



MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO

**Taxonomy of the genus *Brachyteles* Spix, 1823 and its phylogenetic
position within the subfamily Atelinae Gray, 1825**

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São Paulo

2016

MUSEU DE ZOOLOGIA DA UNIVERSIDADE DE SÃO PAULO

MASTOZOOLOGIA

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Taxonomy of the genus *Brachyteles* Spix, 1823 and its phylogenetic position within the subfamily Atelinae Gray, 1825

Dissertação apresentada ao
programa de Pós-Graduação do
Museu de Zoologia da
universidade de São Paulo para o
obtenção de título de Mestre em
Sistemática, Taxonomia Animal e
Biodiversidade

Orientador: Prof. Dr. Mario de
Vivo

São Paulo

2016

Ficha catalográfica

Serrano-Villavicencio, José Eduardo

Taxonomy of the genus *Brachyteles* Spix, 1823 and its phylogenetic position within the subfamily Atelinae Gray, 1825; orientador Mario de Vivo. – São Paulo, SP: 2016.

198 p.; 56 figs; 10 tabs.

Dissertação (Mestrado) – Programa de Pós-graduação em Sistemática, Taxonomia Animal e Biodiversidade, Museu de Zoologia, Universidade de São Paulo, 2016.

1. *Brachyteles*, 2. Filogenia - *Brachyteles*, 3. Atelinae I. Vivo, Mario de. II. Título.

Banca Examinadora

Prof. Dr.

Instituição:

Julgamento

Prof. Dr.

Instituição:

Julgamento:

Prof. Dr. Mario de Vivo (Orientador)

Museu de Zoologia da Universidade de São Paulo



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*Con todo mi amor para Elisa y Juan
que son mi razón para jamás desistir.
Nunca terminaré de agradecer cada
uno de sus sacrificios.*

Agradecimientos

Aunque la gran mayoría del presente trabajo se encuentra redactado en inglés, quise tomarme la libertad de expresar mis agradecimientos más sinceros en mi lengua materna para no dejar ningún sentimiento al aire.

En primer lugar, me gustaría agradecer a mi orientador Mario de Vivo quien se arriesgó a aceptar un desconocido biólogo peruano sin mayor experiencia. Fue gracias a nuestras conversaciones y discusiones que se despertó el sentido crítico que ahora poseo y que lastimosamente no es más común entre científicos. Gracias por las enseñanzas y por la oportunidad Mario.

Me gustaría agradecer también a Marta Maria, Omair e Sônia del servicio de secretaria de posgrado y, al mismo tiempo, pedirles disculpas por las incontables veces que los incomodé. Gracias por todas las respuestas amables y soluciones rápidas que le dieron mis problemas.

A Juliana Gualda, técnica de la sección de mamíferos del MZUSP, por la amistad y toda la ayuda ofrecida desde mi llegada. También a Ismael P. de Jesus, quien siempre se encontró dispuesto a ayudarme y a tener una buena conversación acompañada de un buen café.

A los bibliotecarios del MZUSP, Dione Seripierri, Marta Zamana y Ricardo. Como buenos nunca desisten en la búsqueda de la bibliografía más extraña que se les presente. Su apoyo fue invaluable para hallar las referencias más difíciles que encontré.

Al Dr. João Alves Oliveira y a Sergio M. Vaz del MNRJ por permitir el acceso a los especímenes depositados en esta institución. A Sergio M. Vaz nuevamente por enviarme sin demora la información de los especímenes depositados en el MNRJ.

Al Dr. Castor Cartelle y al personal del laboratorio de Paleontología de la PUC–Minas, a Claudia Guimarães Costa del laboratorio de mastozoología de la PUC–Minas, por permitirme amablemente revisar material que fue de gran importancia para el presente trabajo.

A Alexander Bibl y Frank Zachos del Natural History Museum of Vienna; Jacques Cuisin y Cécile Callou del Muséum National D'Histoire Naturelle de Paris y Pepijn Kamminga del Rijksmuseum van Natuurlijke Historie de Leiden por la cesión de fotos del material tipo y por la siempre rápida respuesta ante mis dudas.

Al Dr. Fernando Perini y al personal del laboratorio de mastozoología de la UFMG por las facilidades y el apoyo brindado durante mi visita en su colección.

A todo el lindo grupo que trabaja en la colección de mamíferos del Museo de Biología Mello Leitão, especialmente a Juliana Paulo da Silva y Cintia Corsini por su ayuda y amabilidad durante mi visita a esa ciudad a la que quiero regresar, Santa Teresa. Aquí quiero aprovechar para agradecer a Dayse Dias por la ayuda que me brindó durante mi viaje a Espírito Santo y por hacerme conocer al menos por unas horas la linda ciudad de Vitoria.

A mi primer asesor, Víctor Pacheco, que siempre me recibe cordialmente en cada visita que hago a mi *alma mater*, el Museo de Historia Natural de Lima. De la misma forma agradezco a Pamela Sanchez y a todos los nuevos alumnos del laboratorio.

A todos mis amigos esparcidos por Brasil y el mundo: Anderson Feijo por la ayuda en mis análisis y en la edición de imágenes; a Guillermo Cassini, Elis Damasceno y Thomas Püschel por el apoyo en mis análisis morfo-geométricos, mil disculpas por tantas incomodidades que les hice pasar; a mi buen amigo andino Sergio “marginal” Bolívar, por la ayuda en la parte estadística y todas las buenas conversaciones a la hora del almuerzo.

A mi gran amiga Cindy Hurtado que, a pesar de la distancia, nuestra amistad perdura y no se convirtió en un impedimento para seguir trabajando juntos. Mil gracias por toda la ayuda brindada en la parte estadística durante el desarrollo de mi trabajo.

Al Dr. Alfred Rosenberger por alentarme a realizar este proyecto, su ayuda y su amistad en los últimos años me han incentivado a ser un mejor científico y una mejor persona.

Al Dr. Marcelo Tejedor, por el apoyo y la buena disposición que siempre me ha mostrado durante tanto tiempo.

A los responsables de que este trabajo haya sido terminado, mis grandes amigos y co-orientadores “no oficiales”, Fabio Oliveira do Nascimento y Guilherme Siniciato Terra Garbino. Faltarían páginas para agradecerles por toda la ayuda brindada además de

todas conversaciones científicas, los debates, los consejos, etc. Gracias por apoyarme siempre.

A Fabiano R. de Melo por la ayuda desinteresada durante el desarrollo de este proyecto y la valiosa información compartida. También me gustaría agradecer a las siguientes personas por la gentil cesión de material fotográfico crucial para la evaluación de caracteres: Paula Breves, Carla Possamai, Dr. Adriano Chiarello, Daniel da Silva Ferraz, Theo Anderson, Luiz Dias y el Prof. Braz Cozenza.

A Sergio Lucena por compartir conmigo información y bibliografía relevante para mi trabajo.

A mi gran amiga Rafaela “xili” Vendramel, que además de ser mi colega (y traductora oficial), alegró mi estancia en São Paulo y en el laboratorio, gracias por las clases de Portugués Paranaense y por ayudarme en cada etapa de esta maestría.

Quiero agradecerle también a mi amiga Yolanda “pirulito” Salgueiro por la ayuda en la redacción de mi trabajo, sin tu ayuda hubiera dormido muchas menos horas.

A mis compañeros de casa Tulio, Michel y Diego “huachin” Evangelista, por los buenos y los malos momentos que pasamos durante nuestra convivencia.

A ti Camila Cardoso por todo el amor, comprensión y apoyo que me has brindado desde que nos conocimos y especialmente durante estos últimos meses de tanta presión. Mil gracias por quedarte siempre a mi lado.

Por último, pero no menos importante, a mis padres mi gordita Elisa y mi viejo Juan, porque a pesar de no estar físicamente a mi lado nunca dejaron de apoyarme. A mi hermana Paola por todo tu apoyo. A mis abuelos Irene y Miguel, que desde mis primeros años me brindaron todo su ayuda y que, al igual que mis padres, se preocuparon por mi educación. Gracias a todos ustedes estoy aquí ahora.

Estoy más que seguro que lamentablemente estoy dejando de mencionar a muchas personas que me ayudaron de una u otra manera durante el desarrollo de mi trabajo y a todas ellas les pido mi más sinceras disculpas.

Este trabajo fue financiado por CAPES. Agradezco también a Idea Wild por la gentil donación de una cámara fotográfica profesional que fue de vital importancia para el desarrollo de mi proyecto.

Abstract

Muriquis, genus *Brachyteles* Spix, 1823, are the largest of the extant New World primates, and they are one of the three extant genera of the subfamily Atelinae along with *Ateles* (spider monkeys) and *Lagothrix* (wooly monkeys). The taxonomy of *Brachyteles* has constantly changed since its first description in the 19th century. First treated as a monotypic genus, and after several modifications in the number of species, *Brachyteles* currently contains two species, *B. arachnoides* (Southern muriqui) and *B. hypoxanthus* (Northern muriqui). The morphological evidence for this taxonomic arrangement relies on two diagnostic characters: the occurrence of a black-pigmented face and the absence of the first digit (thumb) in Southern muriqui populations vs. mottled face and fully-developed thumb in Northern muriqui populations. In addition, the phylogenetic relationship between atelines is disputed: on the one hand, the molecular evidence suggests an (*Ateles* (*Brachyteles* + *Lagothrix*)) clade and, on the other, most morphological evidence supports a clade (*Lagothrix* (*Ateles* + *Brachyteles*)) based on the high degree of postcranial and locomotory resemblances between *Ateles* and *Brachyteles*. My aims here are: 1) to verify how many taxa at the species level group there are in *Brachyteles*, and 2) to estimate the phylogenetic relationships among Atelinae using morphological characters. To achieve these goals, I have performed a qualitative analysis of external morphological characters as the presence or absence of the thumb, pelage coloration, and face pigmentation to test sexual dimorphism or dichromatism and intrapopulational variation. I also performed linear and geometric morphometrics analyses to test sexual dimorphism and geographical variation in both size and shape of the skull. Finally, I carried out a morphological phylogeny using 74

discrete morphological characters, two ecological and one karyological. This analysis includes 11 species of extant and fossil atelids and the outgroup was composed of *Sapajus nigrinus* and *Callicebus personatus*. The analysis of the pelage coloration reveals that there is no sexual dimorphism or dichromatism in *Brachyteles*; besides, the pelage presents a high degree of individual variation. The development of the thumb and the facial pigmentation do not exhibit uniformity; thus, they have no taxonomic meaning. Linear and geometric morphometrics failed on to discriminate between sexes and populations based on the size and shape of the skull. For these reasons, I consider *Brachyteles* as a monotypic genus with no subspecies. Lastly, the morphologic phylogenetic analysis shows that *Brachyteles* is more closely related to *Lagothrix* than to *Ateles*, suggesting that the postcranial similarities between muriquis and spider monkeys could be a plesiomorphic condition in Atelidae, and the arboreal quadrupedalism of *Alouatta* and *Lagothrix* evolved convergently in alouattines and atelines.

Resumo

Os muriquis ou monos-carvoeiros, gênero *Brachyteles* Spix, 1823, são os maiores primatas existentes do Novo Mundo, fazendo parte da subfamília Atelinae, juntamente com os gêneros *Ateles* (macaco-aranha) e *Lagothrix* (macaco-barrigudo). A taxonomia de *Brachyteles* tem sofrido constantes alterações desde sua primeira descrição no século XIX. Inicialmente foi tratado como um gênero monotípico, entretanto, após diversas alterações no número de espécies, atualmente considera-se composto por duas espécies, *B. arachnoides* (muriqui-do-sul) and *B. hypoxanthus* (muriqui-do-norte). O suporte para este arranjo taxonômico baseia-se em dois caracteres diagnósticos: a ocorrência de face com coloração preta e a ausência do primeiro dígito (polegar) nos muriquis-do-sul vs. face com manchas e polegar totalmente desenvolvido em populações de muriquis-do-norte. Adicionalmente, as relações filogenéticas entre os atelinos é contestada: por um lado, a evidência molecular sugere o clado formado por (*Ateles* (*Brachyteles* + *Lagothrix*)), por outro, a evidência morfológica suporta o clado (*Lagothrix* (*Ateles* + *Brachyteles*)), baseando-se na grande similaridade pós-craniana e locomotora. Desta forma, o meus objetivos neste trabalho são: 1) verificar quantos taxa do grupo da espécie existem em *Brachyteles*, e 2) estabelecer as relações filogenéticas entre os Atelinae utilizando caracteres morfológicos. Para isso, analisei qualitativamente os caracteres morfológicos externos, como a presença ou ausência de polegar, a coloração da pelagem, e a pigmentação facial, a fim de testar a ocorrência de dimorfismo sexual ou dicromatismo e a variação intraespecífica. Além disso, realizei análises morfométricas lineares e geométricas para testar o dimorfismo sexual e a variação geográfica do tamanho e forma do crânio. Por fim, realizei uma filogenia morfológica

utilizando 74 caracteres morfológicos, dois ecológicos e um cariotípico. Estas análises incluíram 11 espécies de atelídeos viventes e fósseis e um grupo-externo composto por *Sapajus nigritus* e *Callicebus personatus*. A análise da coloração da pelagem revela que não há dimorfismo sexual ou dicromatismo em *Brachyteles*; além disso, a pelagem apresenta um alto grau de variação individual. O desenvolvimento do polegar e a pigmentação facial não apresentam uniformidade, assim, não tem relevância taxonômica. A morfometria linear e geométrica falharam em discriminar entre os sexos e as populações com base no tamanho e forma do crânio. Finalmente, as análises filogenéticas mostraram que *Brachyteles* está mais estreitamente relacionado com *Lagothrix* do que com *Ateles*, sugerindo que a similaridade pós-craniana entre os muriquis e os macacos-aranha poderia ser uma condição plesiomórfica dos atelídeos, e o quadrupedalismo arborícola de *Alouatta* e *Lagothrix* teria evoluído convergentemente em alouatíneos e atelíneos.

DISCLAIMER ACCORDING TO ARTICLE 8.2 ICZN

This dissertation, although dealing with topics that may affect the taxonomy of certain taxa involved, is explicitly not issued for the purpose of zoological nomenclature and does not intend to make new names available or to contain any other nomenclatural act.

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1. INTRODUCTION

1.1 The family Atelidae and its taxonomic diversity

The New World Monkeys (hereafter NWM) are included in the Infraorder Platyrrhini, and the number of genera and species has risen in recent decades. Currently, five families of NWM are considered: Callitrichidae, Cebidae, Aotidae, Pitheciidae and Atelidae (Mittermeier and Rylands 2013, but see Schneider and Sampaio 2015). The number of genera varies according each author: 16 for Hershkovitz (1977) and Napier and Napier (1976); 19 for Rylands and Mittermeier (2009); 20 for Mittermeier and Rylands (2013); and 23 genera due to the recent splits of the genera *Saguinus* (Rylands et al. 2016) and *Callicebus* (Byrne et al. 2016). All these genera are found in North, Central, and South America, from southern Mexico to northwestern Argentina and Southern Brazil.

The Family Atelidae was formerly classified as subfamily of Cebidae by several authors (Hill 1962, Napier and Napier 1967, Hershkovitz 1977). Currently, Atelidae is subdivided into two subfamilies: Alouattinae (containing the genus *Alouatta*) and Atelinae (containing the genera *Ateles*, *Brachyteles*, and *Lagothrix*). The howler monkeys, genus *Alouatta* Lacépède 1799, are the most widespread genus of platyrrhine, occurring from Southern Mexico to Northern Argentina (Crockett and Eisenberg 1987). The Spider monkeys, genus *Ateles* É. Geoffroy, 1806, are also fairly widespread, occurring from Southern Mexico through the Amazon basin (Kellogg and Goldman 1944). The wooly monkeys, genus *Lagothrix* É. Geoffroy 1806, are found in the upper Amazonian basin and adjoining regions, and also in the cloud forests of a portion of the

Peruvian Andes (Fooden 1963). The Muriquis, genus *Brachyteles* Spix 1823, are restricted to the southeastern Atlantic rainforest of Brazil (Aguirre 1971, Nowak 1991, Strier 2004). The atelids have as synapomorphies a prehensile tail covered ventrally by bare skin with friction ridges, a large body size, and very long forelimbs about the hindlimbs (Schneider and Rosenberger 1996).

1.2 Brief history of the genus *Brachyteles*

Due to the endangered conservation status of *Brachyteles*, this genus has been the focus of several ecological and biogeographical studies (Aguirre 1971, Mittermeier et al. 1987, Nishimura et al. 1988, de Oliveira et al. 2005, Mendes et al. 2005, among many others). Nevertheless, systematics and taxonomic studies focus on *Brachyteles* are scarce and, generally, with a limited number of samples. This problem is mainly caused by the rarity of *Brachyteles*' samples on scientific collections. The first works involving *Brachyteles* were based on individuals of unknown provenance, some of them as the product of the primate trade, which was common at Brazilian ports (Texeira and Papavero 2010). With the arrival of the Portuguese Royal family to Brazil, the ports were opened for trading with all friend nations and to the scientific community (Bulmer-Thomas 2008). Naturalists as Prince Maximilian of Wied-Neuwied, Johann Baptist von Spix, Carl von Martius, and Johann Natterer were the first to collect *Brachyteles*' samples, providing detailed information of the specimens and the site of collection.

Isidore Geoffroy Saint-Hilaire (1829) was the first to describe meticulously the morphology of *Brachyteles*, based on a few samples held at the Muséum National D'Histoire Naturelle (Paris, France) and using the information given by the naturalists above mentioned. After this, there were some studies made with material held mainly in European collections and North American (Slack 1862, Pelzeln 1883, Elliot 1913, Hill 1962, Napier and Napier 1976).

After the establishment of two of the most important Brazilian scientific collections (the Museu Nacional do Rio de Janeiro and the Museu de Zoologia da Universidade de São Paulo) that started the storage of Brazilian fauna. Gradually, these collections gathered the largest number of *Brachyteles*' samples around the world. Vieira (1944) was one of the first researchers to examine these Brazilian collections and recognized two subspecies of this genus based on some morphological differences such as facial skin pigmentation and the presence or absence of a vestigial thumb. He suggested that *Brachyteles arachnoides* should be separated into *Brachyteles arachnoides arachnoides*, occurring in the states of Rio de Janeiro, São Paulo and Paraná along the Serra do Mar; and *B. a. hypoxanthus*, occurring in southern Bahia, Minas Gerais, and Espírito Santo South to the Serra da Mantiqueira.

Vieira (1955) reexamined the taxonomic status of *Brachyteles* and decided to keep it as a monotypic genus without any subspecies. Aguirre (1971), made the first comprehensive study of *Brachyteles* including several aspects (ecological, behavioral, biographical and taxonomic). Following the taxonomic considerations of Vieira (1944,

1955), Cabrera (1958), and Hill (1962), Aguirre (1971) made a remarkable contribution to the knowledge of this genus.

This taxonomic arrangement of *Brachyteles arachnoides* as single species was followed by several years until Groves (2001), based on the studies of Lemos de Sá et al. (1990, 1993), da Fonseca et al. (1991), Lemos de Sá and Glander (1993) and Rylands et al. (1995), indicated that Vieira's (1944) standing was valid. Nevertheless, the differentiation between Northern and Southern populations was even more extreme and would justify the classification of the two forms as separate species: *Brachyteles hypoxanthus* and the *Brachyteles arachnoides* (Fig. 1).

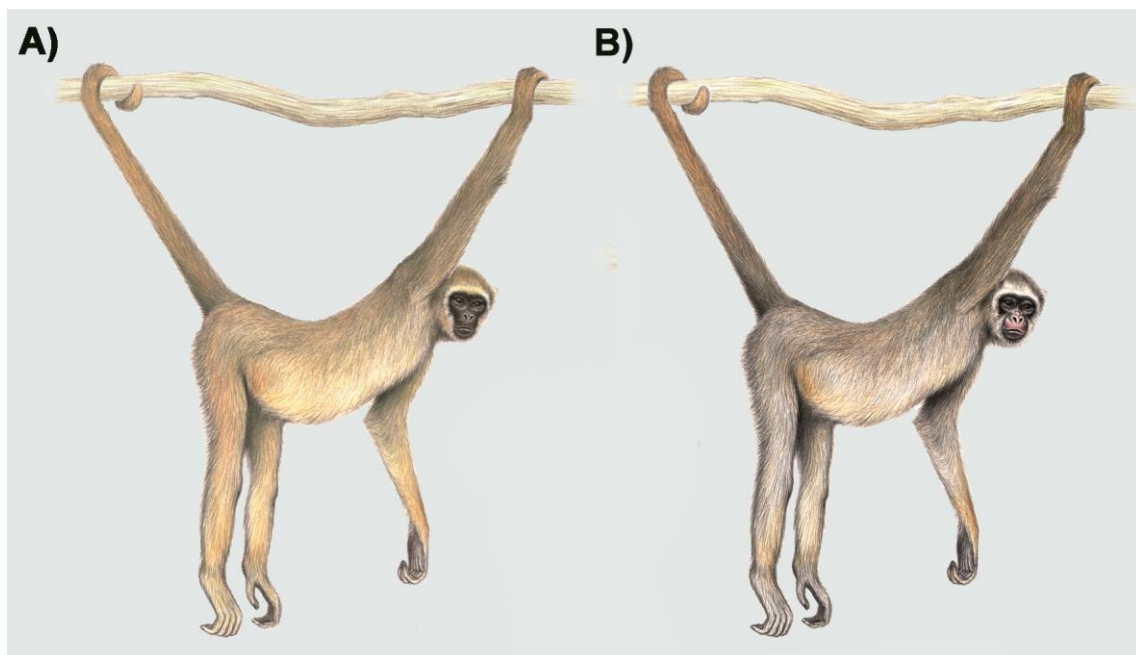


Figure 1. *Brachyteles arachnoides* (a) and *Brachyteles hypoxanthus* (b), modified from Mittermeier et al. 2013 (Pag. 546, plate 24 and 25). Illustrations by Stephen Nash.

Even nowadays, it remains questionable if the presence or absence of vestigial thumbs is a diagnostic morphological character to separate these species of muriquis (Fagundes 2005). Interpretations of some of the interpopulation variation remain controversial (Leigh and Jungers 1994). The most relevant taxonomic arrangements of *Brachyteles* are shown in the Table 1.

1.3 The clade (*Brachyteles*, *Lagothrix*, *Ateles*)

The largest primates of the NWM are in the subfamily Atelinae (Peres 1994). . These primates exploit a clear niche in the Neotropical forest canopy via suspensory postures and brachiating movements, the skeletal adaptations to which seem readily apparent (Hartwig 2005). The alpha-taxonomy of atelines has profoundly changed over the last decades (see Table 1). The monophyly of Atelinae is strongly supported by morphology (Rosenberger 1981, 1984; Ford 1986, Kay et al. 1987), as well as behavior and ecology (Rosenberger and Strier 1989).

Morphological and behavioral analyses of the phylogenetic relationships of atelids revealed two distinct patterns that distinguish *Alouatta* from the other three ateline genera (Strier 1992). *Alouatta* appears to follow a strategy that minimizes energy expenditure while the atelines seem to maximize energy intake (Rosenberger and Strier 1989). These strategies have been associated with folivory in *Alouatta* (Milton 1980) and frugivory in *Ateles* (Klein and Klein 1977, van Roosmalen 1980, Symington 1988) and *Lagothrix* (Defler 1987, Soini 1987). In *Brachyteles*, however, this dichotomy is confounded; although *Brachyteles* resembles *Alouatta* in its folivorous diet, it resembles

the other atelines in other behavioral traits. These latter resemblances support the accepted phylogenetic separation between *Alouatta* on the one hand and *Ateles*, *Brachyteles*, and *Lagothrix* on the other. The marked craniodental and dietary similarities between *Brachyteles* and *Alouatta* suggest at least a functional convergence between them (Zingesser, 1973).

For all the reasons mentioned above, it seems to be supported the divergence of *Alouatta* from the other atelids genera. However, the phylogenetic relationships among the remaining atelid genera are still uncertain. On the one hand, morphological and ecological evidence points out that an *Ateles/Brachyteles* group would be the logical resolution for the ateline trichotomy (Erikson 1963, Rosenberger and Strier 1989, Hartwig 1993) (Fig. 2a). On the other hand, the molecular evidence indicates that a *Brachyteles/Lagothrix* grouping would better explain the phylogenetic relationships within the atelines (Lemos de Sá et al. 1990, da Fonseca et al. 1991, Lemos de Sá and Glander 1993, Schneider et al. 1993, Harada et al. 1995, Horovitz and Meyer 1995, Schneider et al. 1996, Meireles et al. 1999, Von Dornum and Ruvolo 1999) (Fig. 2b).

Table 1. Key taxonomic arrangements of *Brachyteles*' species proposed over time, arranged chronologically.

É. Geoffroy (1806)	<i>Ateles arachnoides</i>		
Wied (1820)	<i>Ateles arachnoides</i>	<i>Ateles hypoxanthus</i>	
Spix (1823)		<i>Brachyteles macrotarsus</i>	
É. Geoffroy (1827)	<i>Ateles arachnoides</i>	<i>Ateles hypoxanthus</i>	
I. Geoffroy (1829)	<i>Eriodes arachnoides</i>	<i>Eriodes hemidactylus</i>	<i>Eriodes tuberifer</i>
Gray (1843)	<i>Brachyteles arachnoides</i>	<i>Brachyteles hypoxanthus</i>	<i>Brachyteles frontatus</i>
Vieira (1944)	<i>Brachyteles arachnoides arachnoides</i>	<i>Brachyteles arachnoides hypoxanthus</i>	
Vieira (1955)	<i>Brachyteles arachnoides</i>		
Hill (1962)	<i>Brachyteles arachnoides</i>		<i>Brachyteles brasiliensis</i>
Groves (2001)	<i>Brachyteles arachnoides</i>	<i>Brachyteles hypoxanthus</i>	

However, all these *Atelids/Atelines* molecular and chromosomal data disagree with the morphology (Schneider and Rosenberger 1996). Rosenberger and Strier (1989) supported an *Ateles/Brachyteles* link based on an extensive series of derived postcranial traits, balanced by the demonstration of convergence in the dental morphology of *Alouatta* and *Brachyteles*.

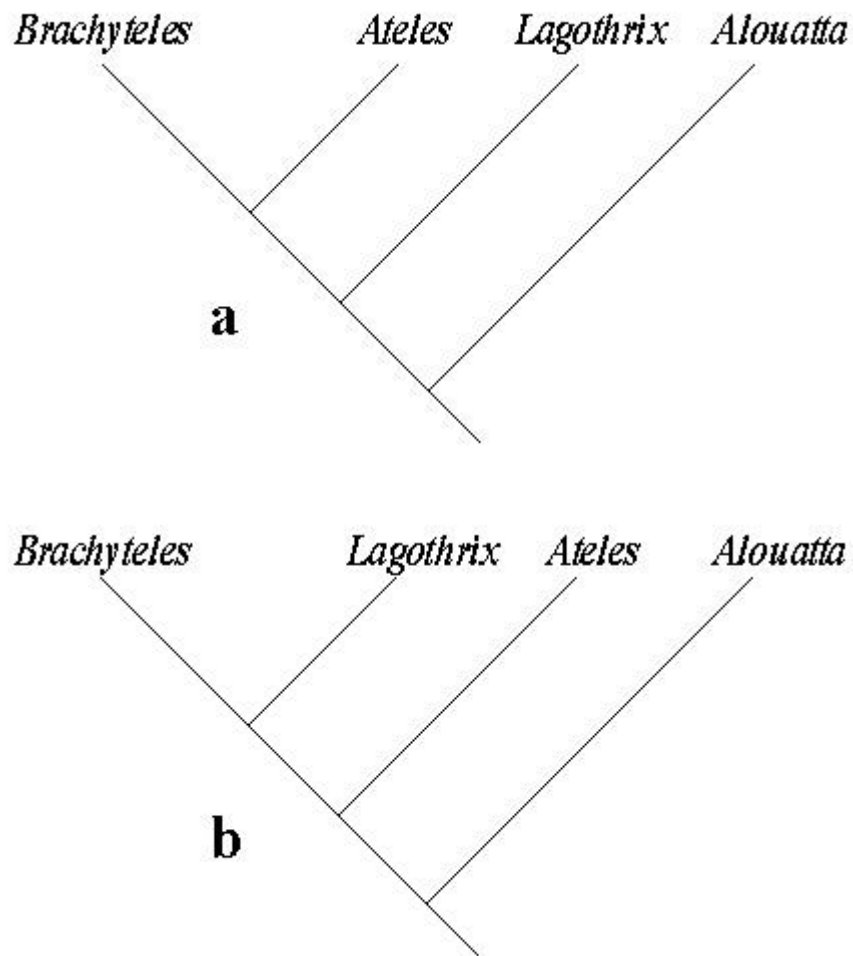


Figure 2. Cladistic relationships among the atelids as supported historically by (a) morphological studies and (b) molecular studies

Equally of arguably as the phylogenetic relationships among atelines is the number of current species of *Brachyteles*, the reasoning used for recognizing two allopatric species remains questionable. The diagnostic characters, which support the full species rank of these populations, are the presence/absence of a vestigial thumb and the facial depigmentation present in the northern population. Furthermore, between primatologists there is still no consensus about the number of species of *Brachyteles*,

this because molecular and morphological works in this genus are not in accord (Rosenberger pers. comm.). For all these reasons the main objectives of this study were:

- To quantify the size and shape variation of the skull in the populations of *Brachyteles*.
- To establish if there is sufficient quantitative and qualitative information to support the recognition of two allopatric species of *Brachyteles*.
- To clarify the phylogenetic relationships among the extant atelines *Ateles*, *Brachyteles*, and *Lagothrix*, and the fossil *Caipora* and *Cartelles*.

2. MATERIALS AND METHODS

2.1 Species concept applied

Cracraft (1983) proposed a new concept to the already large list of the existing species' concepts, the Phylogenetic Species Concept (PSC). This concept claims that "A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent" (Cracraft 1983, p. 170). The PSC was firstly used by ornithologists; nevertheless, in recent decades, the use of this concept in primatology has increased. The PSC is mainly used by researchers of phylogenetics systematics; in this concept, a species is defined on the basis of morphological or genetic distinctions from other taxa (Cracraft, 1983). In principle, this could be based on a single or particular feature. Nowadays, most phylogenetic analyses, and most systematic revisions, are following the PSC to discriminate species based on morphological features or aspects of their DNA (Fleagle 2013).

On average, the PSC recognizes more species than other species concepts (Agapow et al. 2004). The poor understanding or incorrect application of the PSC has generated a phenomenon denominated as "taxonomic inflation" by Isaac et al. (2004). This phenomenon is one of the principal causes for the recent disproportionate increase of well-analyzed and charismatic taxa, such as primates (Mace 2004). Although the PSC has been widely adopted by primatologists (Rylands and Mittermeier 1995; Groves 2001, 2005), there have been serious criticisms to this concept (see Zachos and Lovari 2013 and references therein).

Zachos (2009) stated that the two main requirements proposed by the PSC: reciprocal monophyly and diagnosability are a poor guide to species delimitation. I agreed with Zachos' reasoning; I found the PSC impractical and too simplistic. A criticism to the use of the PSC in recent molecular works is the question of how many genetic differences are needed to discriminate species; this is a critical, but largely unresolved, issue in primate phylogeny (Groeneveld et al., 2009). Interestingly, within primatologists those focused on conservation are the ones who feel an attachment to the PSC, even though, a sound taxonomic knowledge based on the evolutionary history of a group is key to its conservation (Zachos and Lovari 2013).

For this reason, I looked for a species concept, which could be more adequately applied for the conditions I encountered in my research. In this context, I selected the Evolutionary Species Concept (ESC) proposed by Wiley (1978) offers a wider applicability given our current knowledge of evolutionary and speciation processes. The ESC is defined as follows: "A species is a lineage of ancestral descent which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate" (Wiley 1978, p. 18). The ESC implies a critical component that the PSC does not: that species are historical, temporal, and spatial entities. These are three core criteria to try to understand how the species that we study have differentiated along their particular evolutionary processes.

2.2 Specimens and Collections

The material analyzed totaled 42 skins and 71 skulls, including specimens examined in several collections and photographs of international collections. This is study with the largest *Brachyteles*' samples until now which also includes all the type material of this genus. Furthermore, I had the opportunity to see and photograph six individuals in captivity. The catalog numbers of the samples, as well as the acronyms of each collection in which they are deposited, are listed in the appropriate sections of each taxon. All illustrations are mine, except when noted. The collections that contained the analyzed material with their respective acronyms in alphabetical order, and henceforth use the abbreviations in the text, when referring to the respective collections:

MBML - Museu de Biologia Mello Leitão, Santa Teresa, Espírito Santo

MNHN-ZM - Muséum National D'Histoire Naturelle, Paris, France

MNRJ - Museu Nacional do Rio de Janeiro, Rio de Janeiro

MUSM - Museo de Historia Natural - Universidad Nacional Mayor de San
Marcos, Lima, Peru

MZUSP - Museu de Zoologia da Universidade de São Paulo, São Paulo

NHMW - Natural History Museum of Vienna, Vienna, Austria

PUC/MG - Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte

RNH - Rijksmuseum van Natuurlijke Historie, Leiden, Holanda

UFMG - Universidade Federal de Minas Gerais, Belo Horizonte

Living specimens are in the following institutions:

- PZMQB - Parque Zoológico Municipal Quinzinho de Barros, Sorocaba, São Paulo
- Parque de las Leyendas, Lima, Peru

The specimens used for all the analysis in the present work are listed in Appendix 2.

2.3 Localities

The localities and geographical coordinates were raised through the data contained in the specimen's label or by direct consultation with field notebooks, after verification of this data. In most cases, the coordinates have been raised by consulting gazetteers as Paynter and Traylor (1991), Vanzolini (1992), "Cartas do Brasil" to Millionth (IBGE, 1972), or *Global Gazetteer* Version 2.2 sites (see, <http://www.fallingrain.com/world/index.html>) and *Google Earth*. When possible, data some specimens which contained incomplete information on their labels was recover, in this sense, the work of Pinto (1945), which recounts ancient collection expeditions of some naturalists of MZUSP was crucial. The maps were produced using the ArcGIS 9.3 software and edited with Photoshop CS4 software.

2.4. Age groups

The specimens were separated into six age groups according to the eruption teeth and ossification of the cranial sutures, features commonly used in mammalogy. This separation is useful for the study of morphometric and ontogenetic analysis. Only adults were used in quantitative analysis. All the skulls have been assigned to the following age groups:

Infantile: specimens with at least some and at most all deciduous teeth;

Juvenile I: specimens with one to four first permanent molars and such middle permanent incisors as occasionally appear before the upper M1 have fully erupted;

Juvenile II: specimens which possess more permanent teeth than in the juvenile I stage, but without having the last permanent teeth (M3 and/or C) fully erupted, basisphenoid and basioccipital cranial bones not fused;

Adult 0: specimens with completed second dentition, but as yet without noteworthy wear the teeth, basisphenoid and basioccipital cranial bones with small remnants of visible suture;

Adult 1: specimens with moderate to marked wear of the teeth (“middle-aged adults”), basisphenoid and basioccipital cranial bones fused or with small remnants of visible suture;

Adult 2: specimens with very marked to extreme wear of the teeth, basisphenoid and basioccipital cranial bones completely fused.

2.5 Cranial and dental measurements

Using a digital caliper with precision of 0.10 mm, I took 18 crania-dental linear measurements. The measurements involving dental series were taken from the base teeth in the alveoli, allowing them to be also measured in skulls that not possessed those teeth. The measures are described below and the dimensions of the measurements are illustrated in Figure 3.

- 1. BABR:** Basicranial breadth. Greatest breadth of braincase measured between the inferior midline of the external auditory meati.
- 2. BCAB:** Bicanine breadth. Distance between the outer lateral surfaces of the canine alveolus at the septum between the canine and second premolar.
- 3. BPTB:** Bipterygoid breadth. Distance between the outer lateral surfaces of the lateral pterygoid plates.
- 4. BRDT:** Breadth. Greatest breadth of braincase perpendicular to midsagittal plane above the roots of the zygomatic arches on the temporal squamae or parietals.
- 5. BZYB:** Bizygomatic breadth. Distance between the outer lateral surfaces of the zygomatic arches, measured at the inferior-most aspect of the temporozygomatic suture.

6. **GCLT:** Greatest cranial length. Distance between opisthocranion (disregarding processes or crests) to prosthion.
7. **IBIB:** Inner biorbital breadth. Frontomolare orbitale to frontomolare orbitale.
8. **MANL:** Mandible length. Distance between the anterior region of the mandible, between the alveoli of the internal incisors until the most prominent part of the posterior mandible edge, taken with the mandible and caliper positioned straight in parallel, following the tooththrow's line.
9. **NEHT:** Neurocranial height. Basion to bregma.
10. **PALL:** Palatine length. Prosthion to the midline point on a tangent between the most aboral (posterior) portions of the right and left alveolar processes.
11. **PALW:** Distance between the inner edges of the alveoli of the third molars.
12. **POCL:** Postcanine length. Greatest straight distance from the septum between the right upper canine and second premolar to the distal border of the right upper third molar alveolus.
13. **POCW:** Postorbital constriction width. Width across the greater constriction of the skull, located just after the orbits.
14. **UCBL:** Upper canine buccal-lingual. Maximum buccal-lingual dimension of maxillary canine tooth.
15. **UCMD:** Upper canine mesial-distal. Maximum mesial-distal dimension of maxillary canine tooth.
16. **UCM2:** Upper canine to second molar. Distance between the mesial-most point of the maxillary canine alveoli to the middle distal edge of the second molar tooth.

- 17. UM1B:** Upper first molar buccal-lingual. Buccal-lingual dimension of the maxillary first molar crown taken at the occlusal level at the mesial-distal midpoint.
- 18. UM1M:** Upper first molar mesial-distal. Mesial-distal dimension of maxillary first molar crown taken at the occlusal level, in line with the buccal cusps.

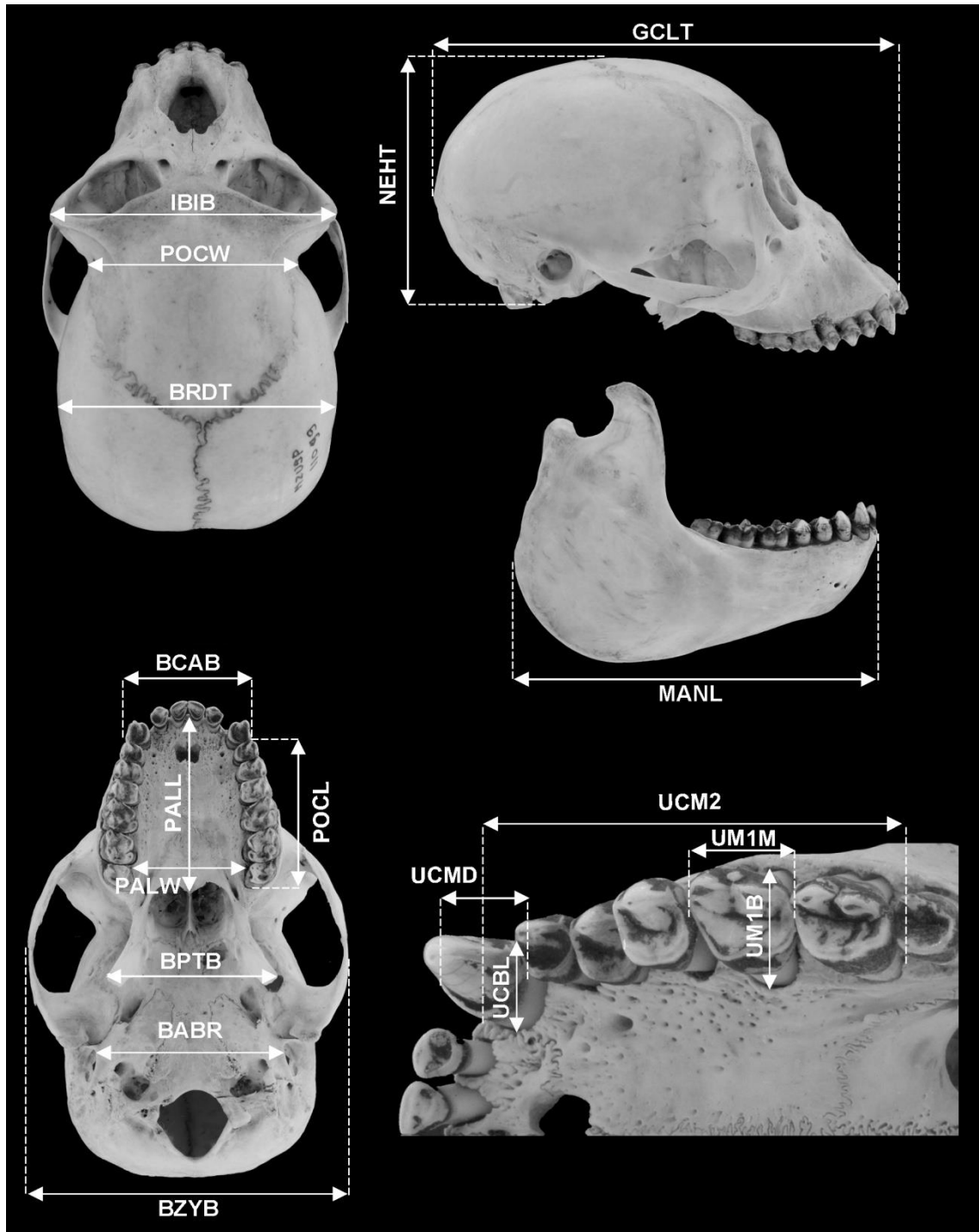


Figure 3: Skull of *Brachyteles arachnoides* in dorsal, ventral, and lateral view; mandible in lateral view and upper tooththrow in occlusal view, showing the linear measurements that were used in this study.

2.6 Definition of the geographic groups

In order to perform the analysis of sexual, individual, ontogenetic populational and geographic variation, I grouped some nearby localities. To achieve this, the following criteria were considered: a morphological homogeneity sample, geographical proximity and ecological similarity of locations, and the absence of significant geographical barriers between them, like rivers of large areas or altitudinal differences. Some geographically isolated locations made impossible its grouping with any other group; these were treated individually and were important to help definining the geographical limits of the morphological patterns found. I use these same groups to test univariate, multivariate and geometric morphometrics analyses. The groups are: BA = Bahia, ES = Espírito Santo, MG = Minas Gerais, RJ1 = Rio de Janeiro 1, RJ2 = Rio de Janeiro 2, SP1 = São Paulo 1, SP2 = São Paulo 2, and SP3 = São Paulo 3

Table 2. List of the grouped localities for the analysis of geographic morphometric variation.

Acronym	Total N	Individual N	ASSOCIATED LOCALITIES
BA (Bahia)	1	1	Rio Congoji
ES (Espírito Santo)	13	1	Colatina
		1	Córrego Jequitibá, Santa Leopoldina
		1	Jahibocas, Itarana
		10	Santa Leopoldina
RJ1 (Rio de Janeiro 1)	1	1	Itatiaia
RJ2 (Rio de Janeiro 2)	11	2	Mambucaba, Angra dos Reis
		3	Pedra Branca, Paraty
		6	Teresopolis
SP1 (São Paulo 1)	5	1	Boraceia
		1	Paranapiacaba (Alto da Serra)
		1	Piedade (Água Doce)
		2	Ubatuba
SP2 (São Paulo 2)	4	1	Iporanga
		2	Itararé
		1	São Bartolomeu
SP3 (São Paulo 3)	2	1	São Paulo
		1	São Paulo

2.7 Analytical methods

In this section, I explain the methods applied to the analysis of sexual dimorphism or dichromatism, geographical and intrapopulation variation.

2.7.1 Pelage, development of the thumb and facial pigmentation

In this section, I evaluated the coloration patterns of juvenile and adult individuals to determine if there is ontogenic differentiation, I also compared the general coloration of adult males and females to determine if there is a marked sexual dichromatism. Finally, I evaluated the absence or presence and the degree of

development of the thumb and the facial pigmentation to test the persistence of these characters among *Brachyteles*' populations.

2.7.2 Statistical analysis

Statistical analyses were performed to test the morphometric differences between geographical groups in order to verify the canine sexual dimorphism and intra- and interpopulational variation. Only skulls of adult individuals were used in these analyses because at this stage the growth of animal ceases. The results were considered significant when presented a probability less than 5% ($p < 0.05$). All the tests were performed using the software the free software R statistical package version 3.0.2 (R Core Team, 2013). Due to missing measurements, I used a regression equation to predict those values.

First, I performed a Shapiro test to assess the normality of the data. For the multivariate analysis, I used the 18 crania-dental linear measurements. I performed A Principal Component Analysis (PCA) as an exploratory tool to investigate more representatively a possible separation of the samples in different units being supported only by morphometric variables without defining taxa *a priori*.

I also analyzed the geographic variation by the method of Transects proposed by Vanzolini (1970). Initially, all locations are mapped, and near locations are geographically connected by transects and their morphometric characters are compared over these transects. Each skull and dental measurement was compared across

geographical groups using *Dice-Leeras* diagrams (Simpson et al. 2003). In this chart, axis Y contains the measurement scale, in millimeters, while the axis X refers to the geographical groups. In each vertical line plotted on the graph, the central point indicates the average of the variable in question, for each cluster, and the line refers to the Confidence Interval of 95%. This methodology allows viewing abrupt breaks or morphometric trends, directly related to geography.

2.7.3 Geometric morphometrics

In addition to the conventional approach to discriminate populations based on linear data, geometric morphometrics (GM) were applied in order to visualize shape variation among the examined taxa (e.g. Fonseca and Astúa 2015, Damasceno and Astúa 2016). A total of 138 skulls were digitalized using a photographic camera Canon Rebel T5, and all the required precautions were taken to avoid possible distortions. The photographs were transformed into TPS files using the software TpsUtil 1.60 (Rohlf 2013). Using the software TpsDig v.2.26 (Rohlf, 2006; Rohlf and Bookstein, 2003), cranial outlines were generated and 2D landmarks were digitized on three different perspectives of the skull (i.e. 22 on the dorsal view; 21 in the lateral view; and 17 in the frontal view). The landmark configuration of each view is shown in the Figure 4. Landmarks definitions are listed in Appendix 1.

Shape variables were obtained by performing a generalized Procrustes analysis, thus removing the differences due to translation, rotation and scale Rohlf & Slice (1990). The Procrustes Superimposition eliminates the effects of orientation and position of the images, and removes isometric size effect, by scaling all configurations

to the same centroid size. These procedures were repeated for the raw landmark coordinates of each view. The new Cartesian coordinates obtained after the superimposition are the shape coordinates used for statistical comparisons of individuals (Cardini et al. 2007).

After all the effects of orientation, position and size were removed, the resulting landmark configurations retain only shape information. Thus, the shape of the structures was analyzed independently of size (Klingenberg et al. 2002, Zelditch et al. 2004). Using the geometric morphometrics data, the shape differences between pre-established groups and between sexes were tested using a Discriminant Analysis followed by a leave-one-out Cross-validation test (Lachenbruch 1967) and also through a Principal Component Analysis (PCA). Both Discriminant Analysis and Principal Component Analysis were performed in the software MorphoJ (Klingenberg, 2011).

For the discriminant analysis used to test sexual dimorphism in *Brachyteles*, all the specimens were merged in one group due to small sample size of some groups and for methodological requirements.



Figure 4. Landmark configuration in dorsal (A), lateral (B), and frontal (C) view. Landmarks were digitized on both sides but definitions are shown on one side only.

2.7.4 Phylogenetic analysis

For the phylogenetic analysis, I included as terminals at least one species of each extant genus of Atelidae. One *Alouatta* species was included as the only living member of Alouattinae. Among extant Atelinae, I included two species of *Ateles*, all recognized taxa of *Lagothrix* and *Brachyteles*. I also included the extinct Platyrrhini *Cartelles coimbrafilhoi* and *Caipora bambuorum*, initially treating them as “subfamily *incertae sedis*”. One cebid, *Sapajus nigritus* and one pithecid, *Callicebus personatus* were used as outgroups, and the tree was rooted in the latter taxon. I had no access to *Lagothrix lugens*, for this reason, I followed the Paredes’ (2003) codification. The matrix contained 13 terminal taxa and 77 characters of pelage and integument (18), skull (28),

postcrania (7), dental (18), cerebral (3) social organization (2) and karyology (1) were scored. The matrix of characters is presented in Appendix 3.

I conducted a parsimony analysis using the software TNT version 1.5 (Goloboff and Catalano 2016, freely distributed by the “Willi Hennig Society”). Due to relatively small number of terminals, it was possible to carry out an exhaustive search for the shortest trees using the “implicit enumeration” option. Branches with minimal length = 0 were collapsed. All of the characters were unordered. As branch support measure, we calculated the decay index, also known as Bremer’s support.

3. RESULTS AND DISCUSSION

3.1 Ontogeny

Regardless the geographic distribution, all infants of muriqui are born with black faces that become mottled as they age (Fig. 5). Nevertheless, some northern individuals remain with a totally (or almost totally) dark face, even as adults. This dark facial pigmentation is a trend but not a rule and all kinds of pigmentation variation can be found (R. de Melo pers. comm.).



Figure 5. Juvenile individual of *Brachyteles* from Caratinga-Minas Gerais, presenting a completely black face. Photograph by Daniel da Silva Ferraz.

The coloration of juveniles is in general paler than adults (Fig. 6), the brighter tones on the inside of the hindlimbs and base of the tail base are present but fainter than in adults. The crown of the head tends to be darker than in adults. Regarding the thumb's development, I had limited access to young individuals due to the scarcity of samples in scientific collections. Nevertheless, based on my observations it seems likely that the development is regular and uniform with the other fingers and, at some point, stops while the others continue their normal develop. Talking with the staff of the Parque Zoológico Municipal Quinzinho de Barros, who have been working with muriquis for several years, they told me that the size of the thumb is heritable. I saw two juveniles one of these had longer thumbs than the other, which corresponded with the

size of the fathers' thumbs. Unfortunately, I could not register this photographically for logistic reasons.



Figure 6. Juvenile individual of *Brachyteles* (MZUSP 11180, a) and an adult (MZUSP 24604, b), both from Santa Leopoldina, Espírito Santo.

3.2 Sexual dimorphism

In this section, I will present the results of the different analyses that I performed to test the sexual dichromatism, cranial and canine sexual dimorphism.

3.2.1 Qualitative Analysis: pelage variation

The qualitative analysis of the pelage coloration revealed that there is no sexual dichromatism in *Brachyteles*, as can be observed in the Figure 7. Nonetheless, there are some differences between males and females in the majority of analyzed groups. These differences seem to be directionless, without a clear pattern for each sex. In some cases, females can be darker than males (Fig. 8) and, in other cases, the opposite. Based on my observations, *Brachyteles* presents the least uniform coloration pattern between sexes within atelines. In *Ateles* and *Lagothrix* these coloration differences are imperceptible. Furthermore, in dry skins from museum collections, the sexual identification of *Brachyteles* becomes a hard task.



Figure 7. Male of *Brachyteles* (MZUSP 11180, a) and a female (MZUSP 11102, b), both from Santa Leopoldina, Espírito Santo.



Figure 8. Male of *Brachyteles* (MNRJ 7724, a) and a female (MNRJ 8513, b), both from Pedra branca, Rio de Janeiro.

3.2.2 Quantitative analysis

In order to test the sexual dimorphism based on cranial measurements, I only could work with two geographical groups: ES and RJ2. In these two groups, the number of females and males made possible this kind of comparisons. The Shapiro and the Levene tests applied to verify the normality of the samples in geographic clusters with $N > 2$ in both males and females showed a normal and homogeneous distribution in all the variables (Table 3). After this, I performed a t-Student t to test the sexual dimorphism in the groups ES and RJ2. The difference between sexes was significant

only for the variables: BCAB, IBIB, UCMD, and UCM2 for the **ES** group; while only UCMD for **RJ2**. (Table 4).

Table 3. Results of homogeneity and normality tests, indicating the values of the Levene and Shapiro indices for all the variables analyzed according to the ES and RJ2 geographic groups.

Variable	ES		RJ2	
	Levene	Shapiro	Levene	Shapiro
BABR	.806	.784	.127	.992
BCAB	.470	.736	.118	.079
BPTB	.669	.790	.783	.806
BRDT	.351	.166	.741	.977
BZYB	.355	.754	.275	.509
GCLT	.137	.440	.945	.416
IBIB	.826	.473	.282	.221
NEHT	.228	.408	.151	.545
PALL	.818	.484	.888	.514
POCL	.514	.310	.327	.584
UCBL	.572	.810	.066	.078
UCMD	.161	.333	.110	.061
UCM2	.318	.067	.080	.230
UM1B	.164	.301	.245	.904
UM1M	.084	.199	.127	.740
POCW	.519	.924	.152	.442
PALW	.534	.392	.532	.139
MANL	.004	.273	.942	.282

Table 4. Results of sexual dimorphism test in ES-and RJ2, indicating the values of t index Student (t), the 5% significance (Sig.), number of samples of males and females for each variable tested. *Variables with significant values.

<i>t-Student</i>								
ES					RJ2			
Variable	<i>t</i>	Sig.	m	f	<i>t</i>	Sig.	m	f
BABR	-.366	.723	7	6	1.238	.242	7	4
BCAB	3.163	.011*	7	6	.592	.566	7	4
BPTB	.055	.957	7	6	1.099	.295	7	4
BRDT	.259	.801	7	6	.476	.644	7	4
BZYB	.925	.379	7	6	1.244	.239	7	4
GCLT	1.118	.292	7	6	1.010	.334	7	4
IBIB	3.137	.012*	7	6	.685	.508	7	4
NEHT	.774	.459	7	6	1.711	.115	7	4
PALL	1.134	.286	7	6	1.034	.323	7	4
POCL	1.317	.221	7	6	-.148	.885	7	4
UCBL	1.738	.116	7	6	.538	.601	7	4
UCMD	2.608	.028*	7	6	3.016	.012*	7	4
UCM2	2.428	.038*	7	6	.836	.421	7	4
UM1B	1.272	.235	7	6	-.130	.899	7	4
UM1M	.479	.643	7	6	-1.436	.179	7	4
POCW	-.257	.803	7	6	.800	.441	7	4
PALW	-.167	.871	7	6	-.673	.515	7	4
MANL	1.197	.262	7	6	.676	.513	7	4

3.2.3 Discriminant analysis based on geometric morphometrics

The Discriminant Analysis using Mahalanobis distances was not able to differentiate between sexes in the three views of the *Brachyteles*' populations (Fig. 9). In these three views all the T-square values were not significant (>0.05). The highest Mahalanobis distance between males and females was found in the frontal view (Table 5). This analysis reveals that the sexual dimorphism in *Brachyteles* based on skull shape is not significant.

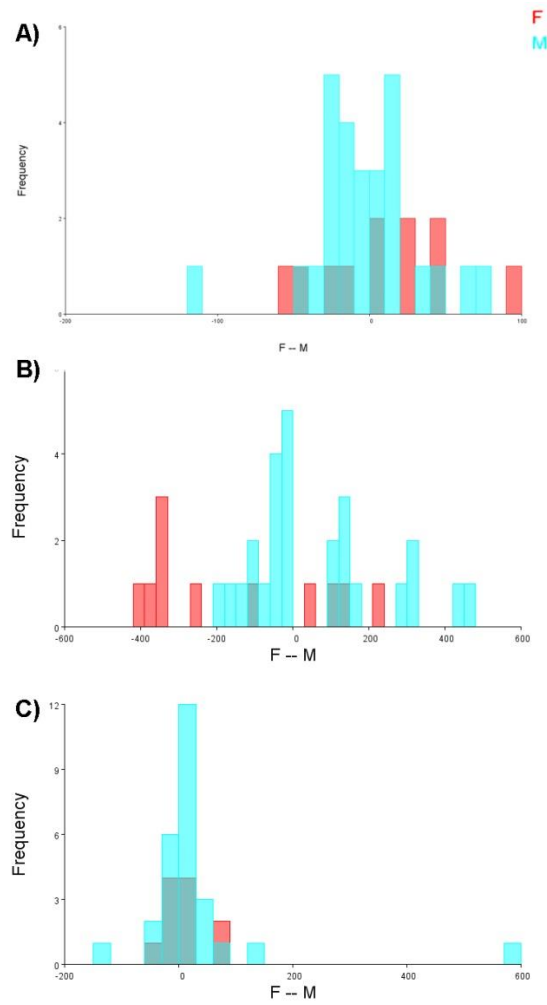


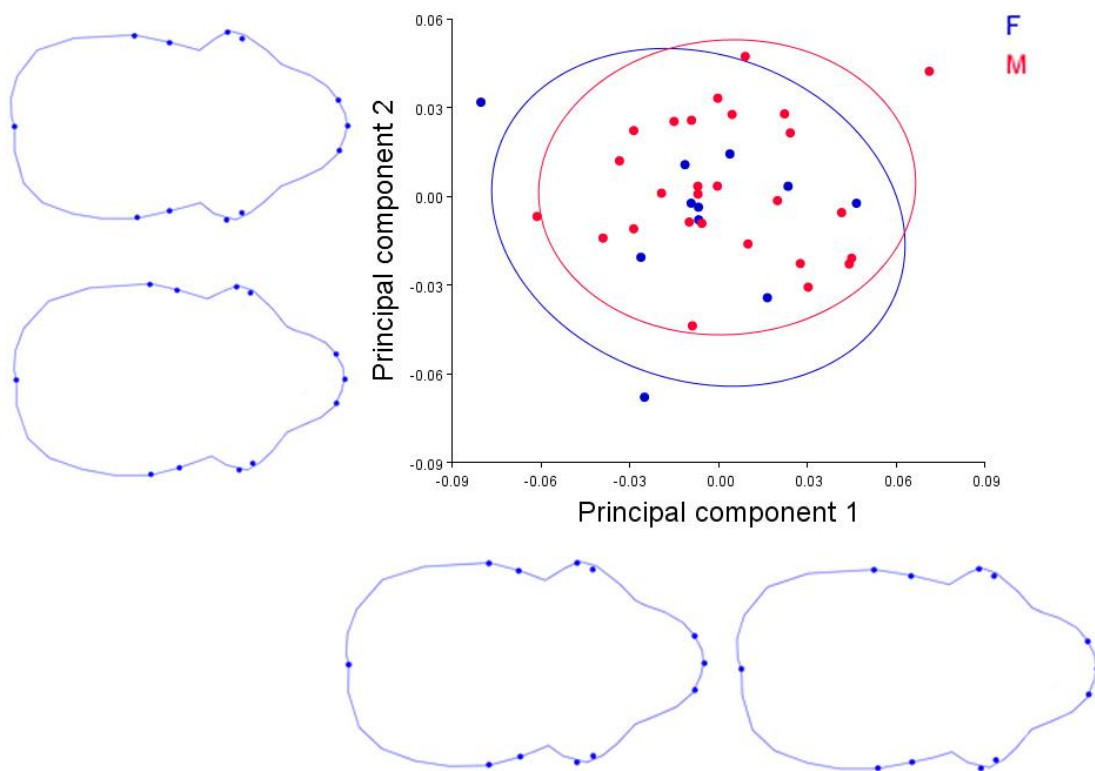
Figure 9. Discriminant function showing the leave-one-out cross-validation between sexes of *Brachyteles* in three different views: dorsal (a), frontal (b), and lateral (c) (f = female, m = male).

Table 5. Mahalanobis distances between both sexes of *Brachyteles* as given by the Pairwise discriminant analyses for shape. T-square values are shown between parentheses. Letters indicate view of the cranium D = dorsal, L = lateral, and F = frontal.

Mahalanobis distances	<i>Brachyteles</i> ♀		
	D	F	L
<i>Brachyteles</i> ♂	4.70 (0.66)	20.37 (0.16)	5.31 (0.33)

3.2.4 Skull shape variation between sexes

The PCA of the dorsal and lateral view of the cranium did not distinguish males from females (Fig. 10). PC1 showed little variation on the postorbital constriction, becoming deeper throughout the negative end of the PC1. In the same way, a very subtle width reduction of the braincase and the maxilla is observed in PC2. The same morphological variations were exhibited in both sexes (PC1 and PC2 in this case). The values of the first three Principal Components are shown in the Table 6.



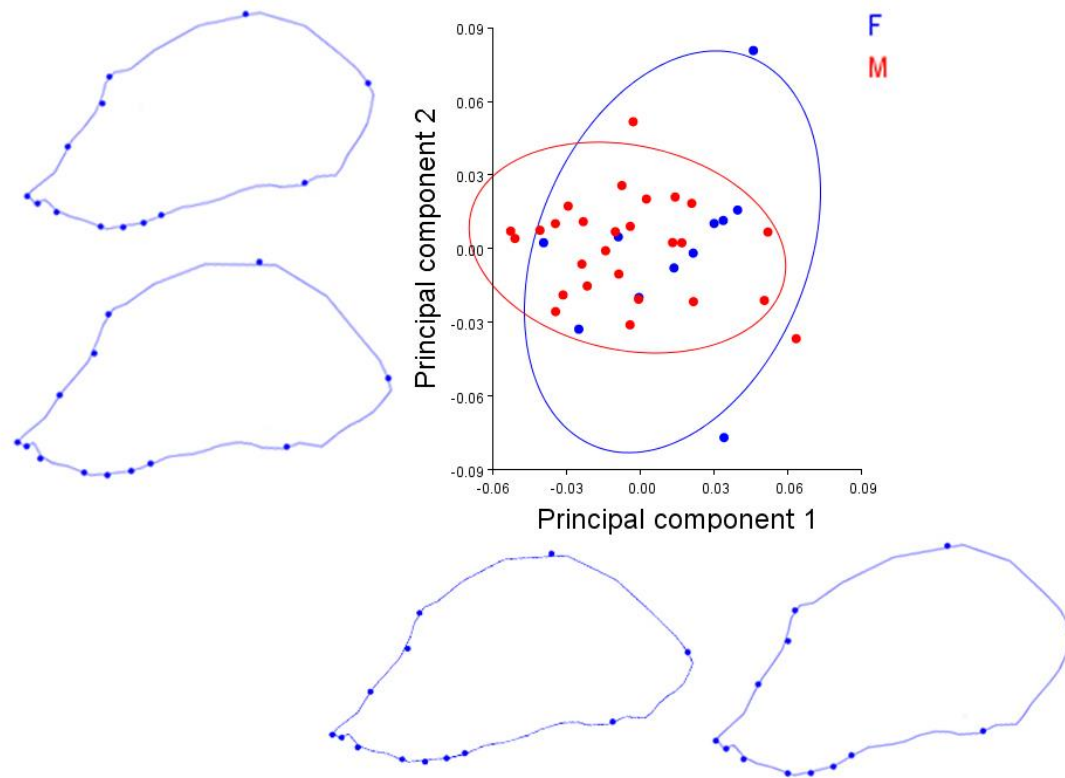


Figure 10. Skull variation of the shape grouped by sexes in dorsal (above) and lateral (below) view of *Brachyteles* determined for PC 1 and PC 2 (F = female, M = male). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.03, right 0.03).

Table 6. Values (expressed in %) of the first three Principal Components of each view.

View	PC1	PC2	PC3
Dorsal	27.79	17.76	13.16
Frontal	29.16	15.22	12.44
Lateral	24.93	18.21	12.03

The PCA on the frontal view of the cranium showed some differentiation between males and females (Fig. 11); although, there is still a major overlap between their confidence intervals. The variation along PC1 can be described in the following

manner: males tend to have broader oval orbits oriented downwards and more flattened skulls. On the other hand, females have slender skulls with orbits that are more circular and a more elevated frontal bone. All the variation explained by PC2 is presented both in males as females equally.

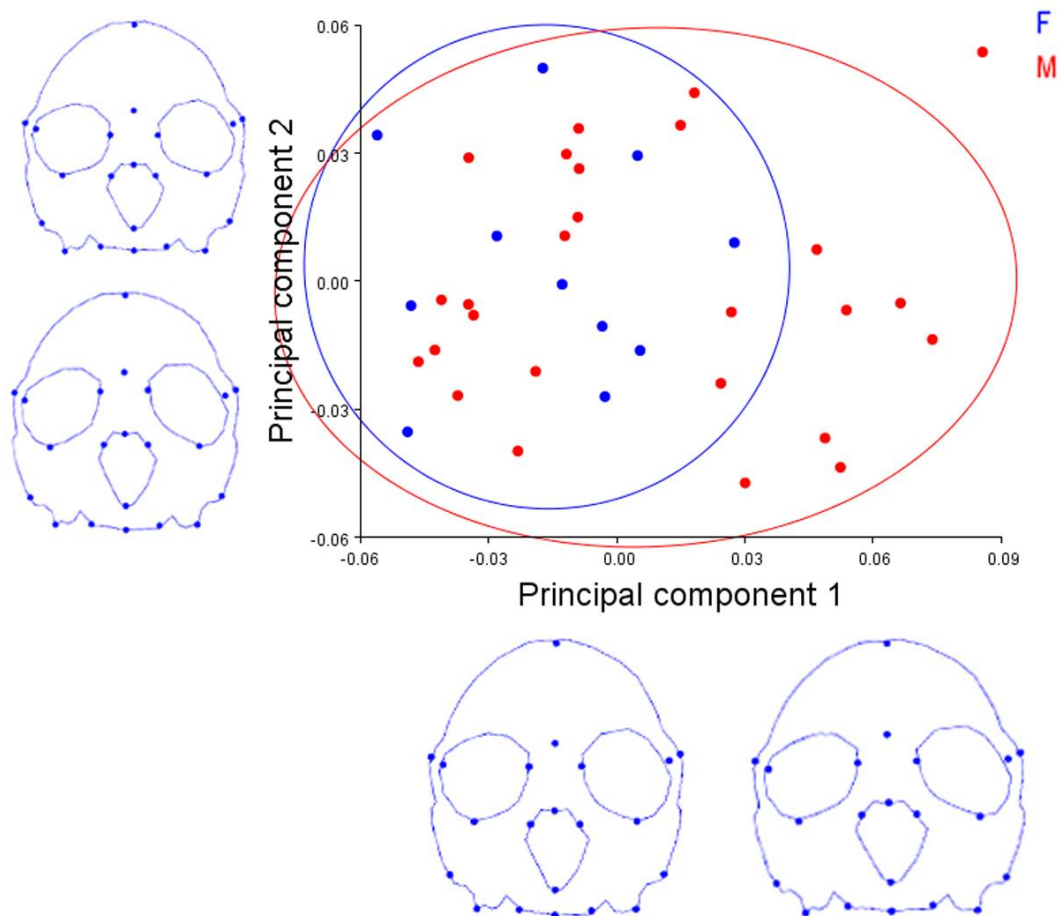


Figure 11. Skull variation of the shape grouped by sexes in frontal view of *Brachyteles* determined by PC 1 and PC 2 (F = female, M = male). The negative and positive extremes of both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.03, right 0.03).

Leutenegger and Cheverud (1982, 1985) proposed the hypothesis that larger primates should present a higher degree of sexual dimorphism in body weight and canine size than smaller primates. They cited no evidence for heritability; nevertheless,

they showed some examples suggesting that males are (or could be) more variable than females (Plavcan and Kay 1988). Following Leutenegger and Cheverud's reasoning, it would be expected that atelids present this high degree of dimorphism. Nonetheless, between atelids this marked sexual dimorphism is only observed in *Alouatta*, and it is present at different levels: body mass (Plavcan and van Schaik 1997), canine length (Plavcan and van Schaik 1992), pelage coloration (*Alouatta caraya* dichromatic), and cranial morphology (Hershkovitz 1977, van Schaik et al. 1999, Crook 1972, and Fleagle 2013). In remaining genera of atelids (*Ateles*, *Brachyteles*, and *Lagothrix*), this sexual dimorphism varies but never reach the degree of *Alouatta*.

The published data about sexual dimorphism in *Brachyteles* is based mainly on canine length and body mass (Ruschi 1964, Zingezer 1973, Kay et al. 1988, Lemos de Sá and Glander 1993). Zingezer (1973) and Kay et al. found no sexual differences in canine lengths, while, Lemos de Sá and Glander (1993), analyzing living animals from two different localities and few museum specimens of *Brachyteles*, found sexual dimorphism only in the canine lengths of southern populations. Based on my observations, I agree with Lemos de Sá and Glander's (1993) results that there is canine sexual dimorphism in *Brachyteles*. Nevertheless, this dimorphism is only significant in the upper canine mesial-distal width and does not in the upper canine buccal-lingual length.

Regarding cranial morphology, there is little information about *Brachyteles*' sexual dimorphism. In the present work, I found no sexual dimorphism in either size or shape of the skull. These results are congruent with the low dimorphism exhibited in

other atelines (*Lagothrix* and *Ateles*) which support the monophyly of this subfamily. Furthermore, in the GM analyses, *Brachyteles* resulted to be the less dimorphic extant ateline; this is consistent with the results of Plavcan and van Schaik (1992, 1997).

Plavcan et al. (1988) proposed that the social structure and the mating competition level would influence in the degree of dimorphism. One of the most interesting results of Plavcan et al.'s (1988) was that monogamous and polyandrous social structures species have the smallest canines, while species with dominance hierarchies of males tend to have bigger canines. In species with fission-fusion social structures and polygamous mating (as atelines), this canine dimorphism would be intermediary. *Ateles* and *Lagothrix*, indeed, present this intermediary degree of canine dimorphism but *Brachyteles* does not. Canines have a primary function during the feeding, being the responsible for breaking hard structures; *Ateles* and *Lagothrix* are genera mainly Amazonian. Thus, their primary food items are Amazonian fruits, which are known for their hardness.

Brachyteles in an Amazonian context would be in disadvantage with its ateline relatives. Therefore, the development of the canines is not only related to sexual selection forces but to ecological and functional factors too. Although the intermale competition in *Brachyteles* is low, its diet does not include hard Amazonian fruits, which may turn the development of the canines unnecessary for its soft fruit and folivore diet. The evolutionary path that *Brachyteles* (and *Alouatta*) took was different from the other atelids; their dental modifications became them in folivore-adapted species in response to the marked seasonality in the Atlantic Forest. The similarity of

Alouatta and *Brachyteles* may represent the ancestral atelid phenotype, but considering dental shearing in both taxa is probably a homoplastic adaptation linked to diet (Rosenberger and Strier 1989). *Alouatta*, unlike *Brachyteles*, possesses a dominance rank competition social structure in which its large canines would also represent a character of sexual selection.

Given the results of pelage variation, and cranial size and shape here obtained, I did not discriminate between males and females and the specimens with undetermined sex for the following analyses.

3.3 Geographic variation

In this section, I will present the results of univariate, multivariate and geometric morphometrics analyses that I applied in order to find geographical clusters of *Brachyteles*.

3.3.1 Qualitative analysis: geographical pelage variation

Two general patterns of coloration were observed; the populations inhabiting the coast tend to be darker than those from the interior, excepting Paraná's populations that could not be analyzed due to the lack of samples in museums or photographic registers. In the ES group, the pattern is also different from the general; here two differentiated morphotypes coexist. In the Figure 12 are shown the frequencies of each morphotypes follow by the description of each pelage variation per group.

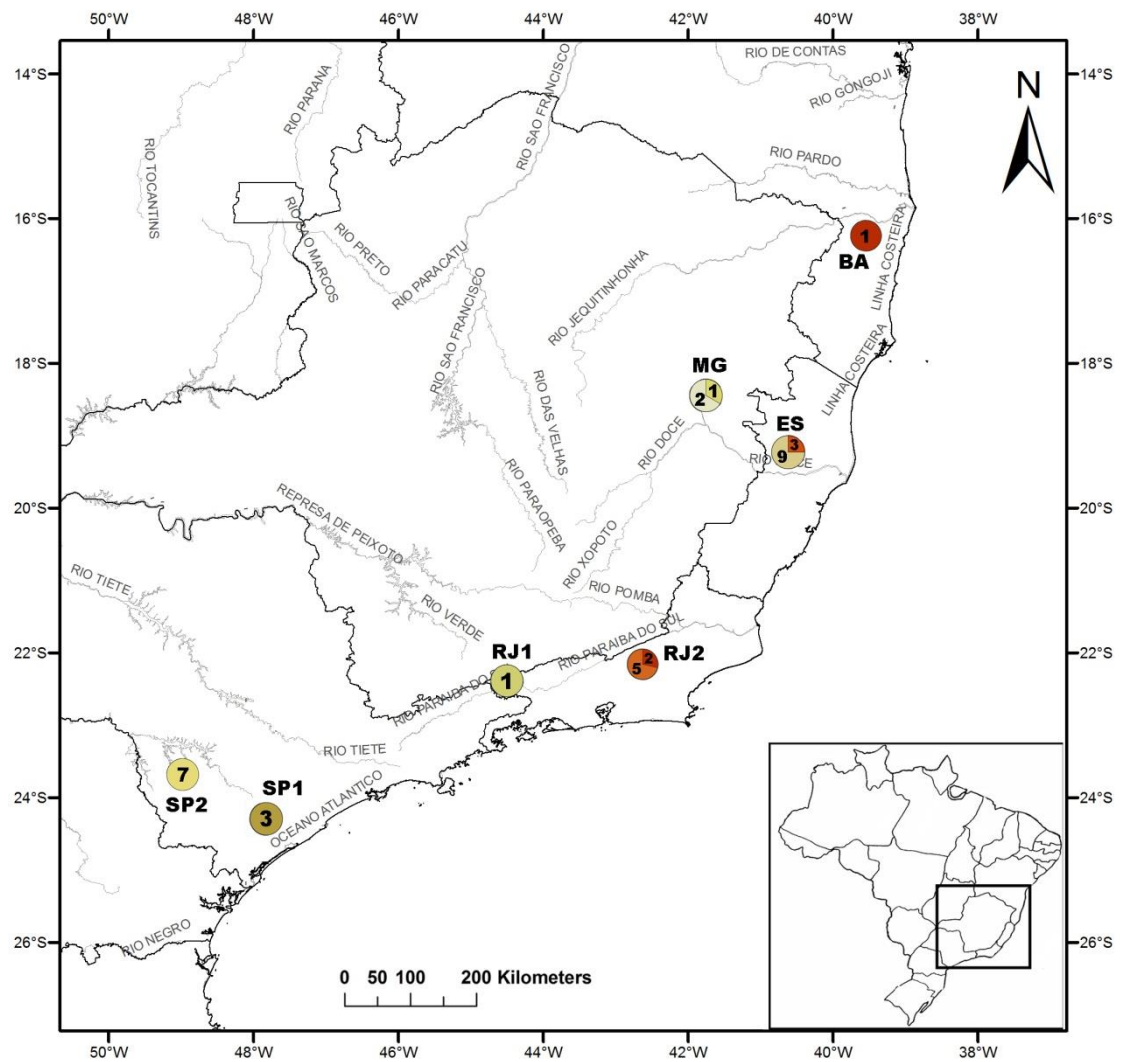


Figure 12. Frequency's distribution of the general coloration in each geographical group. The numbers in each spot represent the number of individuals presenting that specific coloration.

Group BA

The material and registers of *Brachyteles* in this region are quite scarce, all the populations from this state have been almost extinct and there is one known remaining population at the Parque Nacional do Alto Cariri, in Guaratinga. The evidences gathered from Bahia were photography registers from the Alto Cariri's population and from the type material collected by the Prince Maximilian Wied-Neuwied in "As Barreiras",

close to the Rio das Contas. The type material of *Brachyteles hypoxanthus* has a reddish brown coloration; unfortunately, these populations no longer exist but using Kuhl's and Wied's description we can know that those miquis had speckled faces (Fig. 13)



Figure 13. Type material collected by the Prince Maximilian Wied-Neuwied in “As Barreiras” (top; photograph by Pepijn Kamminga); individuals from the Parque Nacional do Alto Cariri, in Guaratinga, (bottom; photograph by Adriano Garcia Chiarello)

Group ES

Here two different morphotypes were observed. The muriquis of the morphotype one are reddish-brown with a lighter belly and lighter contrasting circumfacial coloration. There is no marked contrast between the top of the head and this circumfacial coloration. The coloration of limbs and tail is almost the same as dorsum. While in morphotype 2, the coloration turns pale with a greyish dorsum, the belly is lighter than the Interior populations. The head, which is also greyish, contrasts with the whitish circumfacial ring. Even in the most greyish individuals, the inner portion of the posterior limbs and the initial portion of the tail have a contrasting coloration that could be yellow or orange (Fig. 14).





Figure 14. Two individuals from Santa Maria de Jetibá, one of them presenting a pronounced reddish-brown coloration (top; photograph by Marlon Lima); adult female and a juvenile from the Reserva Biológica Augusto Ruschi, in Santa Teresa (bottom; photograph by Carla Possamai).

Group MG

Here the population is more uniform than in any other locality. The pelage is predominantly beige, with light or dark brown tail, fore- and hindlimbs; although, some individuals can be darker with a predominant grayish coloration. The facial depigmentation varies, and it is possible to find individuals with almost-complete black faces (Fig. 15).

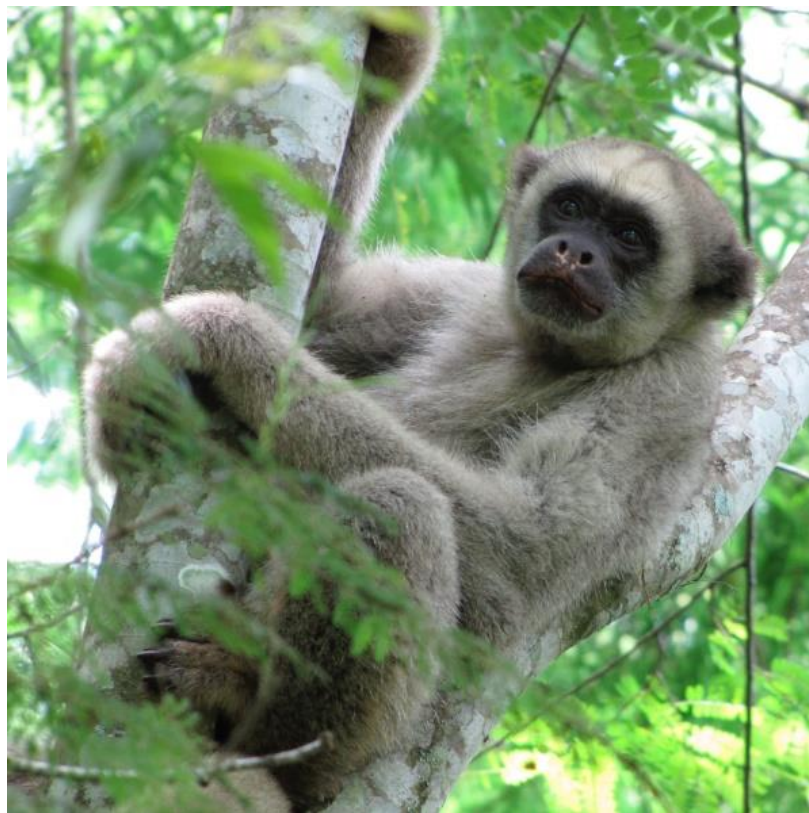


Figure 15. Adult female (top) and adult male from Caratinga, Minas Gerais (bottom; photographs by Carla Possamai).

Groups RJ1 – RJ2

In the RJ2 group, the coloration in the whole body is uniform with slightly darker coloration at crown of the head. The RJ1 is a lighter version of the RJ2 group, these two populations with black face (Fig. 16). There are unpublished reports of depigmented face individuals also from Rio de Janeiro and in contact with these black-pigmented individuals (Breves pers. comm.).



Figure 16. Adult male from the Parque Nacional Serra dos Órgãos, presenting the general coloration of the RJ2 group. (left); adult individual from the Parque Nacional de Itatiaia, presenting the general coloration of the RJ1 group. (right; photographs by Paula Breves).

Groups SP1 – SP2

SP2 populations have a light beige uniform coloration in the dorsum, lighter ventrally; the circumfacial ring is only present in the lateral sides of the face; the crown of the head is a little contrasting (Fig. 17). As in RJ2, SP1 population is a darker version

from the interior populations, being generally brown with the crown, fore- and hindlimbs darker and contrasting with the rest of the body coloration (Fig. 18). Both groups have the face completely black pigmented.



Figure 17. Adult male (NMW-ST 679) from Ypanema (=São João de Ipanema) collected by Johann Natterer (photograph by Alexander Bibl). Presenting the general coloration of the SP2 group.



Figure 18. Adult male from the Parque Zoológico Municipal Quinzinho de Barros, São Paulo, brought from the Parque Estadual Carlos Botelho. Presenting the general coloration of the SP1 group.

3.3.2 Variation of the thumb and the facial pigmentation

These two characters have been accepted as morphological evidence to separate the northern and southern populations of muriquis (Rylands et al. 1995; Groves 2001, 2005). The logic was simple: northern populations (*Brachyteles hypoxanthus*) with a rudimentary thumb (Fig. 19) and a mottled black and pink face; while the southern populations (*Brachyteles arachnoides*) with no external thumb (Fig. 20) and an entirely black face.

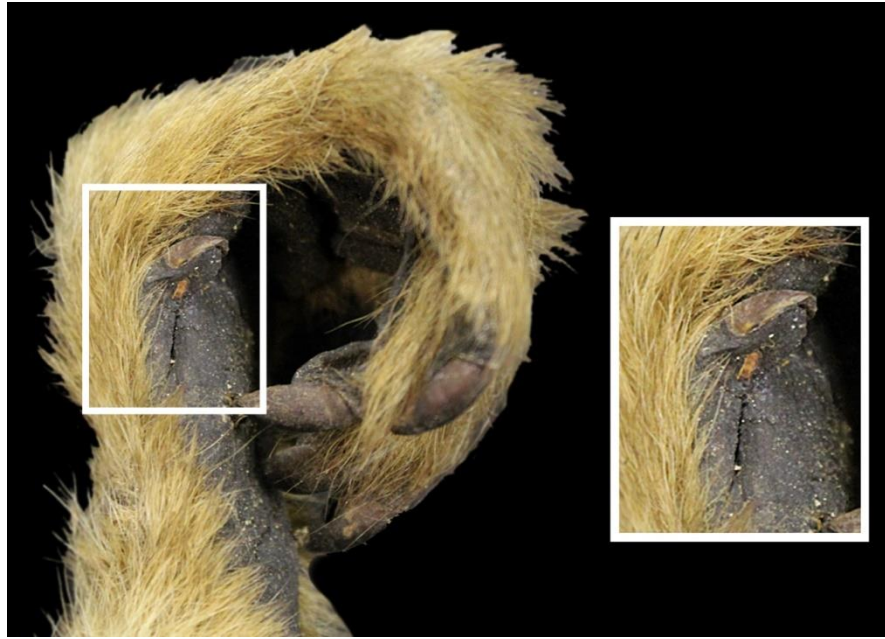


Figure 19. Left hand of *Brachyteles arachnoides* (MZUSP 11098) from Santa Leopoldina, Espírito Santo, exhibiting a full-developed nailed thumb.

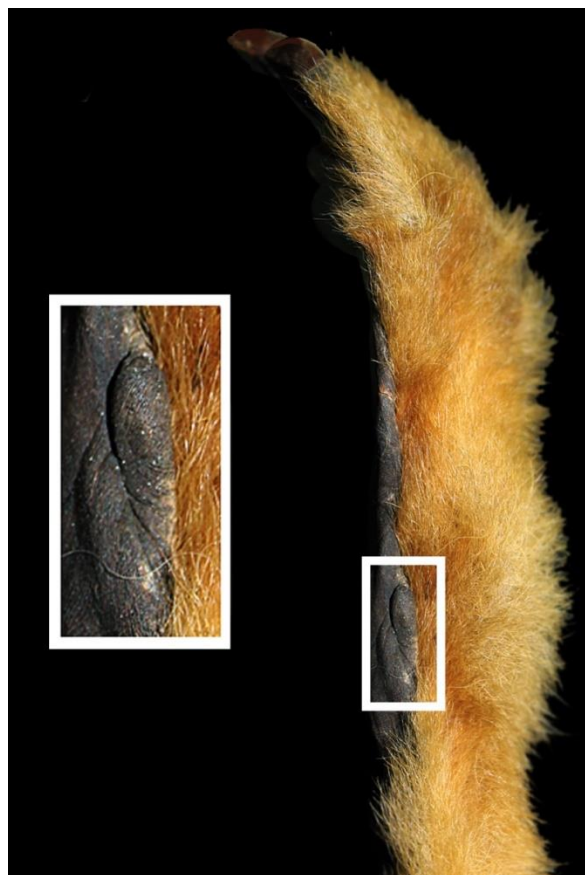


Figure 20. Right hand of *Brachyteles arachnoides* (MZUSP 6482) from Agua Doce, São Paulo, exhibiting a vestigial thumb.

The presence or absence and even the degree of development of the thumb have been recorded by several authors in the past. Slack (1862) was the first to expressed his doubts about the taxonomic significance of this character, he found specimens having upon one hand a nailless tubercle or verruca, and upon the other a nailed thumb, others had the tubercle upon one hand, but lacked on the other (Pag. 514). Elliot (1913) also stressed in this issue, he argued that this character would have no specific value due to the lack of regularity for the presence or absence of the thumb, and this presents individual features. Hill (1962) stated that the condition of having a vestigial thumb on one or both hands is present in both *Ateles* and *Brachyteles*. Therefore, he concluded that this condition has no taxonomic value.

In the present work, I also observed the condition reported by Slack (1862), Elliot (1913), and Hill (1962). The specimen MZUSP 11102, a female adult, possesses a developed nailed thumb on the left hand (Fig. 21), while on the right hand a nailless tubercle (Fig. 22).

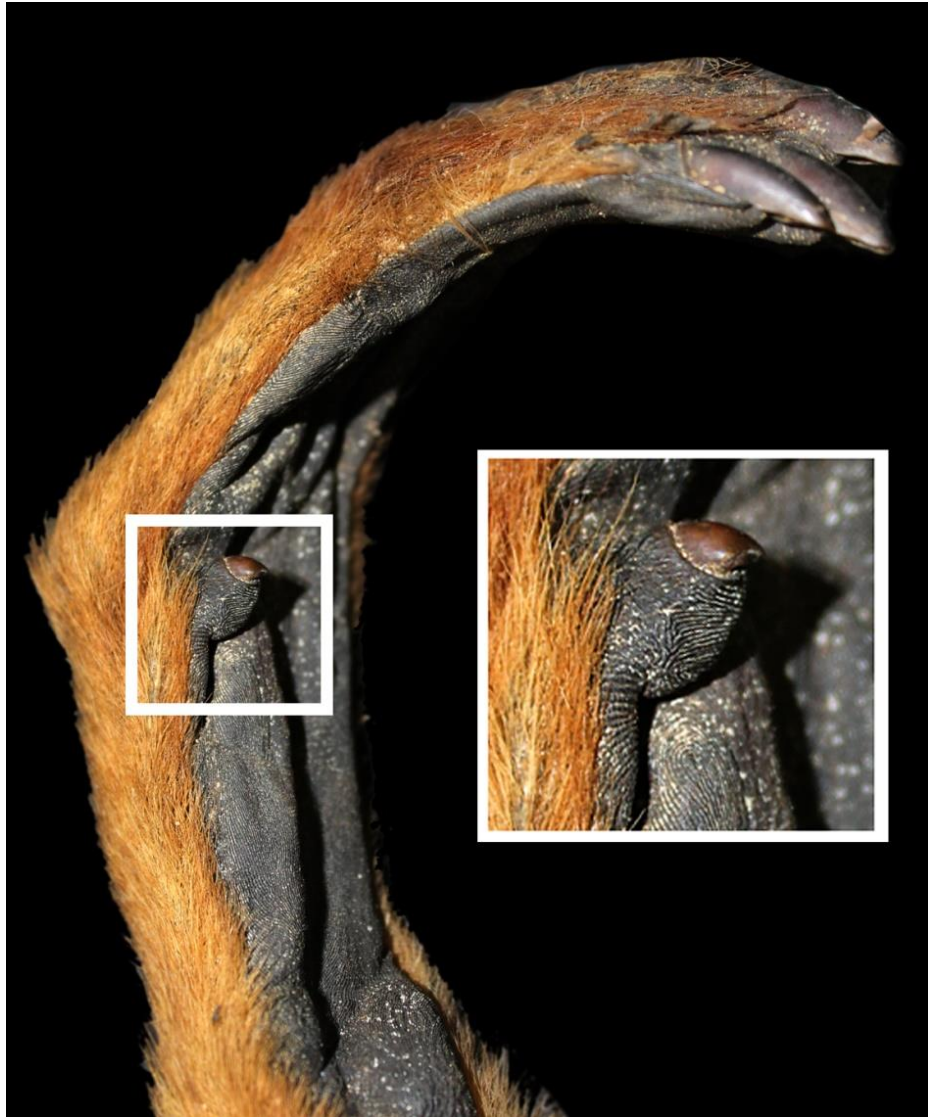


Figure 21. Variation of the thumb's development in the same individual (MZUSP 11102, female), from Santa Leopoldina, Espírito Santo. nailed thumb on the left hand.



Figure 22. Variation of the thumb's development in the same individual (MZUSP 11102, female), from Santa Leopoldina, Espírito Santo. nailless tubercle on the right hand.

Another example of the variation of this character was found in two adult specimens from the MZUSP (catalog number 11099, 11104); both specimens were collected in Santa Leopoldina, specifically in the proximities of the Rio da Pedra, by Leonidas Deane in February of 1968. In these two specimens are present the two conditions of the thumb used by Rylands et al. (1995) and Groves (2001, 2005) for separating the two murequi's species. The specimen, catalog number MZUSP 11099 (Fig. 23), possesses an almost imperceptible nailless vestigial thumb; nevertheless, the

specimen MZUSP 11104 (Fig. 24) exhibits a full-developed nailed thumb. In agreement with Slack (1862), Elliot (1913), and Hill (1962), the absence or presence and the development of the thumb have no taxonomic meaning due to its high individual variation.



Figure 23. Left hand of *Brachyteles arachnoides* (MZUSP 11099), exhibiting a vestigial thumb from Santa Leopoldina, Espírito Santo.



Figure 24. Left hand of *Brachyteles arachnoides* (MZUSP 11104), exhibiting a full-developed nailed thumb from Santa Leopoldina, Espírito Santo.

Regarding the facial pigmentation in *Brachyteles*, the argument used by Lemos de Sá et al. (1993); Strier and da Fonseca (1996/1997); and Groves (2001) to distinguished southern from northern populations would be the former possesses a black face, while the latter, a black face mottled with pink (Figure 25).

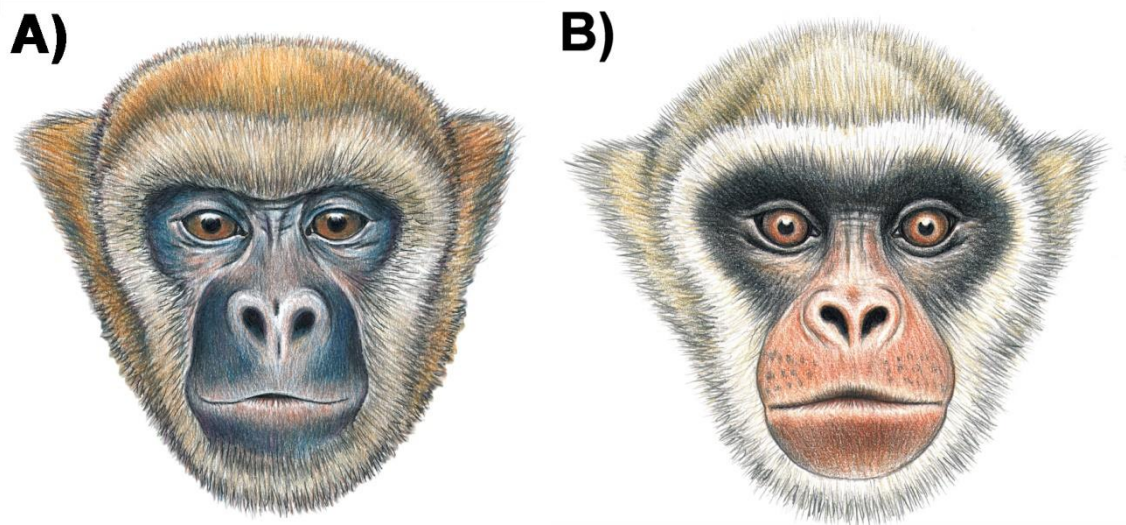


Figure 25. Faces of *Brachyteles arachnoides* (a) and *Brachyteles hypoxanthus* (b), modified from Mittermeier et al. 2013 (Pag. 546, plate 24 and 25). Illustrations by Stephen Nash.

There is, nonetheless, a clear pattern for the southern muriqui populations (Paraná, São Paulo, and Rio de Janeiro) of having an entirely black face in along their ontogenetic development. No depigmented individuals have been reported in Paraná or São Paulo, but there are reports of pigmented and depigmented individuals in sympatry at the Parque Nacional Do Itatiaia - Rio de Janeiro (Aximoff 2015). However, there is no confirmation of interbreeding or a continuous gene flow between pigmented and not pigmented populations at the Parque Nacional Do Itatiaia. Furthermore, the presence of complete black pigmented faces in more northern populations (e.g. Minas Gerais and Espírito Santo) would suggest that the face pigmentation is regulated by factors that we still do not understand (e.g. genetics and environmental) and, also, present a high intrapopulation variation (Fig. 26).

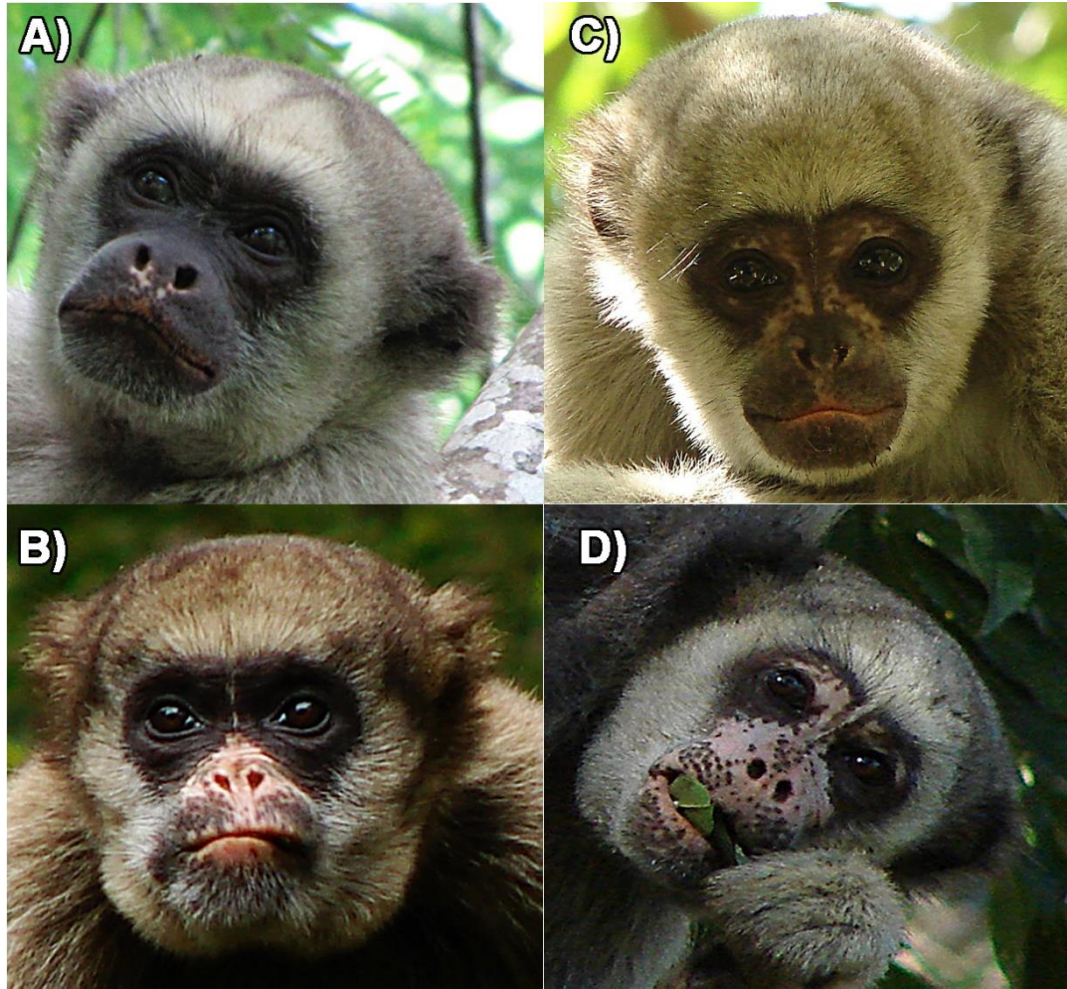


Figure 26. Facial pigmentation variation of northern *Brachyteles arachnoides*' populations: adult male from Caratinga, Minas Gerais (a, c, d), adult female from Caratinga, Minas Gerais (b). Photographs by Carla Possamai (a,b) and Daniel da Silva Ferraz (c,d).

In conclusion, due to high intrapopulation variation of thumb's development and facial depigmentation, these characters do not represent well-marked, geographically restricted characters. For this reason, these characters have no taxonomic value.

3.3.3 Transect definition and *Dice-Leeras* diagrams

At this point, I decided to explore the data before setting any transect. In the Figure 27, is shown that there are no clear cuts between nearby groups making any transect arrangement pointless. Given these results, I declined to go further in this analysis, to put more emphasis in the multivariate and geometric morphometrics analyses.

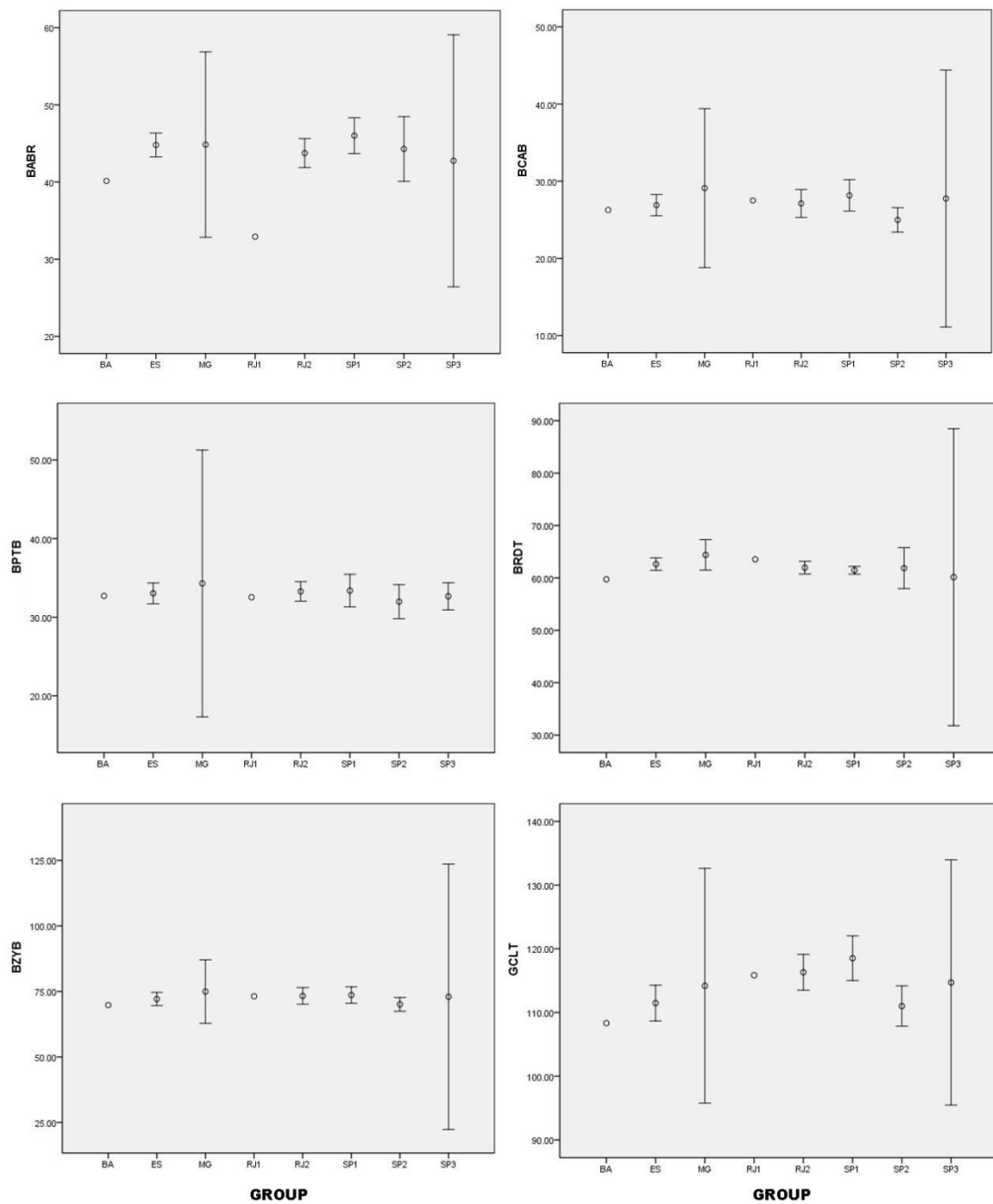


Figure 27. Dice-Leeras diagrams of the cranial variables applied to all the groups. The central circle represents average, the bars comprise 95% of the average confidence interval.

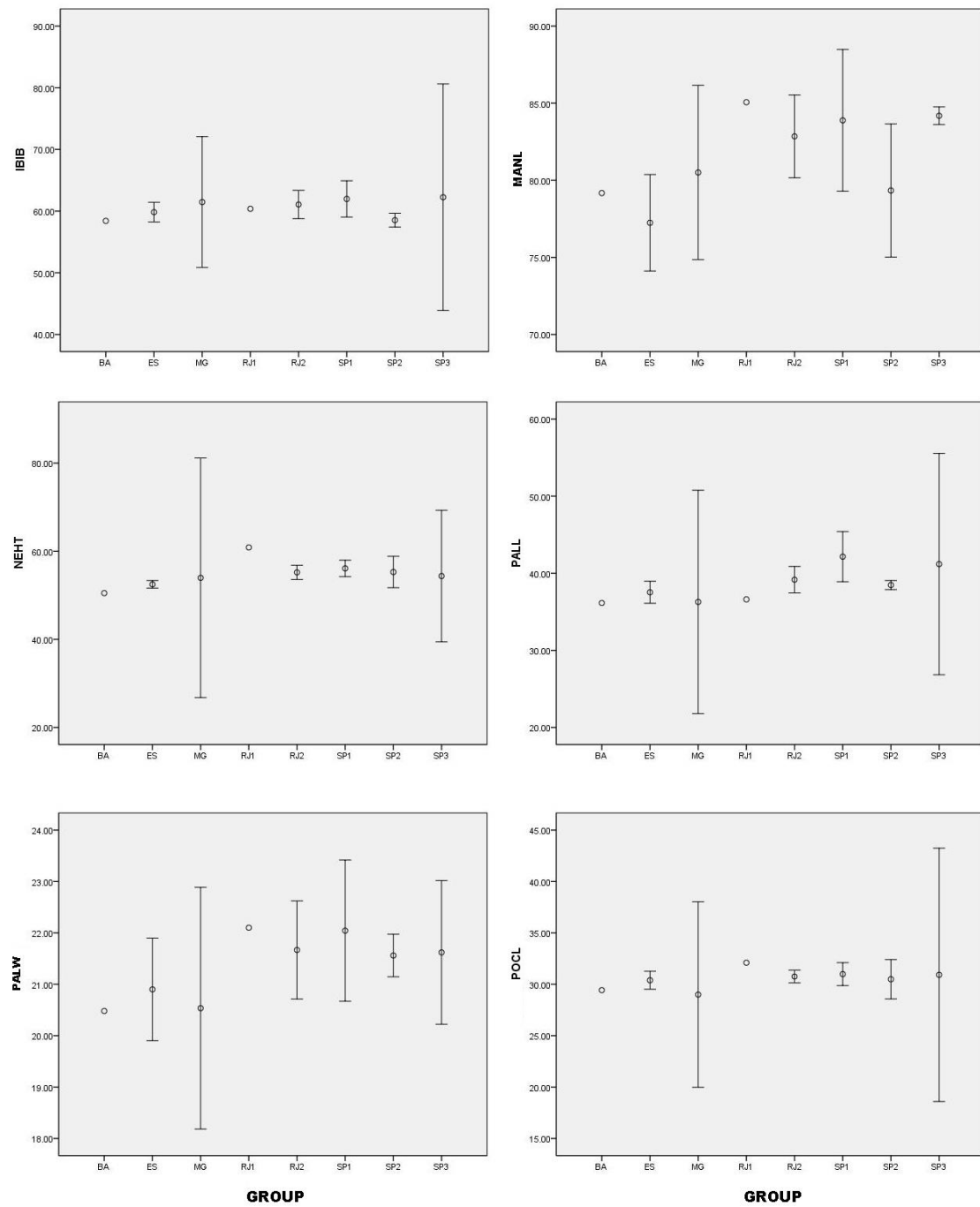


Figure 27 (continued). *Dice-Leeras* diagrams of the cranial variables applied to all the groups. The central circle represents average, the bars comprise 95% of the average confidence interval.

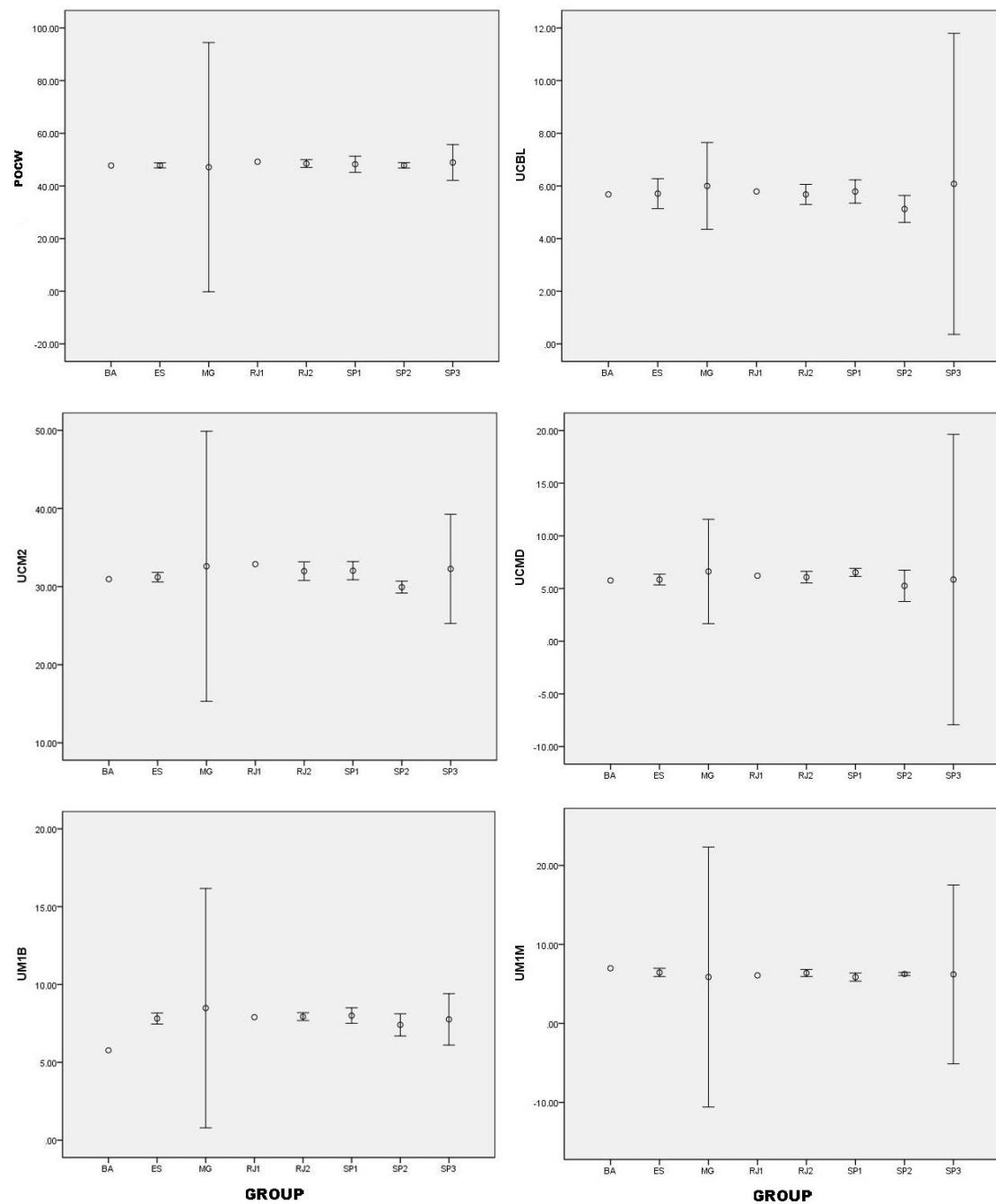


Figure 27 (continued). *Dice-Leeras* diagrams of one cranial and five dental variables applied to all the groups. The central circle represents average, the bars comprise 95% of the average confidence interval.

3.3.4 Principal Components Analysis (PCA)

For the multivariate analyses, I used 39 skulls which had all the measurements complete. In the Table 7 are shown the results of Principal Component Analysis (PCA) relating the variables which contributed most to the total variance in the sample. Three components were generated by the analysis, where the first and second components explained the 50.54% of the total variance, each contributing with 40.85 and 10.36%, respectively. In the first component, which is usually associated with size, only the variable UM1M contributed negatively, and those which contributed most to the variation in descending order were: GCLT, IBIB, BCAB, BZYB, and MANL. Regarding the second component, which is usually associated with the shape, the variables that contributed most to the variation in descending order were: PALL, PALW, UM1M, and GCLT. In this component, BCAB, UCBL, UM1B, and BRDT contributed negatively.

Table 7. Results of the PCA, with their respective eigenvalues and percentage of variance. In bold are the five variables with the greatest value for each component.

Variables	Component		
	1	2	3
GCLT	.858	.231	-.005
IBIB	.855	.160	-.025
BCAB	.854	-.126	.029
BZYB	.828	-.050	-.408
MANL	.750	.372	-.020
UCMD	.738	-.227	.344
UCBL	.729	-.327	.268
UCM2	.691	-.081	.563
PALL	.653	.554	-.172
BPTB	.640	-.183	-.374
POCL	.534	.241	.434
UM1B	.522	-.448	.103
PALW	.457	.421	-.250
NEHT	.389	.179	.368
BRDT	.393	-.692	-.144
UM1M	-.321	.372	.228
BABR	.378	-.140	-.565
POCW	.287	.135	-.357
Eigenvalues	7.233	1.864	1.761
Variance (%)	40.19	10.36	9.78

In the Figure 28 are shown the scores of the first and second Principal Components generated by the PCA, to find possible sample patterns of variation as a whole in the multivariate space without setting taxa *a priori*. Regarding the first component, it can be observed that the groups BA, ES, and SP2 are located on the negative end of the PC1, while MG, RJ1, RJ2, SP1, and SP3 into the positive. In relation to the second component, there is a slight separation between the ES and MG from the remaining groups. Although there is some tendency of the groups ES and MG to separate from the remaining groups in the PC2, almost all the groups are clustered in the center of the axis X and Y. The groups ES and RJ2 present dispersed points in the four quadrants of the plot, reflecting their high variability which cannot be included into

the 95% confidence ellipses. Due to the small number of samples in some groups as BA, SP3, and MG, this results should be taken carefully.

I declined to apply any further analysis owing to the small number of samples present in some groups. For instance, a Canonical Variate Analysis (CVA) perform with this limited number of samples could generate artificial clusters which would not reflect the real diversity of *Brachyteles*, as pointed out by Barcikowski and Stevens (1975). These authors recommend that to arrive at reliable estimates for two canonical roots, the study should include, at least, 40 to 60 times as many cases as variables.

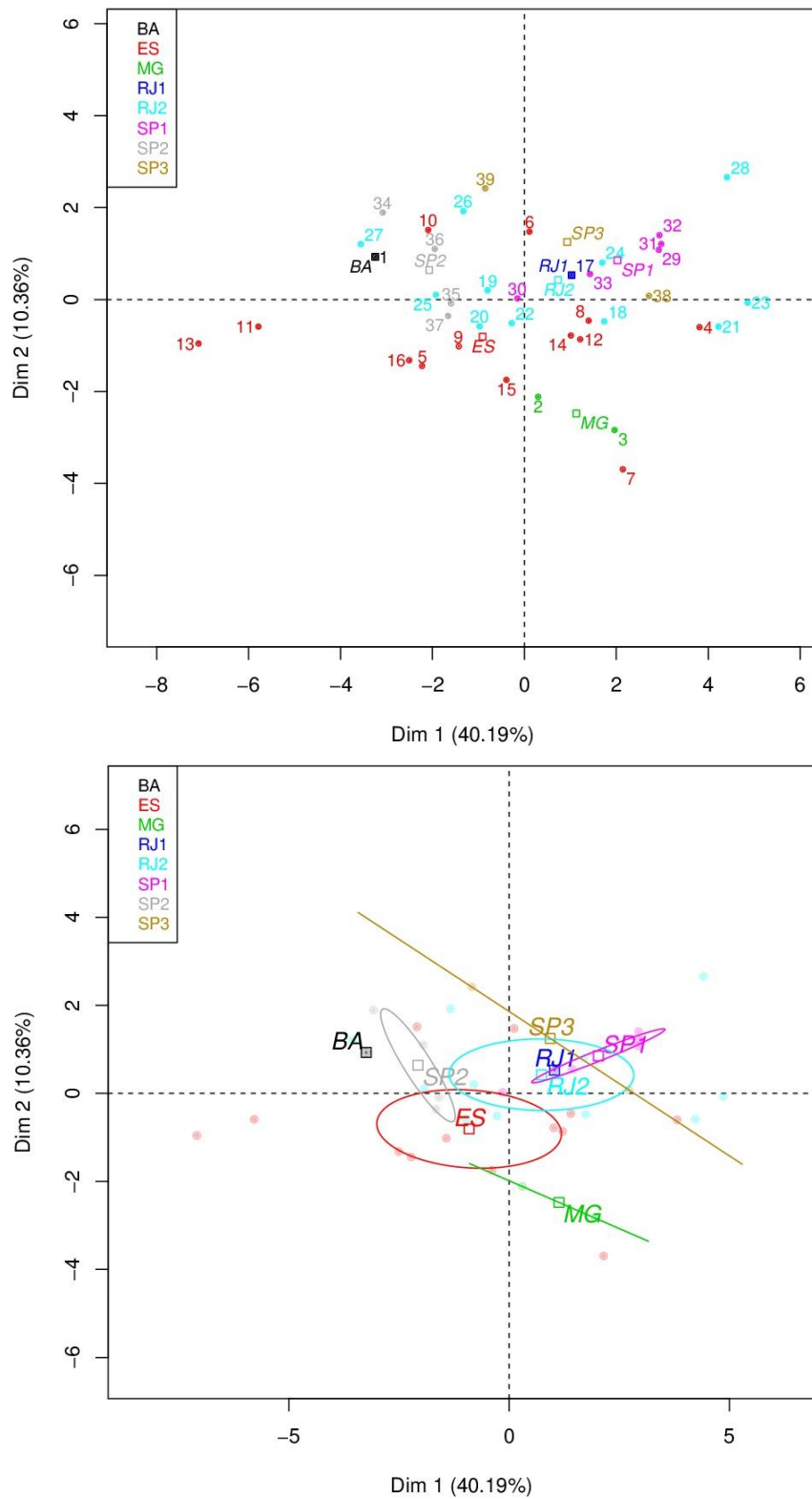


Figure 28. Principal component analysis based on 18 skull measurements from eight geographical groups determined by PC1 and PC2 (BA = Bahia, ES = Espírito Santo, MG = Minas Gerais, RJ1 = Rio de

Janeiro 1, RJ2 = Rio de Janeiro 2, SP1 = São Paulo 1, SP2 = São Paulo 2, SP3 = São Paulo 3). Showing the distribution of all the individuals (above), and grouped by 95% confidence ellipses (below).

3.3.5 Shape variation between geographical groups

The PCA on each dorsal, frontal, and lateral view of the cranium showed no cranial differentiation between groups; the variation explained by the first three components is shown in Table 8. The variation of the skull morphology along the PC1 and PC2 axes in the three views is basically the same as in the previous analyses of sexual dimorphism in *Brachyteles*. These variations are presented in Figures 29, 30 and 31.

Table 8. Values (expressed in %) of the first three Principal Components of each view.

View	PC1	PC2	PC3
Dorsal	27.79	17.76	13.16
Frontal	29.16	15.22	12.44
Lateral	24.93	18.21	12.03

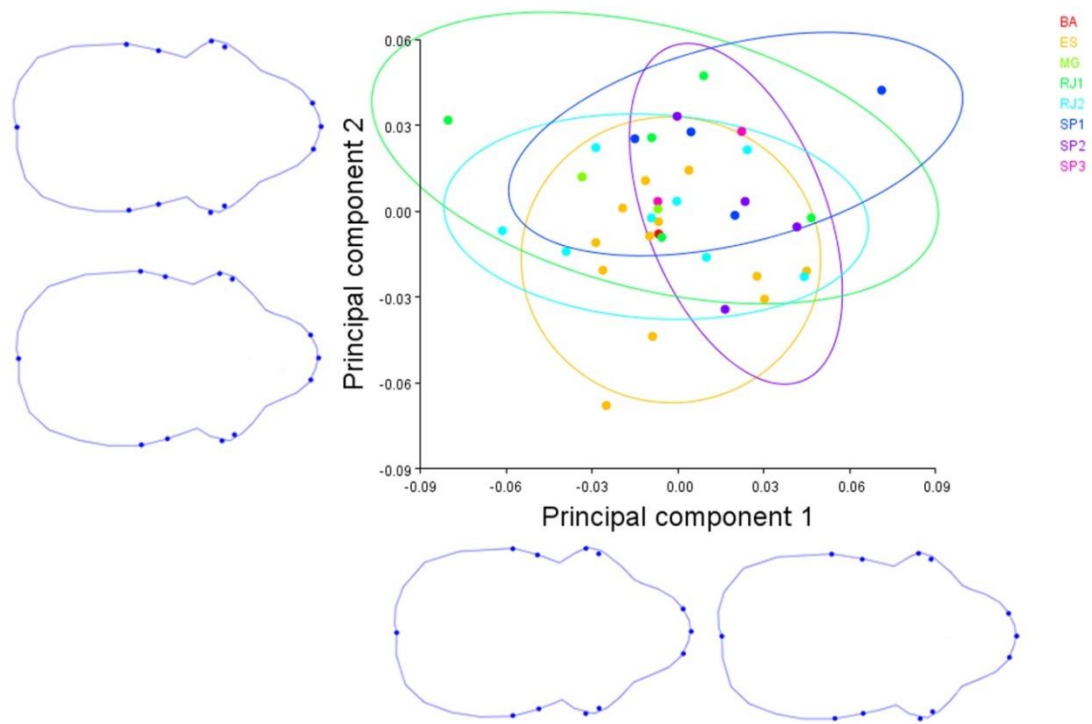


Figure 29. Shape variation of the skull grouped by geographical data in dorsal view of *Brachyteles* determined by PC1 and PC2 (BA = Bahia, ES = Espírito Santo, MG = Minas Gerais, RJ1 = Rio de Janeiro 1, RJ2 = Rio de Janeiro 2, SP1 = São Paulo 1, SP2 = São Paulo 2, SP3 = São Paulo 3). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.03, right 0.03).

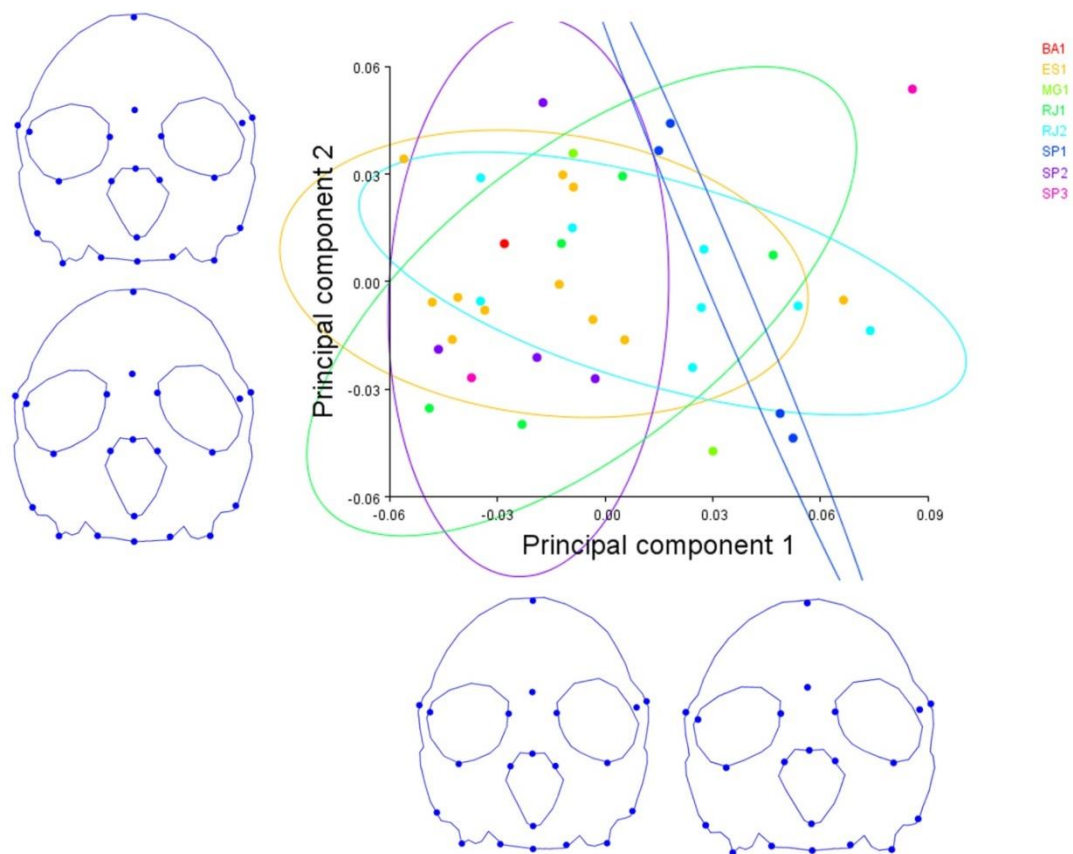


Figure 30. Skull variation of the shape grouped by geographical data in frontal view of *Brachyteles* determined for PC1 and PC2 (BA = Bahia, ES = Espírito Santo, MG = Minas Gerais, RJ1 = Rio de Janeiro 1, RJ2 = Rio de Janeiro 2, SP1 = São Paulo 1, SP2 = São Paulo 2, SP3 = São Paulo 3). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.03, right 0.03).

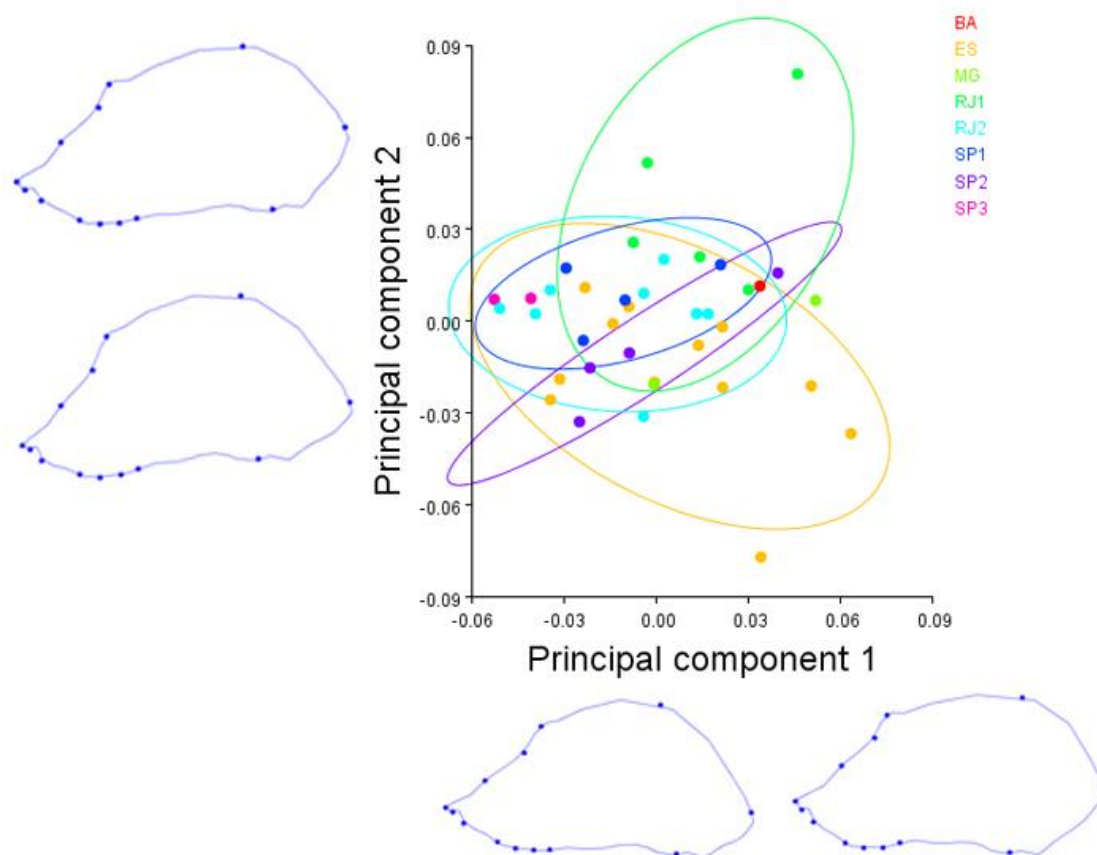


Figure 31. Skull variation of the shape grouped by geographical data in lateral view of *Brachyteles* determined for PC1 and PC2 (BA = Bahia, ES = Espirito Santo, MG = Minas Gerais, RJ1 = Rio de Janeiro 1, RJ2 = Rio de Janeiro 2, SP1 = São Paulo 1, SP2 = São Paulo 2, SP3 = São Paulo 3). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.05, right 0.05).

3.3.6 Skull variation in Atelidae

In this PCA, the variation explained by the first two components on the dorsal view of the cranium is 56.92% and 18.99%, respectively. PC1 clearly distinguishes *Alouatta* from any other atelids, *Ateles*, *Brachyteles* and *Lagothrix* (Fig. 32). The main morphological features responsible for this *Alouatta*'s differentiation are an elongated premaxilla, longer maxilar bones, a narrower and longer braincase and wider parietal bones at the occipital region. The lateral wall of the orbits is wider in *Alouatta* than other atelids. The PC2 separated *Callicebus* from all the other analyzed taxa, this genus has a particularly short premaxilla and rostrum, while the braincase is rounded and elongated.

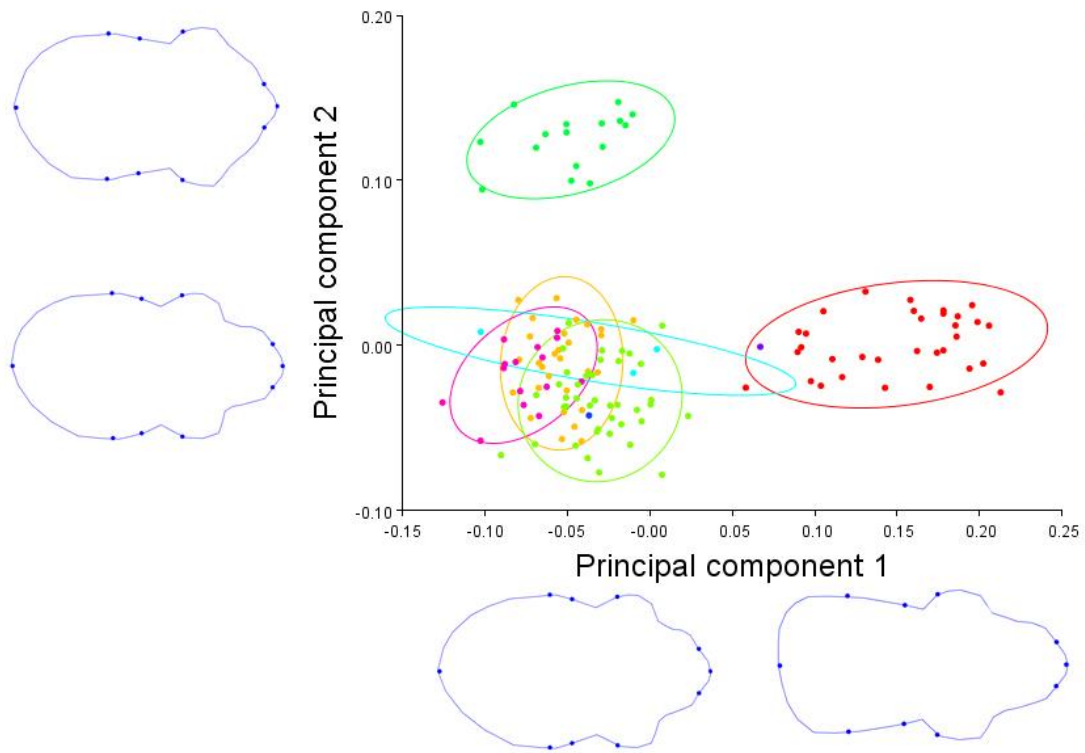


Figure 32. Skull variation of the shape grouped by geographical data in dorsal view of six extant and two extinct (†) Platyrrhine genera determined for PC1 and PC2 (al = *Alouatta*, at = *Ateles*, br = *Brachyteles*, ca = *Callicebus*, ce = *Cebus*, ci = *Caipora* †, cr = *Cartelles* †, la = *Lagothrix*). The view of each

landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.05, right 0.05).

The variation explained by the first two components on the frontal view of the cranium is 30.54% and 20.66%, respectively. PC1 also distinguishes *Alouatta* from any other atelids, *Ateles*, *Brachyteles* and *Lagothrix* (Fig. 33). *Alouatta* has a broader skull; short premaxilla, rectangular orbits; maxilla surpasses the lateral wall of the orbits. On the other hand, the PC2 does not discriminate any of the analyzed genera.

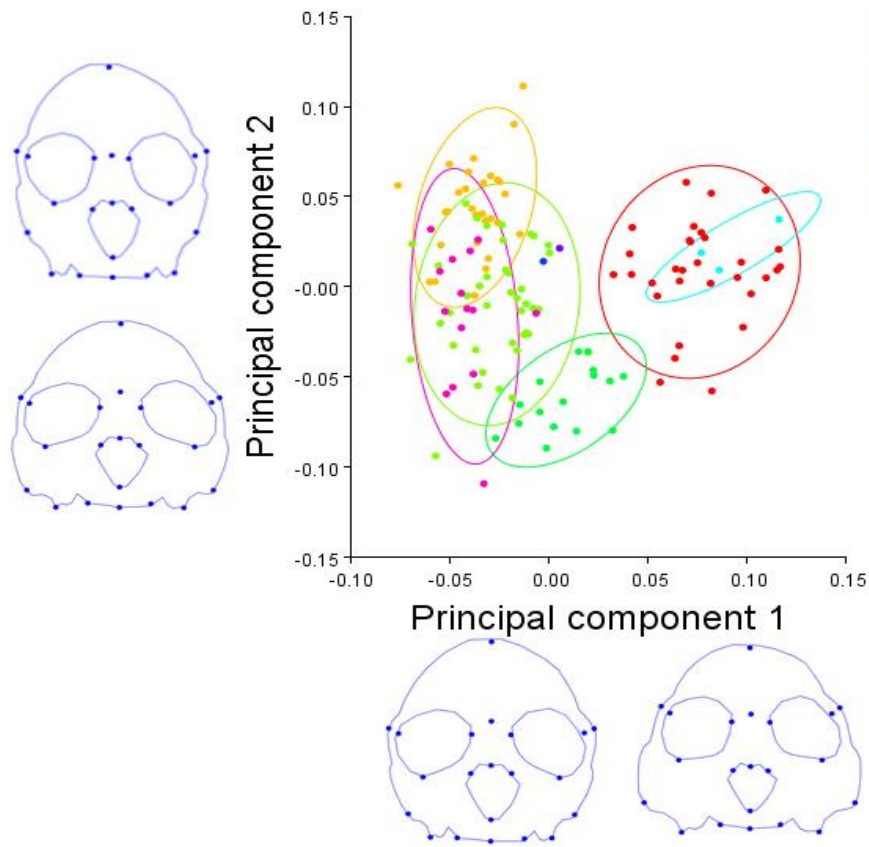


Figure 33. Skull variation of the shape grouped by geographical data in frontal view of six extant and two extinct (†) Platyrrhine genera determined for PC1 and PC2 (al = *Alouatta*, at = *Ateles*, br = *Brachyteles*, ca = *Callicebus*, ce = *Cebus*, ci = *Caipora* †, cr = *Cartelles* †, la = *Lagothrix*). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.05, right 0.05).

The variation explained by the first two components on the dorsal view of the cranium is 64.03% and 7.81%, respectively. The PC1, as in dorsal and frontal view, distinguishes *Alouatta* from any other analyzed taxa (Fig. 34). *Alouatta* has an extremely elongated skull with a projected premaxilla; low braincase; flatter frontal bone. The PC2, as in dorsal view, separated *Callicebus* from all the analyzed taxa, this genus has a particularly short angulated premaxilla and rostrum; the braincase is rounded and elevated at the final portion of the parietals; occipital bone elongated; bone long nasals; glabella and lambda almost at the same level.

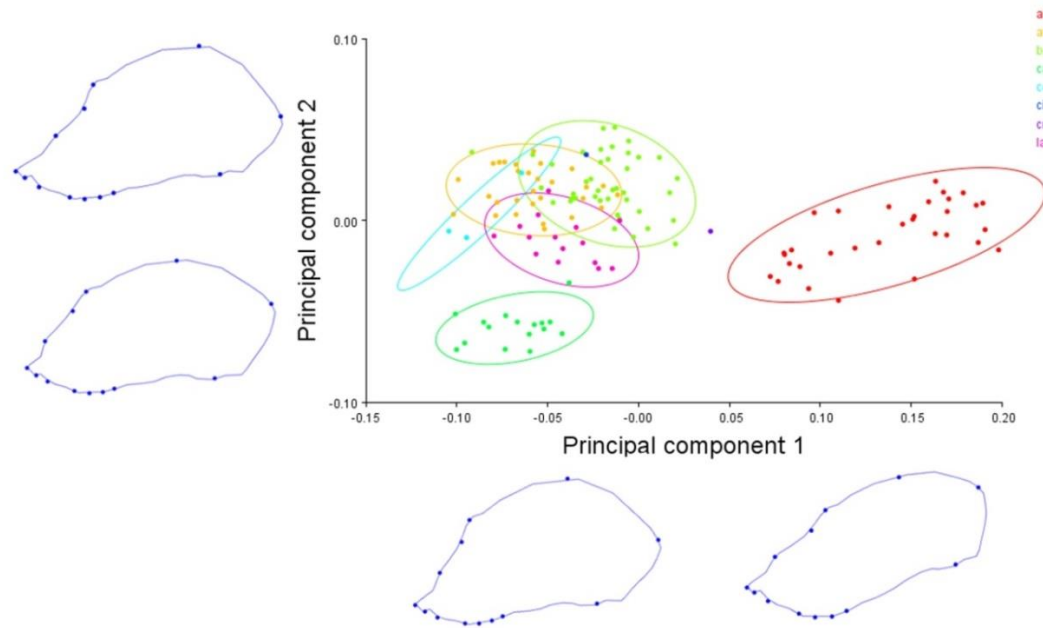


Figure 34. Skull variation of the shape grouped by geographical data in lateral view of six extant and two extinct (†) Platyrrhine genera determined for PC1 and PC2 (al = *Alouatta*, at = *Ateles*, br = *Brachyteles*, ca = *Callicebus*, ce = *Cebus*, ci = *Caipora* †, cr = *Cartelles* †, la = *Lagothrix*). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.05, right 0.05).

3.3.7 Skull variation in Atelinae

The Discriminant Analysis using Mahalanobis distances was able to differentiate between the three Atelinae genera in most of the views (Fig. 34). The lateral view seems to be the most informative for significant between-genera differences. Nevertheless, the differences between *Ateles* and *Lagothrix* in dorsal and frontal view were no significant (see Table 9).

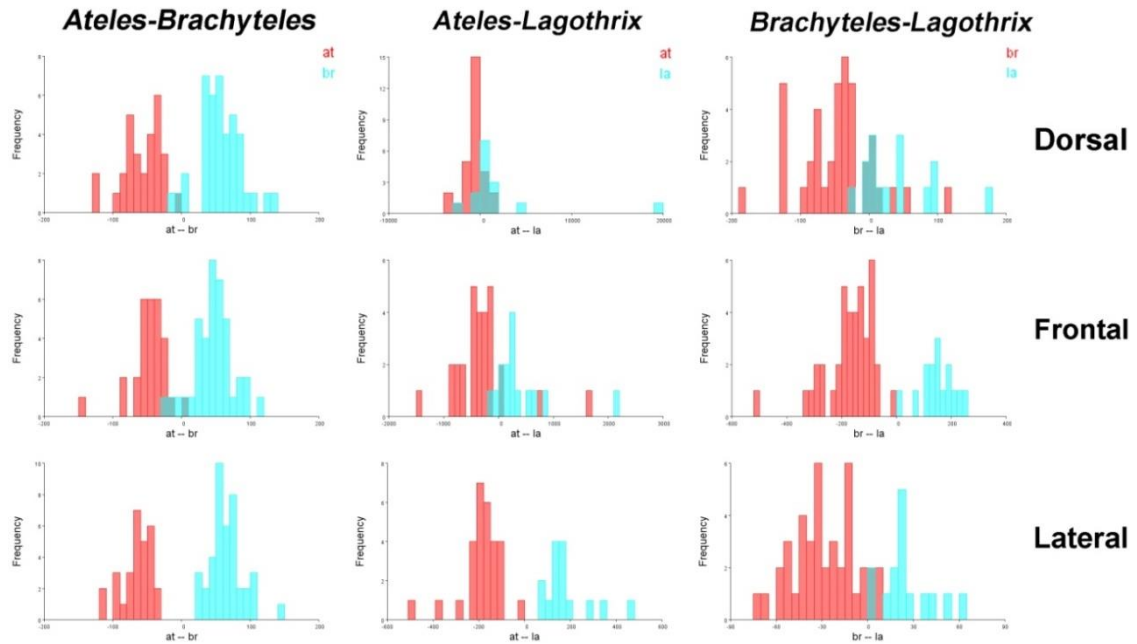


Figure 35. Discriminant function showing the leave-one-out cross-validation between Atelinae genera (al = *Alouatta*, at = *Ateles*, la = *Lagothrix*, br = *Brachyteles*) in three different views: dorsal, frontal, and lateral.

Table 9. Mahalanobis distances between Atelinae genera as given by the Pairwise discriminant analyses for shape. Letters indicate view of the cranium D = dorsal, L = lateral, and F = frontal. Significant pairwise differences are indicated in bold.

Mahalanobis distances View	<i>Ateles</i>			<i>Lagothrix</i>		
	D	F	L	D	F	L
<i>Lagothrix</i>	24.48	24.48	18.75			
<i>Brachyteles</i>	9.78	9.78	11.51	17.84	17.84	7.69

The PCA on the dorsal view of the cranium distinguished between *Ateles* and *Bachyteles*, occupying *Lagothrix* an intermediate position (Fig. 35). When compared with *Ateles*, *Bachyteles* presents a less pronounced postorbital constriction; less projected premaxilla; rounded parietal ending and a wider maxilla.

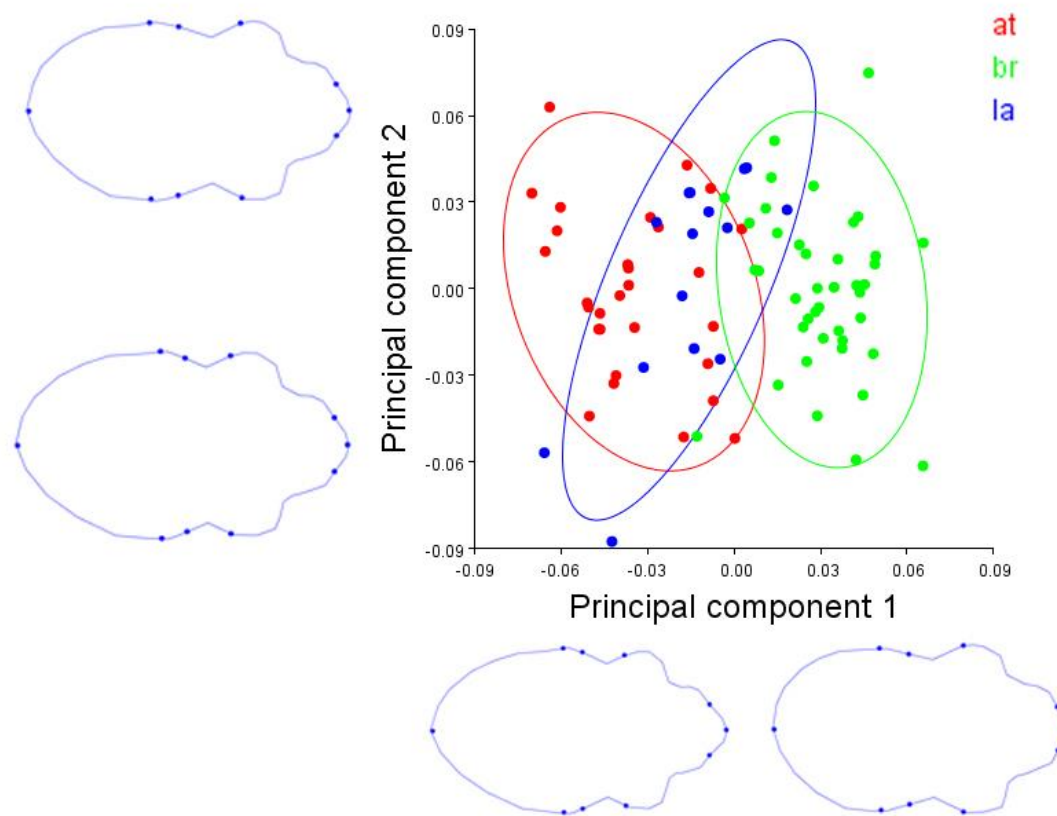


Figure 36. Skull variation of the shape grouped by genera in lateral view of atelines determined for PC1 and PC2 (at = *Ateles*, br = *Brachyteles*, la = *Lagothrix*). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.05, right 0.05).

The PCA on the frontal view of the cranium distinguished between *Brachyteles* and *Lagothrix*, leaving *Ateles* as an intermediary group (Fig. 36). In this case of the PC2, differentiated *Bachyteles* from *Lagothrix* due to the fact that the former showed a shorter braincase; more separated orbits; larger maxillae; longer nasals with a larger nasal aperture.

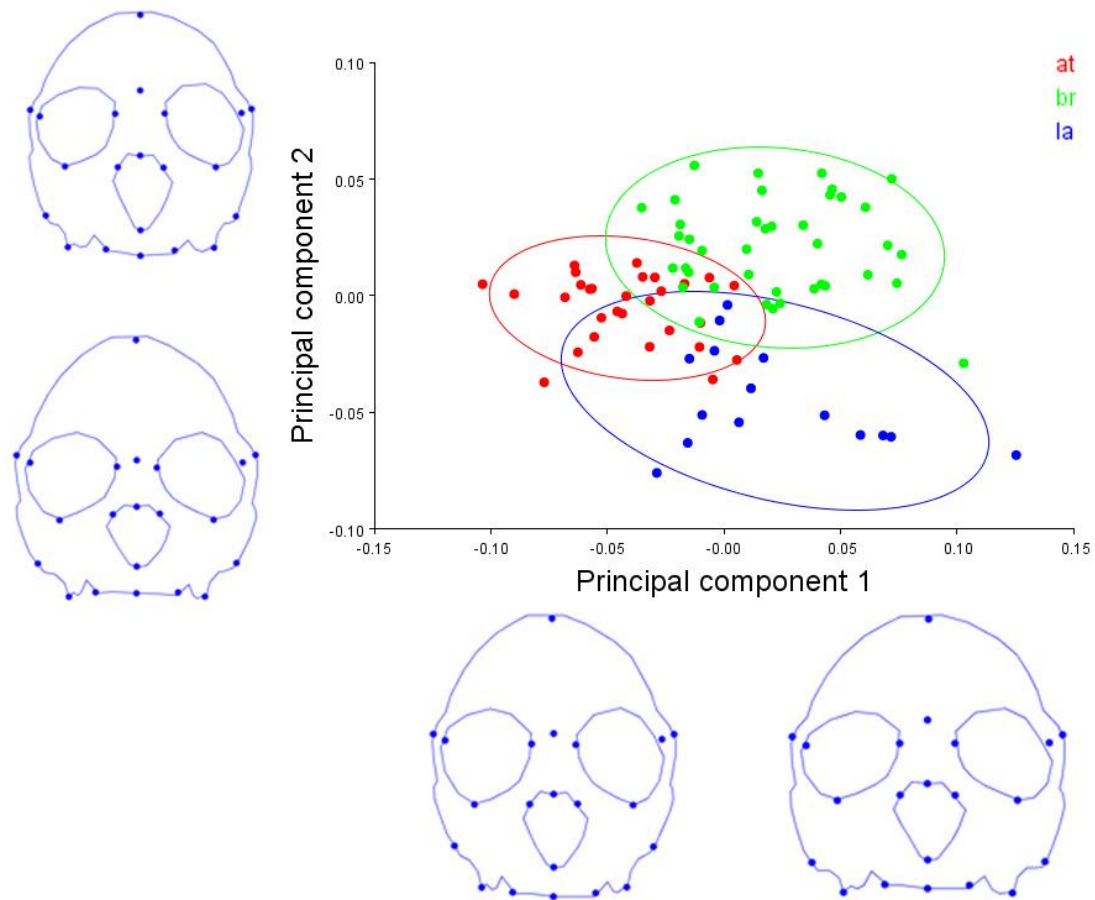


Figure 37. Skull variation of the shape grouped by genera in frontal view of atelines determined for PC1 and PC2 (at = *Ateles*, br = *Brachyteles*, la = *Lagothrix*). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.05, right 0.05).

The PCA on the lateral view of the cranium distinguished between *Ateles* and *Brachyteles*, leaving *Lagothrix* as an intermediary group again (Fig. 37). The PC1 differentiated *Brachyteles* from *Ateles* by having shorter braincase; shorter occipital bone; shorter frontal bone and less pronounced premaxilla.

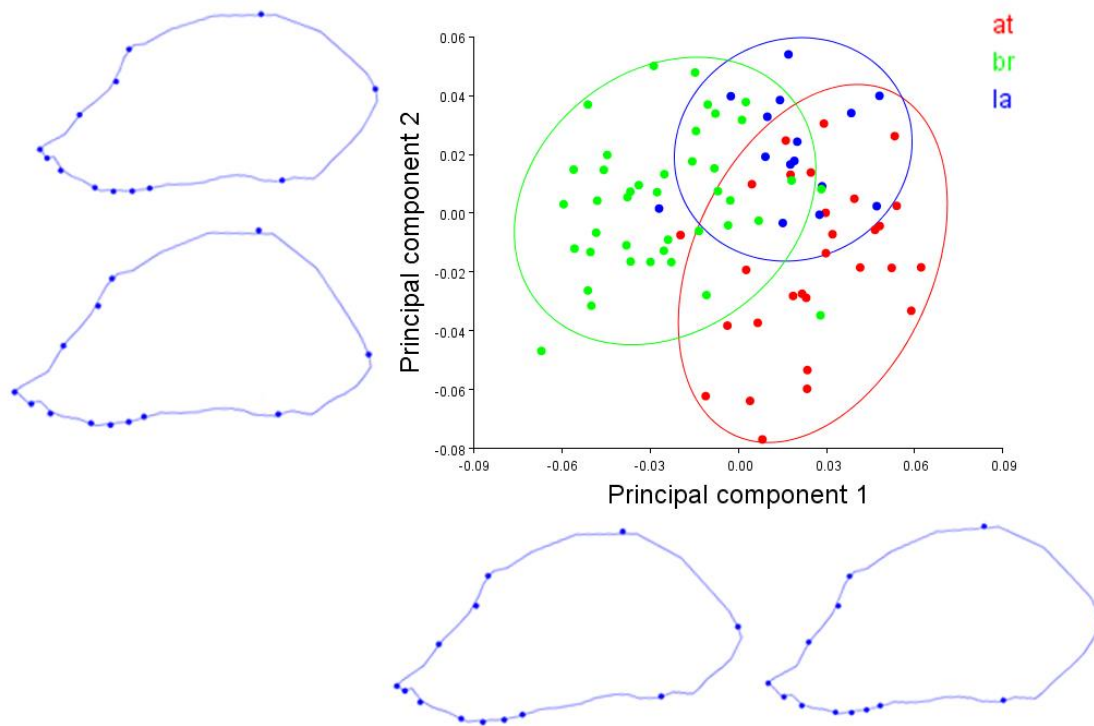


Figure 38. Skull variation of the shape grouped by genera in lateral view of atelines determined for PC1 and PC2 (at = *Ateles*, br = *Brachyteles*, la = *Lagothrix*). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: left -0.05, right 0.05).

3.4 Taxonomy of *Brachyteles*

Given the high intrapopulational and interpopulational morphological variation, I can only recognize one species of *Brachyteles*. As the specific name, *arachnoides* has the priority over any other available name; the sole species in this genus is *Brachyteles arachnoides*. Bellow I present the results of my study, the variation in the samples of *Brachyteles* and the consequences of this research to its taxonomy.

***Brachyteles* Spix, 1823**

Ateles É. Geoffroy St.-Hilaire 1806:270; part. Type species *Simia paniscus* Linnaeus, 1758, by subsequent designation (Miller and Rehn 1901).

Simia: Humboldt 1812:354; part; not *Simia* Linnaeus, 1758. Unavailable name (ICZN 1929, Opinion 114).

Atèle Demarest 1820:75; vernacular, unavailable name.

Brachyteles Spix 1823:36. Type species *Brachyteles macrotarsus*, by monotypy.

Cebus: Fischer 1829:38; not *Cebus* Erxleben, 1777.

Eriodes I. Geoffroy St.-Hilaire 1829:160. No type species selected; *Eriodes arachnoides* here selected as type species.

Brachyteleus Elliot 1913:49; invalid emendation.

***Brachyteles arachnoides* (É. Geoffroy St.-Hilaire, 1806)**

Ateles arachnoides É. Geoffroy St.-Hilaire, 1806:271; type locality “le continent américain”; based on “The large brown Monkey” of Browne (1756:489) and the “brown long-limbed four-finger'd Monkey” of Edwards 1758-1764:222.

Simia arachnoides Humboldt 1812:355; name combination; based on *Ateles arachnoides* of É. Geoffroy St.-Hilaire (1809:92).

Ateles hypoxanthus Wied 1820:91; type locality “Bahia”; restricted by Avila-Pires (1965:9) to "As Barreiras," a beach on the Rio Belmonte or Jequitinhonha, Bahia, Brazil.

Atèle arachnoïde Demarest 1820:75; vernacular, unavailable name; based on *Ateles arachnoides* of É. Geoffroy St.-Hilaire (1809:92).

Atèle hypoxanthe Demarest 1820:72; vernacular, unavailable name; based on *Ateles hypoxanthus* of Wied (1820:91).

Brachyteles macrotarsus Spix 1823:36; type locality “St. Pauli, Rio de Janeiro, Espirito Santo et Bahiae”.

Eriodes arachnoides: I. Geoffroy St.-Hilaire 1829:160; name combination; type locality “le Brésil”; based on *Ateles arachnoides* of É. Geoffroy St.-Hilaire (1809:92).

Eriodes tuberifer I. Geoffroy St.-Hilaire 1829:161; type locality “le Brésil”

Eriodes hemidactylus I. Geoffroy St.-Hilaire 1829:163, plate 22; type locality “le Brésil”.

Cebus hypoxanthus: Fischer 1829:38; name combination; based on *Ateles hypoxanthus* of Wied (1820:91).

Cebus arachnoides: Fischer 1829:38; name combination; based on *Ateles arachnoides* of É. Geoffroy St.-Hilaire (1809:92).

Ateles hemidactylus: Boitard 1842:51; name combination.

Brachyteles arachnoides: Gray 1843:10; type locality “Tropical America”; name combination; based on *Ateles arachnoides* of É. Geoffroy St.-Hilaire (1809:92).

Brachyteles hypoxanthus: Gray 1843:11; type locality “Tropical America”; name combination; based on *Ateles hypoxanthus* of Wied (1820:91).

Ateles eriodes Brehm 1876:188; name combination.

Brachyteleus arachnoides: Elliot 1913:50; unjustified emendation; plate III.

Neotype: adult, mounted skin, sex unknown, Muséum National d'Histoire Naturelle, Paris, number MNHN-ZM-2007-1475, coming from the Museu de Zoologia–USP (São Paulo), collection data unknown, probably collected or bought by Alexandre Ferreira Rodrigues. The individual, catalog number MNHN-ZM-2007-1475, listed by É. Geoffroy St.-Hilaire (1809:92) here designated as neotype.

Type Locality: originally designated by É. Geoffroy St.-Hilaire (1806:271) as “le continent américain”, restricted by the same É. Geoffroy St.-Hilaire (1809:92) to “lé Brésil”, and finally restricted by Vieira (1944:15) to Rio de Janeiro.

Distribution: the distribution of *Brachyteles arachnoides* extends along the Brazilian Atlantic Forest, through the coastal Serra do Mar in the states of Paraná, São Paulo, Rio de Janeiro, Espírito Santo, Minas Gerais and Bahia, excluding the lowland forests in the extreme South of Bahia and North Espírito Santo (see Figure 38).

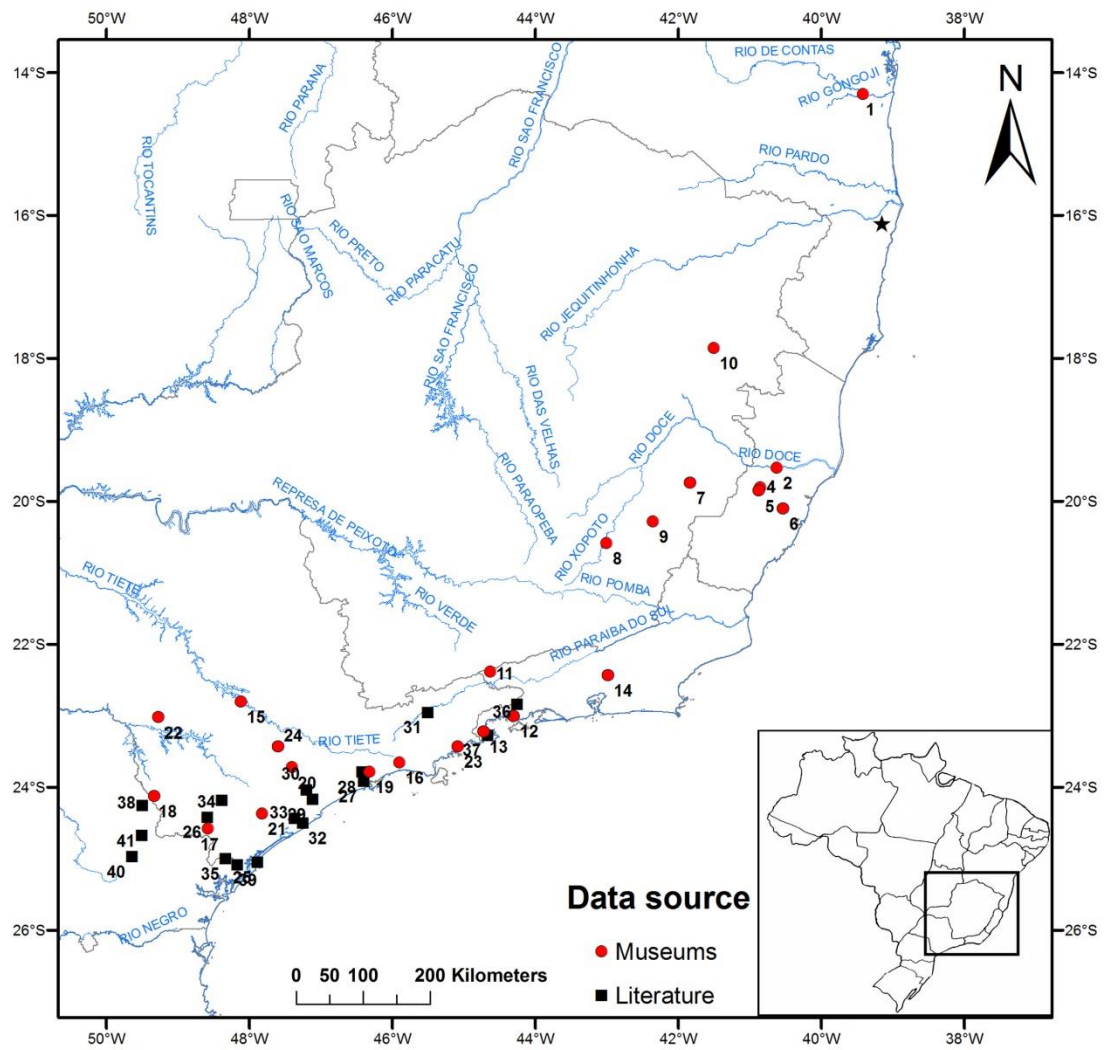


Figure 39. Geographic distribution of *Brachyteles arachnoides*: ★ Wied's *Brachyteles hypoxanthus* type locality; ■ records confirmed by museum specimens; ● records raised from literature.

Table 10. Information about the locations of the map in Figure 39. The locations 1 to 23 are referring to the examined material from museums, and 24 to 40 to localities taken from literature.

NUMBER	LOCALITY	SOURCE
1	Rio Gongoji, Bahia	-
2	Colatina, Espírito Santo	-
3	Itaguaçu, Espírito Santo	-
4	Jahibocas, Itarana	-
5	Santa Leopoldina, Espírito Santo	-
6	Caratinga, Minas Gerais	-
7	Rio Bacalhau, Minas Gerais	-
8	Rio Matipó, Minas Gerais	-
9	Teófilo Otoni, Minas Gerais	-
10	Itatiaia, Rio de Janeiro	-
11	Mambucaba, Angra dos Reis, Rio de Janeiro	-
12	Pedra Branca, Paraty, Rio de Janeiro	-
13	Pedra de Frade (Serra dos Orgãos), Teresópolis, Rio de Janeiro	-
14	Anhembi (Fazenda Barreiro Rico), São Paulo	-
15	Boraceia, São Paulo	-
16	Iporanga, São Paulo	-
17	Itararé, São Paulo	-
18	Paranapiacaba (Alto da Serra), São Paulo	-
19	Piedade (Água Doce), São Paulo	-
20	Poço Grande, São Paulo	-
21	São Bartolomeu, São Paulo	-
22	Ubatuba, São Paulo	-
23	Ypanema, São Paulo	-
24	Ilha do Cardoso State Park, São Paulo	Martuscelli et al. 1994
25	Alto Ribeiro, São Paulo	Martuscelli et al. 1994
26	Mongaguá, São Paulo	Martuscelli et al. 1994
27	Curucutu, São Paulo	Martuscelli et al. 1994
28	Pedro de Toledo/Itariri, São Paulo	Martuscelli et al. 1994
29	Jurupará, São Paulo	Martuscelli et al. 1994
30	São Francisco Xavier, São Paulo	Martuscelli et al. 1994
31	Juréia, São Paulo	Martuscelli et al. 1994
32	Itatins, São Paulo	Martuscelli et al. 1994
33	Fazenda Intervalles, São Paulo	Martuscelli et al. 1994
34	Jacupiranga, São Paulo	Martuscelli et al. 1994

35	Bocaina, Rio de Janeiro	Martuscelli et al. 1994
36	Cairucu, Rio de Janeiro	Martuscelli et al. 1994
37	Jaguariaíva, Paraná	Martuscelli et al. 1994
38	Guaraqueçaba, Paraná	Martuscelli et al. 1994
39	Municipalidad de Castro, Paraná	Koehler et al. 2002
40	Fazenda Olho d'Água, Paraná	Ingberman et al. 2016

A chain of mountains along the coast of Brazil, the Serra do Mar, divides two types of forests (Nishimura et al. 1988). The first, tropical evergreen mesophytic broadleaf forest originally covered the most Brazilian east slope extending to the coast. This type of forest has an annual precipitation mean of 2000 mm and an annual temperature mean of 16° - 19°C (Hueck 1972). The second type is a tropical semideciduous mesophytic broadleaf forest (Eiten 1974), which runs along the western range of the coastal hills, reaching the Plateau region. The annual precipitation mean is about 2000 mm with a pronounced dry season of 5-6 months occurring in the winter season, when average monthly rainfall is around 50 mm (Passos 1992). Despite the low amount of precipitation, tall forests are still present, containing both evergreen and semideciduous species (Cullen et al. 2004).

Aguirre (1971) considered the southern limit of the range of the species to be about 25°S, in the region of the Rio Ribeira in Paraná. Aguirre's hypothesis was corroborated by Martuscelli et al. (1994) who informed of two localities where they found populations of *Brachyteles* in Paraná. One was in the municipality of Jaguariaíva, on the northern coast of Paraná (about 24° 15'S, 49° 30'W), the other in the Guaraqueçaba Environmental Protection Area, on the Serra do Mar massif of Paraná (25° 05'S, 48° 10'W). Recent reports in the Castro municipality (Koehler et al. 2002)

and the Fazenda Olho d'Água (Ingberman et al. 2016) also confirmed the presence of *Brachyteles* in Paraná.

Vieira (1944), in an attempt to enclose the north distribution of *Brachyteles*' populations, proposed that historically this distribution reached the coastal area, covering with thick forests, which runs through the Cabo de São Roque, state of Rio Grande do Norte. Nevertheless, Aguirre (1971) considered that there was no concrete evidence of the species' actual or historical presence in Rio Grande do Norte. He instead proposed that the northern limit was probably the Rio Jequiriçá basin, which flows into the Baía de Todos os Santos, and including the forests of the right bank of the Rio Paraguaçu.

Diagnostic characters: woolly and thick yellowish brown to reddish brown fur; completely or partially pigmented naked face; nailed or nailless vestigial (if present) or absent thumb; body build robust; rounded head; flattened face; prominent abdomen; elongated forelimbs; incisors of equal size; canines small; square shaped molars.

External characters: *Brachyteles* morphologically resembles both *Ateles* and *Lagothrix*, having the bulky and woolly appearance of the latter, but the elongated limbs, harsh hairs and the reduced or absent thumb of the former. The pelage is shorter on the head than on any other part of the body as in *Lagothrix*. The hair is absent or is very scarce on the throat, axillae, chest, palms, soles and the terminal portion of the tail as in other atelids. In adult males, the general body coloration varies from reddish-brown to yellowish-brown, darker at the occipital region of the head; dense, some harsh

and woolly pelage. The face is naked, with a black or flesh-colored pigmentation; upon the brows a few long black hairs; buttocks, circumanal area, perineum, basal portion of the tail and inner parts of the forelimbs dark reddish brown. In adult females, the general color is lighter than males, being more greyish-brown, yellow tonality varies considerably in each individual. In juvenile individuals, the coloration is lighter than adults generally light beige; face entirely black pigmented. In all individuals, a whitish-yellow circumfacial area is unique among atelines.

Cranial morphology: The maximum length of the adult male skull varies between 100.1 mm and 122.54 (N = 39). The rostrum is relatively flattened with narrow nasals. Premaxillae are long and slightly forward projecting. The dorsal plane of the nasals are concave, with their greatest combined width more than one-half distance between alveoli of canines. Facial or nasal angle low, leaf-like nostrils; braincase not markedly inflated, maximum width similar or slightly more than biorbital breadth; metopic suture closed in subadult stage; frontal region high, slightly depressed in the angle between supraorbital bridges; temporal ridges do not form a sagittal crest; lateral border of orbit inclined backward, its angle about 60° relative to Frankfurt plane; median length of frontal bone greater than median length of parietal bone; interpterygoid fossa shallow; mesopterygoid fossa U- shaped; distance between outer bases of hamular processes of pterygoid bones approximately equal to greatest distance between outer incisors; width of basioccipital-presphenoidal suture less than one-half median length of basioccipital bone; position of perpendicular plate of vomer from well in front of to even with posterior border of palate, wings behind narrowly spread to expose the medianly crested presphenoid; the proximal portion of auditory bulla usually

broad but the anterior half not markedly tapering; basicranial exposure of carotid foramen partially to completely concealed by curvature of bulla; paraoccipital process poorly developed, mastoid process ill-defined (cf. Hershkovitz, 1977:170); nasoturbinal (superior turbinate) bone larger than ethmoturbinate I (concha nasalis media); orbits well separated, interorbital septum at level of ethmoid broad, pneumatized; foramen magnum directed backward more than downward relative to Frankfurt plane; mandibular angle broadly expanded and produced well behind condylar-basal axis; temporo-mandibular joint elevated (see Fig. 40). **External body measurements (mm):** Head and body: 586 ± 34.17 (n=5); tail: 714.2 ± 32.3 (n=5); foot: 177.2 ± 8.76 (n=5); ear: 38 ± 1.87 (n=5).



Figure 40. Cranial and mandibular morphology of *Brachyteles arachnoides* (MNRJ 1426) in dorsal, lateral, frontal, and occlusal view. Scale bar: 5 cm.

3.4.1 Cranial variation in *Brachyteles*

Along this study, I observed several cranial variations. These variations do not follow any geographic or sexual pattern. Moreover, there was not observed intrapopulation cranial uniformity in any population. In the figure 40 are shown three adult male skulls from the same locality, Santa Leopoldina - Espírito Santo, presenting various cranial differences as: the shape of the orbits, width and height of cranial vault, shape of the nasals, shape of the piriform aperture, projection of the premaxilla and rostrum, dimensions of the auditory meatus, thickness of the zygomatic arch, among other differences. These cranial variation patterns are similar in other populations as those from Rio de Janeiro (Fig. 41), and São Paulo (Fig. 42) to mention some examples.

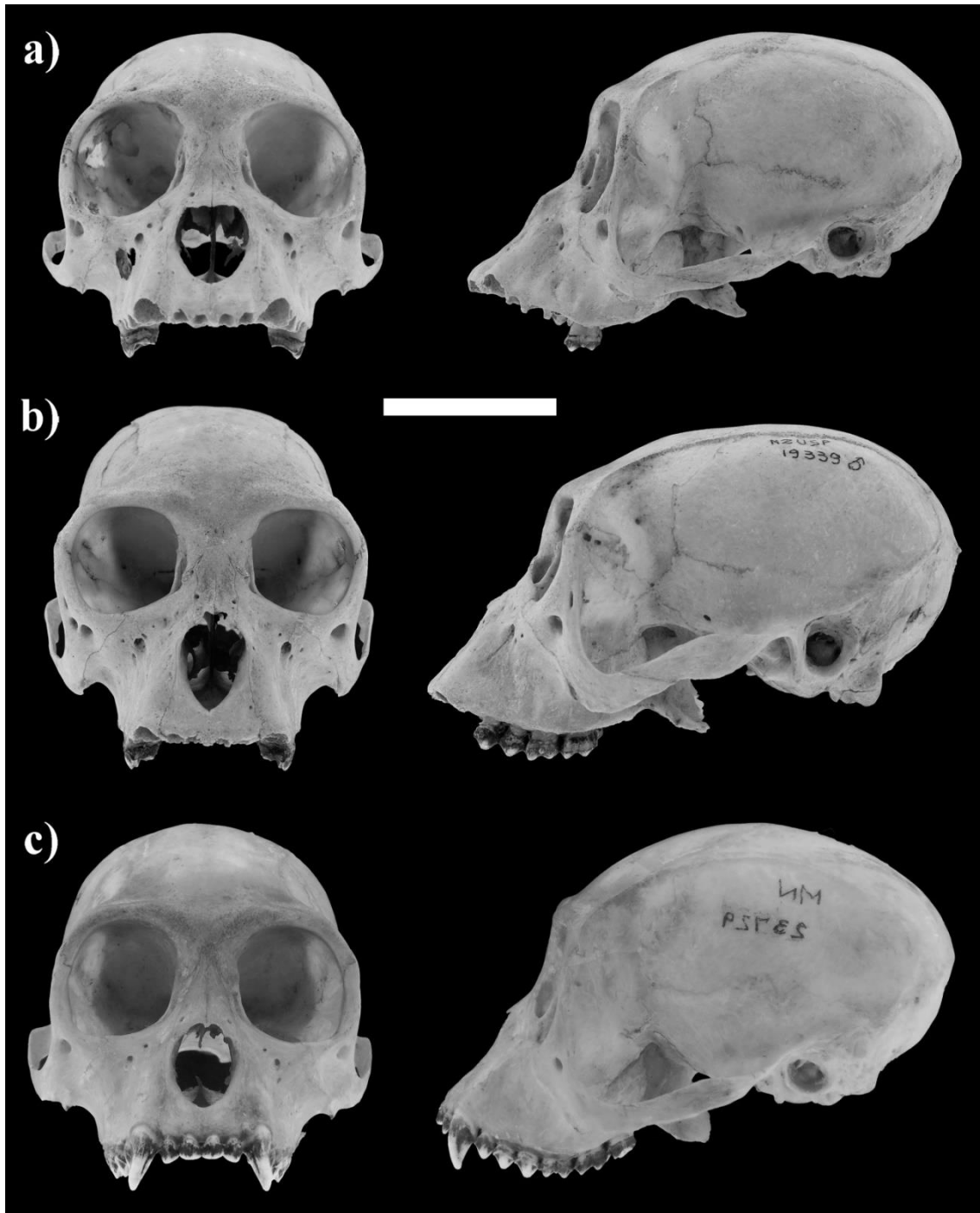


Figure 41. Cranial variation of *Brachyteles* in three different adults from Espírito Santo: a) MZUSP 19337, b) MZUSP 19339, and c) MNRJ 23729.

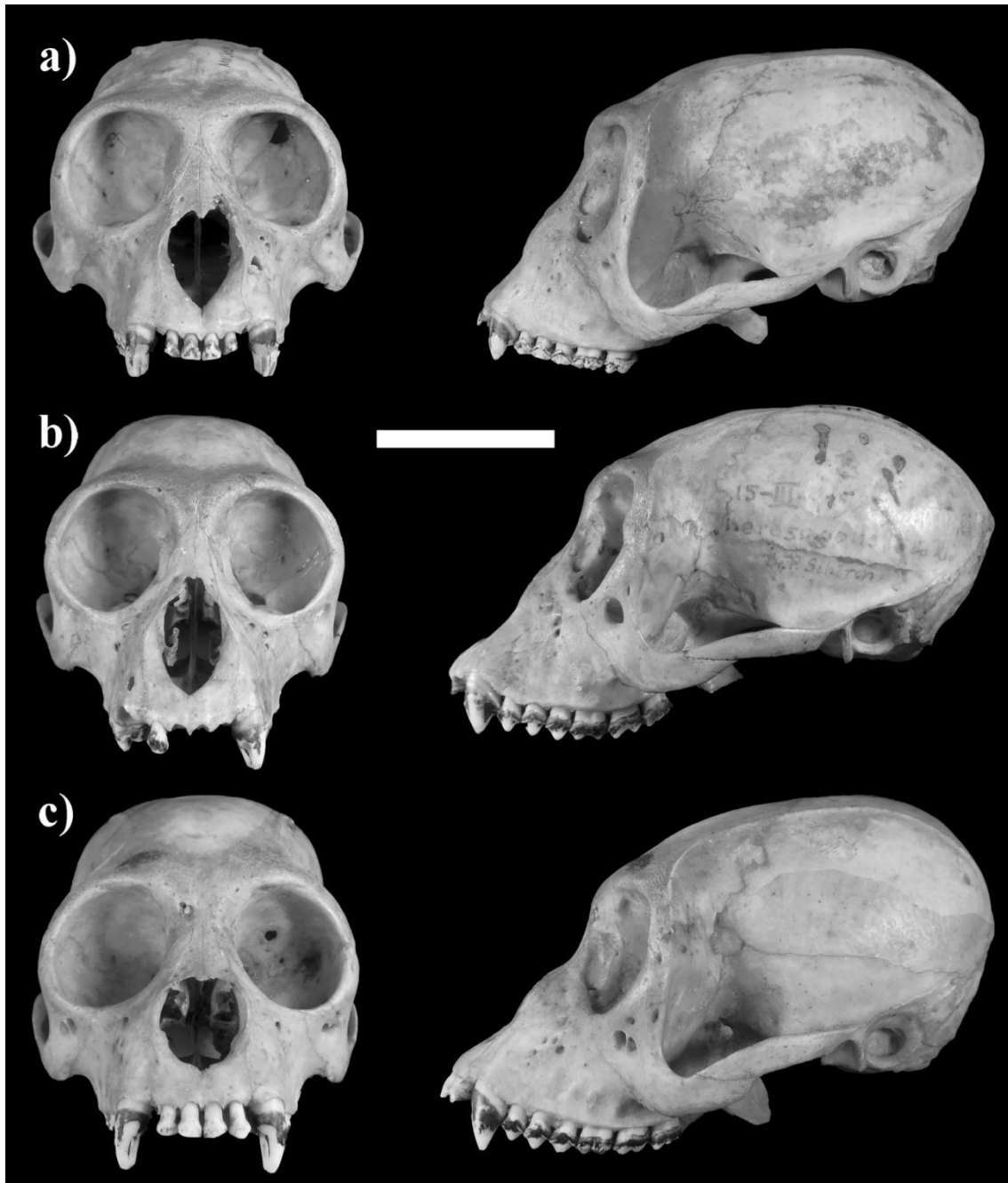


Figure 42. Cranial variation of *Brachyteles* in three different adults from Rio de Janeiro: a) MNRJ 30189, b) MNRJ 1422, and c) MNRJ 1426

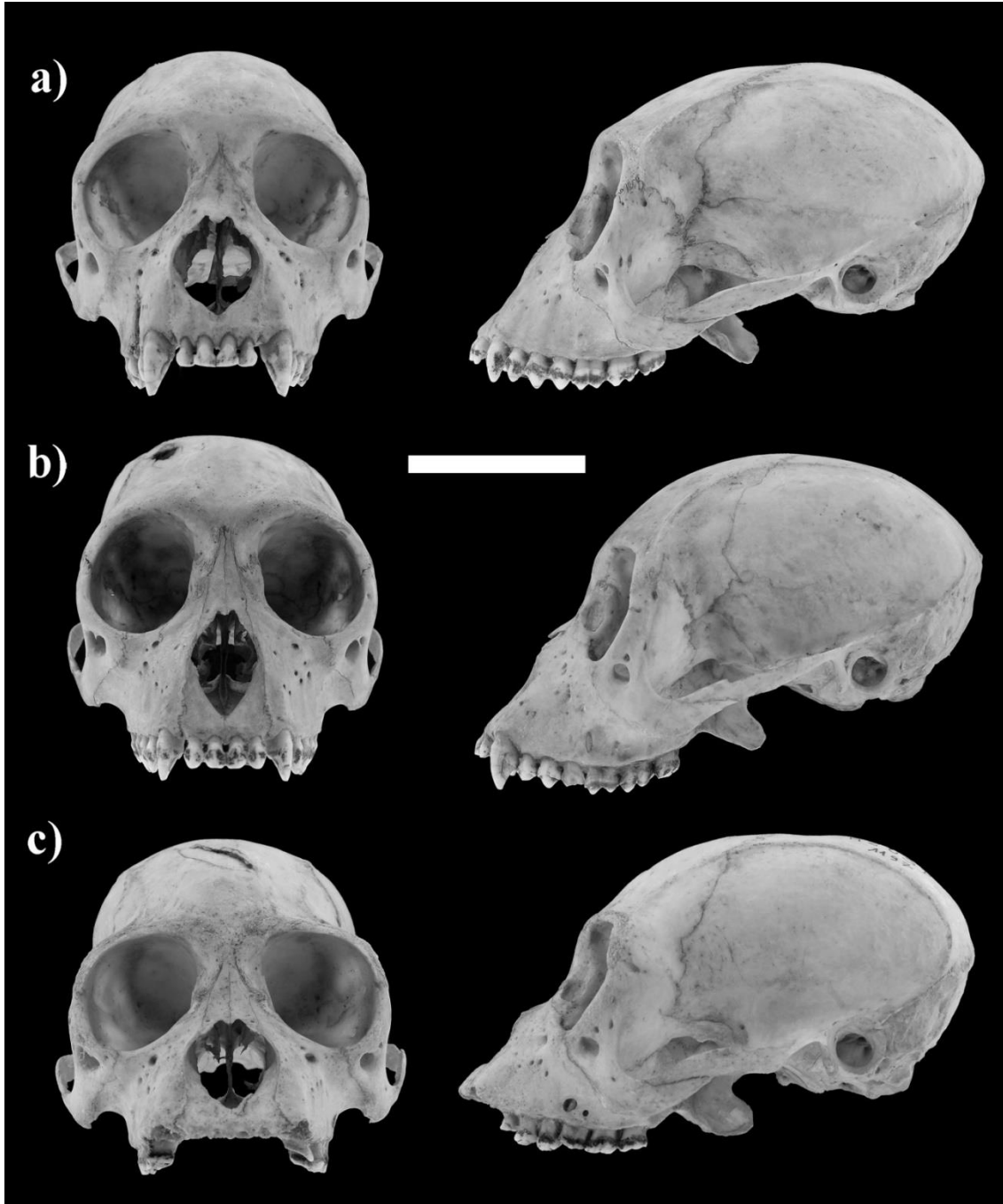


Figure 43. Cranial variation of *Brachyteles* in three different adults from São Paulo: a) MZUSP 1863, b) MZUSP 1159, and c) MZUSP 1197

3.4.2 Taxonomic notes

The German Hans Staden, on one of the earliest European accounts of Brazilian fauna, describes a dog-sized monkey, which was bearded and reddish-colored. Although the animal described most likely was an *Alouatta*, the name the natives called this monkey was, according to him “*Pricki*”, similar to the *buriquí*, the name of the *Brachyteles* in southeastern Brazil (Staden 1557). The Jesuit priest Leonardo do Valle mentioned in his Portuguese-Tupi dictionary four kinds of monkeys living along Brazil’s coast: the small Caguê (callitrichids, *Callithrix* and *Leontopithecus*), the larger Caí (probably *Sapajus* spp.), the bearded and reddish Çaguaçu (probably *Alouatta*), and the long legged Bîrigui, the muriqui or *Brachyteles* mentioned by Valle 1585 (Papavero and Texeira 1999). Manoel Cardoso de Abreu (1783) refers to *Brachyteles* for the first time by its common name in Portuguese, *Mono*.

According to Hill (1962), the first time that *Brachyteles* was mentioned in the literature was in Dr. Patrick Browne’s “History of Jamaica” (1756, 2nd ed. 1789, p. 489). Hill (1962) mentioned that in Browne’s book the author described a large brown, thumbless monkey with a prehensile tail. Nevertheless, what Browne (1756, 1789) described were actually two different animals. SIMIA 1 (The large brown monkey), and SIMIA 2 (The four-fingered monkey) giving a description of the last. Browne’s description of this SIMIA 2 does not include the color of the monkey; nonetheless, there is no doubt that this description was based on an atelid, likely an *Ateles*. From this SIMIA 1 we have no detailed information, for this reason, it is impossible to know if the author saw a *Brachyteles* or any other brown atelid.

The second earlier allusion of *Brachyteles*, still according by Hill (1962), was given by Edwards (1758-1764, p. 222) who reported two four-fingered and long-limbed monkeys: a Black Monkey, called as Spider Monkey, and another monkey quite similar to the former except with hair brown. The author claimed that he had never seen that kind of primates. There is no doubt that Edwards' Black Monkey is an individual of *Ateles*; nevertheless, due to the vague description of the Brown Monkey, this has the same odds of being both a brown species of *Ateles* (probably *Ateles fusciceps*) or an individual of *Brachyteles*, we will never know.

Étienne Geoffroy Saint-Hilaire (1806, p. 270), used Edwards' Brown Monkey description and used to describe a new species of *Ateles*, arguing that Edwards' report could not refer to a female or a young specimen of Edwards' Black Monkey, naming it *Ateles arachnoides*. Due to this, the species was described based only on Edwards' description and the best clue about the type locality was only that the specimen came from the American continent. In 1808 the French Empire sponsored a scientific mission carried by É. Geoffroy, the goal was simple, to "kindly request" the Brazilian material collected by several Portuguese expeditions in Brazil (mainly made by Alexandre Rodrigues Ferreira, who himself help in preparing the material sent to Paris), that were deposited at the Museu da Ajuda (Antunes 2011). Among the material "requested" É. Geoffroy St.-Hilaire, were two individuals of two different *Ateles*' species, one was a new species of this genus (*A. marginatus* É. Geoffroy St.-Hilaire, 1809) and, the second, matched with the *A. arachnoides* that he had described some years before (Fig. 43). With this material in hand, É. Geoffroy St.-Hilaire (1809) gave a more detailed

description of the species; he even presented the first illustration of the species (Fig. 44) and established “Le Brésil” (= Brazil) as the country of provenance of this specimen.



Figure 44. Neotype of *Brachyteles arachnoides* brought to Paris from the Museu da Ajuda (Lisboa) (Photograph by Cécile Callou)



Figure 45. *Ateles arachnoides* É. Geoffroy St.-Hilaire 1809, the earliest illustration of *Brachyteles arachnoides*.

Another reference of É. Geoffroy's *Ateles arachnoides* was made by Humboldt and Bonpland (1812) in their list of American primates, naming it *Simia arachnoides* and also designating Brazil as a possible place of provenance.

Between 1815 and 1817, the Prince Alexander Philipp Maximilian Zu Wied-Neuwied collected a large amount of specimens during his travels in Eastern Brazil (Vanzolini 1996). Wied's discoveries were presented in the two-volume *Reise nach Brasilien in den Jahren 1815 bis 1817* (Wied 1820, 1821). Wied (1820) described several new species of mammals; one of them was *Ateles hypoxanthus*. This new species differed from É. Geoffroy's *Ateles arachnoides* in the presence of a rudimentary thumb. At the same time, Kuhl (1820) published his *Beiträge zur Zoologie und vergleichenden Anatomie* describing, also, Wied's *Ateles hypoxanthus*. Due to the uncertainty of Wied's publication date there has been a complex debate about the authority of *Ateles hypoxanthus* (after the apparition of the International Code of Zoological Nomenclature). This issue has recently discussed by Garbino and Costa (2015); these authors found a Wied's letter sent to Carl Friedrich August Meisner dated 29 March 1820 in which he mentioned the publication of the first volume of the *Reise*. As the preface of Kuhl (1820) is dated 9 April 1820, Wied (1820) would predate Kuhl's book and, therefore, the authority of *Ateles hypoxanthus* should be attributed to Wied as *Ateles hypoxanthus* Wied, 1820 (Garbino and Costa 2015).

During the years 1817 to 1820, Johann Baptist Ritter von Spix and Carl Friedrich Philipp von Martius traveled to Brazil, as leaders of the Bavarian Expedition; they passed through Rio de Janeiro and São Paulo. In the latter, Spix collected a female

individual that would represent the holotype of his *Brachyteles macrotarsus* (Spix 1823) (Fig. 45a, b). This author also restricted the distribution of this species to the States of Bahia, Espirito Santo, Rio de Janeiro and São Paulo (Hill, 1962).

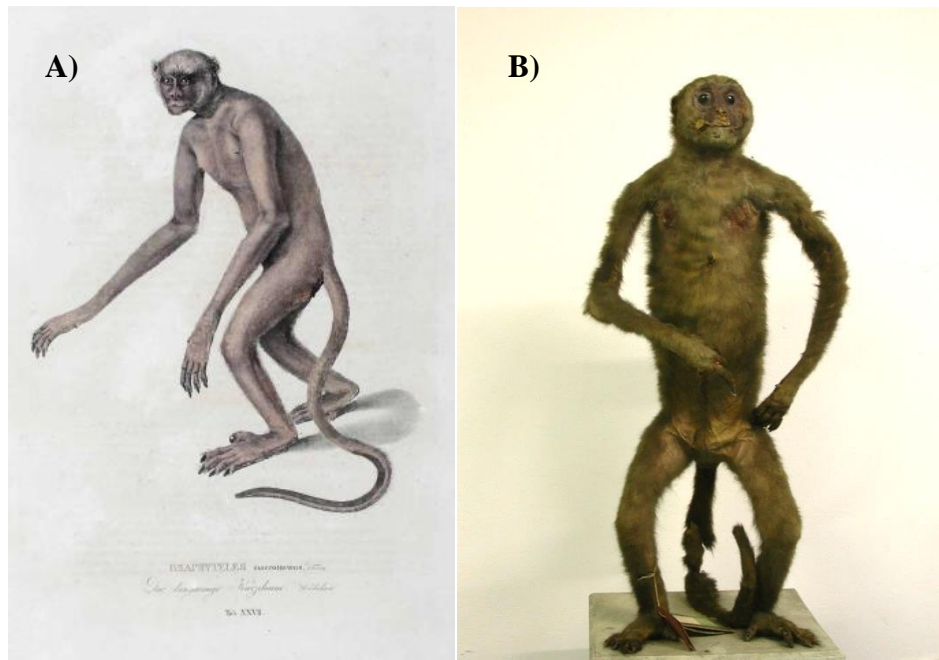


Figure 46. *Brachyteles macrotarsus* Spix, 1823, (a) Spix's original illustration of the holotype (Tab. XXVII); (b) holotype of *Brachyteles macrotarsus* housed at the Zoologische Staatssammlung München (Germany) (Photograph taken from SysTax web site).

É. Geoffroy St.-Hilaire (1827) listed the two species of muriquis, *Ateles arachnoides*, and the recently described *A. hypoxanthus*. This author proposed as a diagnostic character the presence of a rudimentary thumb in *A. hypoxanthus* versus its absence in *A. arachnoides*.

Fischer (1829) also listed both species of muriqui, this time as *Cebus arachnoides* (distributed "In Brasilia?") and *C. hypoxanthus* (distributed between the

23° to 14° *lat. austr.*). This work could be considered as the first mentioning that the Spix's *Brachyteles macrotarsus* was, in fact, a muriqui species, considering *B. macrotarsus* as a synonym of *Cebus hypoxanthus*.

Isidore Geoffroy Saint-Hilaire (1829) based on cranial, dental and pelage characters separated the muriquis to a new genus different from *Ateles*, coining the name *Eriodes*. He also stressed that Spix's *Brachyteles* was an artificial and poorly delimited genus, arguing that the only difference with *Ateles* would be the presence or absence of the thumb. Under this reasoning, I. Geoffroy St.-Hilaire (1829) suggested avoiding the use of *Brachyteles* in order to eradicate any nomenclatural confusion. This author also reported three species of his new genus *Eriodes*: *E. arachnoides* (maintaining the specific name proposed by his father) (Fig. 46), *E. tuberifer* and *E. hemidactylus* (Fig. 47). The main difference within these species was the presence or absence of the thumb and, in the case of being present, the size of this thumb. In this context, the characters were distributed as follows: *Eriodes arachnoides*, with no visible vestige of thumb; *E. tuberifer* with an extremely reduced thumb (almost a verruca) and, finally, *E. hemidactylus* with a more developed thumb which could reach the second digit.



Figure 47. Holotype of I. Geoffroy's *Eriodes arachnoides* (Photograph by Cécile Callou)

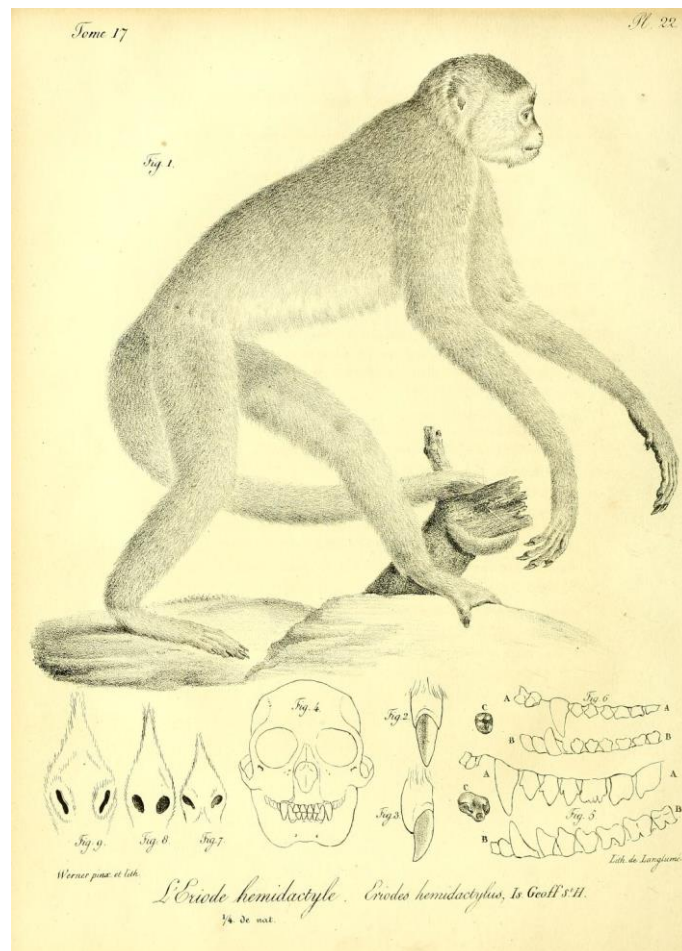


Figure 48. I. Geoffroy's *Eriodes hemidactylus*, Plate 22.

Jardine (1833) decided to follow É. Geoffroy's (1827) taxonomic arrangement listing *Ateles arachnoides* and *A. hypoxanthus* as distinct species of murequi. In a reprint of Jardine (1833), with additional material and new plates (none of them representing any murequi's species), presented the same two species of murequi (Jardine 1854).

Schreber (1840) divided *Ateles* into two groups, which would be equivalent to today's subgenera:

- a) Group *Ateles sensu stricto*, with the following species: *Ateles paniscus*, *A. marginatus*, *A. belzebuth*, *A. geoffroyi*, and *A. hybridus*.
- b) Group *Eriodes*, with two species: the first species was *Ateles hypoxanthus*, subdivided according to the length of the thumb following the criterion of I. Geoffroy (1829), *A. hypoxanthus sensu stricto* (which represented I. Geoffroy's *Eriodes tuberifer*), and *Eriodes hemidactylus*. The second species was *Ateles arachnoides*, with no external thumb (Fig. 48).

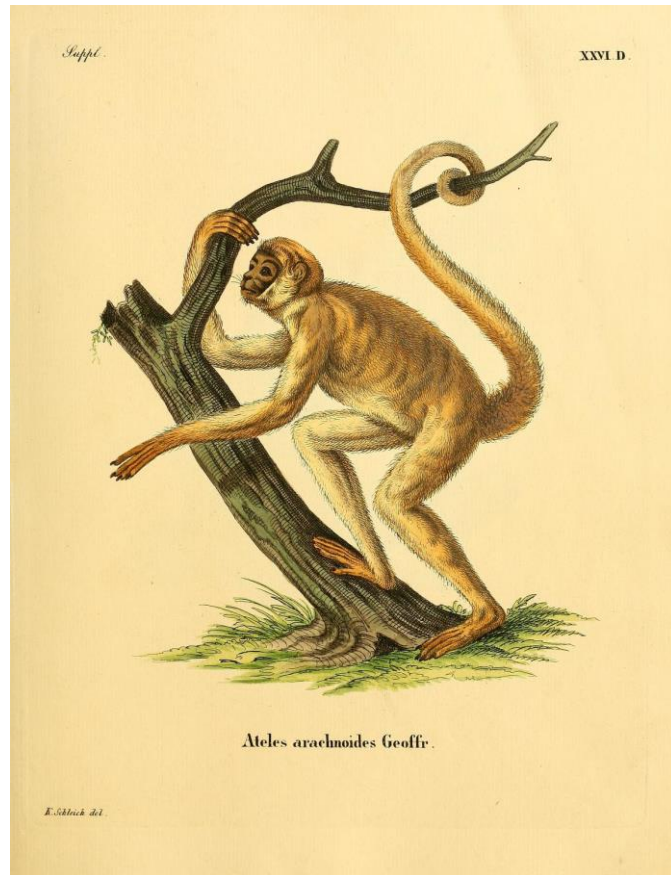


Figure 49. Illustration of *Ateles arachnoides* presented by Schreber (1840). Suppl., Plate XXVI.D

Gray (1842) described a new species of miqui, *Eriodes frontatus*, based on two individuals (one adult and one juvenile) collected by the Captain Sir Edward Belcher in South America. The same author reported three species of miqui, assigning them to Spix's *Brachyteles* Gray (1843). These three species were: *Brachyteles arachnoides* ("The Five-fingered Miqui"); the second species was *Brachyteles frontatus* ("The Black-forehead Miqui"), corresponding to Gray's (1842) *Eriodes frontatus* and, finally, the third species was *Brachyteles hypoxanthus* ("The Miqui"). It seems to be a misconception about Gray's *B. arachnoides*. For all the previous authors, *B. arachnoides* was the only species with only four fingers and no vestige of thumb. Gray's reasoning to call it as a five-fingered monkey remains unclear. All these three

species were distributed in “Tropical America”, without giving any detailed information on the distribution of each species.

Gray (1844) expanded his original description of his *Brachyteles frontatus*; in this, he rectified the distribution of the species to Central America. Gray also gave the exact location where the Captain E. Belcher collected the two individuals used for Gray’s first description and an illustration of this species (Fig. 49). The locality was “harbour of Culebra, Leon” in Nicaragua. With all this information, it is impossible that this species represented a *Brachyteles*’ species, which is endemic to Brazil. Gray’s *B. frontatus* was, in fact, an *Ateles*’ species nowadays known as *Ateles geoffroyi* (Geoffroy’s spider monkey). This author was the first on advocate the use of *Brachyteles* as a formal genus for the muriqui, arguing that Spix’s *Brachyteles* was published several years before I. Geoffroy’s *Eriodes*.

Slack (1862) was the first on questioning the validity of the three species of muriqui proposed by I. Geoffroy (1829): *Eriodes arachnoides*, *E. tuberifer*, and *E. hemidactylus*. Slack argued there were no distinct characters on the coloration of the pelage or skull morphology to separate all these species. Furthermore, Slack demonstrated that the “heaviest” character used by almost all the previous author, the presence or absence of a vestigial thumb (the same that could have or not a nail), was in fact variable. Slack also disagreed with I. Geoffroy’s arguments to consider incorrect the genus proposed by Spix (1823), *Brachyteles*. For all these reasons, he decided to keep only one species into the Spix’s genus, *Brachyteles arachnoides*, erroneously attributing the authority of this name to John Edward Gray.

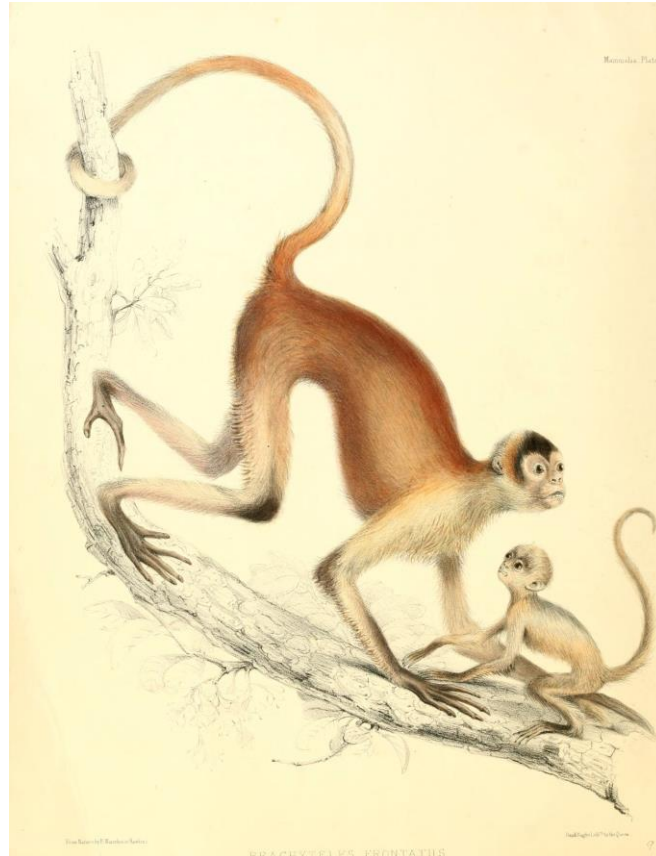


Figure 50. Gray's (1844) *Brachyteles frontatus*, Plate 1.

Gray (1870) grouped *Brachyteles* in the tribe Lagotrichina (which included *Ateles*, *Brachyteles*, and *Lagothrix*); listing only one species, *Brachyteles arachnoides*. He recognized three varieties: without any thumb, with a well-developed thumb, and with a rudimentary thumb. These three varieties were distributed in Brazil without any further locality information.

At this point, started the disagreement about whether the muriqui genus (independently of the generic name used by each author) had one or two species. Schlegel (1876) revised the specimens collected by the naturalist Johann Natterer in “Ypanema” (=São João de Ipanema) in São Paulo (Fig. 50), and decided to return to É.

Geoffroy's (1827) taxonomic arrangement listing two species of murequi, *Ateles arachnoides*, and *A. hypoxanthus*.



Figure 51. *Brachyteles arachnoides* (number NMW-ST 682), collected by Johann Natterer in 1819 and held at the Natural History Museum of Vienna (Photograph by Alexander Bibl).

Pelzeln (1883) listed only one species of murequi, *Eriodes arachnoides*; while for Jentink (1892) there were two species, *Ateles arachnoides*, and *A. hypoxanthus*. Elliot (1913), arguing that *Brachyteles* was an uncorrected Latinization of βραχύς = short and τέλειος = perfection, completion, proposed that the correct generic name

would be *Brachyteles*. This author listed *Brachyteles arachnoides* as the single species of the genus.

Vieira (1944) recognized two subspecies of *Brachyteles*, based on some morphological differences such as facial skin pigmentation and the presence or absence of vestigial thumbs. One subspecies, *Brachyteles arachnoides arachnoides*, occurring in the states of Rio de Janeiro, São Paulo and Paraná along the Serra do Mar; and *B. arachnoides hypoxanthus* occurring in southern Bahia, Minas Gerais, and Espírito Santo South to the Serra da Mantiqueira. Vieira (1955) later decided that the two subspecies were not valid, leaving a monotypic *Brachyteles arachnoides* in the genus and established Rio de Janeiro as type locality of this species.

Cabrera (1958) and Hill (1962) both considered *Brachyteles arachnoides* as the single extant species of the genus, although the latter author classified Lund's *Protopithecus brasiliensis* as an extinct species of *Brachyteles*, naming it *B. brasiliensis*. Aguirre (1971) and Napier and Napier (1976) recognized only one species of *Brachyteles* (*B. arachnoides*) with no subspecies.

This taxonomic arrangement was widely accepted until Rylands et al. (1995), based on Lemos de Sá et al. (1990), Fonseca et al. (1991) and Lemos de Sá and Glander (1993), indicated that Vieira's (1944) arguments to consider the Southern and Northern populations of *Brachyteles* as distinct were valid. Nevertheless, these authors found that the molecular and morphological differentiation between these two groups was even more extreme and would justify the classification of full rank species (Coimbra-Filho et

al. 1993; Groves 2001), the Northern muriqui, *Brachyteles hypoxanthus* and the Southern muriqui, *Brachyteles arachnoides*. Finally, Groves (2001, 2005) followed Rylands et al.'s (1995) proposal and listed the two populations of muriqui as allopatric species, which is the taxonomic arrangement currently accepted.

3.4.3 Specimens examined

(42 skins, 71 skulls). **BAHIA: Rio Congoji:** MZUSP 3830; **As Barreiras:** R.N.H. 17688. **ESPÍRITO SANTO: Colatina:** MZUSP 2236; **Itaguaçu:** MNRJ 24114; **Jahibocas:** MNRJ 24113, 74686, 74687; **Santa Leopoldina:** MZUSP 11098 11099, 11100, 11102, 11104, 11106, 11180, 19336, 19337, 19338, 19339, 19340, 24604, MNRJ 24104, 23729. **MINAS GERAIS: Estação Biológica de Caratinga:** MBML 2095, UFMG 3132, 3130, 3131, MNRJ 69783; **Rio Bacalhau:** MNHN-ZM AC-A1512; **Rio Matipó:** MZUSP 3533; **Teófilo Otoni:** MZUSP 8582. **RIO DE JANEIRO: Itatiaia:** MZUSP 9962; **Mambucaba- Angra dos Reis:** MNRJ 24115, 30189, 30193, 31304, 31321; **Pedra Branca-Paraty:** MNRJ 5651, 6699, 7724, 8513, 8514, 8515; **Teresópolis:** 1426, 1420, 1422, 1424, 1425, 2717, 2718. **SÃO PAULO: Anhembi-Fazenda Barreiro Rico:** MZUSP 8463, 8909; **Boraceia:** MZUSP 7422; **Iporanga:** MZUSP 24801; **Itararé:** MZUSP 1158, 1159, 1160; **Paranapiacaba-Alto da Serra:** MZUSP 2940; **Piedade-Agua Doce:** MZUSP 6482; **Poço Grande:** MZUSP 282; **São Bartolomeu:** MZUSP 1689, 1690; **Ubatuba:** MZUSP 1863, 1864; **Ypanema (=São João de Ipanema):** NMW-ST 679, 682, 680A, 680B, 1539. **Locality unknown:** MNRJ 515, 523, 524, 525, 526, 2719, 6107, 25700, 26888, 30188, 30190, 30191,

30192, 30194 MZUSP 19360, 19361, 19362, 19363; MNHN-ZM 2007-1475, 2007-1474, AC-1949-67, AC-1950-41, MO-1847-1853.

3.5 Phylogenetic position of *Brachyteles* within the Atelinae

In this section, I will describe all the characters used in the phylogenetic analysis, follow by the results of each codification. Finally, I will discuss the phylogenetic relationships found between the different taxa.

3.5.1 Pelage characters

1. Texture of body pelage

(0) hard;

(1) soft.

Alouatta seniculus, *Ateles belzebuth*, *A. chamek*, and *Callicebus personatus* present the character (0). This character was first used in the unpublished phylogeny of Paredes (2003).

2. Length of body hair

(0) long;

(1) short to medium.

Lagothrix flavicauda, *Lagothrix cana*, *Lagothrix poeppigii*, *Lagothrix lugens*, *Lagothrix lagotricha*, *Brachyteles arachnoides* and *Sapajus nigritus* present the character (1).

3. Abundance of hairs

- (0) scarce;
- (1) abundant.

Alouatta seniculus, *Ateles belzebuth*, and *A. chamek* present the character (0). This character was first used in the phylogeny of Paredes (2003).

4. Shade of pelage in ventral region

- (0) same as dorsum;
- (1) darker than dorsum;
- (2) lighter than dorsum.

The tone of the coat of the ventral and dorsal region is equal in *Ateles chamek* and *Alouatta seniculus*. In all the species of *Lagothrix*, the ventral pelage has a darker tone than the dorsum. In *Lagothrix lugens*, this difference of tones is not as evident in the darker individuals, but it is noticeable in the lighters. In *Ateles belzebuth*, *Brachyteles arachnoides*, *Sapajus nigritus*, and *Callicebus personatus* this ventral coloration is lighter than dorsum. This character was used in the phylogeny of Auricchio (1999).

5. Pelage length in pectoral region:

- (0) same length as in dorsum;
- (1) larger than dorsum and scarce;
- (2) larger the dorsum and abundant;
- (3) shorter than the dorsum and abundant.

Alouatta seniculus and *Sapajus nigritus* present the ventral pelage of equal length or slightly longer than the dorsal and sparse fur; in *Ateles chamek*, *Ateles belzebuth*, and *Brachyteles arachnoides* the pelage on the pectoral region is approximately 1.5 times longer than on dorsal region and wispy, while in all the species of *Lagothrix*, the pelage of the pectoral region is about 3 times longer than the pelage on the dorsal region. *Callicebus personatus* is the only species presenting the character (3). This character was first used in the phylogeny of Paredes (2003).

6. Shade of the pelage on the crown:

- (0) same as dorsum and rest of the body;
- (1) darker than dorsum;

In *Lagothrix cana*, *L. flavicauda*, *L. poeppigii*, *Sapajus nigritus*, and *Callicebus personatus* the tone of the fur on the crown is always darker than on the dorsum, showing a marked contrast between the color of this area and the dorsal pelage. *Alouatta seniculus*, *Ateles belzebuth*, *Ateles chamek*, and *Brachyteles arachnoides* have no color contrast between the fur on the crown and the rest of the dorsum. This character was used in the phylogeny of Paredes (2003).

7. Marked contrast between hand/foot and arm/leg pelage color:

- (0) absent;
- (1) present.

Lagothrix flavicauda, *L. cana*, *L. lagotricha*, and *L. poeppigii* show that the tone of the pelage which is present on the hands, forearms, feet and legs is markedly darker than the rest of the pelage of the limbs. Unlike these, *Alouatta seniculus*, *Ateles belzebuth*, *Ateles chamek*, and *Brachyteles arachnoides* have no color contrast between in these areas. This character was used in the phylogeny of Paredes (2003).

8. Facial pigmentation:

(0) partial, with freckles;

(1) total.

Only *Ateles belzebuth* and *A. chamek* have the character (0) presenting a zoned depigmentation in the face, around the eyes, along the entire nose and around the lips. Nevertheless, *Brachyteles arachnoides* is polymorphic and, for this reason, was coded as (0, 1). This character was used in the phylogeny of Paredes (2003).

9. Color of the pelage in the scrotal region and above and around the callosity of the tail tip relative to surrounding areas:

(0) same color as the surrounding pelage or different color in all three regions;

(1) color contrasting with the surrounding pelage;

Only *Lagothrix flavicauda* presented the character (1). This character was used in the phylogeny of Paredes (2003).

10. Shade of triangular patch of inter-scapular pelage:

- (0) same as dorsum;
- (1) lighter than dorsum;
- (2) darker than dorsum.

This triangular pelage of inter-scapular pelage starts in the neck and becomes more contrasting from the top edge of the shoulder blades and may extend to the low dorsum, as in the case of *Lagothrix cana* and *Brachyteles arachnoides* where this line is dark, blackish, equal as the shade as the crown or may be short and not reach beyond the lower edge of the shoulder blades as in *L. lagotricha* and *Sapajus nigritus*, which have a lighter color than the surrounding fur on the dorsum. *Lagothrix poeppigii*, *L. flavicauda*, and *L. lugens* do not have this strip, as *Ateles chamek*, *A. belzebuth*, *Alouatta seniculus* and *Callicebus personatus*. This character was used in the phylogeny of Paredes (2003).

11. Middorsal tracks of dark pelage:

- (0) absent;
- (1) present, very faint;
- (2) present, well-marked.

In *Lagothrix lagotricha* and *L. poeppigii*, the presence of these bands of dark hair is very clear; contrasting strongly with the rest of the coat, while in *L. lugens* and *Brachyteles arachnoides* these dark stripes can be noticed; however, the contrast with the rest of the dorsal pelage is much lower. In *Lagothrix cana*, *L. flavicauda*, *Ateles chamek*, *Ateles belzebuth*, *Alouatta seniculus*, *Sapajus nigritus*, and *Callicebus*

personatus these bands are absent on the dorsal pelage. This character was used in the phylogeny of Paredes (2003).

12. Patches of colored pelage in face:

(0) absent;

(1) present.

Only *Lagothrix flavicauda* presented the character (1). This character was used in the phylogeny of Paredes (2003).

13. Presence of glabrous ventral surface of the tail:

(0) absent;

(1) present.

Sapajus nigritus and *Callicebus personatus* present the character (0). This character has been recognized as synapomorphic for Atelidae (Horovitz and Meyer 1997).

14. Proportion of touch pad:

(0) half the length;

(1) one third the length.

The portion devoid of hairs on the distal ventral surface of the prehensile tail, with fingerlike patterns, is known as "digital pad" and it is a synapomorphy of Atelidae (Pocock 1925, Horovitz and Meyer 1997). In *Alouatta seniculus* and *Brachyteles*

arachnoides, this digital pad terminal occupies nearly half of the tail. While, in the other atelids the digital pad occupies a third of the tail. This is the first phylogenetic analysis to code this character differentially among Atelidae, although it was used in the phylogeny of Paredes (2003), with a more limited amount of terminal taxa.

15. Small hairs in the middle phalange of hands and feet of different color than surrounding pelage:

(0) absent;

(1) present.

Ateles belzebuth, *Lagothrix flavicauda*, *Brachyteles arachnoides*, and *Sapajus nigritus* present the character (1). This character was used in the phylogeny of Paredes (2003).

16. Color of hair tufts over external ear:

(0) same as hair in crown;

(1) brighter contrasting hair than found in the crown;

(2) darker contrasting hair than found in the crown.

In *Alouatta seniculus*, *Ateles chamek*, *Ateles belzebuth*, *Lagothrix cana*, *L. poeppigii*, *L. lagotricha*, and *Callicebus personatus* present no difference between the coloration of these tufts and the hair of the crown. *Lagothrix flavicauda* and *L. lugens* have a lighter coloration on the tufts than in the rest of the crown. *Brachyteles arachnoides* is the only taxon presenting the character (2). This character was used in the phylogeny of Paredes (2003).

17. General aspect of pelage color:

- (0) solid red (pheomelanin);
- (1) solid black (eumelanin);
- (2) Agouti brown tones;
- (3) Agouti greyish black.

Callicebus personatus, *Brachyteles arachnoides*, and all the species of *Lagothrix* (except *L. flavicauda*) present agouti brown tones in the pelage. In a general aspect, *Lagothrix flavicauda* and *Alouatta seniculus* present a solid saturated color which varies from red to mahogany. On the other hand, *Ateles belzebuth* and *A. chamek* present a solid black saturated color, while *Lagothrix cana* and *L. lugens* present an agouti greyish black coloration. This character was used in the phylogeny of Paredes (2003).

3.5.2 Cranial characters

18. Alignment of incisive foramina:

- (0) parallel;
- (1) oblique.

Incisive foramina are located between the maxillary – palatal suture below the row of the incisors (Fig. 51). These could be total or partially separated by the palatal process and its arrangement can be variable. Such variations may be related to the rostrum thinning and lengthening of the premaxilla (Rosenberger and Coimbra-Filho 1984). *Lagothrix flavicauda*, *Brachyteles arachnoides*, and *Caipora bambuorum* present

oblique foramina, joining them at the distal edge where they merge. All the remaining taxa present oval and parallel foramina, separated by a well-developed process palatal sometimes fused to the middle or at the base of the foramina. This character was used in the phylogeny of Paredes (2003).

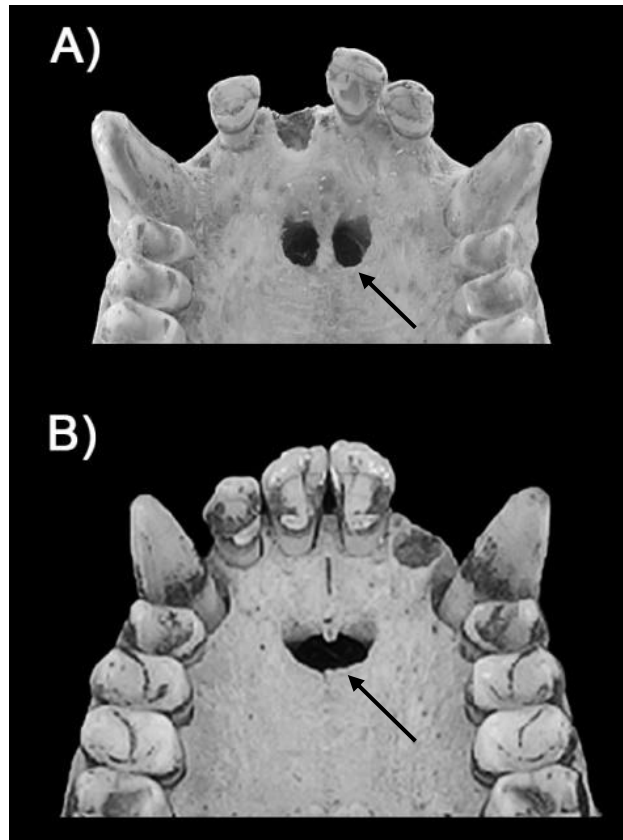


Figure 52. Occlusal view of the Maxillary bone where is observed the arrangement of the oval and parallel incisor foramina separated by the Palatal process in *Lagothrix lagotricha* MUSM 10382 (a) and oblique in *Lagothrix flavicauda* MUSM 52 (Character 18).

19. Shape of the horizontal plate formed by the palatine bones:

- (0) rectangle;
- (1) triangular or semilunar, wide;
- (2) triangular, narrow.

The horizontal plate of the palatine is located behind the premaxilla and both elements form the osseous roof of the palate. The shape and dimensions of the horizontal plate of the palatine can be variable, and this variation is related to diet changes (Hershkovitz 1977). Only *Ateles chamek*, *A. belzebuth*, and *Callicebus personatus* present this horizontal plate, usually forming a rectangular frame with rounded edges. *Lagothrix flavicauda* present an autapomorphic triangular and narrow horizontal plate. The remaining taxa have the horizontal plate of the palatine forming a triangular or semilunar structure with rounded edges. This character was used in the phylogeny of Paredes (2003).

20. Curvature of the anterior border of the premaxilla:

- (0) strong or pronounced curvature;
- (1) soft, less pronounced curvature.

The premaxilla supports all the incisors, forms the lateral and lower margins of the nasal aperture and is involved in defining the profile of the individual. In the evolution of the premaxilla, there is a tendency to a reduction in size, correlated with changes in the shape of the rostrum, decrease in number and the alteration of the form and function of the incisors (Hershkovitz 1977). In all the species of *Lagothrix* and in *Sapajus nigritus* the premaxilla is curved, presenting a soft or poor-pronounced curvature, while *Alouatta seniculus*, *Ateles belzebuth*, *A. chamek*, *Brachyteles arachnoides*, *Cartelles coimbrafilhoi*, and *Caipora bambuorum* present a pronounced premaxillary curvature. This character was used in the phylogeny of Paredes (2003).

21. Inferior border of Frontal bone in pterionic region:

- (0) extended towards the pterionic foramen;
- (1) restricted to the superolateral angle of the orbit.

The temporal fossa is completely closed in some species of primates, this leads to the formation of the pterionic foramen. The area around this foramen is called pterionic region, in this area are in contact the frontal, parietal, malar, temporal and alisphenoid bones (Fig. 52). The extension of the frontal in this region is variable. Groves (2001, character 10) uses this character in his analysis of atelids but maintains that the front in this region extends into the pterionic foramen in *Ateles* and *Lagothrix flavicauda*, being restricted in *Lagothrix* and *Alouatta*. Here I found that *Lagothrix flavicauda*, *Sapajus nigritus*, and *Callicebus personatus* present the frontal bone restricted to the superolateral region of the orbital wall, while in all *Lagothrix* species, *Ateles chamek*, *Ateles belzebuth*, and *Brachyteles arachnoides* present the frontal bone extended over the pterionic region. *Alouatta seniculus*, *Cartelles coimbrafilhoi*, and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

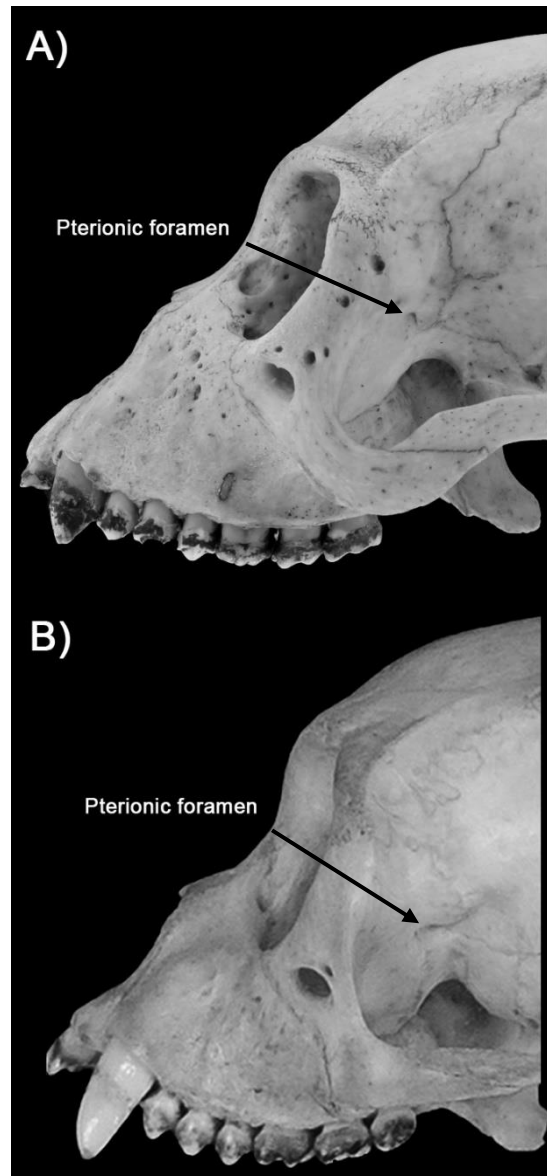


Figure 53. Pterionic region in lateral view of the skull. Front extended towards the pterionic foramen in *Brachyteles arachnoides* (MZUSP 2940) (a), and restricted to bone of the superolateral region of the orbital wall in *Lagothrix flavicauda* (MUSM 52) (character 21).

22. Engrossment around the pterionic foramen:

- (0) not very pronounced;
- (1) very pronounced.

Ateles belzebuth, *A. chamek*, and *Lagothrix flavicauda* present the character (0). *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

23. Dimension of the pterionic foramen:

- (0) small or reduced (≤ 0.7 mm across);
- (1) medium to large (2-3mm across).

In primitive primates, the degree of postorbital closure is partial with a complete separation of the temporal and orbital cavities. In Platyrrhini, this degree of closure is greater, with the fossa temporal and orbital completely separated by the lateral extensions of the malar and alisphenoid. However this closure is never complete, vestigial fissures persist. The pterionic foramen is a vestigial persistent fissure in Platyrrhini, covered by a membrane. Its size varies from 1 to 5 mm between different taxa (Hershkovitz 1977). In this study *Alouatta seniculus*, *Lagothrix cana*, *L. lagotricha*, *L. poeppigii*, *Brachyteles arachnoides* and *Callicebus personatus* present a small or very small pterionic foramen, not reaching 0.7 mm. of diameter; while *Ateles chamek*, *Ateles belzebuth*, *Lagothrix flavicauda*, *Sapajus nigritus* and *Caipora bambuorum* have a larger pterionic foramen which dimensions varies between 2 to 3 mm in diameter. *Lagothrix lugens* presented a variable pterionic foramen, for this reason, was coded as polymorphism (0, 1). Groves (2001) codifies this character in his analysis of atelids, but in this character the variability among species of *Lagothrix* is not

reflected. *Cartelles coimbrafilhoi* was coded as "?" due to the impossibility to verify the status.

24. Shape of the inferior border of the malar bone, at the suture with the temporal bone:

- (0) angular sutural apex;
- (1) sutural apex non-angular.

All the species of *Lagothrix*, *Brachyteles arachnoides*, and *Sapajus nigrinus* present the malar bone with a sutural apex non-angular. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

25. Angle formed by the prolongation of the lateral orbital wall and the maxillary section of zygomatic arch:

- (0) almost straight;
- (1) acute.

Lagothrix flavicauda, *Brachyteles arachnoides*, *Sapajus nigrinus*, *Callicebus personatus*, *Cartelles coimbrafilhoi*, and *Caipora bambuorum* present the character (1).

26. Projection of the malar and temporal bones suture:

- (0) goes over both malar and maxillary borders but do not reach the upper second molar alveolus;

(1) reaches the alveolus of the second upper molar.

In nearly every Platyrrhini, the entire zygomatic arch is on the dental series. Some of the ventral projection may be present but rarely exceeds the level of the plane of the alveolar ridge (Horovitz 1999). In this study *Alouatta seniculus*, *Ateles belzebuth*, *A. chamek*, *Lagothrix cana*, *L. lagotricha*, *L. poeppigii*, *L. lugens*, *Brachyteles arachnoides*, *Cartelles coimbrafilhoi*, *Caipora bambuorum* and *Sapajus nigritus* have the sutural projection of the malar and temporal which does not reach the upper edge of the tooth row. *Lagothrix flavicauda* and *Callicebus personatus* have a very elongated sutural projection of the malar and temporal, reaching the upper second molar alveolus. This agrees with Horovitz (1999, character 23) in the codification of *Alouatta* and *Ateles*; nevertheless, this author did not include *Lagothrix flavicauda* which presents variations in this character.

27. Inferior angle of the Malar bone and orientation of the zygomatic arch relative to Frankfurt plane:

(0) angle pronounced, arch oblique;

(1) angle not pronounced, arch straight or slightly oblique.

The malar bone extends laterally forming a notch which is the initial portion of the zygomatic arch, its inclination is variable. This inclination seems to be associated with the depth of the mandibular angle and shape of the malar (HersHKovitz 1977). *Alouatta seniculus*, *Sapajus nigritus*, *Cartelles coimbrafilhoi* and *Callicebus personatus* present a fairly deep notch, with an oblique zygomatic arch, while *Ateles belzebuth*, *A. chamek*,

all the species of *Lagothrix* and *Caipora* have a slightly pronounced notch and a slightly oblique zygomatic arch. This character was used in the phylogeny of Paredes (2003).

28. Position of the major axis of the body of the Malar bone (lateral view):

(0) almost vertical;

(1) oblique.

The portion of the malar which is between the maxillar and below the ocular orbit can be oblique with a strong inclination or may occur oblique or nearly vertical (Fig. 53).

Alouatta seniculus, *Sapajus nigritus*, *Lagothrix flavicauda*, *Callicebus personatus* and *Caipora* present this malar region almost vertical. All the remaining species of *Lagothrix*, *Ateles belzebuth*, *A. chamek*, *Brachyteles arachnoides*, and *Cartelles coimbrafilhoi* present this region with a strong lateral inclination.

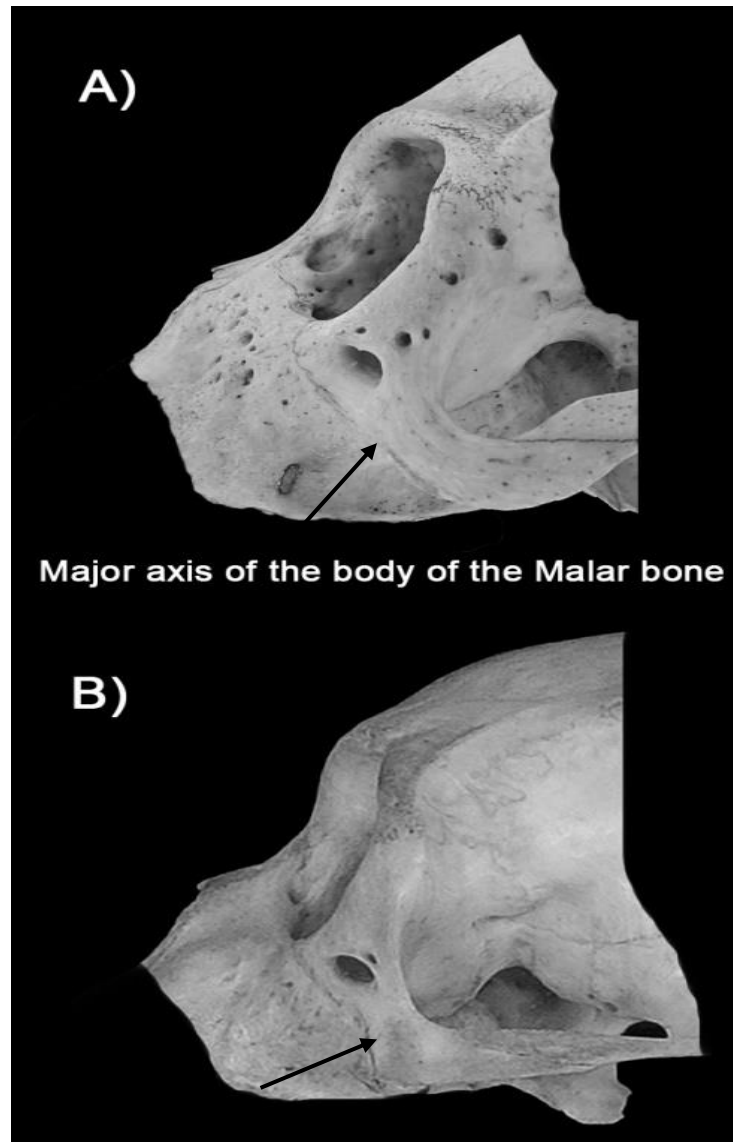


Figure 54. Lateral view of the skull (below the orbit). The position of major axis of the malar body oblique *Lagothrix lagotricha* (MUSM 10380) (a), and the major axis almost vertical in *Lagothrix flavicauda* (MUSM 52) (b) (character 29).

29. Size of malar foramen:

(0) less than 4mm;

(1) greater than 4mm.

Alouatta seniculus, *Ateles chamek*, *Lagothrix flavicauda*, *Caipora* and *Cartelles* present the character (2).

30. Shape and width of the anterior border of the quadrilateral surface of the

Tympanic Bulla:

- (0) broad, rounded or blunt edge;
- (1) narrow, angular edge.

The tympanic Bulla comes from the petrous portion of the temporal. In atelids, the bulla is relatively large but not the largest among Platyrrhini (HersHKovitz 1977). *Ateles belzebuth*, *A. chamek*, *Brachyteles arachnoides*, and *Sapajus nigritus* have a narrow front end and an angled edge, while all the species of *Lagothrix*, *Alouatta seniculus*, *Caipora* and *Callicebus personatus* have a wide end and truncated or rounded edge. *Cartelles* was coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

31. Development of the styloid process of the temporal bone:

- (0) vestigial or absent;
- (1) regular (0.5-0.6mm);
- (2) enlarged (1-2mm).

The styloid process is located in the braincase, positioned on the tympanic Bulla, before the stylomastoid foramen. In the styloid process are inserted the stylohyoid, stylopharyngeus and styloglossus muscles. In *Lagothrix flavicauda* this process is present but is poorly developed, while in all the remaining species of *Lagothrix*, *Ateles belzebuth*, *Brachyteles arachnoides*, *Callicebus personatus*, and *Sapajus nigritus* this process is extremely reduced or absent. In *Alouatta seniculus* and *Ateles chamek*, the

styloid process is enlarged. *Cartelles coimbrafilhoi* and *Caipora bambuiorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

32. Dimensions of the styloid-mastoid foramen:

- (0) small (≤ 1.2 mm);
- (1) medium or large (1.7-2.4 mm).

The styloid-mastoid foramen is located in the braincase, below the auditory meatus, posterior to the styloid process. *Ateles belzebuth*, *A. chamek*, *Brachyteles arachnoides*, and *Caipora* present the character (1). This character was used in the phylogeny of Paredes (2003).

33. Dimension and shape of the hamulus:

- (0) very long, could surpass the lateral plate of the pterygoid bone, claw-like end;
- (1) short, do not surpass the lateral the lateral plate of the pterygoid, of strong curvature and blunt end;
- (2) short, do not surpass the pterigoid plate, regular curvature and styloid end.

The hamulus is the terminal spinous process of the medial pterygoid plate. This medial plate is attached to lateral pterygoid plate (Fig. 54). Its form can vary from stylar extensions strongly curved and elongated blunt and short extensions or be completely degenerate in some genera (Herskovitz 1977). *Alouatta seniculus*, *Lagothrix poeppigii*,

L. lagotricha, and *Sapajus nigritus* possess a very long hamulus which surpasses the lateral plate of the pterygoid bone. *Ateles belzebuth*, *A. chamek*, *Lagothrix flavicauda*, *L. cana*, *L. lugens*, and *Brachyteles arachnoides* have shorter hamulus with blunt end which do not surpass the plate of the pterygoid. *Callicebus personatus* has short hamulus with styloid end. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

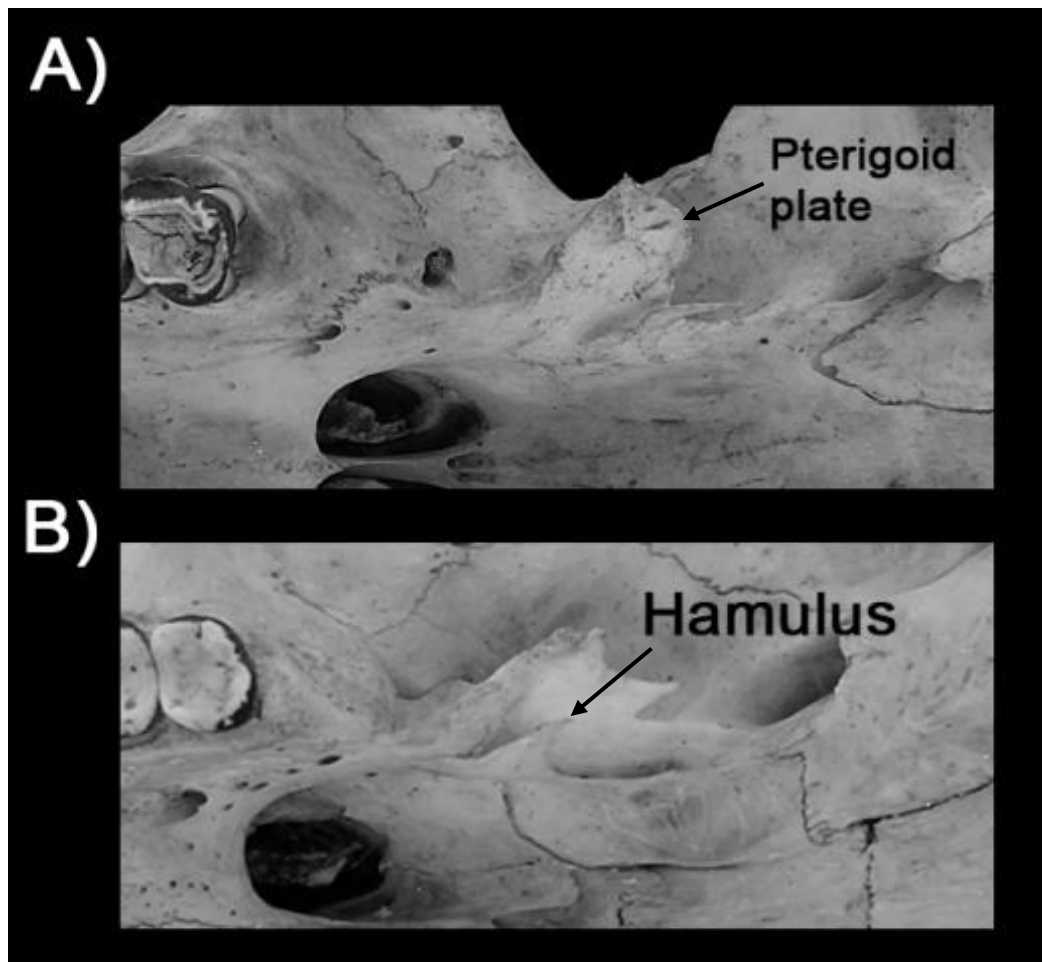


Figure 55. Occlusal view of the maxilla where is shown: a very long hamulus surpassing the lateral plate of the pterygoid bone, claw-like end in *Alouatta seniculus* MUSM 11108 (a), and a hamulus which does not excess the lateral pterygoid plate, in *Lagothrix lagotricha* (MUSM 11122) (character 34).

34. Length and extension of the lacrimal bone:

- (0) long, reaches the interior superior angle of the orbit wall and protrudes laterally;
- (1) reaches only half the height of the intraorbital wall, edges do not protrude.

The intraorbital wall is formed by the lacrimal, frontal and ethmoid bones. The extension of the lacrimal on the front and towards the upper inner angle of the orbit is variable. In *Ateles belzebuth*, *A. chamek*, *Sapajus nigritus*, *Carteles*, *Caipora*, and *Callicebus personatus* the lacrimal bone reaches only half the height of the intraorbital wall. This character was used in the phylogeny of Paredes (2003).

35. Impression left by the nerve-vascular package on the orbital floor:

- (0) pronounced;
- (1) not pronounced.

The infraorbital nerve is a branch of the trigeminal or 5th cranial nerve that runs through the floor of the orbital cavity (maxilla) emerging from the infraorbital foramen (Ankel-Simons 2000). The passage of this nerve and associated vessels produces a mark on the floor of the cavity, which is pronounced in *Alouatta seniculus*, *Brachyteles arachnoides*, *Cartelles*, *Caipora*, and all the species of *Lagothrix*. This character was used in the phylogeny of Paredes (2003).

36. Dimension of the posterior ethmoidal foramen:

- (0) reduced and narrow;

- (1) notorious and wide.

The posterior ethmoid foramen is located in the orbital cavity, on the ethmoid-frontal suture, in the intraorbital wall. Through this foramen pass branches olfactory nerve (Ankel-Simons 2000). The posterior ethmoid foramen is very low or virtually absent in *Alouatta seniculus*, *Ateles belzebuth*, *A. chamek* and *Sapajus nigritus*. While *Brachyteles arachnoides* and all the species of *Lagothrix* have a notorious ethmoidal foramen. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

37. Position of the foramen rotundum (anterior view):

- (0) below the inferior fissure in the orbit;
- (1) inferolateral.

All the species of *Lagothrix* and *Callicebus personatus* present the character (0). This character was used in the phylogeny of Paredes (2003).

38. Opening of the inferior orbital fissure (spheno-maxillary) in the floor of the orbit:

- (0) wide, greater than that of the superior orbital fissure and optic foramen together;
- (1) regular, greater than that of the superior orbital fissure and optic foramen together with the formation of an bony canal at the base of the orbit cavity;

- (2) almost completely closed, of lesser extent than the optic foramen, covered bony canal.

The inferior orbital fissure is located at the base of the posterior wall of the orbital cavity and communicates with the pterygoid region. The degree of closing of this fissure in the Platyrrhini is almost total, through the extensions of the malar, alisphenoides and malar bones, leaving only a small orifice. In *Sapajus nigritus* and all the species of *Lagothrix* this opening is regular and greater than that of the superior orbital fissure and optic foramen together. *Ateles belzebuth*, *A. chamek* and *Brachyteles arachnoides* have a wide opening, while *Callicebus personatus* has an almost completely closed opening. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

39. Position of the malar-frontal suture in the external orbital wall:

- (0) at the supralateral angle of the orbit level;
(1) at mid height of the lateral wall of the orbit.

The anterior portions of the frontal and malar bones form the outer side wall of the orbit, with the frontal-malar suture located either at the superolateral angle or at mid-height of the lateral wall of the orbit. *Alouatta seniculus*, *Sapajus nigritus*, and *Callicebus personatus* present the character (0). This character was used in the phylogeny of Paredes (2003).

40. Projection of the rostrum and width of its anterior border:

- (0) projected and wide;
- (1) projected and narrow;
- (2) not projected and narrow.

The rostrum is the portion of the skull that begins at the lower edge of the orbits reaching the front edge of the maxilla. The projection of the rostrum, is the extension of this significant region in the profile of the face, and appears to be related by the extension of the premaxilla, maxilla and by the depth of the mandibular angle. The width of the anterior rostrum (at level of the incisors' row) seems to be related to the size of the canines (Herskovitz 1977). *Callicebus personatus* together with all the species of *Lagothrix* present a not projected and narrow rostrum, while *Ateles belzebuth*, *A. chamek*, *Brachyteles arachnoides*, *Sapajus nigritus*, and *Caipora* have a projected and narrow rostrum. *Alouatta seniculus* and *Cartelles* present the most projected and wide rostrum. This character was used in the phylogeny of Paredes (2003).

41. Shape of the nasal bones:

- (0) rectangular;
- (1) triangular, long;
- (2) triangular, short, base narrow;
- (3) triangular, short, base wide.

Alouatta seniculus, *Ateles belzebuth*, *A. chamek*, *Caipora* and *Cartelles* have rectangular and long nasals. On the other hand, *Lagothrix flavicauda*, *Brachyteles arachnoides*, and

Callicebus personatus have long triangular nasals, while *Lagothrix poeppigii*, *L. lugens*, and *Sapajus nigritus* have triangular nasals with the base narrow. Finally, *Lagothrix cana* and *L. lagotricha* present short triangular nasals with the base wide. This character was used in the phylogeny of Paredes (2003).

42. Profile of the palate roof at the second superior molar (posterior view):

- (0) vaulted, curved superiorly;
- (1) blunt, forming a plateau.

The profile of the mouth's roof can be "square", "arched", "gothic", etc. and thus it is affected by the position of the dental series and alveoli (HersHKovitz 1977). *Alouatta seniculus*, *Lagothrix cana*, *L. lagotricha*, *Sapajus nigritus*, and *Callicebus personatus* present the character (0). This character was used in the phylogeny of Paredes (2003).

43. Visibility and shape of the fenestra rotunda (lateral view):

- (0) partially exposed, covered by the lateral edge of the ectotympanic, oval or rounded;
- (1) exposed and rounded.

The fenestra rotunda is located in the middle ear, below the fenestra oval. The fenestra rotunda is partially exposed, covered by the lateral edge of the ectotympanic in all the species of *Lagothrix* (except *L. flavicauda*), *Brachyteles arachnoides*, *Sapajus nigritus*, and *Caipora*. *Cartelles coimbrafilhoi* was coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

44. Engrossment of the carotid canal:

- (0) engrossed, clear delimitation of carotid canal from cochlear promontory;
- (1) slightly engrossed;
- (2) not engrossed, no delimitation between carotid canal and cochlear promontory.

The carotid canal (lateral view) is present in the middle ear and is noticeable through the auditory meatus (mesotympanic cavity) (Hershkovitz 1977). This conduct is located immediately below the cochlear promontory, at the bottom of the mesotympanic cavity. The carotid artery runs through this canal (Ankel-Simons 2000). The conduct may or may not be engrossed, differentiating externally from the cochlear promontory. *Lagothrix flavicauda* and *Sapajus nigritus* present no engrossment and no delimitation between carotid canal and cochlear promontory. In *Lagothrix lugens*, *L. lagotricha*, *Brachyteles arachnoides*, and *Callicebus personatus* the carotid canal is slightly engrossed. In *Alouatta seniculus*, *Ateles belzebuth*, *A. chamek*, *Lagothrix cana*, and *L. poeppigii* this canal is engrossed, generating a clear delimitation of the carotid canal from the cochlear promontory. This character was used in the phylogeny of Paredes (2003).

45. Position of the distal part of the M2 in relation to the anterior edge of the maxillary-zygomatic suture:

- (0) before the suture;
- (1) after the suture.

Lagothrix flavicauda, *L. cana*, and *L. poeppigii* present the character (1).

46. Insertion of zygomatic arch, in lateral view:

- (0) level with M1;
- (1) level with distal border of M2 - mesial border of M3.

Sapajus nigritus and *Callicebus personatus* present the character (1).

47. Foramen magnum, orientation:

- (0) ventral;
- (1) caudal.

The spinal cord passes through the foramen magnum. The many other smaller foramina vary considerably in size and position among living primates and are widely used in systematics (Fleagle 2013). Only *Alouatta seniculus*, *Cartelles coimbrafilhoi*, and *Callicebus personatus* present this foramen magnum caudally orientated (1).

48. Anterior projection of premaxilla, in dorsal view:

- (0) does not project more than its lateral with;
- (1) projects anteriorly, longer than its lateral width.

Sapajus nigritus and *Callicebus personatus* present the character (1).

49. End of hard palate:

- (0) posterior to M3;
- (1) level with M3;

(2) level with M2.

The hard palate is a thin horizontal bony plate of the skull, located in the roof of the mouth. It is formed by the palatine process of the maxilla and horizontal plate of palatine bone, and spans the arch formed by the upper teeth. Only in *Alouatta seniculus* and *Sapajus nigritus* the hard palate ends posteriorly to M3.

50. Lambdoid crest in males:

(0) present;

(1) absent.

The lambdoid crest is formed by the suture of the parietals and the occipital (basioccipital), seeming as an osseous extension of the skull. They are much more frequent in males and its main function is to provide for insertion surface for the masticatory muscles. In *Sapajus*, the sagittal crest is used as a diagnostic character to differentiate species (HersHKovitz 1977). This crest is only present in *Alouatta seniculus*, *Lagothrix cana*, *L. lagotricha*, and *Sapajus nigritus*. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the lack of certainty about the sex of the specimens.

3.5.3. Mandibular characters

51. Dimensions of the ascending ramus of the mandible:

(0) regular width and length;

- (1) narrow and regular length;
- (2) wide and long.

The elements of the mandible have been described by Hartwig et al. (1996) as variable characters within atelids. Herskovitz (1977) stated that the ascending ramus of the mandible of Platyrrhini shows a wide range of variations, closely related to the differences in the diet. *Alouatta seniculus*, *Lagothrix flavicauda*, and *Brachyteles arachnoides* present a wide and long ascending ramus. *Callicebus personatus* and the remaining species of *Lagothrix* present a narrow ascending ramus with regular length. *Ateles belzebuth*, *A. chamek*, and *Sapajus nigritus* present an ascending ramus with regular width and length. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status. This character was used in the phylogeny of Paredes (2003).

52. Relative height of coronoid process:

- (0) level with condylar;
- (1) lower than condylar;
- (2) higher than condylar.

In *Ateles belzebuth*, *A. chamek*, and all the species of *Lagothrix* present a relative height of coronoid process at the same level with condylar process. In *Alouatta seniculus* this is lower than the condylar process, while in *Sapajus nigritus* and *Callicebus personatus* is higher. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

53. Relative depth of the mandibular angle:

- (0) shallow;
- (1) regular;
- (2) deep.

The mandibular angle is formed by the union of the ascending and horizontal mandibular ramus. This angle provides the insertion surface for the masticatory muscles: the anterior and posterior temporalis. The evolution of the mandibular morphology includes the extension, the rounding of the edges and the thickening of the mandibular angle (Ankel-Simons 2000). *Lagothrix flavicauda* and *Sapajus nigritus* present a shallow relative depth of the mandibular angle, while *Ateles belzebuth*, *A. chamek*, *Lagothrix cana*, *L. poeppigii*, *L. lugens*, *L. lagotricha*, *Caipora*, and *Callicebus personatus* present a regular angle. Only *Alouatta seniculus* and *Brachyteles arachnoides* present a deep mandibular angle. *Cartelles coimbrafilhoi* was coded as "?" due to the lack of this structure.

54. Form of the mandibular arch at symphysis point:

- (0) narrow and angular;
- (1) blunt, not angular.

Alouatta seniculus, *Ateles belzebuth*, *A. chamek*, *Lagothrix flavicauda*, *Brachyteles arachnoides*, *Cartelles*, *Caipora*, and *Callicebus personatus* present the character (0).

55. Mandibular tooththrow, orientation in dorsal view:

- (0) parallel;

(1) posteriorly divergent.

Sapajus nigrinus and *Callicebus personatus* present the character (1). *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

3.5.4. Dental characters

56. Shape of I1 (occlusal view):

(0) spatular shape, wide medially, short and robust;

(1) spatular shape, long and narrow medially.

Alouatta seniculus, *Lagothrix poeppigii*, *L. lugens*, *L. lagotricha*, and *Callicebus personatus* present the character (1). This character was used in the phylogeny of Hartwig et al. (1996).

57. Size of P2, relative to P3 and P4:

(0) P2 smallest;

(1) P2 not the smallest.

Sapajus nigrinus and *Callicebus personatus* present the character (0). This character was used in Horovitz (1999)

58. P2, presence of metaconid:

(0) absent;

(1) present.

The absence of the metaconid in atelids is constant. This metaconid was only present in *Sapajus nigritus* and *Callicebus personatus*. *Cartelles coimbrafilhoi* was coded as "?" due to the impossibility to code it.

59. Diastema between P2 and C:

(0) absent;

(1) present.

This diastema is present in all the analyzed taxa with the exception of *Sapajus nigritus* and *Callicebus personatus*.

60. M1, mesostyle in buccal aspect:

(0) absent;

(1) present and reduced;

(2) present and developed.

The cingulate elements, buccal or lingual are abundant in Platyrrhini; however, in Atelidae (except for *Brachyteles* and *Alouatta*) are scarce (Kinzey 1973). *Alouatta seniculus* and *Lagothrix lugens* presents a well-developed mesostyle. In *Lagothrix cana*, *L. poeppigii*, *Brachyteles arachnoides*, and *Callicebus personatus* present this mesostyle but it is reduced. *Ateles chamek*, *Lagothrix favicauda*, *L. lagotricha*, *Sapajus*

nigritus and *Caipora* do not present mesostyle. *Ateles belzebuth* was codified as “?” due to the damages in biological material. In *Cartelles* this character was impossible to codify. This character was used in the phylogeny of Horovitz (1999).

61. M1, lingual cingulum:

(0) absent;

(1) present.

A cingulum is an enamel belt around the tooth's cusps; this is only present in the M1 of *Alouatta seniculus* and *Callicebus personatus*. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

62. M2, Relative size of metacone:

(0) highly developed;

(1) reduced relative to the paracone.

The metacone is one of 4 cusps of the upper molars, located in the buccal distal portion of the dental element. The development of this cuspid has been analyzed by other authors. Rosenberger (1981) notes that *Ateles* and *Brachyteles* share a strong metacone reduction of the upper molars and Ford (character UM5, 1986) indicates that *Lagothrix* shows a less degree of metacone reduction than *Ateles* and *Brachyteles*. *Alouatta seniculus*, *Cartelles coimbrafilhoi* and *Callicebus personatus* present the character (0).

63. M3 shape:

- (0) longer mesiodistally than bucolingually;
- (1) approximately as long as wide.

All the species of *Lagothrix*, *Ateles belzebuth*, *A. chamek*, *Sapajus nigritus* and *Caipora* present the character (1).

64. M3, size relative to P2:

- (0) subequal;
- (1) smaller.

Ateles belzebuth, *A. chamek*, and *Sapajus nigritus* present the character (1). *Cartelles coimbrafilhoi* was coded as "?" due to the impossibility to verify their status.

3.5.5. Postcranial characters

65. Fully developed pollex:

- (0) absent;
- (1) present.

Ateles belzebuth, *A. chamek*, and *Caipora bambuorum* present the character (0). *Brachyteles arachnoides*, was codified as (0,1) due to the presence of a fully-developed pollex in some individuals.

66. Type of locomotion:

- (0) semi-brachiator;
- (1) arboreal quadrupedalism.

Arboreal quadrupedalism is more suitable for movement on a continuous network of branches and is probably less hazardous than leaping, especially for larger species (Fleagle 2013). While suspensory behavior allows larger species to spread their weight among small supports and also to avoid the problem of balancing their body above a support. *Ateles belzebuth*, *Ateles chamek*, *Brachyteles arachnoides*, and *Caipora* present the character (0). According to Halenar (2011), *Cartelles coimbrafilhoi* would have presented both types of locomotion, for this reason this species was codified as (0, 1).

67. Intermembral index:

- (0) < 0.85;
- (1) > 0.95;
- (2) > 1.0.

The intermembral index describes the body proportions of the different primate species, and is particularly informative in phylogenetic analyses (Ford 1986; Horovitz and Meyer 1997). This index is correlated with the type of locomotion and it is easily calculated as follows:

$$\text{Intermembral index} = \frac{\text{Humerus length} + \text{radius length}}{\text{Femur length} + \text{tibia length}} \times 100$$

In general, leapers have a low intermembral index (longer hindlimbs), suspensory species have a high intermembral index (longer forelimbs), and quadrupedal species have intermediate indices (forelimbs and hindlimbs similar in size) (Fleagle 2013). *Callicebus personatus* and *Sapajus nigritus* have an intermembral index lower than 0.85, while in *Alouatta seniculus*, *Lagothrix flavicauda*, *L. cana*, *L. poeppigii*, *L. lugens*, and *L. lagotricha* is higher than 0.95 but lower than 1.0. *Ateles belzebuth*, *A. chamek*, *Brachyteles arachnoides*, *Cartelles*, and *Caipora* present an intermembral index higher than 1.0.

68. Hypertrophy of the hyoid bone in males:

(0) absent;

(1) present.

The hyoid bone is a small bone suspended in the throat beneath the mandible, in some Platyrrhini species this bone is expanded into a very large, hollow resonating chamber (Fleagle 2013). *Alouatta seniculus* and *Callicebus personatus* present the character (1). *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

69. Entepicondylar foramen of the humerus:

(0) absent;

(1) present.

Character mentioned by Rosenberger and Coimbra-Filho (1984), used also by Ford (1986) in her phylogenetic analysis (character PC104). *Sapajus nigritus* and *Callicebus personatus* present the entepicondylar foramen (character state 1).

70. Lumbar vertebrae: (Horovitz 1999)

- (0) more than 5;
- (1) 5 or fewer.

This character is used as was codified by Horovitz (1999). *Sapajus nigritus* and *Callicebus personatus* present the character (1). *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

71. Body mass in males:

- (0) < 4000g;
- (1) > 5000g.

Sapajus nigritus and *Callicebus personatus* present the character (0).

3.5.6. Cerebral characters

72. Sulcal patterns of the brain: confluence of Sylvian and intraparietal sulci

- (0) Sylvian and intraparietal sulci discrete
- (1) Sylvian and intraparietal sulci confluent

This brain character is based on Falk (1979, 1980) and in its subsequent use in the phylogeny of Ford (1986). According to Falk (1980), this character may be related to the presence of prehensile tail. *Sapajus nigritus* and *Callicebus* present the character (0). *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

73. Visibility of occipitotemporal sulcus, in lateral view

(0) not visible

(1) visible

Alouatta seniculus, *Sapajus nigritus*, and *Callicebus personatus* present the character (0). *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

74. Expansion of the paraflocculi of the cerebellum

(0) not expanded

(1) expanded

Alouatta seniculus and *Sapajus nigritus* present the character (0). *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

3.5.7. Karyotypical characters

75. 2n chromosomal number:

- (0) 34;
- (1) 40;
- (2) 44;
- (3) 54;
- (4) 62.

There is great karyological variability in Platyrrhini with chromosome numbers ranging from 16 (titi monkey) to 62 (woolly monkey), most species of this group have been subject of classical chromosome banding analyses for several decades (de Oliveira et al. 2012). All the species of *Lagothrix* and *Brachyteles arachnoides* have a **2n=62** (Egozcue and Perkins, 1970; De Boer 1974; Koiffmann and Saldanha 1974, 1978; Viegas-Péquignot et al. 1985; de Oliveira et al. 2005); **2n=54** for *Sapajus nigritus* (Amaral et al. 2008); 2n=44 for *Callicebus personatus* (Rodrigues et al., 2004); **2n=40** for *Alouatta seniculus* (Romagno 2014); and, **2n=34** for *Ateles belzebuth* and *A. chamek* (Medeiros et al. 1997).

3.5.8. Ecological characters

76. Social organization

- (0) monogamy
- (1) multimale-multifemale groups
- (2) fission-fusion

Callicebus personatus, as all the species of *Callicebus*, present a monogamous social organization, while *Alouatta seniculus* and *Sapajus nigrinus* present multimale-multifemale groups. All the remaining taxa present fission-fusion groups. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

77. Male dominance:

(0) absent;

(1) present.

The composition of primate social groups differs considerably, however, from species to species. Several distinct types of group are particularly common in Platyrrhines: pair group, one-male groups (polygynous), single reproducing female and several sexually active males (polyandrous groups), several reproductively active adult males and females (polygynandrous groups) (Fleagle 2013). Only *Alouatta seniculus* and *Sapajus nigrinus* present a one-male group social structure. *Cartelles coimbrafilhoi* and *Caipora bambuorum* were coded as "?" due to the impossibility to verify their status.

The parsimony analysis resulted in four most parsimonious trees (CI = 0.563, RI = 0.553 each) with 201 step. The strict consensus resulted in a tree with 206 steps, a Consistency Index (CI) = 0.551, and a Retention Index (RI) = 0.533 (Fig. 55).

The family Atelidae was supported by 13 synapomorphies, and had a Bremer

support of 4, the second highest value in the phylogeny. The Atelinae clade was supported by six characters, while the Alouattinae by three. The extinct *Caipora bambuorum* was found to be an Atelinae, and *Cartelles coimbrafilhoi* an Alouattinae. The topology recovers a sister group relationship between *Ateles* and *Lagothrix*, this being the first study based in discrete morphological characters to recover such topology.

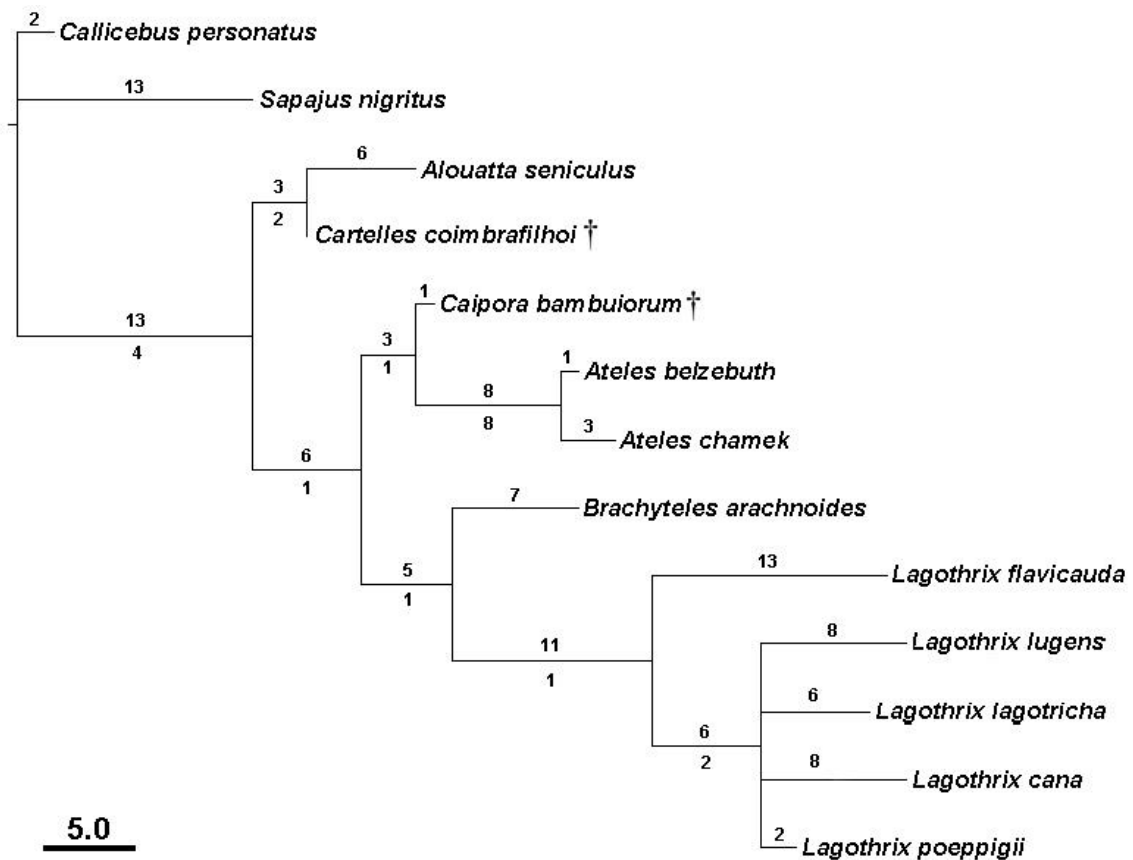


Figure 56. Strict consensus diagram of the four most parsimonious trees obtained from the analysis of the 77 characters (CI = 0.553, RI = 0.533, length = 206 steps). The numbers above and below the branches show the length of each branch (i.e. number of autapomorphic characters supporting them) and the Bremer support values, respectively. † = fossil taxa.

The *Brachyteles* + *Lagothrix* clade corroborates previous molecular findings (Lemos de Sá et al. 1990, da Fonseca et al. 1991, Lemos de Sá and Glander 1993, Schneider et al. 1993, Harada et al. 1995, Horovitz and Meyer 1995, Schneider et al. 1996, Meireles et al. 1999, Von Dornum and Ruvolo 1999).

Contrastingly, most morphological studies propose a closer phylogenetic relationship between *Ateles* and *Brachyteles* based on similarity in craniodental morphometry, locomotor behavior and postcranial adaptations as advanced brachiators (Cole 1995; Hartwig 1993; Rosenberger 1984; Rosenberger and Strier 1989). My phylogenetic analyses found no support for an *Ateles* + *Brachyteles* clade and, accordingly, I agree with the general cranial resemblances between *Brachyteles* and *Lagothrix* described by Rosenberger et al. (2008), which are the moderately large skulls, broad faces and braincases that are less rounded in shape than in *Ateles*.

It seems to be that this semi-brachiator locomotor behavior appeared more than once in the ateline evolutionary history. The postcranial evidence points out that *Cartelles*, which is closely related to *Alouatta* (Halénar and Rosenberger 2013), could have presented this highly suspensory locomotion as *Ateles*, *Brachyteles*, and *Caipora*. The question is whether this suspensory locomotion evolved independently in Alouattines, as *Cartelles*, and also in Atelines, as *Brachyteles*, and *Ateles* + *Caipora*, or if this was a primitive condition of the proto-atelid model that was lost in some genera as *Alouatta* and *Lagothrix*.

I found plausible the hypothesis that postcranial adaptations in *Ateles* and *Brachyteles* would be homoplastic (Jones 2008, Bjarnason et al. 2015), evolving independently in these two genera. This hypothesis would explain the presence of

suspensory postcranial resemblance in only these two genera but does not in the remaining atelid genera. The presence of these suspensory postcranial elements in fossils as *Caipora* and *Cartelles* would make less probable that this feature is homoplastic evolving, at least, three independent times in atelids. For this reason, I propose that a more parsimonious view would be to assume that the suspensory locomotion in atelids is plesiomorphic and was lost in *Alouatta* and *Lagothrix*. With the discovery of more atelid fossils that include postcranial material this hypothesis will be refuted or verified.

4. CONCLUSIONS

- *Brachyteles* does not present sexual dimorphism or dichromatism;
- *Brachyteles* shows a considerable variation in pelage coloration; this variation does not correspond to any geographical pattern;
- The presence or absence of the thumb and the facial pigmentation show a high individual variation. Thus, these characters have no taxonomic relevance;
- The morphological evidence supports the recognition of only one *Brachyteles*' species;
- Atelidae and Atelinae are monophyletic groups, well supported by morphological characters;
- Based on morphological characters *Cartelles coimbrafilhoi* and *Caipora bambuorum*, are members of alouattinae and atelinae, respectively.
- Within Atelinae, *Brachyteles* is closely related to *Lagothrix* based mainly on cranial and tegumentary characters;
- The postcranial resemblance between *Ateles* and *Brachyteles* would be a plesiomorphic condition in Atelidae, and the arboreal quadrupedalism exhibit in *Alouatta* and *Lagothrix* evolved convergently in alouattines and atelines.

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Appendix 1 – Landmark definitions

Dorsal view:

1. Prosthion: antero-inferior point on projection of pre-maxilla between central incisors.
2. Nasospinale: inferior-most midline point of piriform aperture.
3. Anterior-most point of canine alveolus.
4. Rhinion: most anterior midline point on nasals.
5. Meeting point of nasal and pre-maxilla on margin of piriform aperture.
6. Nasion: midline point on fronto-nasal suture.
7. Zygo-max superior: antero-superior point of zygomaticomaxillary suture taken at orbit rim.
8. Supraorbital notch.
9. Frontomalare orbitale: where frontozygomatic suture crosses inner orbital rim.
10. Frontomalare temporale: where frontozygomatic suture crosses lateral edge of zygoma.
11. Posterior-most point on curvature of anterior margin of zygomatic process of temporal bone.
12. Posterior-most point of zygomatic process of temporal bone.
13. Bregma: junction of coronal and sagittal sutures.
14. Lambda: junction of sagittal and lamboid sutures.

Frontal view:

1. Prosthion: antero-inferior point on projection of pre-maxilla between central incisors.
2. Nasospinale: inferior-most midline point of piriform aperture.
3. Anterior-most point of canine alveolus.
4. Meeting point of nasal and pre-maxilla on margin of piriform aperture.
5. Rhinion: most anterior midline point on nasals.
6. Nasion: midline point on fronto-nasal suture.
7. Zygo-max superior: antero-superior point of zygomaticomaxillary suture taken at orbit rim.
8. Frontomolare orbitale: where frontozygomatic suture crosses inner orbital rim.
9. Frontomolare temporale: where frontozygomatic suture crosses lateral edge of zygoma.
10. Bregma: junction of coronal and sagittal sutures.
11. Zygo-max inferior: antero-inferior point of zygomaticomaxillary suture.
12. Lateral midpoint onto alveolar margin of M3.

Lateral view:

1. Prosthion: antero-inferior point on projection of pre-maxilla between central incisors.
2. Anterior-most point of canine alveolus.
3. Mesial P3: most mesial point on P3 alveolus, projected onto alveolar margin.
4. Contact point between adjacent P4/M1, projected labially onto alveolar margin.
5. Contact point between adjacent M1/M2, projected labially onto alveolar margin.
6. Contact point between adjacent M2/M3, projected labially onto alveolar margin.
7. Posterior midpoint onto alveolar margin of M3.
8. Anterior tip of the external auditory meatus.
9. Posterior-most point of zygomatic process of temporal bone.
10. Posterior tip of the external auditory meatus.
11. Lambda: junction of sagittal and lamboid sutures.
12. Bregma: junction of coronal and sagittal sutures.
13. Glabella: most forward projecting midline point of frontals at the level of the supraorbital ridges.
14. Nasion: midline point on fronto-nasal suture.
15. Rhinion: most anterior midline point on nasals.
16. Frontomolare orbitale: where frontozygomatic suture crosses inner orbital rim.
17. Zygo-max superior: antero-superior point of zygomaticomaxillary suture taken at orbit rim.

Appendix 2 - Biological Material

***Alouatta fusca*: BRAZIL. ESPÍRITO SANTO: Pau Gigante: MZUSP 2209; Rio Doce: MZUSP 2208. PARANÁ: Castro: MZUSP 2464; Porto Camargo: MZUSP 7711. SANTA CATARINA: Corupá: MZUSP 426, 430, 579; Jacinto Machado: MZUSP 11190; Joinville: MZUSP 1669, 1670, 1671, 1672, 1687; Praia Grande: MZUSP 11181, 11182. SÃO PAULO: Anhembi: MZUSP 8464, 8466, 8907; Apiaí: MZUSP 2442; Embu: MZUSP 19532; Lins: MZUSP 5899, 5900; Pinheiros: MZUSP 317; Paranapiacaba: MZUSP 407, 408, 412; São Paulo: MZUSP 314, 2346, 6737; Serra da Cantareira: MZUSP 5864, 5868, 6487.**

***Alouatta seniculus*: PERU. CAJAMARCA: Namballe: MUSM 9436. HUÁNUCO: Pachitea River: MUSM 33. LORETO: Yaquerana: MUSM 11108; Samiria River: MUSM 1853. MADRE DE DIOS: MUSM 15552; Castañal: MUSM 15555, 15556; Loero: MUSM 15574; Jorge Chavez: MUSM 15570, 15568. UCAYALI: MUSM 34; kilometer 207 road to Pucallpa: MUSM 32.**

***Ateles belzebuth*: PERU. LORETO: Iquitos: MUSM 40, 23117.**

***Ateles chamek*: PERU. LORETO: Yaquerana: MUSM 11109, 11110. MADRE DE DIOS: Las Piedras River: MUSM 49, 50; Parque Nacional del Manu: MUSM 47. UCAYALI: MUSM 35.**

***Ateles marginatus*: BRAZIL. PARÁ: Taperinha: MZUSP 3565.**

***Ateles paniscus*: BRAZIL. PARÁ: Cachimbo: MZUSP 8070; Caxiricatuba:**

MZUSP 5281, 5282, 5284, 5605; **Foz do Curuá-Uma:** MZUSP 5288, 5600; **Fordlandia:** MZUSP 10158, 19313, 19317, 19318, 19319, 19320, 19322, 19323, 19324, 19325, 19327, 19329, 19330; **Obidos:** MZUSP 3641; **Piquiatuba:** MZUSP 5279, 5286, 5606; **Rio Amazonas:** MZUSP 5277, 5278; **Santarém:** MZUSP 19328; **Tapaiuna:** MZUSP 10159.

Caipora bambuiorum: **BRAZIL. BAHIA: Toca da Boa Vista:** MCL 05.

Callicebus personatus: **Brazil. ESPÍRITO SANTO: Colatina:** MZUSP 2221, 2224, 2225, 2226, 2227; **Rio Doce:** MZUSP 2411, 2412, 2413; **Sooretama:** MZUSP 11152, 11164, 11713, 11805. **MINAS GERAIS: Teófilo Otoni:** MZUSP 2712, 2713; **Baixo Rio Suaçuí:** MZUSP 5931, 5932.

Cartelles coimbrafilhoi: **BRAZIL. BAHIA: Toca da Boa Vista:** MCL 06.

Lagothrix cana: **PERU. CUSCO: Paucartambo:** MUSM 15908. **PASCO: Cerro Chontiya:** MUSM 10379, 10380, 10381; **Cerro Jonatan:** MUSM 10382; **Cacazu River:** MUSM 5847. 1959.

Lagothrix flavicauda: **PERU. AMAZONAS: Alva:** MUSM 41, 42, 43, 45; **La Roca:** MUSM 1300; **Santiago River:** MUSM 5356. **SAN MARTIN: García, road to Pedro Ruiz:** MUSM 52; **Parque Nacional Río Abiseo:** MUSM 59. **WITHOUT LOCALITY:** MUSM 1857, 1858, 1942, 2005, 5070, 5133, 9391.

Lagothrix lagotricha: **Brazil. AMAZONAS: Rio Juruá:** MZUSP 692, 805,

806, 917, 1183; **Igarapé Grande:** MZUSP 5533, 5536; **Rio Negro:** MZUSP 19674.

Lagothrix poeppigii: **PERU. LORETO: Cerros de Contamana:** MUSM 1859, 1860; **Requena-Yaquerana Galvez River:** MUSM 11122, 11123, 11124; **Cocha Coconilla:** MUSM 17557. **MADRE DE DIOS: Inambari River:** MUSM 51. **UCAYALI: Cerros de Orellana:** MUSM 687, 688; **Coronel Portillo:** MUSM 18108, 18110, 18111.

Sapajus nigrinus: **BRAZIL. SÃO PAULO: Alto da Serra:** MZUSP 400; **Bauru:** MZUSP 491; **Itararé:** MZUSP 1155.

Appendix 3 – Matrix of characters

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
<i>Alouatta seniculus</i>	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	1	0	-	0	0	0	0	0	0	0	2	0	0	0	0	0	-	0	2	2
<i>Ateles belzebuth</i>	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	0	1	0	0	0	0	1	1	0	0	1	1	0	0	1	0	1	1	1	1	0	1	0
<i>Ateles chamek</i>	0	0	0	2	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	1	1	0	2	1	0	1	1	1	1	0	1	0
<i>Lagothrix flavicauda</i>	1	1	1	1	2	1	1	1	1	0	0	1	1	1	1	1	0	1	2	1	1	1	1	1	1	1	0	1	1	0	2	0	1	0	0	1	0	1
<i>Lagothrix cana</i>	1	1	1	1	2	1	1	1	0	2	0	0	1	1	0	0	3	0	1	1	0	0	0	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1
<i>Lagothrix poeppigii</i>	1	1	1	1	2	1	1	1	0	0	2	0	1	1	0	0	2	0	1	1	0	0	0	1	0	1	1	0	0	0	2	0	0	0	0	1	0	1
<i>Lagothrix lugens</i>	1	1	1	1	2	2	0	1	0	0	1	0	1	1	0	1	3	0	1	1	0	0	2	1	0	1	1	0	0	0	1	0	1	0	0	2	0	1
<i>Lagothrix lagotricha</i>	1	1	1	1	2	3	1	1	0	1	2	0	1	1	0	0	2	0	1	1	0	0	0	1	0	1	1	0	0	0	2	0	0	0	0	1	0	1
<i>Brachyteles arachnoides</i>	1	1	1	2	1	0	0	[01]	0	2	1	0	1	0	2	2	2	2	1	0	0	0	0	1	1	0	0	1	0	1	0	1	1	0	0	1	1	0
<i>Cebus nigritus</i>	1	1	1	2	0	1	1	1	0	1	0	1	0	-	1	1	2	0	1	1	1	0	1	1	1	0	0	1	0	1	1	0	0	1	1	0	1	1
<i>Cartelles coimbrafilhoi</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	0	?	?	?	?	1	0	0	0	0	?	?	?	?	1	0	?	1	?
<i>Caipora bambuorum</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	0	?	?	1	?	1	0	1	1	0	0	?	1	?	1	0	?	1	?
<i>Callicebus personatus</i>	0	0	1	2	3	1	1	1	0	0	0	0	0	-	0	0	2	0	0	0	1	0	0	0	1	1	0	1	0	0	2	0	2	1	1	0	0	2

Taxa	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
<i>Alouatta seniculus</i>	0	0	0	0	1	0	0	1	1	1	0	0	2	1	2	0	0	1	1	0	1	0	1	0	0	0	1	1	1	1	0	1	1	1	0	0	1	1	1
<i>Ateles belzebuth</i>	1	1	0	1	1	0	0	1	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	1	1	1	0	0	2	0	0	2	1	1	1	1	0	2	0
<i>Ateles chamek</i>	1	1	0	1	1	0	0	1	0	1	1	1	0	0	1	0	0	0	1	0	1	0	0	1	1	1	0	0	2	0	0	2	1	1	1	1	0	2	0
<i>Lagothrix flavicauda</i>	2	2	0	1	2	2	1	?	0	1	?	1	2	-	0	0	0	0	1	0	1	0	0	1	?	?	1	1	1	0	0	2	1	1	1	1	4	2	0
<i>Lagothrix cana</i>	2	3	1	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	1	0	1	1	0	1	1	0	1	1	1	0	0	2	1	1	1	1	4	2	0
<i>Lagothrix poeppigii</i>	2	2	1	1	0	0	1	1	0	1	1	1	1	0	1	1	0	1	1	0	1	1	0	1	1	0	1	1	1	0	0	2	1	1	1	1	4	2	0
<i>Lagothrix lugens</i>	2	2	1	1	0	1	0	1	0	1	1	1	1	0	1	1	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	2	1	1	1	1	4	2	0
<i>Lagothrix lagotricha</i>	2	3	1	0	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	2	1	1	1	1	4	2	0
<i>Brachyteles arachnoides</i>	1	1	1	1	0	1	0	1	0	1	1	1	2	0	2	0	0	0	1	0	1	2	0	1	0	0	[01]	0	2	0	0	2	1	1	1	1	4	2	0
<i>Cebus nigritus</i>	0	1	2	0	0	2	0	0	0	0	0	0	0	2	0	1	1	0	0	1	0	0	?	1	1	1	1	1	0	0	1	0	0	0	0	0	3	1	1
<i>Cartelles coimbrafilhoi</i>	1	0	0	1	?	?	0	1	1	1	1	?	?	?	?	1	?	0	1	?	1	?	?	0	0	?	1	0	?	1	0	?	1	?	?	?	?	?	?
<i>Caipora bambuorum</i>	1	1	1	1	0	?	0	1	0	1	1	?	?	?	2	0	?	0	1	0	1	0	0	1	1	0	0	0	2	0	0	?	1	?	?	?	?	?	?
<i>Callicebus personatus</i>	0	2	1	0	1	1	0	0	1	0	1	1	1	2	1	0	1	1	0	1	0	1	1	0	0	0	1	1	0	1	1	0	0	0	0	1	2	0	0