutaí, RDS Cujubim (MPEG 41716-17, 41740-44, 41749, 41759, 41797-99), RESEX Auati-Paraná (IDSM AP 001,006,030, 029, IDSM JT030), Santo Antônio do Içá (IDSM ICA004-6); COLOMBIA – *Caquetá*, Florencia (FMNH 71001, AMNH 33874 [holotype of *S. caquetensis*], AMNH 33875), La Tagua (FMNH 70658-60, 70662-64, 70667), La montanita (LACM 27320-24), Leticia (LACM 27325), *Guaviare*, Campo Grito (FMNH 89480), *Huila*, Acevedo (FMNH 70643-51, 70653-54), Pitalito (FMNH 70655, 70657), *Putumayo*, San Antonio (FMNH 70669); ECUADOR – *Napo*, upper Payamino River (FMNH 31100-31105), Copaza River (BMNH 1880.5.615.2 [holotype of *S. macrodon*]; PERU – *Loreto*, Maynas, Nanay River

(FMNH 86970), Maniti River (FMNH 86977), Maynas, isla de Iquitos (FMNH 125387-96); Alto Amazonas (FMNH 88863, 88865), Alto Yavari Mirim (FMNH 88866-67), Tigre River (FMNH 122802-03, 122805-13, 122815-23), Yurac Yacu, San Martin (BMNH 1904.2.7.1 [holotype of *S. petrina*].

Saimiri sp. n.

Saimiri sciureus macrodon 2. Paim *et al*. (2013: 1063) – BRAZIL

Saimiri cassiquiarensis macrodon B. Lynch Alfaro *et al*. (2015: 445) – BRAZIL

Holotype: MPEG 37101, adult male, stuffed skin, skull and skeleton, tissue, collected by João Valsecchi do Amaral on June 28, 2004 on the left bank of Solimões River, Reserva de Desenvolvimento Sustentável Mamirauá, comunidade Barroso (02°26’55”S, 65o6’57”W), Uarini municipality, Amazonas state, Brazil

Paratype: MPEG 37102, adult female, stuffed skin and skull, tissue, collected by João Valsecchi do Amaral on June 28, 2004 on the left bank of Solimões River, Reserva de Desenvolvimento Sustentável Mamirauá, comunidade Barroso (02°26’55”S, 65°6’57”W), Uarini municipality, Amazonas state, Brazil; IDSM 1081, adult female, field number RDSMAS-01, stuffed skin and skull, collected on February 2nd, 2012 on left margin of Lago Parauá, Setor Aramapu, Reserva de Desenvolvimento Sustentável Mamirauá, Maraã, Amazonas state, Brazil. MPEG 39869, adult male, stuffed skin and skull, tissue, collected by Izaura Muniz Maschio on January 15, 2008 on comunidade São Francisco do Boá (02°23’3”S, 65°13’57”), Amazonas state, Brazil.

Type locality: São Francisco do Boá, Maraã, Amazonas, Brazil (2°23’3”S, 65°13’57”W).

Diagnosis: Gothic arch above the eyes; ears tufted; crown grayish; forearms and hands are grizzled gray; back is grizzled gray speckled with yellow; grizzled gray in the extremities of hindlimbs extends from the feet up to the heels; throat and chest whitish; tail pencil bushy.

Variation: *Saimiri* sp. n. can present variation in two traits, coloration of the hands and of the feet, some specimens present the hands and feet yellowish (MPEG 39874) or just the fingers with yellow (MPEG 39871). Females present blackening in the sideburns.

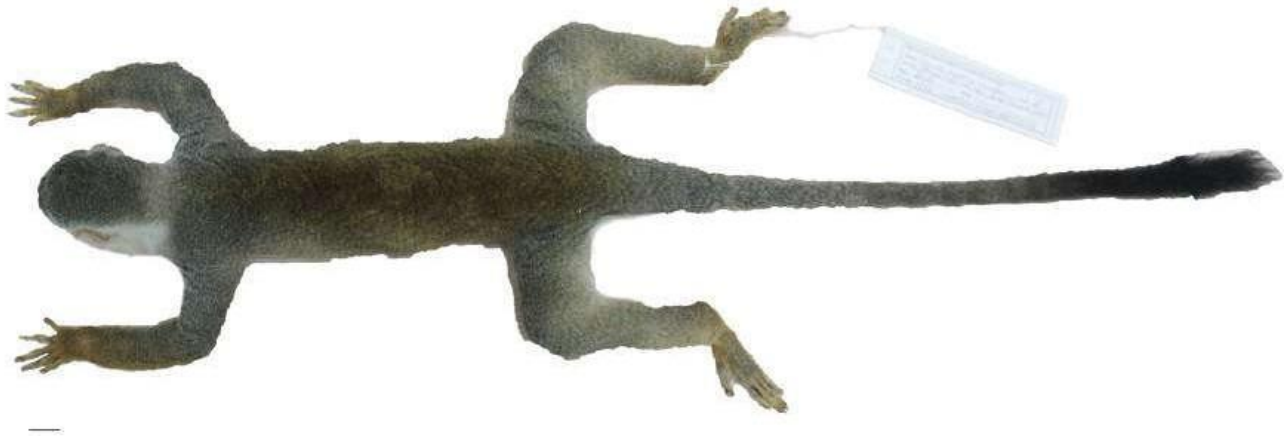

Figure 19. Dorsal view of *Saimiri* sp.n. (IDSM1081), scale bar = 20 mm.

Comparison: *Saimiri* sp. n. can be distinguished from *S. macrodon* by the coloration of the back (grizzled gray speckled with yellow vs. chestnut with orange), forelimbs (grizzled gray vs. yellowy orange), and feet (grizzled gray vs. yellowy orange). *Saimiri* sp. n. differs from *S. cassiquiarensis* by the coloration of the crown (grayish vs. yellowish), back color (grizzled gray speckled with yellow vs. brighter reddish), coloration of the forelimbs (grizzled gray vs. orange), and hindlimbs (grizzled gray vs. orange). *Saimiri* sp. n. differs from *S. vanzolinii* by arch format (gothic vs. roman), the coloration of the crown (grayish vs. blackish), coloration of the back (grizzled gray speckled with yellow vs. blackish), coloration of the forelimbs (grizzled gray vs. golden yellow), coloration of the hindlimbs (grizzled gray vs. golden yellow), coloration of the chest (whitish vs. burnt yellow), and tail pencil (bushy vs. thin).

Distribution: *Saimiri* sp. n. is endemic to Brazil. Occurs in the Solimões-Japurá interfluvium, extending south of Solimões River to the middle Juruá River in both sides. The western record is in the left margin of Javari River. This record indicates a possible sympatry between *Saimiri* sp. n. and *Saimiri macrodon* in the Javari-Jutaí interfluvium. The northern limit is likely to be Japurá River, while the southern and eastern limit is not known.

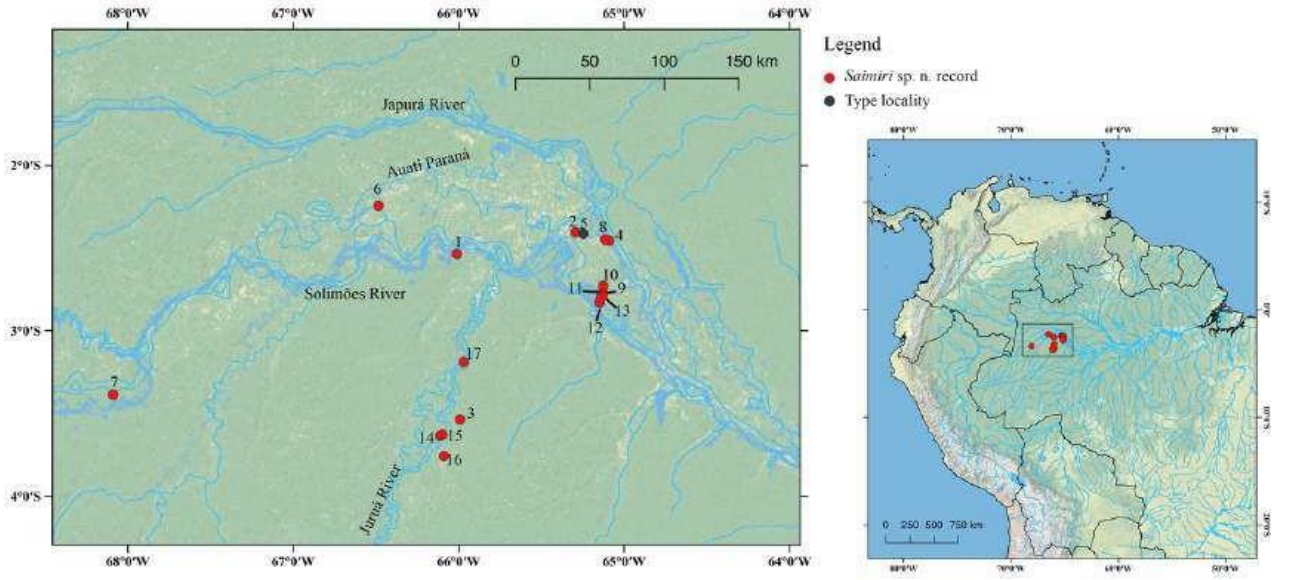

Figure 20. Geographic distribution of the specimens of *Saimiri* sp. n. studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality.

Remarks: Saimiri sp. n. was provisionally called as *Saimiri sciureus macrodon* 2 by Paim *et al.* (2013) and as *Saimiri cassiquiarensis macrodon* B (Lynch Alfaro *et al*., 2015). Paim *et al.* (2013) were able to distinguish *Saimiri* sp. n. from *S. macrodon*, but they considered that the morphological divergence among these species was low (only four-character states). They commented that the phenotype observed in *S. s. macrodon* 2 was described by Lönnberg (1940) for *Saimiri madeirae juruana*. However, after we analyze all the synonymous of *Saimiri macrodon*, including *S. m. juruana*, we observed that the morphology presented by *Saimiri* sp. n. does not correspond to the morphology of *S. m. juruana*. Lynch Alfaro *et al*. (2015) considered that was necessary a deeper investigation including more samples from a wider geographic area and nuclear data analysis to better understand the status of *Saimiri cassiquiarensis macrodon* B.

Status: Not accessed.

Specimens examined (n=45): BRAZIL, *Amazonas*, Fonte Boa (MN 2885, 23703, 23711, 23713) – Fazenda São José (MPEG 7035, 7037, 7039-43), Maraã – cano do Lago do Preguiça (MPEG 38973-75), comunidade São Francisco do Boá (MPEG 39869 [paratype] - 39872), comunidade do Jarauá (MPEG 39877), Setor Aramapu (IDSM 1080[paratype]-1083), Tefé - Lago do Boiá (MPEG 13209), Porto da castanha (MPEG 13210), Uarini (MPEG 39867) – comunidade Aiucá (39863-66, 39868), cano do Lago Mamirauá (MPEG 39882), comunidade Barroso (MPEG 37101[holotype], 37102 [paratype], 37103, 37011, 37120, 37128), Paraná do Jarauá (MPEG 39876), Paraná do Aiuapiá, Auati Paraná (MZUSP 18894-95), São Paulo de Olivença (MN 23705-08).

***Saimiri madeirae* Thomas, 1908**

Saimiri madeirae Thomas, 1908: 90; original description (see below for type locality).

Type material: Adult male with skin and skull. Collected by W. Hoffmanns in August 17th, 1906. Housed at British Museum of Natural History, number BMNH 1908.5.9.6.

Type locality: "Humayta, Middle Rio Madeira, about 63ºW., 7º 30'S."

Emended diagnosis: Gothic arch with well-delineated edge above the eyes; ears without tuft; crown bluish-gray; back orange speckled with black; forelimbs grayish; hands orange; feet orange up to the ankles; throat and chest whitish to pale yellow; tail pencil bushy (Figure 21).

Figure 21. Dorsal and ventral view of *Saimiri madeirae* (MPEG 21995).

Variation: Females present preauricular patch that extends from in front of the ears until the arch above the eyes and in the back of the crown forming a ring. They can present some blackening in the shoulders.

Comparison: *Saimiri madeirae* can be distinguished from *S. ustus* by the coloration of the crown (bluish gray vs. bluish orange), coloration of the forelimbs (gray vs. burnt yellow/orange) and coloration of the back (orange speckled with black vs. golden speckled with black). *Saimiri madeirae* and *S. ustus* differ from the other *Saimiri* species due the absence of hair tufts on the ears.

Distribution: This species is endemic to Brazil (Figure 22). The northern limit is the Amazon River. The western limit seems to be Purus River, with one record at Urucu River. Occurs on both sides of the middle and lower Madeira River, with some records in northern Rondônia state (north bank of Ji-Paraná River). One confirmed record in Mato Grosso state, is the southernmost record of the species.

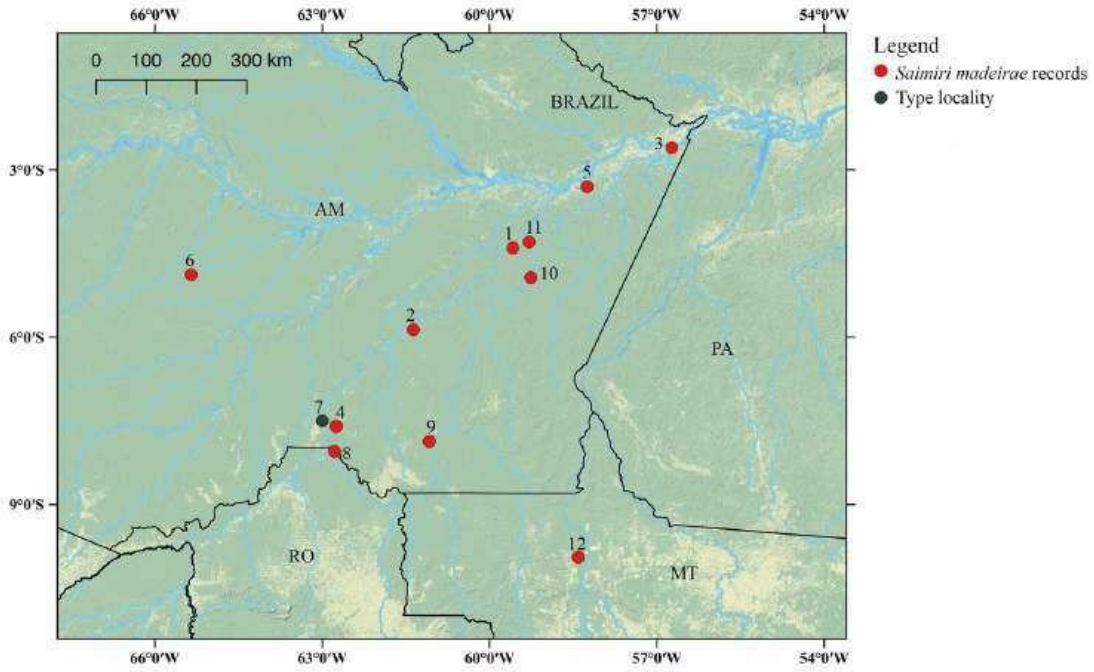

Figure 22. Geographic distribution of the specimens of *Saimiri madeirae* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality.

Remarks: Saimiri madeirae was considered valid by Elliot (1913), Hill (1960) and Thorington (1985) and regarded as synonym of *S. ustus* by Cabrera (1958), Hershkovitz (1984) and Groves (2001, 2005). The main differences between *S. madeirae* and *S. ustus* were considered to be morphological variation within *S ustus* by Hershkovitz (1984), Groves (2001) and Rylands *et al*. (2013).

Status: Not accessed.

Specimens examined (n=60)*:* BRAZIL, *Amazonas*, Borba (AMNH 91764, 91772-73, 91775-78, 92044, MPEG 23969), Humaitá (MPEG 21990-93, BMNH 1908.5.9.6 [holotype]), Lago do Baptista, Manicoré, Rosarinho (AMNH 92306-12, 92782, 92787-91, 92795, MZUSP 5204-09, 5211-18, 10506, 10508, 10521, 10523-25), Novo Aripuanã (MPEG 42809), Parintins (AMNH 93063, 93065, 93067, 93069-70, 93072-74, 93122, 93672); *Rondônia*, Calama (MPEG 21994, 21995).

***Saimiri ustus* I. Geoffroy, 1843**

Saimiri ustus I. Geoffroy, 1843: 1152; original description (see below for type locality).

Type material: Male, mounted skin without skull housed at Muséum National d'Histoire Naturelle, Paris (MNHN-ZM-2007-1540, Figure 23), collected by Alexandre Rodrigues Ferreira. Initially this material was at Museo da Ajuda, Lisbon, Portugal. The specimen was also illustrated by I. Geoffroy (1845: Pl. I).

Type locality: In the original description I. Geoffroy (1843) only mentions that the specimen is "du Brésil". Cabrera (1958) restricted the type locality to "al Rio Madeira, en el estado de Amazonas", posteriorly Hershkovitz (1984) restricted to "Humaitá, Rio Madeira, Amazonas, Brazil". We suggest

that the Hershkovitz (1984) restriction was not accurate, as the specimens from the left bank of the Madeira River at Humaitá region do not present *S. ustus* morphology and the original tag from Alexandre Rodrigues Ferreira was lost. Here we propose a new type locality, the east bank of Madeira River, Porto Velho, Rondônia, Brazil, which agrees with the route of Alexandre Rodrigues Ferreira and with the morphology of *Saimiri ustus*.

Figure 23. Lateral view of the holotype of *Saimiri ustus* (MNHN-ZM-2007-1540) provided by MNHN - L. Flame RECOLNAT – 2014.

Emended diagnosis: Gothic arch above the eyes; bare ears; crown bluish orange; back chestnut speckled with black; forelimbs burnt yellow from hands up to the elbows; hindlimbs burnt yellow restricted to the feet and ankles; throat and chest whitish.

Variation: Females present the preauricular patch black that extends until the arch above the eyes and the ears with some black hairs scattered on the crown.

Comparison: Saimiri ustus can be distinguished from *S. madeirae* by the coloration of the crown (golden yellowish vs. bluish gray) and the forelimbs (burnt yellow/orange vs. gray). *Saimiri ustus* and *S. madeirae* differ from the other species of *Saimiri* because they have bare ears while hair tufts are present on the ears of all other *Saimiri* species.

Distribution: *Saimiri ustus* is endemic to Brazil, occurring in the states of Pará on both sides of Tapajós River to the left bank of Xingu River and in Rondônia occurs on the right bank of the Madeira River, between Guaporé and Ji-Paraná rivers (Figure 24). It is unknown if in Mato Grosso and Amazonas states this species occurs in sympatry with *S. madeirae*.

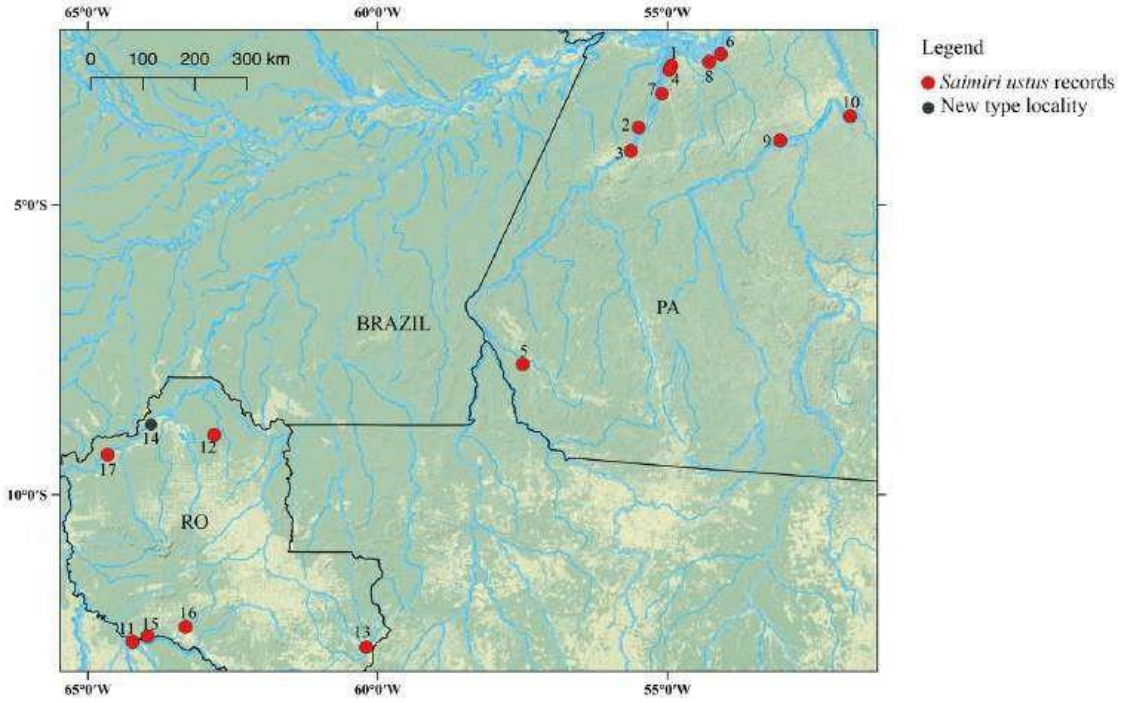

Figure 24. Geographic distribution of the specimens of *Saimiri ustus* studied. Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality. Acronyms of Brazilian states are only provided for those entities where the species is known to occur. Acronyms: PA: Pará, RO: Rondonia.

Remarks: This taxon has been accepted as valid by several authors (Cabrera, 1958; Hill, 1960; Hershkovitz, 1984; Groves, 2001, 2005; Rylands *et al*., 2013). Phylogenies constructed with mitochondrial loci (Lynch Alfaro *et al*., 2015; Ruiz-Garcia *et al*., 2015) have indicated that what we currently recognized as *S. ustus* is polyphyletic. Based in our genomic data (Mercês *et al*., in preparation), morphological, and cranio-dental analyses we restrict the golden-backed squirrel monkey *Saimiri ustus* to the southwest part of the currently recognized distribution; the northwest part of the distribution is instead inhabited by another taxon of bare-eared squirrel monkey, *Saimiri madeirae*.

Status: Near threatened (IUCN, 2015). After our taxonomic change and update of the geographic distribution, the level of threat to this taxon might have increased, considering that its area was reduced to more than half of the original size, and the species occurs in the "arc of deforestation" region.

Specimens examined (n=126): BRAZIL – *Pará*, Carixicatuba (AMNH 95007, MZUSP 5523, 5525-30, 10515), Fordlândia (MZUSP 10101-02, 19142-53,19711-15, 19717-19, 19721, 19723-25), Monte Cristo (MZUSP 3613-14), Piquiatuba (AMNH 95012, MZUSP 5524, 10531), Cururu River (LACM 27264, 27265), Santarém (AMNH 95003), Santarém, Curuá-Tinga (MN 11579), Santarém, Curuá River (MN 21643, 23537, 33598); *Rondônia*, Costa Marques (AMNH 209935), UHE Samuel (MPEG 21712-21747, 21915-21923, 2950-21953, 22992, 23030, 23031, 23033, 23180, 35305, MN 27960,

28490-94), Porto Velho, UHE Jirau (MPEG 43710-43710 [the type locality restricted here]), São Francisco do Guaporé (MPEG 42958).

***Saimiri collinsi* Osgood, 1916**

Saimiri sciurea collinsi Osgood, 1916: 215; original description (see below for type locality).

Saimiri collinsi Mercês *et al.*, 2015: 432. First binomial current use.

Type material: "Adult male. Field Museum of Natural History no. 19534 (Figure 25). Collected November 15, 1911 by E. Snethlage". Emilie Snethlage collected three specimens in Fazenda Teso. She sent two to the Field Museum of Natural History (FMNH 19534, 19535) and the third stayed at Goeldi Museum (MPEG 1378).

Type locality: "Fazenda Teso, near Soure, Marajó Island, Brazil".

Emended diagnosis: Gothic arch above the eyes; ears with tuft; crown grayish with yellow; hands and forearms dark tawny; back chestnut; in the hindlimbs the dark tawny goes beyond the ankles up to the knee; throat and chest whitish; tail pencil bushy.

Variation: *Saimiri collinsi* females present a dark preauricular patch that progresses until the lateral side of the crown or temporal region. In some females the preauricular patch is restricted to in front of the ears.

Comparison: *Saimiri collinsi* differs from *S. ustus* by the hair tufted on the ears (present vs. absent, coloration of crown (grayish with yellow vs. bluish orange), coloration of the back (chestnut vs. golden speckled with black) and coloration of the limbs (dark tawny vs. burnt yellow-orange). *Saimiri collinsi* can be distinguished from *S. sciureus* by the coloration of the crown (grayish with yellow vs. gray with little yellow), coloration of the back (chestnut vs. reddish chestnut), and coloration of the forelimbs (dark tawny vs. bright yellow).

Figure 25. Dorsal and ventral view of the holotype of *Saimiri collinsi* (FMNH 19534).

Distribution: *Saimiri collinsi* is endemic to Brazil, south of the Amazon River (Figure 26). It occurs in the states of Amazonas, Pará, Maranhão and Tocantins. The western boundary is not yet well delineated, and there are records west of the Tapajós River (Arapiuns River, Itaituba in Pará, and Parintins in Amazonas). The westernmost register (Parintins, Amazonas) of *Saimiri collinsi* indicates sympatry of this species with *S. madeirae*. *Saimiri collinsi* is also sympatric with *S. ustus* on both banks of the Tapajós River and in the Tapajós-Xingu interfluvium. Its eastern limit seems to be the Cerrado biome, with one record in this biome (Mercês *et al*., 2018). Its southern limits are still unknown. The southernmost record (Araguaína, Tocantins) is situated just beyond 7° S (Mercês *et al*., 2018).

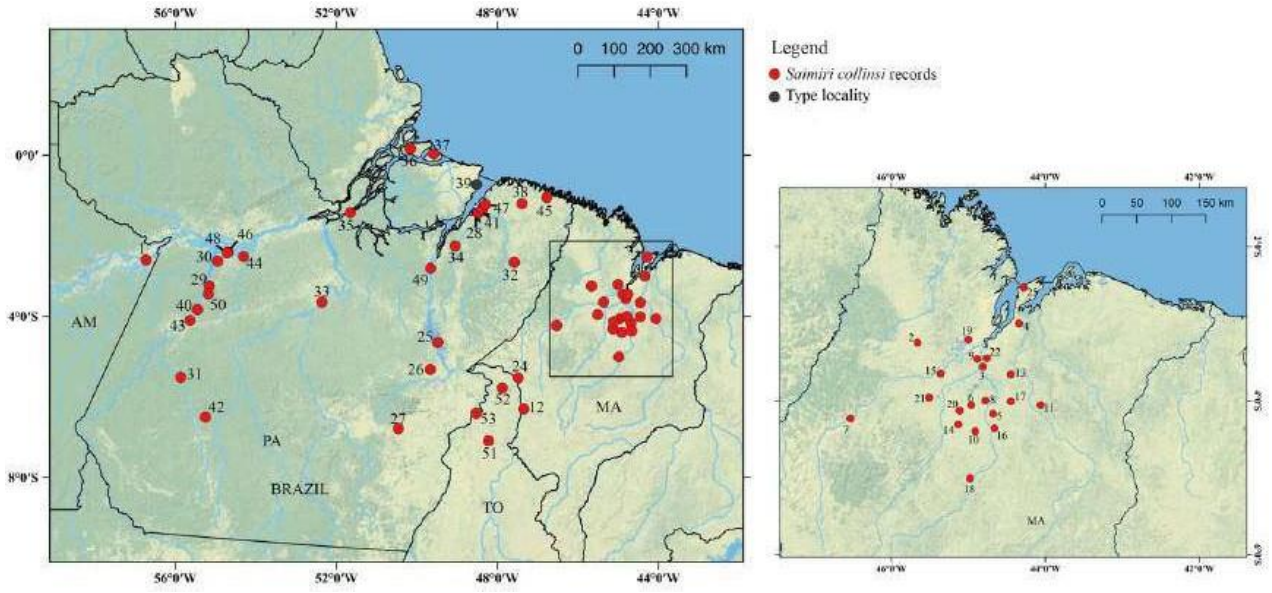

Figure 26. Geographic distribution of the specimens of *Saimiri collinsi* studied and from literature (Mercês *et al*., 2018). Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality. Names of countries and acronyms of Brazilian states are only provided for those entities where the species is known to occur. Acronyms: AM: Amazonas; MA: Maranhão; PA: Pará; TO: Tocantins. The inset square represents the location of the big map which shows sampled localities at Maranhão state

Remarks: *Saimiri sciurea collinsi* was named by Osgood (1916) based on one male from Fazenda Teso, Marajó Island. Lima (1945), Cabrera (1958) and Hill (1960) considered this name valid. Hershkovitz (1984), Thorington (1985), Costello *et al*. (1993) and Groves (2001, 2005) considered this name as a synonym of *Saimiri sciureus sciureus*. Lavergne *et al*. (2010) found evidence in their cytochrome b phylogeny that the Marajó population should be considered distinct from *S. sciureus* and be classified as a subspecies of *S. ustus* (I. Geoffroy, 1843). Chiou *et al*. (2011) considered that this classification to be wrong, due to the priority principle from ICZN, because the oldest name of the species group would be *S. cassiquiarensis* (Lesson, 1840). Mercês *et al*. (in preparation) identified a second lineage, that was called *S. collinsi* 2 from two localities (Faro and Juruti, Pará). This lineage did not form a monophyletic clade with *S. collinsi* 1. In a mitochondrial loci analyses, Mercês *et al*. (2015) recovered this clade as sister to the other samples of *S. collinsi*. Despite the evidence of paraphyly from ddRADseq analysis, thus is necessary further investigation with more samples to better understand the position of this lineage.

Status: Least Concern by Brazilian assessment (Silva Junior *et al*., 2015); Near Threatened (IUCN. 2015).

Specimens examined (n=175): BRAZIL – *Amazonas:* Parintins, Serra de Parintins (AMNH 93673-93676); *Maranhão*: Bacabal, Fazenda Lagoa Nova (MPEG 23174); Bacabal, BR-316, left bank of Mearim River (MPEG 21989); Imperatriz (MPEG 1904, 2448), Lago da Pedra, Pedra Preta, Alto da Liberdade (MPEG 23029, 23032), Rodovia Belém-Brasília (LACM 27267, 27266, 27269); *Pará*: Ananindeua, CENP (MPEG 21452, 21454); Ananindeua, mouth of Traquateua River (MPEG 707-8); Belém, Utinga, Água Preta (MPEG 21460), Utinga (MN 2882); Bragança (MPEG 130); Cametá (MZUSP 5531); Chaves, igarapé Taperebá (MPEG 1784); Chaves, Fazenda São Vicente (MPEG 782-85); Curionópolis, Projeto Cristalino (MPEG 38485, 38489); Faro, Floresta Estadual de Faro (MPEG 39848, 39862); Cachoeira do Espelho, Xingu River (MZUSP 25435); mouth of Tapajós River (MPEG 660); Caviana Island, Fazenda São Luiz (MPEG 22033, 23055, 35284-86, 35296, 35299); Island of Gurupá, Casa Santo Antônio, left bank of Jaburu River (MPEG 21450); Island of Gurupá, Mariony River (MPEG 22974); Mexiana Island (MPEG 35295, 35297); Itaituba (MPEG 2400); Jacundá, 126 km south of Tucuruí, right bank of Tocantins River (MPEG 12182-84), 120 km south of Tucuruí, right bank of Tocantins River (MPEG 12185-90); Juruti, Acampamento Barroso (MPEG 39472-73); Marajó (LACM 27268), igarapé Taperebá (MZUSP 8677-78, 19704-5); Nova Timboteua (MN

33528-46, 33548-63, 33565-75), Timboteua Velha, Fazenda São Francisco da Trombeta (MN 23531-32); Porto de Moz (MN 33526- 27); Santa Bárbara, comunidade Araci (MPEG 37915, 37939, 38175); Santarém (MPEG 21451, 21453, 21458, MN 11942, 11943-50, 11952-53, 11956-60, 11962-63, 11966-73), Santarém, Arapiuns (MPEG 21461), Taperinha (MPEG 36); Santo Antônio, Tocantins River (MZUSP 13473); Arapiuns River, Tapajós (MPEG 664-65); Soure (MPEG 1367, 1379-80); Soure, Fazenda Teso (MPEG 1378, 1387, 1388, FMNH 19534 [holotype of *S. collinsi*], 19535); Tucuruí, Operação Curupira (MPEG 21456), UHE Tucuruí (MPEG 21455, 21462-64), 126 km south of Tucuruí, right bank of Rio Tocantins (MPEG 12180-81); 170 km south of Tucuruí, left bank of Rio Tocantins (MPEG 12192-97); 20 km south of Jacundá, left bank of Rio Tocantins (MPEG 12191); Acampamento Saúde IV (MPEG 12198-99); BR 010, km 93 (MZUSP 8921-22); *Tocantins*: Araguatins (MZJH 53-54).

***Saimiri vanzolinii* Ayres, 1985**

Saimiri vanzolinii Ayres, 1985: 148; original description (see below for type locality).

Type material: The holotype consists of an open skin with complete skeleton of an adult male (MZUSP 15474) collected on July 25, 1983 by J. A. Ayres and P. E. Vanzolini. We analyzed the paratypes (MZUSP 19016 and MZUSP 15472). The skins are well preserved (Figure 27), and the skulls are intact.

Type locality: at "left (north) bank of the Lake Mamirauá, at the mouth of the Rio Japurá, state of Amazonas, Brazil (02º59'S, 64º55'W)".

Figure 27. Paratype of *Saimiri vanzolinii* (MZUSP 19016).

Emended Diagnosis: Roman arch above the eyes; ears with tuft; crown is black; hands, forearms and feet golden yellow; back blackish, forming a continuous blackish area from the head to the tail; throat whitish; chest burnt yellow; tail pencil thin.

Variation: Adult females present darker back than males.

Comparison: *Saimiri vanzolinii* differs from *S. boliviensis* by the coloration of the back (blackish vs. grayish with yellow) and chest (burnt yellow vs. yellowish). *Saimiri vanzolinii* can be distinguished from *S. cassiquiarensis* by the arch format (roman vs. gothic), by the coloration of the crown (blackish vs. yellowish), back (blackish vs. brighter reddish), limbs (burnt yellow vs. orange), and by the tail pencil (thin vs. bushy). *Saimiri vanzolinii* differs from *Saimiri* sp. n. by the arch format (roman vs. gothic), by the coloration of the crown and nape (blackish vs. grayish), by the coloration of the back (blackish vs. grizzled gray speckled with yellow), coloration of the forearms (golden yellow vs. grizzled gray) and coloration of the chest (burnt yellow vs. whitish).

Distribution: *Saimiri vanzolinii* is endemic to Brazil. The northern and eastern limits are formed by the Japurá River. The southern limit is Solimões River. The western limit is the Paraná do Jarauá (Figure 28). The surveys of Paim *et al*. (2013) reduced the original range proposed by Ayres (1985) from 950 km^2 to 870 km^2, because no individuals were found on Cauaçu Island.

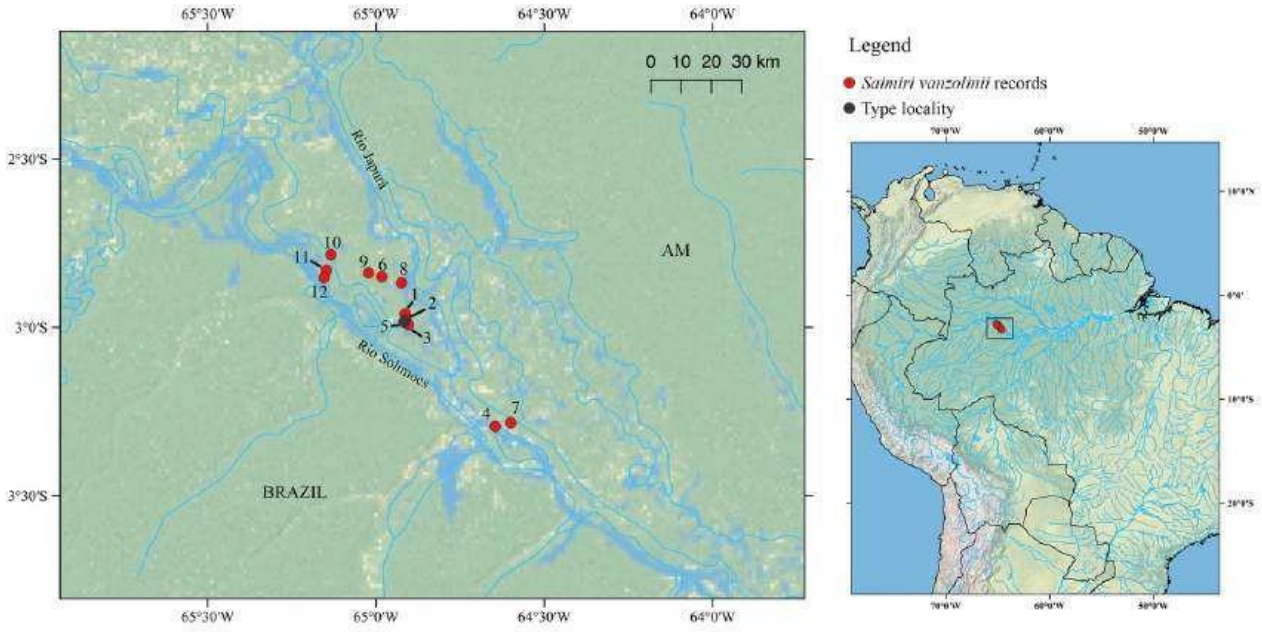

Figure 28. Geographic distribution of the specimens of *Saimiri vanzolinii* studied and from literature (Paim *et al*., 2013). Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality. Acronym: AM: Amazonas.

Remarks: Hershkovitz (1987a) listed *S. vanzolinii* as subspecies of *S. boliviensis* based in their morphology (Roman arch). Groves (2005) classified it as a valid species. This species was widely accepted as valid based on morphology (Groves, 2001; Silva-Júnior & Queiroz, 2008; Rylands *et al*., 2013). Lynch Alfaro *et al*. (2015) included this taxon in their mtDNA phylogeny, which established *S. ustus* as their sister species; however in our genomic-wide study with ddRADseq (Mercês *et al*., in preparation), we recovered *S. vanzolinii* as most closely related to *S. boliviensis*, forming a clade that

shares the same morphology, the Roman group. This is concordant with the classification proposed by Ayres (1985) and Hershkovitz (1987a).

Status: Vulnerable (IUCN, 2015).

Specimens examined (n=4): BRAZIL – *Amazonas*, Alvarães (IDSM 1219, IDSM 1221), Lago Mamirauá, Foz do Japurá (MZUSP 15472, 19016).

Saimiri boliviensis **(I. Geoffroy & De Blainville, 1834)**

Callithrix boliviensis I. Geoffroy & De Blainville, 1834: 89; original description (see below for type locality).

Calitrix entomophagus d'Orbigny, 1835: pl. 14. Type locality "Guarayos Mission, Rio San Miguel, Santa Cruz, Bolivia".

Saimiri boliviensis nigriceps Thomas, 1902: 246. Type locality: "Cosnipata, Eastern Peru".

Saimiri boliviensis Elliot, 1913:315. First use of the current binomial.

Saimiri boliviensis jaburuensis Lönnberg, 1940: 10. Type locality: "Jaburú, W. of the Rio Purús", Amazonas, Brazil.

Saimiri boliviensis pluvialis Lönnberg, 1940: 12. Type locality: "Lago Grande, rio Jurua", Amazonas, Brazil.

Type Material: Male, mounted skin with skull. The lectotype is housed at Muséum d'Histoire Naturelle, Paris (MNHN-ZM-2005-930; Figure 29).

Type locality: "Guarayos Mission, Rio San Miguel, Santa Cruz, Bolivia".

Figure 29. Lateral view of *Saimiri boliviensis* (MNHN-ZM-2005-930) lectotype provided by MNHN - L. Flame RECOLNAT – 2014.

Emended diagnosis: Roman arch above the eyes; ear with tuft; crown blackish with the hair tips black and the basal part cream; hands and forearms golden yellow; feet golden yellow to a little beyond the ankles; back grayish yellow; tthroat whitish; chest is yellowish; tail pencil thin.

Variation: Morphological variation can be individual or sexual in *Saimiri boliviensis*. The crown can vary from dark agouti to blackish depending on the sex. Males have less variation in the crown, usually presenting a dark agouti crown, while in females the crown varies from black agouti to fully black. Adult females may also present darkening in the shoulder, back and upper tail region.

Individual variation can be observed in males from the same locality. For instance, of the specimens from Lago Grande, Juruá River, one presented blackening in the back and in the upper part of the tail (NRM 602446) and the other had a greyish yellow back (FMNH 50878), with a generally lighter appearance compared to the first specimen.

Distribution: western of Brazilian Amazonia, south of Solimões River, between Juruá and Purus Rivers in the states of Amazonas and Acre, extending south until southeastern of Peru (in the departments of Madre de Dios, Cuzco, Huánuco and Ucayali), and the north and central region of Bolivia (departments of Beni, Cochabamba, Pando and Santa Cruz) in the upper Madeira River (Figure 30).

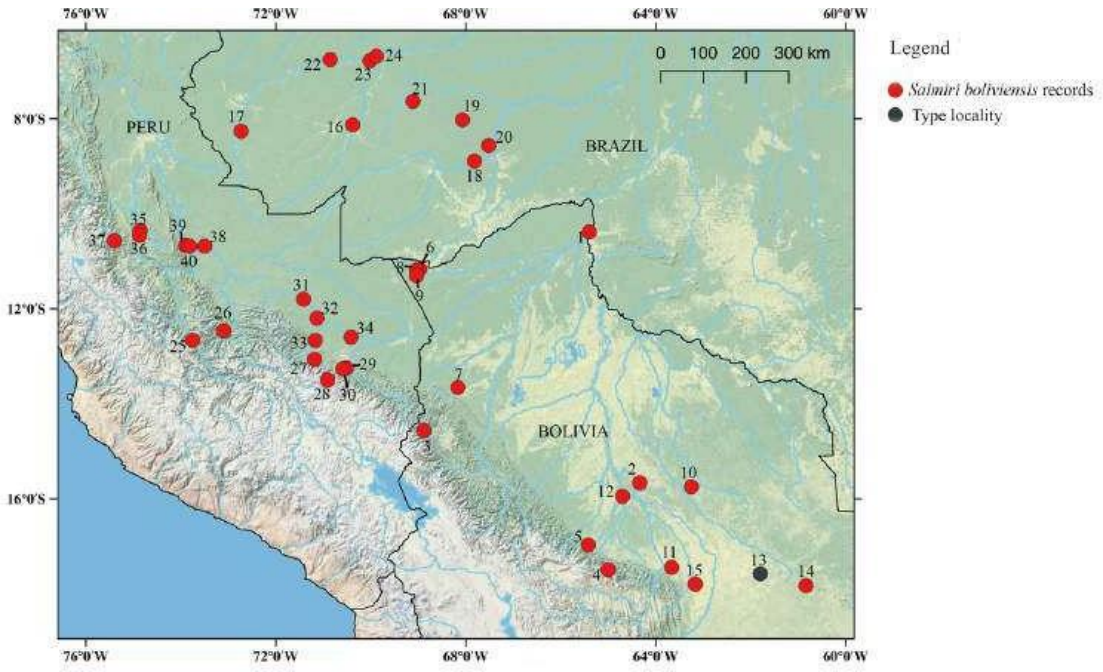

Figure 30. Geographic distribution of the specimens of *Saimiri boliviensis* studied and from literature (Hershkovitz, 1984). Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality. Names of countries are only provided for those entities where the species is known to occur.

Remarks: *Callithrix boliviensis* was named in a footnote by I. Geoffroy & De Blainville (1834). One year later d'Orbigny illustrated *Calitrix entomophagus*, based on the same specimen. Although I. Geoffroy & De Blainville (1834) mention in their note that d'Orbigny was the author, the ICZN ruled

that the authors were those who had written the description first (Article 50.1). Thomas (1902) described *Saimiri boliviensis nigriceps* as presenting the colors of *S. boliviensis* but with a deep black head. Regarding other synonyms of *S. boliviensis*, Lönnberg (1940) argues that *S. b. jaburuensis* is generally darker and more colored then the specimens from Beni, Bolivia, but the crown is agouti to blackish, while *S. b. pluvialis* is much darker in the back with the crown blackish. Lönnberg (1940) considered that *S. b. jaburuensis* was different from *S. b. nigriceps* Thomas, 1902. Hershkovitz (1987a), after analyzing the type material of S. *b. jaburuensis* and *S. b. pluvialis* considered both as valid subspecies that differ from *S. b. boliviensis* by the crown pelage. After our analysis of all *S. b. boliviensis* synonymies we decided to keep all as junior synonyms, and considered *Saimiri boliviensis* as a full species, separated from other species of the Roman group.

Status: Least Concern (Wallace *et al*., 2018).

Specimens examined (n= 70): BOLIVIA – *Beni*: Mamoré (AMNH 211591), Marban (AMNH 211592, 211594); *Pando*: Tahuamanu (FMNH 123966); *Santa Cruz*: Guarayos Mission, San Miguel River (MNHN-ZM-2005-930 [holotype of *S. boliviensis*]), Ichilo (AMNH 211635-211639, 211641, 211643, FMNH 21409, 51874); Cochabamba (AMNH 38795, 40835, FMNH 21538); BRAZIL – *Acre*: Feijó (MPEG 21858, 21859), Porto Walter (MPEG 22979); *Amazonas*: Eirunepé (MPEG 22977-78), Eirunepé, Lago Miranda (IDSM FES 55-56), Jaburu, West of Purus River (NRM 590247 [syntype of *S. b. jaburuensis*]), Lago Grande, Juruá River (FMNH 50878, NRM 602446 [syntype of *S. b. pluvialis*]). PERU – *Ayacucho:* Huamanga (AMNH 208075); *Cuzco*: Quispicanchi, Quincemil (FMNH 68322, 75129, 75130, 78674-76), Cosnipata (BMNH 1902.69.5.13.1 [holotype of *S. b. nigriceps*]); *Loreto*: Upper Ucayali (AMNH 147373); *Madre de Dios*: Manu (FMNH 84222-25, 98038-39, 170289); *Pasco*: Oxapampa, Nevati Mission (AMNH 230814, 230816-230817, 239868-239874, 240000), San Pablo (AMNH 230819-230823); *Ucayali*: Atalaya (AMNH 76003, 76005, 76007, 76008, 98271), Lagarto (AMNH 76581-76586).

***Saimiri peruviensis* Hershkovitz, 1984**

Saimiri boliviensis peruviensis Hershkovitz, 1984: 183; original description (see below for type locality).

Type material: Adult male with skin and skull, housed at Field Museum of Natural History (FMNH 122800; Figure 31), collected on November 25, 1980, by Philip Hershkovitz.

Type locality: "Rio Samiria, right bank opposite Biological Station Pithecia, Reserva Nacional Pacaya – Samiria, Loreto Province, Loreto, Peru; altitude about 130 above the sea".

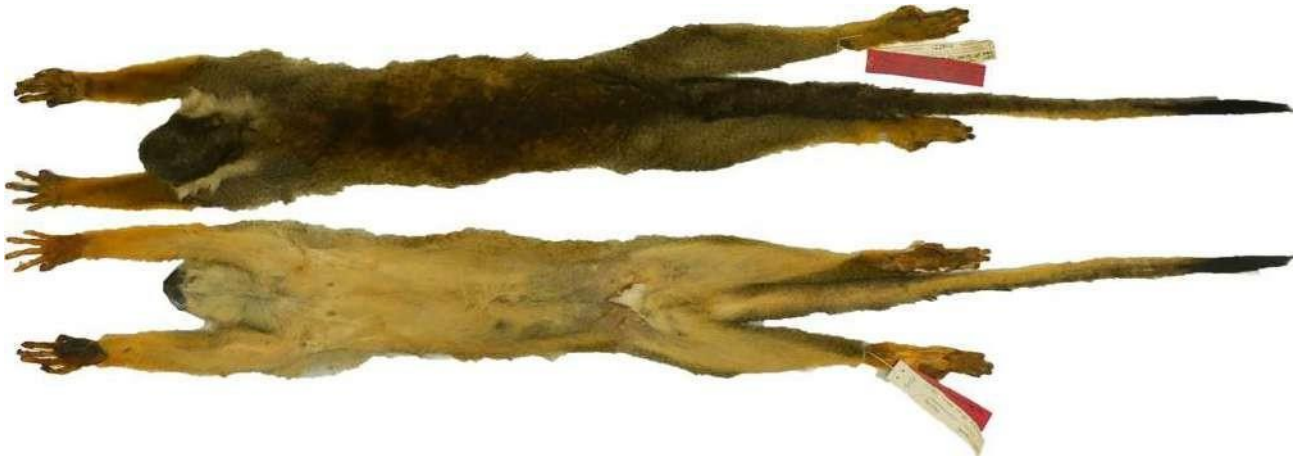

Figure 31. Dorsal and ventral view of *Saimiri peruviensis* (FMNH 122800) holotype.

Emended diagnosis: Roman arch above the eyes; ear with tuft; crown agouti; hands and forearms golden yellow; feet golden yellow; back dark chestnut; throat and chest yellowish; tail pencil thin.

Comparison: *Saimiri peruviensis* can be distinguished from *S. boliviensis* by the coloration of the crown (agouti vs. blackish) and back (dark agouti vs. grayish yellow). *Saimiri peruviensis* differs from *S. vanzolinii* by the coloration of the crown (agouti vs. blackish) and back (dark chestnut vs. blackish). *Saimiri peruviensis* can be distinguished from *S. macrodon* by the arch format (roman vs. gothic), by the coloration of the crown (agouti vs. grayish olivaceous), back (dark chestnut vs chestnut with orange), forelimbs (golden yellow vs. yellowy orange) and chest (yellowish vs. whitish).

Distribution: Saimiri peruviensis is endemic to central and north region of Peru (Figure 32). The north limit is Marañón-Amazonas River, from west bank of Tapiche River to west of the Huallaga River, and south through the departments of San Martin, Huánuco and Ucayali.

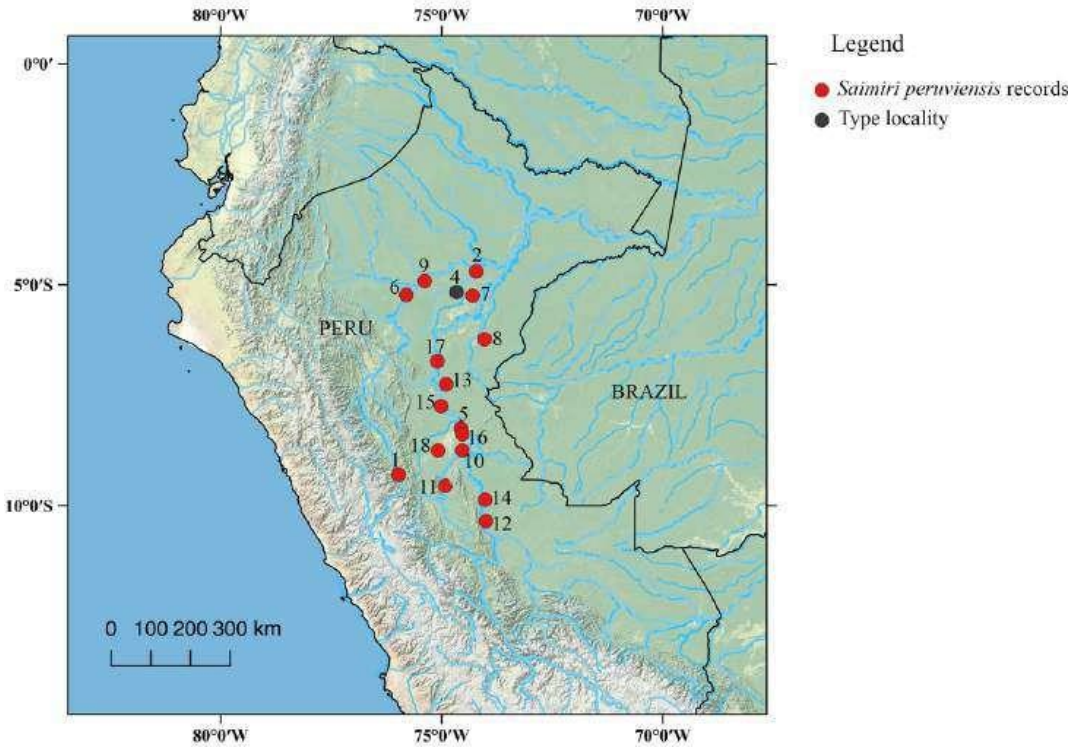

Figure 32. Geographic distribution of the specimens of *Saimiri peruviensis* studied and from literature (Hershkovitz, 1984). Numbers correspond to collection localities listed in the gazetteer (see Appendix 1) and the black dot refers to the type locality.

Remarks: *Saimiri boliviensis peruviensis* was named by Hershkovitz (1984) based on one holotype and two paratypes from Samiria River. This subspecies was regarded as valid by Groves (2001), while Groves (2005) classified it as a synonym of *S. boliviensis*. Boinski & Cropp (1999), Lavergne *et al.* (2010), Chiou *et al*. (2011) with the mitochondrial genome and Ruiz Garcia *et al.* (2015) recovered *S. boliviensis* and *S. peruviensis* as sister clades, while Lynch Alfaro *et al*. (2015) did not observe any difference between *S. boliviensis* and *S. peruviensis*. Considering that Lynch Alfaro *et al*. (2015) analysis was based only in two mitochondrial markers, after analyzing the morphology (four of eleven morphological traits presented differences between the taxa) and cranio-dental characters (presented statistical support for separation between *S. boliviensis* and *S. peruviensis*), and molecular data available in literature we decided to elevate *S. b. peruviensis* to species status, and here it is considered a full species, *Saimiri peruviensis.*

Status: Least Concern (IUCN, 2015).

Specimens examined (n=53): PERU – *Huánuco*: Tingo María (FMNH 24196-206, 24209, 56848-49), *Loreto*: Maynas (FMNH 35083, AMNH 98265-66), Samiria River (AMNH 188072, 188074, 188076), Santa Elena (FMNH 86972-76), Biological Station Pithecia (FMNH 122799, 122800 [holotype of *S. b. peruviensis*], 122801), *Ucayali*: Coronel Portillo, Yarinacocha (FMNH 55495-55500, 62073, 62075), Sarayacu (AMNH 76369-75, 76377-83), Tapiche River (AMNH 99251, 99253).

CONCLUSION

This work represents a comprehensive overview of the systematics of the squirrel monkeys, compiling information about their taxonomy, geographic distribution, individual variation, differentiation between species and species history. Based on the largest sample of the genus thus far examined, we recognize thirteen species of *Saimiri*. We identified an unnamed species (*Saimiri* sp. n.), elevate three taxa to the species level (*S. albigena*, *S. peruviensis* and *S. citrinellus*), and resolve the debate about the taxonomy of the bare-eared group, recognizing two species with this morphology (*S. madeirae* and *S. ustus*). Through the designation of a neotype for *Saimiri cassiquiarensis* (Lesson, 1840) the taxon has now a name-bearing type specimen that is crucial for any further taxonomic study.

Despite our extensive sampling, some species remain imperfectly known and characterized. The absence of specimens of *Saimiri madeirae* from central Amazonia prevents robust delimitations of their distribution limits. For instance, only a single picture record is available in northwestern Brazil, in Urucu region, to document the eastern and northern limits of *S. madeirae*. The lack of

information from Mato Grosso also restricts our understanding about *S. ustus* and *S. madeirae* in this region.

From the conservation perspective, IUCN (2015) indicated that six of the thirteen species presented some degree of threat (*S. citrinellus, S. oerstedii, S. albigena, S. vanzolinii, S. ustus,* and *S. collinsi*). The most threatened species among squirrel monkeys is *Saimiri citrinellus,* that is classified as Endangered. The entire population is fragmented (Rylands *et al*., 2013). Three species were assessed as Vulnerable (*S. oerstedii, S. albigena* and *S. vanzolinii*). They are endemic species and present small geographic distribution. *Saimiri vanzolinii* presents one of the smallest geographic distribution among Neotropical primates, occurring in 870 km^2. The fifth species that presented some degree of threat is *S. ustus*. After our taxonomic proposal, the split of the two species of bare-eared squirrel monkey (*S. ustu*s and *S. madeirae*) may change our understanding about the risk of extinction of these taxa. *Saimiri ustus* as previously recognized was classified as near threatened (IUCN, 2015), mainly due to the high rate of habitat loss. Now the geographic distribution was reduced to almost the half of the previous estimated the risk of extinction increases. *Saimiri collinsi* was assessed as Near Threatened because it occurs in area with a high rate of habitat loss in the "arc of deforestation" in the Amazon. In some areas of its distribution the populations have been reduced or extirpated (see Mercês *et al*., 2018).

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Appendix 1

Gazetteers

***Saimiri sciureus* (Linnaeus, 1758)** – The numbers in the map (Fig. 8) refers to the following localities: Brazil – 1. Amazonas, Nhamundá, Paraná do Bom Jardim; 2. Amapá, Cachoeira de Santo Antonio, Jari River; 3. Amapá, Fazenda Nova California, Araguari River; 4. Amapá, igarapé Novo, Iratapuru River; 5. Amapá, Iracema, Aporema River; 6. Amapá, Itaubal, Fazenda Lago Novo; 7. Amapá, Tracajatuba River; 8. Amapá, Tracajatuba River; 9. Amapá, RDS Iratapuru River, Igarapé Baliza; 10. Amapá, RDS Iratapuru River, Cupixi River; 11. Amapá, Amapari River; 12. Amapá, Anacui River; 13. Amapá, Vila Nova River; 14. Amapá, Oiapoque, Vila Velha de Caciporé; 15. Pará, Cachoeira Porteira, Trombetas River; 16. Pará, Cachoeira Porteira, Mapuera River; 17. Pará, Lago Paru, Trombetas River; 18. Pará, Paiçandu, Paraná do Bom Jardim; 19. Pará, Uchizal, Paru do Leste River; 20. Pará, Faro, Nhamundá River; 21. Pará, Alenquer, ESEC Grão Pará Sul; 22. Pará, Almeirim, FLOTA Paru; 23. Pará, FLOTA de Faro, Nhamundá River; French Guiana – 24. 20km West of Tonate; 25. Entre Trois Sauts en Mont Saint Marcel, Sud Oyapock; 26. Environ crique Arouani; 27. Forêt à palmier pinot sur le canal de Kaw; 28. Ouanary; 29. St Jean du Maroni; 30. Trois-Sauts, sur l'Oyapock; 31. Guyana, Kartabo (type locality); 32. French Guiana, Cayenne; 33. Guyana, Cuyuni-Mazaruni Region; 34. Guyana, East Demerara West Coast Berbice, Essequibo R, Rockstone; Suriname – 35. rokopondo, Saramacca, Loksie Hattie; 36. Brokopondo, Saramacca, Finisanti; 37. Nickerie, Kayser Gebergte Airstrip, Zuid; 38. Nickerie, Wilhelmina Mountains; 39. Saramacca, La Poule.

***Saimiri cassiquiarensis* (Lesson, 1840)** - The numbers in the map (Fig. 10) refers to the following localities: *Brazil* – 1. Amazonas, Codajás; 2. Amazonas, Japurá river; 3. Amazonas, Barcelos; 4. Amazonas, Manacapuru, ilha Maracati; 5. Amazonas, Manacapuru; 6. Amazonas, Maraã, RDS Amanã; 7. Amazonas, Maraã, comunidade Boa Esperança; 8. Amazonas, Maraã, Coracizinho River; 9. Amazonas, Paraná do Manacabi; 10. Amazonas, Parauari; 11. Amazonas, RDS Mamirauá, ponto A; 12. Amazonas, RDS Mamirauá, ponto B; 13. Amazonas, RDS Mamirauá, ponto C; 14. Amazonas, Panema River; 15. Amazonas, Uarini, cano do Lago Mamirauá; 16. Amazonas, Uarini, cano do Lago Mamirauá B; 17. Amazonas, Uarini, rio Japurá; 18. Roraima, Mucajaí river; 19. Roraima, Apiaú; 20. Roraima, colônia do Apiaú; 21. Roraima, Mucajaí, 42km South of Boa Vista; *Venezuela* – 22. Amazonas, mouth of Ocamo River; 23. Amazonas, Cassiquire 15 mile above Capibara; 24. Amazonas, Cassiquire River, El Merey; 25. Amazonas, Atapabo, Mount Duida; 26. Boca Mavaca River; 27. Cassiquire River; 28. Mavaca River, 108 km southeast of Esmeralda; 29. San Juan, Manapiare River; 30. Amazonas, Atures, Ocamo River; 31. Tamatama, Orinoco River.

***Saimiri albigena* (Pusch, 1941) –** The numbers in the map (Fig. 12) refers to the following localities: *Colombia* – 1. Meta, San Juan; 2. Guaviare, Lower Guayabero River; 3. Arauca; 4. Medina (type locality); 5. Huila, Gabinete; 6. Huila, San Antonio de Anaconia; 7. Huila, Vegalarga; 8. Huila, Tarqui; 9. Huila, Brusela; 10. Huila, Palestina; 11. Huila, Palestina b; 12. Huila, Guacalito;. 13. Huila, Guadalupe; 14. Huila, Altamira; 15. Meta, La Uribe; 16. Meta, San Vicente del Caguan; 17. Meta, La Macarena; 18. Guaviare, Granada; 19. Guaviare, San Jose de Guaviare; 20. Meta, Villavicencio A; 21. Meta, Villavicencio B; 22. Cundinamarca; 23. Casanare, Tamara; 24. Casanare, Hato Corozal; 25. Casanare, Agua Azul; 26. Casanare, Mani; 27. Arauca, Saravena; 28. Arauca, Tame.

***Saimiri oerstedii* (Reinhardt, 1872) –** The numbers in the map (Fig. 14) refers to the following localities: *Costa Rica* – 1. Golfito; 2. Puntarenas, Palmar; *Panamá* - 3. Chiriqui, Boqueron; 4. David, Chiriqui (type locality).

***Saimiri citrinellus* Thomas, 1904 –** The numbers in the map (Fig. 16) refers to the following localities: *Costa Rica* – 1. Pirris River, Pozo Azul (type locality); 2. Manuel Antonio; 3. Uvita; 4. Cerros; 5. Esterillos; 6. Damas; 7. Chirraca; 8. Gamalotillo; 9. Isla Damas; 10. Bambú; 11. 2 km north of Cerritos; 12. Quepos; 13. Villanueva; 14. La Managua; 15. La Vasconia.

***Saimiri macrodon* Elliot, 1907 –** The numbers in the map (Fig. 18) refers to the following localities: *Brazil* – Amazonas 1. Altamira, left margin of Juruá River; 2. Atalaia do Norte, Javari River; 3. Auati-Paraná Lago Pema; 4. Eirunepé; 5. Estirão do Equador; 6. Igarapé do Gordão, Juruá River; 7. Ipixuna, left margino of Juruá River; 8. Jutaí, RDS Cujubim; 9. Jutaí, RESEX Jutaí; 10. Santo Antônio do Iça; 11. ESEC Jutaí-Solimões; 12. RESEX Auati-Paraná, Furo do Batelão; *Colombia* – 13. Caqueta, Florencia; 14. Caqueta, La Tagua; 15. Huila, Acevedo, San Adolfo; 16. La Montanita; 17. Leticia; 18. Putamayo, San Antonio, Mecaya River; *Ecuador* – 19. Copataza River (type locality); 20. Napo, upper Payamino River; *Peru* – 21. Loreto, Alto Yavari Mirim; 22. Loreto, Alto Amazonas, Morina River; 23. Loreto, San Fernando, Yavari River; 24. Loreto, Isla de Iquitos, Carococha; 25. Loreto, Isla de Iquitos, San Pedro; 26. Loreto, Isla de Iquitos, Santa Zulema; 27. Loreto, Maniti River, Santa Cecilia; 28. Loreto, Nanay River, Santa Rita; 29, Loreto, Yavari Mirim River, Quebrada Esperanza; 30. Loreto, Tigre River.

***Saimiri* sp. n. Mercês et al., in preparation –** The numbers in the map (Fig. 20) refers to the following localities: *Brazil* – Amazonas: 1. Fonte Boa; 2. Lago do Boiá, Tefé River; 3. Tefé Lake, Porto da Castanha; 4. Maraã, Japurá River, Preguiça Lake; 5. Maraã, right margin of Paraná Aranapú; 6. Paraná do Aiupiá, Auati-Paraná; 7. São Paulo de Olivença; 8. Uarini, left margin of Solimões; 9. Uarini, Paraná do Aiucá A; 10. Uarini, Paraná do Aiucá B; 11. RDS Mamirauá A; 12. RDS Mamirauá B; 13. RDS Mamirauá C; 14. RESEX Juruá A; 15. RESEX Juruá B; RESEX Juruá C; 17. Carauari, right margino f Juruá River.

***Saimiri madeirae* Thomas, 1908 –** The numbers in the map (Fig. 22) refers to the following localities: *Brazil* – 1. Amazonas, Borba, Madeira River; 2. Amazonas, Manicoré, Rosarinho; 3. Amazonas, Parintins, Villa Bella Imperatriz; 4. Amazonas, Humaitá, BR-230 km 16; 5. Amazonas, Lago do Baptista; 6. Amazonas, Coari, Urucu River; 7. Right margin of Madeira River, Humaitá (type locality); 8. Rondonia, Calama; 9. Amazonas, Novo Aripuanã, BR-230; 10. Amazonas, Borba, Santa Barbara

***Saimiri ustus* I. Geoffroy, 1843 –** The numbers in the map (Fig. 24) refers to the following localities: *Brazil* – Pará: 1. Carixicatuba, Tapajós River; 2. Fordlândia; 3. Monte Cristo; 4. Piquiatuba, Tapajós River; 5. Cururu River, Tapajós; 6. Santarém, Curuá River; 7. Santarém tauari; 8. Taperinha; 9. Uruara, Xingu River; 10. Vitória do Xingu, Miguel Xipaia; Rondônia: 11. Costa Marques; 12. Guaporé-Machado interfluvium; 13. Matas do Piroculuía, Guaporá River; 14. Porto Velho, UHE Jirau (type locality); 15. São Francisco do Guaporé, left margin of São Miguel River; 16. Biological Reserve of Guaporé; 17. UHE Samuel, Jamari River.

***Saimiri collinsi* Osgood, 1916 –** The numbers in the map (Fig. 26) refers to the following localities: *Brazil* – Amazonas: 1. Serra do Parintins, Amazon River; Maranhão: 2. Alto Alegre, west of Mearim

River; 3. Arari; 4. Bacabeira; 5, Bacabal, left margin of Mearim River; 6. Bacabal, Fazenda Lagoa Nova; 7. Buriticupu, Fazenda MAPISA; 8. Mangueira, east margin of Mearim River; 9. Vitória do Mearim, Morada Nova; 10. Lago do Junco; 11. Lago Verde; 12.Porto Franco; 13. Matões do Norte, Palmeiral; 14. Lago da Pedra, Pedra Preta; 15. Praia do Açúcar, right margino f Pindaré River; 16. São Luiz Gonzaga do Maranhão; 17. São Mateus; 18. São Roberto; 19. Viana; 20. Olho D'Água das Cunhãs; 21. Santa Luzia, Zutia River; 22. Arari; 23. São Luiz, State Park of Bacanga, Florestal Reserve of Sacavem; 24. Imperatriz, Belém-Imperatriz road; Pará: 25. Jacundá, left margin of Tocantins River; 26. Tucuruí, right margin of Tocantins River; 27. Água Azul do Norte; 28. Belém, Água Preta, Mata do Utinga; 29. Aveiros; 30. Belterra; 31. Bom Jardim; 32. BR-010 km 93; 33. Cachoeira do Espelho, Xingu River; 34. Cametá; 35. Ilha Grande de Gurupá, left margin of Jaburu River; 36. Caviana Island, Fazenda São Luiz; 37. Mexiana Island, Fazenda Santana; 38. Nova Timboteua, Fazenda São Francisco da Trombeta; 39. Fazenda Teso, Soure, Marajó Island (type locality); 40. Tapajós National Forest; 41. Ananindeua, Tracuateua River; 42. Jamanxin-Curá River; 43. Monte Cristo; 44. Os Patos; 45. Bragança, Providencia; 46. Tapajós, Arapiuns River; 47. Santa Barbára do Pará, PA-391 road; 48. Santarém; 49. Santo Antonio, Tocantins River; 50. Tavio, Tapajós; Tocantins: 51. Araguaína, campus of Universidade Federal do Tocantins; 52. Araguatins; 53. Xambioá.

***Saimiri vanzolinii* Ayres, 1985 –** The numbers in the map (Fig. 28) refers to the following localities: *Brazil* – Amazonas: 1. Reserva de Desenvolvimento Sustentável Mamirauá, Lago Teiu; 2. Reserva de Desenvolvimento Sustentável Mamirauá, Lago Mamirauá A; 3. Reserva de Desenvolvimento Sustentável Mamirauá, Lago Mamirauá B; 4. Solimões River; 5. Lago Mamirauá, across from Lago Teiú (type locality); 6. Furo do Buá-Buá; 7. Ilha do Tarará; 8. Setor Jarauá A; 9. Setor Jarauá B; 10. Setor Horizonte A; 11. Setor Horizonte B; 12. Setor Horizonte C.

***Saimiri boliviensis* (I. Geoffroy & De Blainville, 1834) –** The numbers in the map (Fig. 30) refers to the following localities: *Bolivia* – Beni: 1. Mamoré, northwest of Alejandria; 2. Marban, southwest of Buena Hora; 3. Mojos; Cochabama: 4. Carrasco, Todos os Santos; 5. Chapare, Todos os Santos; Pando: 6. Cobija; 7. Ixiamas; 8. Mucden; 9. Narueda; Santa Cruz: 10. Guarayos; 11. Ichilo, Buena Vista; 12. Ichilo, south of Chapare River; 13. San Miguel River; Guarayos Mission (type locality); 14. San Jose de Chiquitos; 15. Santa Cruz de la Sierra; *Brazil* – Acre: 16. left margin of Envira River, 17. Ocidente, right margin of Juruá; Amazonas: 18. Arapixi; 19. National Forest of Purus; 20. Purus River; 21. Pauini River; 22. Eirunepé, São José; 23. Eirunepé, Lago Miranda; 24. Jurua River, Lago Grande; *Peru* – 25. Ayacucho, Huamanga, Apurimac River; Cuzco: 26. Comberciato River; 27. Cosnipata, Marcapata River; 28. Marcapata; 29. Nisiniscato; 30. Quispicanchi, Quincemil; Madre de Dios: 31. Cocha Cashu; 32. Manu, Altamira; 33. Manu, Itahuania; 34. Manu, Colorado River; Oxapampa: 35. Nevati Mission; 36. San Pablo; 37. Pasco, San Juan de Oxapampa; Ucayali: 38. Atalaya, Inuya River mouth; 39. Atalaya, Urubama River mouth; 40. Lagarto, Alto Ucayali.

***Saimiri peruviensis* Hershkovitz, 1984 –** The numbers in the map (Fig. 32) refers to the following localities: *Peru*: 1. Huanuco, Tingo Maria; 2. Loreto, Samiria River; 3. Maynas, Iquitos; 4. Loreto, Samiria River, right bank opposite to Biological Station Pithecia, National Reserve Pacaya (type locality); 5. Ucayali, Yarunacocha; 6. Maynas; 7. Loreto, Pacaya, Ucayali River; 8. Loreto, Punga, left bank of Tapiche River; 9. Loreto, Santa Elena, Samiria River; 10. Pachitae, Pachitae River; 11. Panguana, Pachitae River; 12. Ucayali, Chicosa; 13. Ucayali, Contamana; 14. Ucayali, Cumaria, opposite to Shahuia; 15. Ucayali, Pisque, Ucayali River; 16. Ucayali, Pucallpa; 17. Ucayali, Sarayacu, Ucayali River; 18. Von Humboldt.

Supplementary Material

Graphs of Discriminant Function Analysis of females.

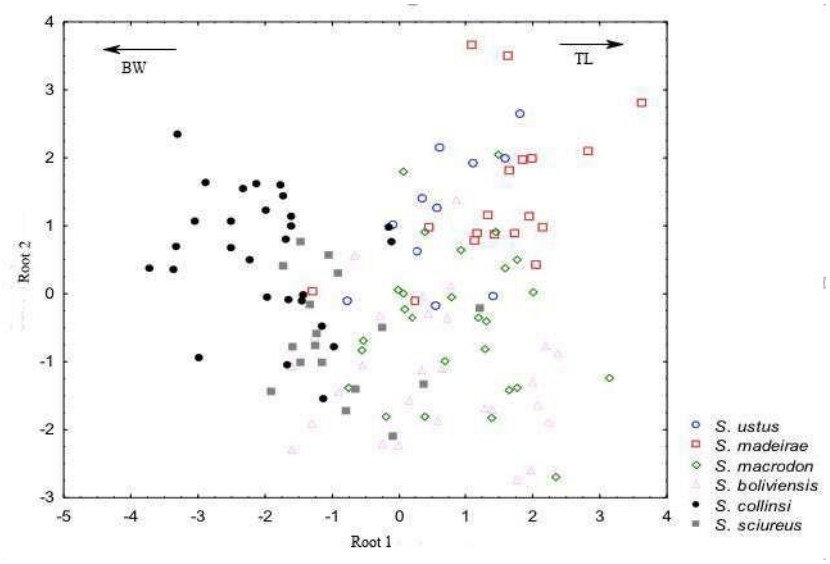

Figure S1. Discriminant function analyses of females for cranio-dental measurements for *Saimiri* based on phylogenomic and morphospecies groups.

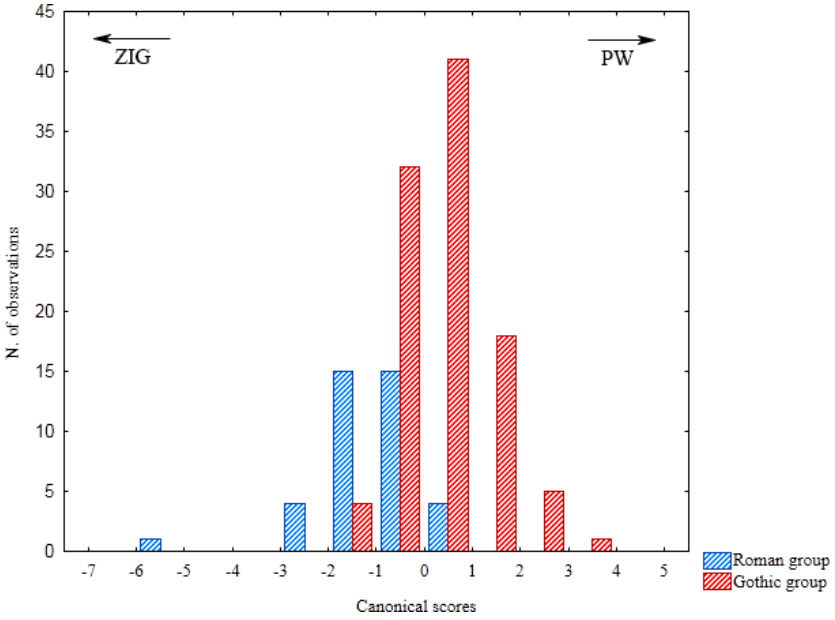

Figure S2. Discriminant function analyses for cranio-dental measurements for *Saimiri* females separated by gothic and roman group.

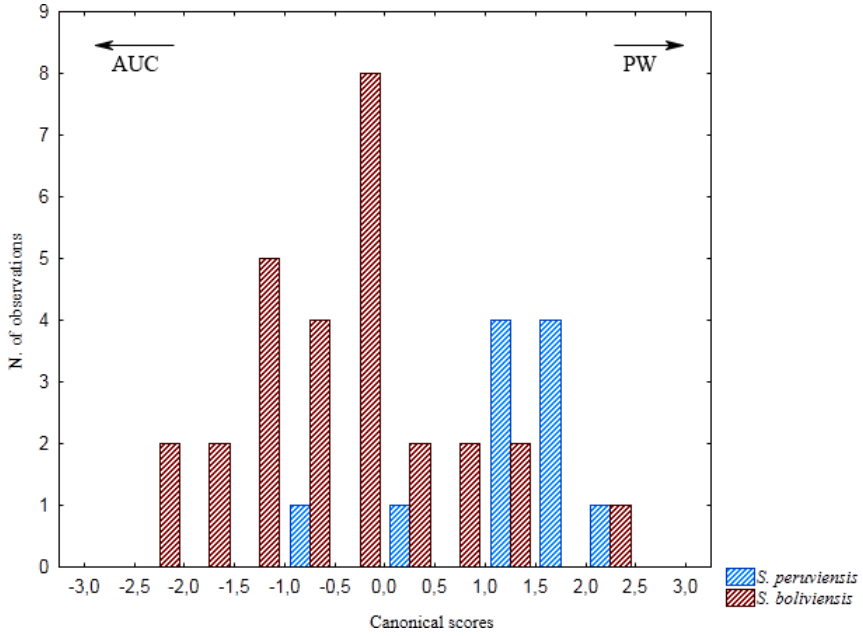

Figure S3. Discriminant function analyses for cranio-dental measurements for females of *S. b. boliviensis* and *S. b. peruviensis.*

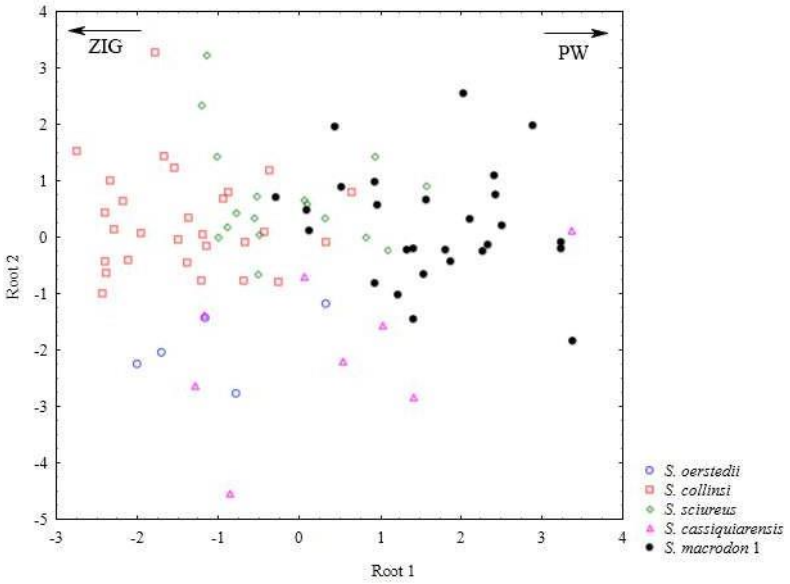

Figure S4. Discriminant function analyses for cranio-dental measurements of females for *S. sciureus* group.

Capítulo 3

New records of *Saimiri collinsi* Osgood, 1916 (Cebidae, Primates), with comments on habitat use and conservation

O Capítulo III desta tese foi elaborado e formatado conforme normas de publicação cientifica da Revista Mammalia, as quais se encontram no Anexo 3.

Short Note

Michelle Pinto Mercês*, Wlainer Silva de Paula and José de Sousa e Silva Júnior

New records of *Saimiri collinsi* Osgood, 1916 (Cebidae, Primates), with comments on habitat use and conservation

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Abstract: *Saimiri collinsi* is a primate that occurs in the Amazon biome and recently was elevated to species status. Despite being an abundant and widespread species, *S. collinsi* distributional limits are still unknown in the transitional region between Amazon and Cerrado biomes. Here we provide 25 new records for the species, obtained through field observation and analysis of museum specimens. Twenty-one records are from Maranhão state, three from Tocantins where the species had not yet been registered and one in Pará state. These records expand its known distribution, which now includes the area of transition between the Amazon and Cerrado, as well as one record in the Cerrado biome. We registered the species in areas with intense forest fragmentation and within different habitat types, including primary and secondary forest, babassu palm forest and capoeira forest. This indicates that *S. collinsi* is a species that can survive in locations with extreme anthropogenic alterations. Nevertheless, out of these new records only the ones in Maranhão are within protected areas. Even these protected areas are undergoing pressures from deforestation, agriculture, livestock and mining, suggesting that these squirrel monkey populations might be threatened in this region.

Keywords: Amazonia; Cerrado; distribution extension; primate; squirrel monkey.

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The squirrel monkey *Saimiri sciureus sciureus* (Linnaeus, 1758) is a widely distributed taxon that occurs throughout the eastern Amazon including four centers of endemism, the Guyanas (east of the Branco and Negro rivers), Belém, Xingu and Tapajós centers, although the southern and eastern limits of this distribution are still unclear (Hershkovitz 1984). Rylands et al. (2013) considered this taxon to be a full species, with two subspecies, *S. s. sciureus* and *S. s. collinsi*, and a further nine taxa in the genus *Saimiri*.

Mercês et al. (2015) recently elevated the two subspecies of *Saimiri sciureus* recognized by Rylands et al. (2013) to full species, and noted that these species were not sister groups. After elevating *Saimiri collinsi* Osgood, 1916 and redefining the ranges of the two taxa, Mercês et al. (2015) observed that each species occurs only in approximately half of the original distribution of *S. sciureus* (sensu Hershkovitz 1984). The Amazon River forms the limit between *S. sciureus* and *S. collinsi*, with the former occurring to the north of this river, and the latter, to the south. The current known range of *S. sciureus* is relatively well defined, being limited to the south by the Amazon River, the west by the Branco and Negro rivers, and the north and east by the Atlantic Ocean. However, the eastern and southern limits of the range of *S. collinsi* are still poorly documented.

In the original description of the species, Osgood (1916) considered *Saimiri collinsi* to be endemic to Marajó Island, although Mercês et al. (2015) verified that the species found on this island is the same that occurs to the south of the Amazon River. While the western limit of the species range is assumed to coincide with the Tapajós River, records of *S. collinsi* from the left bank of this river (Pimenta and Silva Júnior 2005, Mercês et al. 2015) raise a number of doubts with regard to its exact geographical limits. Hershkovitz (1984) defined the eastern limit of this taxon as the Pindaré River, in the Brazilian state of Maranhão, and proposed that the southern limit would not be further south than 6° S.

In this context, the present study aims to provide an extension to the known geographical distribution of *Saimiri collinsi* through new records from the Brazilian states of Tocantins, Maranhão and Pará. Information is also provided on the phytophysiognomies in which the species was observed, and the degree of anthropogenic change evident in the newly recognized extension of the species distribution.

The identification of *Saimiri collinsi* in the field was based on the diagnostic characters defined in the original description of the species and by Mercês et al. (2015). We could identify the animals by the coloration on the nape of the neck, on the shoulders, in the middle of the back (the "saddle"), on the posterior region of the back (the "hip") and of the distal and median portions of the forelimbs. The photographic records were compared with the specimens available in the mammal collection of the Goeldi Museum (Museu Paraense Emílio Goeldi – MPEG) for the confirmation of the characteristics of the external morphology.

Data were collected during fieldwork in the Brazilian states of Maranhão and Tocantins, with additional information being obtained from researchers who have worked in this region and in southern Pará. Visual records were obtained using binoculars during walks along pre-existing trails, as well as by canoe in some areas. Searches were conducted in a number of different Amazonian and

Cerrado phytophysiognomies (primary and babassu palm forests, and secondary forests in varying stages of succession).

The records from Maranhão were collected during a series of expeditions conducted during the 1990s and between 2010 and 2016, based on the inventory of the local fauna through direct observations and the collection of specimens. The records from Tocantins were obtained between 2012 and 2016 during expeditions to localities where the local residents had reported the presence of monkeys, and also consisted of direct observations. Whenever possible, photographic records (Figure 1B) were obtained from researchers working in other areas within the region. We also analyzed two specimens of *Saimiri collinsi* (Figure 1A) deposited in the mammal collection of the José Hidasi Museum of Zoology (MZJH) in Porto Nacional, Tocantins. The record from Pará was obtained during a short expedition (5 days) to the locality of Água Azul do Norte conducted by K. R. A. Silva in December 2016.

We have obtained 25 records of *Saimiri collinsi* in the study region (Figure 2, Table 1). A total of 21 records were obtained from Maranhão, including 20 from east of the Pindaré River. All the records from Tocantins, and those from Porto Franco in Maranhão and Água Azul do Norte in Pará, are located south of 6° S. The record from Araguaína represents the southernmost known locality for the taxon.

The species occurs in the Amazon biome, and in transitional areas between this biome and the neighboring Cerrado, where there are scattered records. Our observations indicated the occurrence of the species in a variety of the different environments found in this region. Some of the records were from environments located far from perennial bodies of water and included fragments of secondary forest in different stages of succession, as well as babassu forests. The species was also recorded in areas of farmland, in particular, the old orchard of the Lagoa Nova farm, where a group of at least 38 animals was observed in 1993. Records were also obtained from early secondary and gallery forests associated with three rivers, the Mearim, in São Mateus, the Pindaré, at Praia do Açúcar, and the Ipixuna-Açu in Morada Nova. The easternmost record, from near São Roberto (M. G. M. Lima, pers. comm.), indicates that *Saimiri collinsi* occurs in the Cerrado biome.

In Tocantins, squirrel monkeys were recorded in three municipalities, Xambioá, Araguatins and Araguaína. Araguaína is the southernmost municipality where the species has been recorded in the state and is characterized by the presence of large trees and palms, typical of the transition between the Amazon forest and the Cerrado savanna. In recent years, the landscape has been altered with the clearing of the native forest for the establishment of *Eucalyptus* plantations. The observation record from this municipality was obtained on the local campus of the Federal University of Tocantins, in a remnant of secondary forest that is connected to other fragments, forming an ecological corridor. The

two specimens deposited in the mammal collection of the José Hidasi Museum were from the municipality of Araguatins and we observed a group in primary forest. In Xambioá the species was observed in primary forest, in the area of the legal reserve of a mining operation.

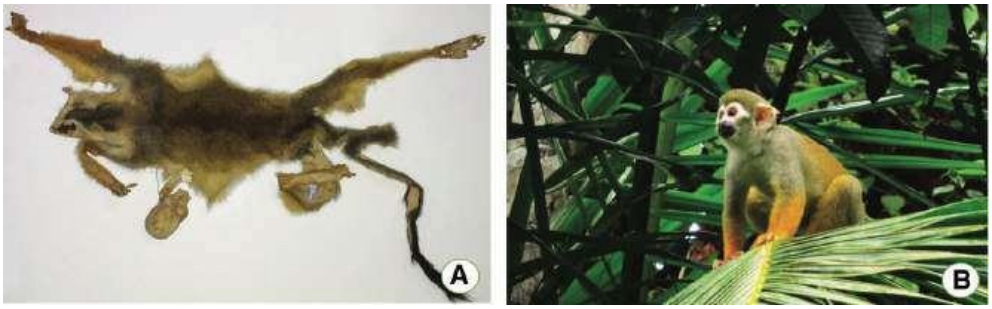

Figure 1: Specimens of squirrel monkey analyzed during this study. (A) Skin and skull of *Saimiri collinsi* (MZJH054) from Araguatins, Tocantins. (B) A female of *Saimiri collinsi* from Araguaína Tocantins. Photo: W. Pascoal.

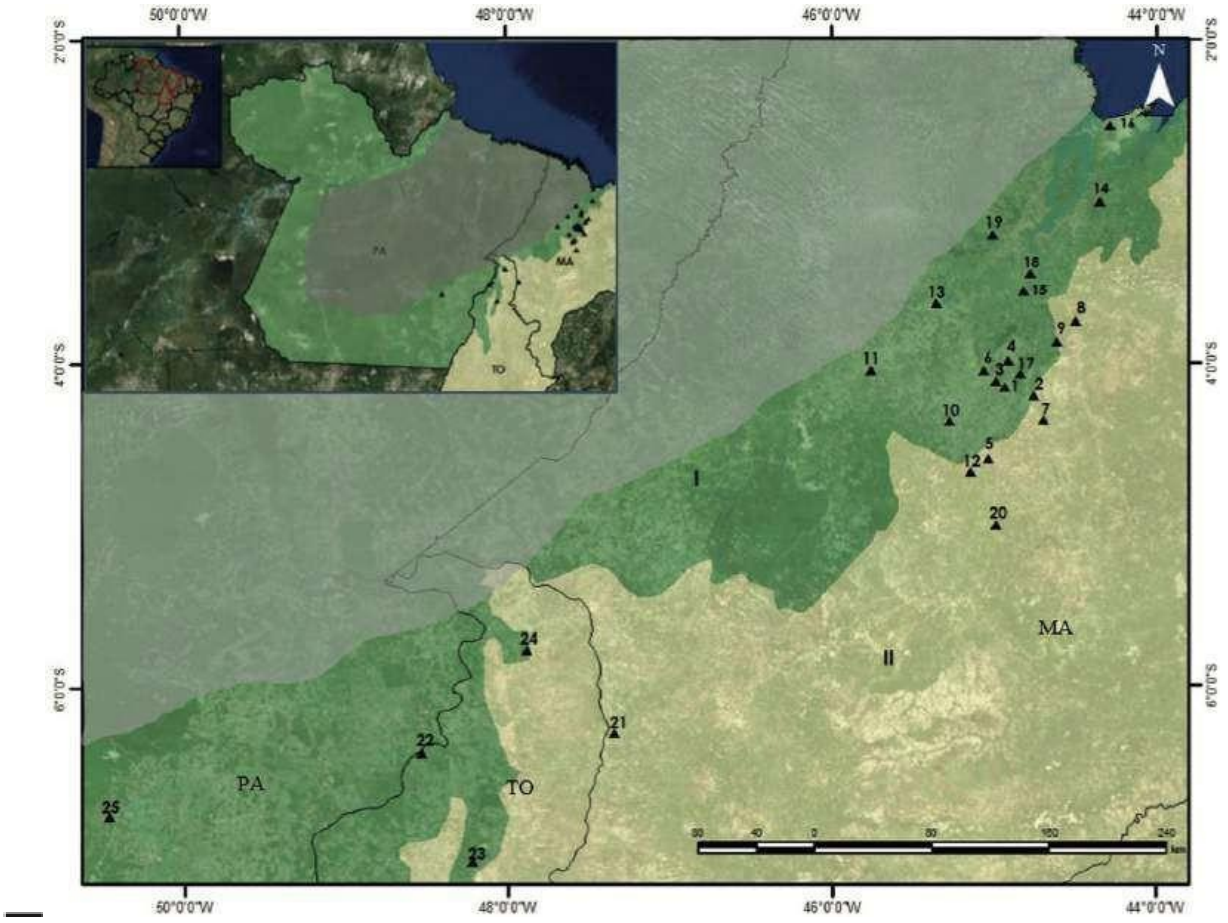

Figure 2: Partial geographic distribution of the squirrel monkey *Saimiri collinsi* in Amazon and Cerrado (main map) and complete geo- graphic distribution (captioned map); I – Amazon (green); II – Cerrado (yellow). Gray shaded area in both maps represents the records of Hershkovitz (1984) and the black triangles in both maps represents the new records: Maranhão (MA) – 1. Alto Alegre (44W 56′ 19″, 4S 9′ 4″); 2. Mangueira (44W 45′ 21″, 4S 13′ 10″); 3. Fazenda Lagoa Nova (44W 59′ 19″, 4S 7′ 15″); 4. Lago Verde (44W 54′ 57″, 3S 59′ 55″); 5. Lago do Junco (45W 2′ 17″, 4S 36′ 22″); 6.

Olho D'Água das Cunhãs (45W 3′ 43″, 4S 3′ 35″); 7. São Luiz Gonzaga do Maranhão (44W 41′ 24″, 4S 21′ 44″); 8. Matões do Norte (44W 29′ 52″, 3S 44′ 56″); 9. São Mateus (44W 36′ 36″, 3S 52′ 19″); 10. Fazenda Mapisa, Buriticupu (46W 31′ 48″, 4S 13′ 48″); 11. Santa Luzia, rio Zutiua (45W 45′ 18″, 4S 3′ 5″); 12. Pedra Preta, Lago da Pedra (45W 8′ 34″, 4S 40′ 48″); 13. Praia do Açúcar, Santa Inês (45W 21′ 20″, 3S 38′); 14. Bacabeira (44W 20′ 24″, 3S); 15. Arari (44W 48′ 36″, 3S 33′ 36″); 16. Reserva Florestal do Sacavém, Parque Estadual do Bacanga (44W 16′ 48″, 2S 31′ 48″); 17. Morada Nova (44W 50′, 4S 4′ 15″); 18. Near Arari (44W 46′ 20″, 3S 27′ 4″); 19. Viana (45W, 3S 12′ 6″); 20. São Roberto (44W 58′ 48″, 5S 00′ 36″); 21. Porto Franco (47W 20′ 24″, 6S 18′); Tocantins (TO) – 22. Xambioá (48W 31′ 48″, 6S 24′ 36″); 23. Campus of the Federal University of Tocantins, Araguaína (48W 13′ 12″, 7S 05′ 24″); 24, Araguatins (47W 52′ 48″, 5S 46′ 48″); Pará (PA) – 25. Água Azul do Norte (50W 28′ 01″, 6S 47′ 28″). Acronyms of Brazilian states are only provided for those entities where the species is known to occur.

In Pará, the record was obtained from the municipality of Água Azul do Norte, in Amazonian forest, approximately 125 km south of the southernmost previous known record, from Curionópolis (Mercês et al. 2015). A number of mining operations are present in this region, and intense farming activity is causing widespread forest fragmentation.

Hershkovitz (1984) determined the limits of the geographical distribution of *Saimiri collinsi* (identified as *Saimiri sciureus sciureus*) based on the information available in the scientific collections consulted. The results of the present study indicate clearly that this is an underestimate of the actual range of the species, due to the limitations of the samples available to Hershkovitz (1984). The new records presented here extend this range to both the east and the south.

Table 1. Summary of the new locality records of *Saimiri collinsi* from southeastern Amazon.

Locality (Federal State, locality and municipality)	**Habitat**	**Region/Biome**	**Type of Record (Voucher/Photo/Observation) and Year**
1 MA - Alto Alegre, west of Mearim River, Bacabal	Secondary forest	CZ	Observation/1990-2000
2 MA - Mangueira, east of Mearim River, Bacabal	Capoeira of babassu	CZ	Observation/1990 and 2010
3 MA - Lagoa Nova Farm, Bacabal	Secondary and babassu palm forest	CZ	MPEG21989 dried skin with skull male; Observation/ 1990-2000
4 MA - Lago Verde	Babassu palm forest	CZ	Observation/1990-2000
5 MA - Lago do Junco	Babassu palm forest	CZ	Observation/2015
6 MA - near of Olho D'Água das Cunhãs	Capoeira of babassu	CZ	Observation/1990 and 2010
7 MA - near of São Luiz Gonzaga do Maranhão	Secondary babassu palm forest	CZ	Observation/1990 and 2010
8 MA - Palmeiral, Matões do Norte	Secondary forest	CZ	Observation/2015
9 MA – near of São Mateus	Capoeira of babassu	CZ	Observation/1990-2000
10 MA - Fazenda MAPISA, Buriticupu	Primary and Secondary forest	AM	Observation/1990-2000
11 MA - near of Santa Luzia, Zutia River	Secondary forest	AM	Observation/1990-2000
12 MA - Pedra Preta, Lago da Pedra	Primary and Secondary forest	AM	Observation/1990-2000

13 MA - Praia do Açucar, right margin of Pindaré River, Santa Inês	Gallery forest	AM	Observation/1990-2000
14 MA - Bacabeira	Babassu palm forest	AM	Observation/2014
15 MA - Arari	Secondary forest	AM	Observation/2014
16 MA - Reserva Florestal do Sacavém, Parque Estadual do Bacanga, São Luís	Secondary forest	BM	Observation/1990-2000
17 MA - Morada Nova, Vitória do Mearim	Secondary forest	BM	Observation/1990-2000
18 MA - Arari	Secondary forest	BM	Observation/1990-2000
19 MA - Viana	Secondary forest	BM	Observation/1990-2000
20 MA - near of São Roberto	-	CE	Observation/2013
21 MA - municipality of Porto Franco	Primary forest	Transition between AM/CE	Observation/2013
22 TO - municipality of Xambioá	Primary forest	Transition between AM/CE	Photo/2013
23 TO - Campus of Federal University of Tocantins, municipality of Araguaína	Secondary forest	Transition between AM/CE	Photo, Female/2016
24 TO - Araguatins	Primary Forest	Transition between AM/CE	MZJH054 dried skin with skull male (Figure 2); MJH053 dried skin; Photo/ 2012
25 PA - Água Azul do Norte	Babassu palm forest	AM	Observation/2016

MA, Maranhão; TO, Tocantins; PA, Pará; CZ, Cocais Zone, AM, Amazon; BM, Baixada Maranhense; CE, Cerrado.

Squirrel monkeys (*Saimiri* spp.) are known to prefer secondary forest in riparian environments, although they will also use primary forest (Stone 2007). The variation in habitat use may be associated with seasonal fluctuations in the availability of feeding resources (Zimbler-DeLorenzo and Stone 2011). This indicates that these animals are able to exploit various different types of environment. The range of *Saimiri collinsi* includes the transition zone between the Amazon and Cerrado biomes (Ab'Sáber 2003, MMA 2007), which includes the Cocais zone, dominated by dense forests of babassu (*Orbignya* sp.) palm and the Maranhão lowlands (Baixada Maranhense), characterized by extensive areas of marshland (Santos-Filho et al. 2013). The poor quality of these environments indicates that *S. collinsi* is a resilient species, being able to maintain small populations in areas of intense fragmentation and direct anthropic impact. As part of the Amazon's "Arc of Deforestation" (Fearnside 2010), the entire study region has been severely degraded. Most of the localities included in the present study have suffered extensive impacts over the past two decades, through the expansion of agricultural frontiers, mining operations and urban development. While *S. collinsi* was considered to be extinct at three localities in Maranhão, these localities were revisited in 2010 (Mangueira, São Luiz Gonzaga, Olho D'Água das Cunhãs), and the species was found in severely degraded environments at four locations (Alto Alegre, Fazenda Lagoa Nova, Palmeiral and Morada Nova), where small groups were observed in extremely fragmented areas.

A number of conservation units – Bacanga State Park, Gurupi Biological Reserve, Buriticupu Forest Reserve, and the Baixada Maranhense Environmental Protection Area – are present within the study area, all in Maranhão. However, even these protected areas are subject to threats such as logging, mining, squatting, and wildfires, and none has an operational management plan (Correia 2011). The Gurupi Biological Reserve is the only fully protected area in the Amazon biome east of the Tocantins River (Rylands and Pinto 1998), but it is also one of the most threatened by logging and deforestation for pasture (Moura et al. 2011). Clearly, the populations of *Saimiri collinsi* found in these protected areas are still vulnerable to habitat modifications.

Some of the ecological characteristics of *Saimiri collinsi* contribute to its resilience, even in highly fragmented environments. Squirrel monkeys are omnivores, feeding mainly on fruit and insects, and they are able to inhabit areas with low densities of fruit trees. In eastern Pará, Stone (2007) found that the fruit of the *Attalea maripa* palm was an important component of the diet of these primates during the dry season. This suggests that *S. collinsi* may be exploiting the region's palm trees as a source of food, in addition to invertebrates.

The records obtained in this study indicate that *Saimiri collinsi* occurs over a much wider area than was previously thought, probably including the entire ecotonal region of central-western Maranhão, northern Tocantins and southern Pará. The record from São Roberto indicates that this range extends to the edge of the Cerrado biome, although there is no conclusive evidence for the occurrence of the species in this biome. The species may also occur in the state of Mato Grosso, which encompasses the Amazon- Cerrado ecotone.

Despite the long-term persistence of some populations confirmed in 2010, in particular in Maranhão, *Saimiri collinsi* populations have declined visibly throughout the study region due to the intense forest fragmentation and modification of the landscape. A survey of the species in the region's protected areas, and the establishment of a monitoring program for these populations are essential measures for the long-term management of *S. collinsi*. The status of these populations is currently unknown.

Acknowledgments: We are grateful to M. G. M. Lima for providing the records from the Cerrado, L. Ramos and A. Lopes for information on the specimens at José Hidasi Museum of Zoology, H. Buratti and W. Pascoal for information on the occurrence of the species in Tocantins, and K. R. A. Silva for information on the specimens from Pará. We would also like to thank M. Bastos for improvements to the manuscript, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior for the doctoral scholarship granted to M. P. M.

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CONCLUSÕES GERAIS

Os resultados aqui documentados representam um grande avanço no conhecimento a respeito da diversificação e taxonomia dos macacos-de-cheiro. No primeiro capítulo, recuperou-se a filogenia e o tempo de divergência entre as linhagens de *Saimiri* a partir de *double digest* restriction-site associated DNA sequencing (ddRADseq). Além disso, os resultados da análise Bayesiana de clusteres indicaram a necessidade de maior amostragem de determinados grupos, devido a possíveis eventos de hibridização ou *incomplete lineage sorting*.

No segundo capítulo, com o uso de dados da morfologia externa e morfometria craniana, mais os dados filogenéticos do capítulo 1, foi possível reconhecer 13 espécies (*Saimiri sciureus*, *S. cassiquiarensis*, *S. albigena*, *S. oerstedii*, *S. citrinellus*, *S. macrodon*, *Saimiri* sp.n., *S. madeirae*, *S. ustus*, *S. collinsi*, *S. vanzolinii*, *S. boliviensis* e *S. peruviensis*). No arranjo taxonômico apresentado, três *taxa* foram elevados à categoria da espécie, um teve um neótipo designado e uma nova espécie foi identificada. Forneceu-se diagnoses e mapas de distribuição geográfica para cada uma das espécies reconhecidas. No terceiro capítulo, ampliou-se a distribuição geográfica de *Saimiri collinsi* para uma parte da região de transição entre Amazônia e Cerrado. Verificou-se que as populações daquela região se encontram em declínio devido à modificação do habitat que vem ocorrendo desde os tempos coloniais e que tem sido drasticamente intensificada nas últimas décadas.

Coletivamente, os capítulos dessa tese forneceram informações a respeito da história evolutiva de *Saimiri* na Bacia Amazônica. Entre os primatas neotropicais, os macacos-de-cheiro são o grupo que se diversificou mais recentemente. Portanto, entender sua história evolutiva traz novos *insights* sobre os processos que ocorreram na Amazônia durante o Pleistoceno. A nova proposta taxonômica é baseada na congruência entre dados morfológicos e do genoma, indicando a grande diversidade nesse grupo.

ANEXOS

Anexo 1 – Normas da Revista Molecular Phylogenetics and Evolution, à qual será encaminhado o capítulo 1 para publicação.

Article structure

Subdivision - numbered sections: Divide your article into clearly defined and numbered sections. Subsections should be numbered 1.1 (then 1.1.1, 1.1.2, ...), 1.2, etc. (the abstract is not included in section numbering). Use this numbering also for internal cross-referencing: do not just refer to 'the text'. Any subsection may be given a brief heading. Each heading should appear on its own separate line.

Introduction: State the objectives of the work and provide an adequate background, avoiding a detailed literature survey or a summary of the results.

Material and methods: Provide sufficient details to allow the work to be reproduced by an independent researcher. Methods that are already published should be summarized, and indicated by a reference. If quoting directly from a previously published method, use quotation marks and also cite the source. Any modifications to existing methods should also be described.

Theory/calculation: A Theory section should extend, not repeat, the background to the article already dealt with in the Introduction and lay the foundation for further work. In contrast, a Calculation section represents a practical development from a theoretical basis.

Results: Results should be clear and concise.

Discussion: This should explore the significance of the results of the work, not repeat them. A combined Results and Discussion section is often appropriate. Avoid extensive citations and discussion of published literature.

Conclusions: The main conclusions of the study may be presented in a short Conclusions section, which may stand alone or form a subsection of a Discussion or Results and Discussion section.

Glossary: Please supply, as a separate list, the definitions of field-specific terms used in your article.

Appendices: If there is more than one appendix, they should be identified as A, B, etc. Formulae and equations in appendices should be given separate numbering: Eq. (A.1), Eq. (A.2), etc.; in a subsequent appendix, Eq. (B.1) and so on. Similarly for tables and figures: Table A.1; Fig. A.1, etc.

Essential title page information:

-***Title.*** Concise and informative. Titles are often used in information-retrieval systems. Avoid abbreviations and formulae where possible.

-***Author names and affiliations.*** Please clearly indicate the given name(s) and family name(s) of each author and check that all names are accurately spelled. You can add your name between parentheses in your own script behind the English transliteration. Present the authors' affiliation addresses (where the actual work was done) below the names. Indicate all affiliations with a lower-case superscript letter immediately after the author's name and in front of the appropriate address. Provide the full postal address of each affiliation, including the country name and, if available, the e-mail address of each author.

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Acknowledgements: Collate acknowledgements in a separate section at the end of the article before the references and do not, therefore, include them on the title page, as a footnote to the title or otherwise. List here those individuals who provided help during the research (e.g., providing language help, writing assistance or proof reading the article, etc.).

Formatting of funding sources: List funding sources in this standard way to facilitate compliance to funder's requirements: Funding: This work was supported by the National Institutes of Health [grant numbers xxxx, yyyy]; the Bill & Melinda Gates Foundation, Seattle, WA [grant number zzzz]; and the United States Institutes of Peace [grant number aaaa]. It is not necessary to include detailed descriptions on the program or type of grants and awards. When funding is from a block grant or other resources available to a university, college, or other research institution, submit the name of the institute or organization that provided the funding. If no funding has been provided for the research, please include the following sentence: This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Units: Follow internationally accepted rules and conventions: use the international system of units (SI). If other units are mentioned, please give their equivalent in SI.

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Inc., New York, pp. 281–304. Reference to a website: Cancer Research UK, 1975. Cancer statistics reports for the UK. http://www.cancerresearchuk.org/aboutcancer/statistics/cancerstatsreport/ (accessed 13 March 2003). Reference to a dataset: [dataset] Oguro, M., Imahiro, S., Saito, S., Nakashizuka, T., 2015. Mortality data for Japanese oak wilt disease and surrounding forest compositions. Mendeley Data, v1. https://doi.org/10.17632/xwj98nb39r.1.

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Anexo 2 – Normas da Revista Zoologial Journal of Linnean Society, à qual será encaminhado o capítulo 2 para publicação.

PREPARATION OF MANUSCRIPT

Manuscript format and structure/style

BASIC FORMATTING GUIDE

Authors should aim to communicate ideas and information clearly and concisely, in language suitable for the moderate specialist. Papers in languages other than English are not accepted unless invited. When a paper has joint authorship, one author must accept responsibility for all correspondence; the full postal address, telephone and fax numbers, and e-mail address of the author who is to check proofs should be provided. Although the Society does not specify the length of manuscripts, it is suggested that authors preparing long texts (20 000 words or more, including references, etc.) should consult the Editor before considering submission. **Please submit your manuscript in an editable format such as .doc, .docx or .rtf, prepared on A4, paginated, double spaced throughout (i.e. including references and quotations), with ample margins. If you submit your manuscript in a non-editable format such as PDF, this will slow the progress of your paper as we will have to contact you to request an editable copy.**

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Article types

Original Article

Review

Invited Review

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This should be uploaded as a separate file, designation 'Title Page'. It should include title, authors, institutions and a short running title. The title should be concise but informative, preferably shorter than 25 words. Catchy titles are encouraged. Where appropriate the title should include mention of family or higher taxon in the form: 'The Evolution of the Brown Rat, *Rattus norvegicus* (Rodentia:

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Abstracts must be on a separate page and must be concise, clearly written and cover the context of the paper. The abstract is of great importance as it may be reproduced elsewhere and is all that many may see of your work. It should be about 100–200 words long and should summarize the paper in a form that is intelligible in conjunction with the title. It is advisable to avoid descriptions, lists or jargon if possible. It should not include references. The abstract should be followed by up to ten keywords additional to those in the title (alphabetically arranged and separated by hyphens) identifying the subject matter for retrieval systems. Taxonomic authorities should not be included in the abstract.

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The paper should be divided into main sections: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION and CONCLUSION, with the hierarchy of headings below these not exceeding two, except in systematic hierarchies. Results are presented in present tense, whereas previous studies that are discussed need to be presented in past tense. Do not merge results and discussions. Please present your work in clear and concise language, keeping the broad readership in mind. Separate Results and Discussion sections provide a clear distinction between results of the study at hand and discussion of results of other studies, so these separate sections generally should be used.

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Use SI units, and the appropriate symbols (mm, not millimetre; µm, not micron; s, not sec; min for minute; c for circa; Myr for million years, Mya for million years ago; etc.). Use an n-dash (–), not a hyphen (-), for ranges and use the times sign × (not the letter x) for multiplication, dimensions, crosses and hybrids. Use the negative index (m-1, l-1, h-1) except in cases such as 'per plant'). Avoid elaborate tables of original or derived data, long lists of species, etc.; if such data are absolutely essential, consider including them as appendices or as online-only supplementary material. Avoid footnotes and keep cross references by page to an absolute minimum. Please provide a full English translation [in square brackets] for any quoted matter that is not in English.

References

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Kamiński MJ, Kanda K, Lumen R, Smith AD, Iwan D. 2019. Molecular phylogeny of Pedinini (Coleoptera, Tenebrionidae) and its implications for higher-level classification, *Zoological Journal of the Linnean Society* 185: 77–97.
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(iii) Other citations such as papers 'in press' may appear on the list but not papers 'submitted', 'in review' or 'in preparation'. These may be cited in the text as 'unpubl. data'. A personal communication may be cited in the text but not in the reference list. Please give the initials and surnames for all authors of personal communications and unpublished data.
(iv) In the case of taxonomic reviews, authors are requested to include full references for taxonomic authorities.
(v) Give foreign language references in Roman alphabet (but include accents in languages that use special letters and accents, like in French, German, Spanish, Swedish, Danish, Czech, etc.). If necessary, transliterate in accordance with a recognized scheme (e.g. pinyin). For the Cyrillic alphabet use British Standard BS 2979 (1958). If only a published translation has been consulted, cite the translation, not the original. Add translations not supplied by the author of the reference in square brackets.

Tables

Keep these as simple as possible, with few horizontal and, preferably, no vertical rules. When assembling complex tables and data matrices, bear the dimensions of the printed page (225 × 168 mm) in mind; reducing typesize to accommodate a multiplicity of columns will affect legibility.

Illustrations

These normally include (1) half-tones reproduced from photographs, (2) black and white figures reproduced from drawings and (3) diagrams. Use one consecutive set of Arabic numbers for all illustrations (do not separate 'Plates' and 'Text-figures' - treat all as 'Figures'). Figures should be numbered in the order in which they are cited in the text. Use upper case letters for subdivisions (e.g. Figure 1A-D) of figures; all other lettering should be lower case.
Half-tones reproduced from photographs: increasingly, authors' original images are captured digitally rather than by conventional film photography. In these cases, please use settings on your equipment for the highest possible image quality (minimum 300dpi). Desktop technology now allows authors to prepare plates by scanning photographic originals and then labelling them using graphics programs such as Adobe Illustrator. These are acceptable provided:
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Type legends for Figures in numerical order on a separate sheet. Where a 'key' is required for abbreviations used in more than one Figure, this should be included as a section of the main text.
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Upon revision papers should be submitted in an editable file format (i.e. not PDF) and figures should be submitted as separate, high-resolution, files.
For information on Latex files, please see: https://academic.oup.com/journals/pages/authors/latex_files You can also send queries about figure files to zoolin_oup@newgen.co.
Supplementary data
Submit all material to be considered as Supplementary Material online at the same time as the main manuscript. Ensure that the supplementary material is referred to in the main manuscript at an appropriate point in the text. Supplementary material will be available online only and will not be copyedited, so ensure that it is clearly and succinctly presented, and that the style conforms with the rest of the paper. Also ensure that the presentation will work on any Internet browser. It is not recommended for the files to be more than 2 MB each, although exceptions can be made at the editorial office's discretion.

Anexo 3 – Normas da Revista Mammalia, na qual foi publicado o capítulo 3.

Submission of manuscripts
Manuscripts must be submitted online at:
http://mc.manuscriptcentral.com/mammalia
At this web site, you will find detailed information on allowable document types and file formats. Check carefully before proceeding with submissions. Each manuscript should be accompanied by a cover letter containing a brief statement by the authors as to the element of novelty upon which they base their request for publication in *Mammalia*. The authors may indicate the names, full postal addresses, telephone and fax numbers, and e-mail addresses of three impartial potential peer reviewers.

Preparation of manuscripts General format and length

Before submitting a manuscript, authors should check to ensure that the following instructions have been followed. Manuscripts that differ from the specifications will be returned for correction before review. The text must be carefully checked for grammatical and typing errors to avoid correction in the proof. All tables and calculations should also be carefully checked. Non-English speakers are strongly encouraged to have their manuscripts checked by a native speaker before submission. Manuscripts must be prepared in 12-point font size, double-spaced throughout, with a left-hand margin of 4 cm and a right-hand margin of 2 cm in A4 or American letter-sized documents. Do not right justify the text. Full-length papers and reviews should not exceed 40 manuscript pages. Short notes should not exceed 10 manuscript pages and allow a
maximum of two figures and one table. Review articles and taxonomic revisions based upon high specimen numbers or covering wide geographical areas may be longer.

Use upper and lower case letters for headings and names. Do not write names in capitals. Do not use the ampersand (&) between names (with the exception of company names). References within the text body are quoted by the author name and year system and, if necessary, by page number(s). If the reference consists of three or more author names, the first name is followed by et al.

Font marking / Dimensions and units

Italics are used for species/genus names and certain parts of chemical formulas. Please do not use italics for standard Latin abbreviations like et al., i.e., ca., vs.). SMALLL CAPITALS are used for M (molar) or N (normal). The metric system must be used (with the exception of nautical mile = one minute of latitude). SI units are required.

Nomenclature

Papers should follow the *International Code of Zoological Nomenclature*. For taxonomical terms authors should refer to Wilson and Reeder (eds.). 2005. *Mammal Species of the World* and McKenna and Bell (eds.). 2000. *Classification of Mammals: Above the Species Level*. Authors are asked to follow the recommendations of the CBE Style Manual (Council of Biological Editors, Committee on Form and Style, American Institute of Biological Sciences, Washington, D.C., USA). The recommendations of the

- – International Union of Pure and Applied Chemistry (IUPAC),
- – International Union of Biochemistry (IUB),
- – International Code of Botanical Nomenclature,
- – Système International d'Unités (SI),
- – American National Standard for the Abbreviation of Titles of Periodicals,
- – World List of Scientific Periodicals are binding. Each voucher specimen described or mentioned must have been deposited in an appropriate institution and bear a catalogue number. DNA sequences associated with the article must be deposited in molecular data banks (GenBank, EMBL, DDBJ).

Structure of the text body

General. Full-length papers should be organised into: Title page, Abstract, Keywords, Introduction, Materials and methods, Results, Discussion and Conclusion, Acknowledgements, References, Tables, and Figure legends.

Short notes should contain a short Abstract, Keywords and a single section of main text without headings. Experimental procedures should be described in legends to figures or footnotes to tables. Acknowledgements and References should be presented as in full-length papers. **Title page.** The title page should contain a concise title, the name(s) of author(s), the complete postal address(es), e-mail addresses and/or fax numbers, and a running title of maximum 50 characters. Footnotes may be added on this page only. **Abstract/Keywords.** A concise abstract of maximum 200 words for full-length papers and reviews (max. 100 words for Short notes) should be on the second page. The content of the title must not be repeated. Do not give authorities for species/genus names in the abstract. Begin the abstract by stating the scientific question of concern. Explain the methods used to tackle the question. The results should be outlined briefly and put into a concise broad perspective.

Up to 5 keywords, specific of the article, are to be listed after the abstract. The journal accepts standard abbreviations. All non-standard abbreviations should be spelled out at first mention in the abstract as well as in the text body. Thereafter, only these abbreviations are to be used.

Introduction. The introduction must define the problem within the context of existing knowledge. Ensure that those not working in your particular field are able to understand the objectives of the work. **Materials and methods.** Be as concise as possible, but with sufficient detail to enable others to repeat your work. All Latin binominals should have the correct authorities quoted at their first citation (but not in the abstract) or at some convenient point such as a list of species.

Results. Only material pertinent to the subject may be included. Data must not be repeated in figures and tables.

Discussion and Conclusion. This part should interpret the results in relation to the problem outlined in the introduction. The discussion should place the results within the context of the broad scientific discipline of the study. A conclusion should be added if results and discussion are combined.

Acknowledgements. Acknowledgements may be used to credit support.

References. The reference section must contain an alphabetical list of all published works cited in the text body, tables or in figure legends. Only the initials of the first author's name are placed behind the surname (family name). Repeated names in consecutive references are typed out in full. All works in the list of references must have author(s), date, title, full details of publication and page numbers. When referring to a thesis, the name of the institution from where it is available must be given. Abbreviate journal titles according to the World List of Scientific Periodicals. If a journal is not within the World List, use the same abbreviation procedure. In case of uncertainty, write out a journal title in full. The number of a fascicle in brackets after the volume number should be given only if the volume is not paginated consecutively. National origin of a journal is to be provided only in cases of possible confusion. Citation of transliterated or translated titles must include an indication of the original language, e.g. (in Russian). Please use *italics* only for genus/species names; all other information should be given in normal font.

Please note the following bibliographical examples: * Articles in journals: Johnsingh, A.J.T. 1992. Prey selection in three large sympatric carnivores in Bandipur. Mammalia 56: 517–526. * Books: Prater, S.H. 1971. The book of Indian animals. Bombay Natural History Society, Bombay. pp. 332. * Articles/Chapters in books: Peres, C.A. and F. Michalski. 2006. Synergistic effects of habitat disturbance and fragmentation on tropical forest vertebrates. In: (W.F. Laurance and C.A. Peres, eds.) Emerging threats to tropical forests. University of Chicago Press, Chicago, IL. pp. 105–126.

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Do not embed figures within the text body of submitted manuscripts. Submit figures separately. Photographs must be of good contrast as there is a loss of contrast in printing. Authors are encouraged to submit illustrations in color

if necessary for conveying their scientific content. Publication of color figures is provided free of charge both in online and print editions. Electronically submitted figures should be provided in a generic graphics format. For reproduction, high resolution images (minimum 600 d.p.i.) are required.

Tables. Tables are numbered in Arabic numerals followed by the title. Additional explanations should go underneath the table. Footnotes are referenced by superscript numbers. No vertical lines will be printed. The maximum width of a printed table is 60 characters in 1 column, 125 characters in two

columns, and 190 characters in landscape format. Each table should be typed on a separate manuscript page with its legend.