



JOSÉ EDUARDO
SERRANO VILLAVICENCIO

**Ecomorphological comparison of *Alouatta*,
Callicebus, and *Cebus* species inhabiting
the Amazonian and Atlantic Forests**

Comparação ecomorfológica das espécies de *Alouatta*,
Callicebus e *Cebus* habitando as florestas Amazônica e
Atlântica

Single Volume

SÃO PAULO

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Thesis submitted to the Graduate Program
of the Museu de Zoologia da Universidade
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requirements for the degree of Doctor of
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Biodiversity).

Advisor: Prof. Dr. Alexandre R. Percequillo

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Para Mariana

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“We are not enemies, but friends. We must not be enemies. Though passion may have strained, it must not break our bonds of affection. The mystic chords of memory will swell when again touched, as surely they will be, by the better angels of our nature”

Abraham Lincoln

RESUMO

A diversidade morfológica é resultado de um processo complexo que envolve interações filogenéticas e ecológicas, sendo a importância relativa de cada um desses fatores dinâmica e variável ao longo do processo evolutivo. Identificando padrões de diversificação morfológica e compreendendo suas causas e efeitos são passos fundamentais para estudos de especiação, evolução e macroecologia. Nesse cenário, utilizei três gêneros de primatas neotropicais pertencentes a três radiações evolutivas diferentes, *Alouatta* (Atelidae), *Cebus* (Cebidae) e *Callicebus* (Pitheciidae), como modelo para explorar a evolução morfológica desse grupo de mamíferos. O objetivo principal foi revelar os padrões da diversidade morfológica presente nesses gêneros de primatas amplamente distribuídos no continente americano, e relacioná-los através de uma abordagem integrada, com fatores ecológicos e filogenéticos. Para tanto, avaliei o material desses três gêneros mantido no Museu de Zoologia da Universidade de São Paulo, São Paulo, Brasil. No total, digitalizei 758 crânios de adultos de *Alouatta* (284), *Callicebus* (188) e *Cebus* (286) em vistas dorsal, frontal e lateral. Obtive as informações filogenéticas de bases de dados online e solicitando diretamente aos autores das revisões sistemáticas mais recentes. Eu extraí 19 variáveis bioclimáticas para cada localidade utilizando o pacote Raster no R. Gerei os dados morfogeométricos digitalizando pontos de referência cranianos em três vistas diferentes, dorsal (12), frontal (12) e lateral (17). Finalmente, para calcular a correlação entre variáveis climáticas e geográficas, realizei Análise de Mínimos Quadrados Parciais de Dois Blocos Separados (PLS) em tamanho e forma. Meus resultados principais em relação ao tamanho apontaram que: (1) as espécies amazônicas de *Alouatta* e *Cebus* são maiores que seus coespecíficos da Mata Atlântica, o contrário de *Callicebus*; (2) há um sinal filogenético significativo no tamanho craniano de *Callicebus*; (3) *Callicebus* é o gênero menos sexualmente dimórfico entre os três gêneros; (4) o efeito alométrico em *Callicebus*, porcentagem do tamanho explicando a forma, é insignificante; (5) diferentemente de *Alouatta* e *Cebus*, o PLS apresentou correlação significativa entre tamanho e clima e geografia apenas no caso de *Callicebus*. Em relação à forma, os resultados mais relevantes foram: (1) a alometria influenciou significativamente a forma em *Alouatta* e *Cebus*, não em *Callicebus*; (2) Embora o coeficiente RV tenha apresentado uma correlação total menor entre os blocos do PLS em *Callicebus* do que em *Alouatta* e *Cebus*, sua correlação ainda é

significativa. Diante desses resultados, posso assegurar que, embora sejam sintópicos na maioria de suas distribuições, o clima e a geografia influenciaram diretamente, mas de forma diferente, esses três gêneros. Na maioria dos casos, *Alouatta* e *Cebus* responderam de forma semelhante à influência de variáveis abióticas o que pode sugerir um processo semelhante de diversificação, levando adiante os processos de expansão e contração da Amazônia e da Mata Atlântica para colonizar novas ecorregiões, contrastando com *Callicebus* para qual uma série de eventos vicariantes têm sido propostos como principal caminho de diversificação.

Palavras-chave: "*Callicebus*". "Amazônia". "*Cebus*". "Floresta Atlântica". "*Alouatta*". "Ecomorfologia".]

ABSTRACT

Morphological diversity is the result of a complex process that involves phylogenetic and ecological interactions, being the relative importance of each one of these factors dynamic and variable throughout the evolutionary process. Identifying patterns of morphological diversification and understanding its causes and effects are fundamental steps for studies of speciation, evolution and macroecology. In this scenario, I used three neotropical primate genera belonging to different evolutive radiations, *Alouatta* (Atelidae), *Cebus* (Cebidae), and *Callicebus* (Pitheciidae), as a model to explore the morphological evolution of this group of mammals. The main objective of this work was to reveal the patterns of morphological diversification present in these genera of primates widely distributed in the American continent, and to relate them through an integrated approach, with ecological and phylogenetic factors. For this purpose, I evaluated the material of these three genera held at the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil. In total, I digitized 758 adult skulls of *Alouatta* (284), *Callicebus* (188), and *Cebus* (286) in dorsal, frontal, and lateral views. I obtained the phylogenetic information from online databases and by requesting directly to the authors of the most recent systematic reviews. I extracted 19 bioclimatic variables for each locality using the Raster package in R. I generated the morpho-geometric data by digitizing cranial landmarks in three different views, dorsal (12), frontal (12), and lateral (17). Finally, to calculate the correlation among climatic and geographical variables I performed a Two Separate Blocks Partial Least Square (PLS) Analysis on size and shape. My main results regarding size pointed out that: (1) Amazonian species of *Alouatta* and *Cebus* are bigger than their conspecifics from the Atlantic Forest, the opposite case of *Callicebus*; (2) there is a significant phylogenetic signal on cranial size of *Callicebus*; (3) *Callicebus* is the least sexually dimorphic genus among the three genera; (4) the allometric effect in *Callicebus*, percentage of size explaining shape, is negligible; (5) differently from *Alouatta* and *Cebus*, the PLS showed a significant correlation between size and climatic and geographical only in the case of *Callicebus*. In regards of shape, the most relevant results were: (1) allometry influenced significantly shape in *Alouatta* and *Cebus*, not in *Callicebus*; (2) Although the RV coefficient showed a lower total correlation between blocks of the PLS in *Callicebus* than in *Alouatta* and *Cebus*, its correlation is still significant. In view of these results, I can assure that, although being syntopic in most of their

distributions, climatic and geographical have influenced directly but differently these three genera. In most cases, *Alouatta* and *Cebus* have responded similarly to the influence of abiotic variables what might suggest a similar process of diversification, taking advantage of the processes of expansion and contraction of the Amazonia and the Atlantic Forest to colonize new ecoregions, contrastingly to *Callicebus* for which a series of vicariant events have been proposed as mainly path of diversification.

Keywords: *“Callicebus”*.*“Amazônia”*.*“Cebus”*.*“Floresta Atlântica”*.*“Alouatta”*.*“Ecomorfologia”*.

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1. INTRODUCTION

Morphological diversity is the result of a complex process involving both phylogenetic and ecological interactions (Alberch, 1982; Thorpe, 1987; Schlichting e Smith, 2002). Ecological factors include abiotic, as climate, and biotic variables, such as diet. Phylogenetic determinants, on the other hand, are related to ancestry, that is, species that share the same common ancestor tend to be more similar when compared to distant lineages (Felsenstein, 1985). The relative importance of each of these factors in the final phenotypic expression is dynamic and variable throughout the evolutionary process (Mayr, 1956; Thorpe, 1987; Dunson and Travis, 1991; Benton, 2009).

Identifying patterns of morphological diversification and understanding causes and effects are fundamental steps for studies of speciation, evolution and macroecology (Mayr, 1956; Gould and Johnston, 1972; Gaston and Blackburn, 1996; Orme et al., 2006). The understanding of the ecological processes that shape the morphological variation is one of the growing aspects of evolutionary ecology, called ecomorphology (Bock, 1994). Ecological morphology or ecomorphology provides one method of investigating the relationship between the phenotype of an organism and its environment (Van der Klaauw, 1948). One important approach of the ecomorphology is to make ecological inferences about species from their phenotypes (often morphology) and use these in further studies related to guild structure (Lewis, 1997; Werdelin and Lewis, 2001; Van Valkenburgh, 1985, 1988).

Geometric morphometrics has emerged as an effective tool capable of exploring, analyzing, and testing differences in the shape of organisms in a taxonomic, evolutionary and ecomorphological approach (Adams et al., 2013; Lawing and Polly, 2009). The main advantage of this technique over traditional morphometry is that the size effect is dissociated from shape (Zelditch et al., 2012). Geometric morphometrics is particularly well suited for capturing subtle variations that might be missed using linear methods. Furthermore, isometric size difference, which is a confounding factor for ecomorphological studies (Klein et al., 2010), is removed in a geometric morphometric analysis.

In vertebrates, the skull and mandible are often used as models to represent the

morphological diversity of organisms (Figueirido et al., 2009; Mehta, 2009; Esteban-Trivigno, 2011; Bubadué et al., 2015). Both are considered morphologically complex structures, originated from different ontogenetic processes and responsible for harboring and participating in the main systems related to the perception of the environment, such as vision, smell, and hearing (Jiang et al. 2002; Schoch 2006), but also to feeding habits (Herrel et al., 2008; Vincent et al., 2009; Klaczko et al., 2016). Therefore, ecological factors are expected to exert a strong influence on the morphological diversification of the skull and mandible. In addition, through the shape of the teeth it is possible to abstract the diet of the animals, being of great applicability in paleoecology (Fiorillo et al., 2001; Larson and Currie, 2013).

Studies of morphological evolution among Neotropical primates exploring the environmental and phylogenetic effects are scarce. There are, nonetheless, some important contributions to the understanding of the evolutionary components that had molded the phenotypic variety of these primates. Marroig and Cheverud (2004, 2005, 2010) demonstrated that there was an important cranial allometric component, *i.e.*, influence of size on shape, in the 16 genera and 110 species of Platyrrhini. Makedonska et al. (2012), using 3D morpho-geometrical data, investigated the skull shape modularity in *Cebus* and found a higher degree of modularity in *C. apella* than in the other studied capuchin species, *C. libidinosus*, *C. nigritus*, *C. olivaceus*, and *C. albifrons*. These results might be explained by the dietary habits of *C. apella* which is a hard-object feeder which would influence in the ecomorphological variation of the skull of capuchin monkeys. More recently, Meloro et al. (2014a), Cáceres et al. (2014), and Meloro et al. (2014b) also investigated the ecogeographical variation of the genera *Cebus* and *Alouatta* from the Amazonian and Atlantic Forests. Analyzing the ventral view of the skull of both taxa, these authors found that there is a significant correlation of latitude, climate, and size influencing the skull shape.

Both *Alouatta* and *Cebus* have been matter of research in recent years mainly due to their wide distributions across America, which extends for almost all the ecoregions of this continent. However, there is another genus of Neotropical primate that present an extensive range of distribution as well, *Callicebus*. The distribution in space and time of these three genera, presenting in some cases isolated populations, make of them

interesting primate models for addressing questions regarding their biogeography, speciation, and morphological and molecular evolution, among others.

Species of the genus *Alouatta*, commonly known as howler monkeys in English, monos aulladores in Spanish, and bugios and guaribas in Portuguese are the most widely distributed across the Americas. They range from southern Mexico to northern Argentina (Fig. 3.1) and can be found in numerous forest types across the region (Neville et al. 1988; Glander and Pinto 2013). They are among the largest of the platyrrhines (Hill 1962; Peres 1994) along with the muriquis (*Brachyteles*), the spider monkeys (*Ateles*), and woolly monkeys (*Lagothrix*).

The distribution of howler monkeys extends from Southern Veracruz State in Mexico, through Central and South America to northern Argentina (Figure 1). *Alouatta* inhabits the widest range of environments of any Neotropical primate species (Crockett and Eisenberg, 1987), and can be found from sea level to 3200 m, although different species vary in habitat preferences (Crockett, 1998). For example, *Alouatta palliata* and *A. seniculus* occur in habitats ranging from closed-canopy wet evergreen forest to highly seasonal deciduous woodlands and riverine forests, whereas *A. belzebul* is basically a forest species (Crockett, 1998). Most of the species also occur in fragments of forest beside cattle ranches or in agricultural areas (see Crockett, 1998).



Figure 1. Distribution of howler monkey species (genus *Alouatta*), taken from Crockett (1998, Figure 1).

The taxonomy of *Alouatta* has been highly variable, mainly because of the scarcity of comprehensive taxonomic revisions of the genus. Most of the current knowledge regarding the diversity of *Alouatta* is based in some taxonomic reviews or accounts and only one taxonomic revision *sensu stricto*. In this context, the number of species has varied greatly from five species proposed by Cabrera (1958) to 12 (including three tentative species) listed by Cortés-Ortiz and Mittermeier (2015). Gregorin (2006), in the most comprehensive taxonomic revision of the Brazilian populations of *Alouatta*, recognized 11 monotypic species: *A. caraya*, *A. belzebul*, *A. discolor*, *A. ululata*, *A. fusca*, *A. clamitans*, *A. juara*, *A. macconelli*, *A. nigerrima*, and *A. puruensis* (Figure 2). One of the most important points to be highlighted in Gregorin's (2006) revision is the information regarding the phenotypical variation and the distribution of each species, aspects deficiently assessed before.



Figure 2. Adult male individual of *Alouatta seniculus* from the Sorocaba Zoo.

The number of *Alouatta* taxa at subspecific level is currently also a matter of discussion. In this case, the main shortcoming with the recognized subspecies relies in the lack of clear diagnoses and geographic boundaries between these taxa. For instance, the taxon *ululata* has been treated as a synonym of *A. belzebul* by some authors (Lönnerberg, 1941; Groves, 2001), a subspecies of *Alouatta belzebul* (Cabrera, 1958; Hill, 1962; Rylands et al., 1995), or even as a full distinct species by others (Gregorin, 2006; Glander and Pinto, 2013; Cortés-Ortiz and Mittermeier, 2015). Viana et al. (2015) conducted a molecular analysis to elucidate the phylogenetic relationships among the taxa *belzebul* and *ululata*. These authors found no clear separation between these two taxa; nonetheless, and as pointed out by them, this result might be an artifact of the poor sampling of *ululata* (only one specimen). As a result, Viana et al. (2015) decline of taking any taxonomic decision regarding the validity of *belzebul* and *ululata*.

The phylogenetic relationships of *Alouatta* have been poorly investigated and Cortés-Ortiz et al. (2003) were the first to investigate the phylogenetic relationships of *Alouatta*, suggesting that the Central and South American howler monkey species were reciprocally monophyletic groups which diverged at 6.8 Ma. Cortés-Ortiz et al. (2003) found eight monophyletic mtDNA haplotypes congruent with six named South American

species (*A. seniculus*, *A. sara*, *A. macconnelli*, *A. caraya*, *A. belzebul*, and *A. guariba*) and two Mesoamerican (*A. pigra* and *A. palliata*). However, this study included few specimens coming from some scarce localities from Central and South America. In view of the current evidence, Cortés-Ortiz et al. (2015) stated that we are far from “resolve” the taxonomy of *Alouatta*, but what becomes urgent is an integrative taxonomic revision that generates a congruent well-supported hypothesis of the true diversity of howler monkeys. Doyle et al. (2021), based on fossil calibrations, estimated a divergence among Mesoamerican and South American howler monkeys of 13.2 MYA.

There are some controversies regarding the divergence time between the *Alouatta* species inhabiting the Amazon and the Atlantic Forest, as Cortes-Ortiz et al. (2003) estimated a divergence of 5.1 MYA, whereas Springer et al. (2012) a split around 3.2 MYA and, more recently, Doyle et al. (2021) stated that the split among howler monkeys from the Amazon and those from Atlantic Forest would happened much earlier, around 10.7 MYA. Regardless the *guariba/clamitans* taxonomic debate, the *Alouatta* populations from Southeastern Brazil seem to be more related with the Amazonian species rather than with those populations from the Cerrado either based on morphological (Gregorin, 2006), cytogenetics (Oliveira et al., 2012) or molecular evidence (Cortés-Ortiz et al., 2003; Villalobos et al., 2004; Doyle et al., 2021). Another interesting fact regarding *Alouatta*'s phylogenetic relationships is the position of *A. caraya* which, although inhabits biomes as Pantanal, parts of the Cerrado and Caatinga, it seems to be more closely related to Amazonian howler monkeys (see Cortés-Ortiz et al., 2003; Villalobos et al., 2004; Doyle et al., 2021). According to Cortés-Ortiz et al. (2003) and Perelman et al. (2011) the split between *A. caraya* and its Amazonian congeneric species occurred approximately at 4 Ma which would coincide with the split of *Alouatta seniculus* in the Amazon.

The capuchin monkeys (genus *Cebus*) are medium-sized monkeys (2–4 kg) with semi-prehensile tails (Freese & Oppenheimer, 1981). The genus was traditionally, and sometimes informally, classified in two groups: the untufted or gracile capuchin monkeys and the tufted or robust capuchin monkeys (Hershkovitz, 1949, Hill 1960). Untufted capuchins are found in lowland, premontane, and montane forests of Central and northern South America, from sea level to over 2000 m (Hershkovitz, 1949; Aquino &

Encarnación, 1994; Hernández-Camacho & Cooper, 1976; Boubli et al., 2012) (Figure 3a). Tufted species of capuchin monkeys, on the other hand, are restricted to South America, inhabiting the Amazon Basin, across Brazil, Paraguay, and northeastern Argentina (Silva-Júnior, 2001; Lynch Alfaro et al., 2012a; Rylands et al., 2013) (Figure 3b).

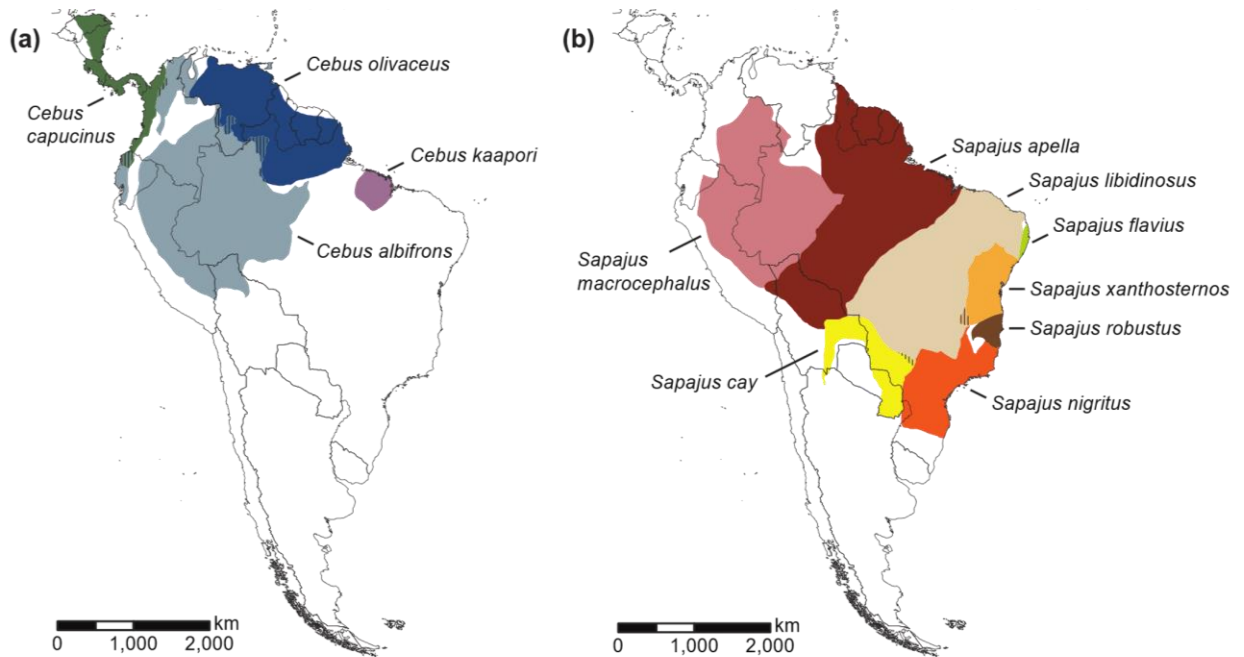


Figure 3. Distribution of capuchin monkeys (genus *Cebus*); a) Untufted and b) Tufted species (taken from Lynch Alfaro et al., 2013).

The capuchin monkeys have suffered various taxonomic changes in recent years both at the specific and generic level. Silva Jr. (2001) recognized two different groups within *Cebus*, proposing that such distinction could be formalized at the subgeneric level, *Cebus* and *Sapajus* (Figure 4). Later, Lynch-Alfaro et al. (2012b) proposed that the genus *Cebus* should be divided into genera *Sapajus* for robust capuchins and *Cebus* for the graceful forms, based on the divergence time between these two lineages. Ruiz-García et al. (2012, 2016b) based on molecular studies of COII indicated that, although the morphological differences between *Cebus* and *Sapajus* are notorious, the molecular and karyotypic differences are relatively small, recommending the use of the genus *Cebus* for all capuchin monkeys. Subsequently, Gutiérrez and Marinho-Filho (2017) proposed that *Sapajus* and *Cebus* should be treated as subgenera, arguing that the use of the generic level in this case would be unnecessary and impractical, generating confusion and a

visible taxonomic inflation; besides that, both groups remain as a monophyletic group; this is the arrangement that I am following at the present contribution.



Figure 4. Male adult *Cebus* (*Cebus*) *albifrons aequatorialis* [left, taken from Hurtado et al. (2016)] and *Cebus* (*Sapajus*) *apella macrocephalus* [right, taken from John C. Mittermeier, available at <https://www.flickr.com/photos/40167965@N05/3746966509/in/photolist-6H7bAR>].

Species of the genus *Callicebus*, commonly known as titi monkeys in English, monos tocones in Spanish, and zogue-zogues and sauás in Portuguese, are small to medium-sized primates. Species of the genus inhabit the tropical forests of the Amazon and Orinoco basins, the Brazilian Atlantic Forest, the Chaco, and the dry forests of Paraguay and Bolivia (Hershkovitz, 1988; Hershkovitz, 1990; van Roosmalen et al., 2002; Byrne et al., 2016; Byrne et al., 2018) (Figure 5).

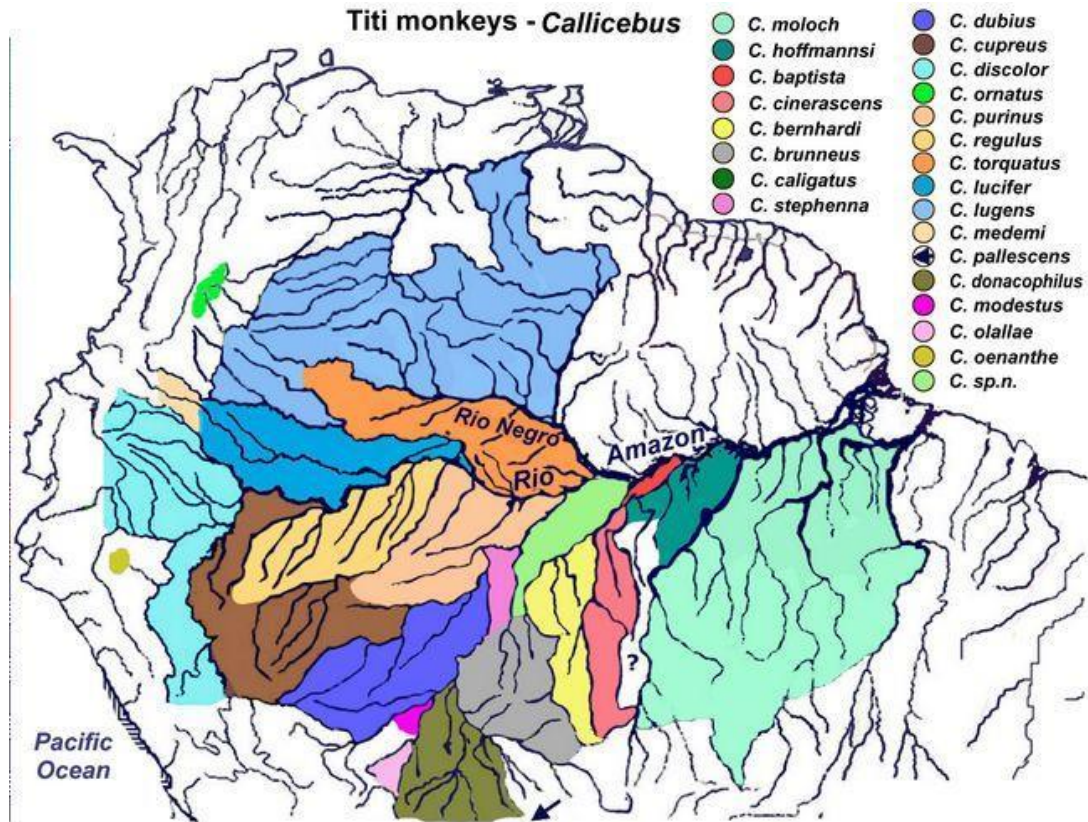


Figure 5. Distribution of *Callicebus*' species (after van Roosmalen et al., 2002).

The taxonomy of *Callicebus* has varied deeply in the last two decades, at both specific and generic levels. Over this time, the number of species has increased from 13 to up to 35 species (Herskovitz, 1990; Byrne et al. 2016, 2021). Although this profound variation on the number of species is in part due the description of new taxa of genus *Callicebus* (van Roosmalen et al., 2002; Gualda-Barros et al., 2013; Dalponte et al., 2014; Boubli et al., 2019; Gusmão et al., 2019), the main cause for this disproportionate increase is the result of the abandonment of the subspecific level in the taxonomy of *Callicebus* by van Roosmalen et al. (2002). These authors claimed that the concept of subspecies would be of “minimal value” when describing the diversity of Neotropical primates, but did not provide any further conceptual discussion regarding this species/subspecies matter.

At the generic level, *Callicebus* has also suffered profound changes. Herskovitz (1963, 1988, 1990) considered all the species of titi monkeys within the genus *Callicebus*, which was followed by posterior authors (Kobayashi, 1995; Kobayashi and Langguth, 1999; Groves, 2001; van Roosmalen et al., 2002). Groves (2001) pointed out that the differences

between the species of the torquatus group would deserve subgeneric recognition as proposed by Goodman et al. (1998). Groves (2005) formally proposed the subgenus *Torquatus* for the species of the torquatus group (as proposed by the aforementioned authors) and for the remaining species of titi monkeys to be allocated in the subgenus *Callicebus*. Finally, Byrne et al. (2016), in the first molecular appraisal of titi monkeys, proposed a new classification of these primates splitting *Callicebus* in three genera, *Cheracebus*, *Plecturocebus*, and *Callicebus* (Figure 6). Nonetheless, Byrne et al.'s (2016) proposal has been criticized because its taxonomic unpracticality besides of creating an unnecessary inflation at generic level and for not improving nothing that the subgeneric level would resolve (Marinho Filho & Gutierrez, 2017; Serrano-Villavicencio, 2017).

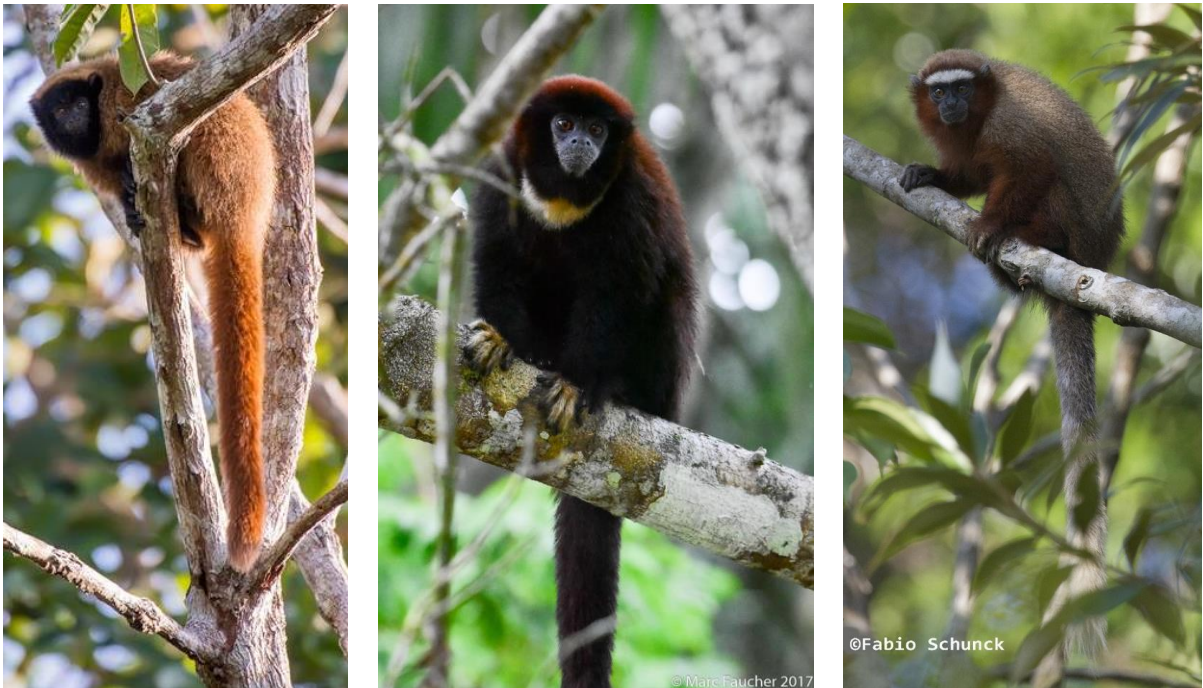


Figure 6. Individuals of *Callicebus* (*Callicebus*) *personatus* [left, photo by Leonardo Merçon]; *Callicebus* (*Cheracebus*) *torquatus* [middle, photo by Marc Faucher]; and *Callicebus* (*Plecturocebus*) *caligatus dubius* [right, photo by Fabio Schunck)].

All these advances in terms of biogeography and systematics have increased our understanding in Neotropical primates' evolution and speciation. Nonetheless, there are several common shortcomings in all the above-mentioned contributions as the lack of species in their analyses and, most importantly, the geographical coverage of the samples. This last shortcoming is understandable because the wide distribution of these

genera but, unfortunately, some regions are extremely relevant in terms of biogeography as the Andes and the cloudy forests for instance, a poorly represented region in Neotropical primates' phylogenetic studies [see Pacheco et al. (2020) for discussion regarding the taxonomy of *Callicebus oenanthe*]. Regardless these limitations, this new data have also provided new tools to link morphological aspects with phylogenetic and evolutionary information.

The contributions of Cáceres et al. (2014), and Meloro et al. (2014a, b) provided important insights regarding the morphological evolution, based on skull shape variation of *Alouatta* and *Cebus*, two genera of the closely related families Atelidae and Cebidae, respectively (Perelman et al. 2011). These authors found the same morphological response of *Alouatta* and *Cebus* to climatic variables. In this scenario, one question arises: Is this response a common pattern in other neotropical primates widely distributed on the continent? In this context *Callicebus* (Family Pitheciidae) stands apart as an interesting group due to its phylogenetic position, a sister clade of *Atelidae* + *Cebidae*, and because its distribution covers almost the same ecoregions as *Alouatta* and *Cebus*.

Considering all the above mentioned, the objectives of this work were: (1) to describe the morphological patterns involve in the diversification present in all the genera examined, and to relate them through an integrated approach, considering ecological and phylogenetic factors; (2) to analyze and describe the morphological variation of each taxon, at individual and geographical levels (3) to evaluate if the three genera have responded equally to non-biological factors and hypothesize about the morphological similarities and/or differences among these three groups.

2. MATERIAL AND METHODS

2.1 Taxonomic arrangement

For the present work, I followed the taxonomic arrangement proposed by Silva (2001), Feijó and Langutth (2013), and Groves (2005) for the genus *Cebus* (Figure 1), considering *Sapajus* and *Cebus* as subgenera of genus *Cebus* (contra Lynch-Alfaro et al. 2012). I included all the species of titi monkeys into *Callicebus* but, acknowledging the

evidence found by Byrne et al. (2016), I used the names *Callicebus*, *Cheracebus*, and *Plectorocebus* as subgenus agreeing with Serrano-Villavicencio et al. (2017), Gutiérrez & Marinho-Filho (2017), Garbino & Aquino (2018), Brandão et al. (2019), and Pacheco et al. (2020). In the case of *Alouatta*, I followed the taxonomic arrangement proposed by Gregorin (2006) for the Brazilian populations of howler monkeys since this work represents the most comprehensive taxonomic revision of this group.

2.2 Scientific collections and species considered

I examined the collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP), that holds 758 skulls specimens belonging to the genera *Alouatta* (284; 146♂, 137♀, 1 NA), *Callicebus* (188; 84♂, 90♀, 14 NA), and *Cebus* (286; 147♂, 132♀, 7 NA) (see Table 1 for a detailed list of species and specimens used for each genus). I classified the specimens into four age classes (infant, juvenile, subadult, and adult) through analysis of tooth eruption and fusion of cranial sutures following de Vivo (1988) and Gregorin (2006). For all analyses I only employed adult and subadult individuals, totalizing 253 individuals of *Alouatta*, 186 of *Callicebus*, and 222 of *Cebus*. See Appendix 1 for biological material and localities.

Table 1. List of specimens by species analyzed in this work.

Species	N
<i>Alouatta belzebul</i> (Linnaeus, 1766)	10
<i>Alouatta caraya</i> (Humboldt, 1812)	7
<i>Alouatta clamitans</i> Cabrera, 1940	78
<i>Alouatta discolor</i> (Spix, 1823)	50
<i>Alouatta fusca</i> (Geoffroy Saint-Hilaire, 1812)	28
<i>Alouatta juara</i> (Linnaeus, 1766)	22
<i>Alouatta macconnelli</i> Elliot, 1910	53
<i>Alouatta nigerrima</i> Lönnberg, 1941	32
<i>Alouatta puruensis</i> Lönnberg, 1941	3
<i>Alouatta ululata</i> Elliot, 1912	1

<i>Callicebus (Callicebus) barbarabrownae</i> Hershkovitz, 1990	2
<i>Callicebus (Callicebus) coimbrai</i> Kobayashi e Langguth, 1999	1
<i>Callicebus (Callicebus) melanochir</i> (Wied, 1820)	1
<i>Callicebus (Callicebus) nigrifrons</i> (Spix, 1823)	12
<i>Callicebus (Callicebus) personatus</i> (Humboldt, 1812)	24
<i>Callicebus (Cheracebus) lugens</i> (Humboldt, 1812)	1
<i>Callicebus (Plectorocebus) baptista</i> Lönnberg, 1939	14
<i>Callicebus (Plectorocebus) bernhardi</i> van Roosmalen et al., 2002	1
<i>Callicebus (Plectorocebus) brunneus</i> (Wagner, 1842)	7
<i>Callicebus (Plectorocebus) cinerascens</i> (Spix, 1823)	6
<i>Callicebus (Plectorocebus) donacophilus</i> (d'Orbigny, 1836)	4
<i>Callicebus (Plectorocebus) hoffmannsi</i> Thomas, 1908	17
<i>Callicebus (Plectorocebus) moloch</i> (Hoffmannsegg, 1807)	57
<i>Callicebus (Plectorocebus) cupreus</i> (Spix, 1823)	41
<i>Cebus (Cebus) olivaceus</i> (Schomburgk, 1848)	2
<i>Cebus (Sapajus) libidinosus</i> Spix, 1823	16
<i>Cebus (Sapajus) apella</i> (Linnaeus, 1758)	95
<i>Cebus (Sapajus) cay</i> Illiger, 1815	31
<i>Cebus (Sapajus) xanthosternos</i> (Wied-Neuwied, 1826)	16
<i>Cebus (Sapajus) robustus</i> (Kuhl, 1820)	30
<i>Cebus (Sapajus) nigritus</i> (Goldfuss, 1809)	96
Total	758

2.3 Localities

I extracted the information of localities and geographical coordinates from each specimen's label or by direct consultation of field notebooks. In most cases, I raised these coordinates 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. Whenever possible, I recovered data from some specimens with incomplete collection information on their label, for this purpose, I reviewed Pinto (1945), which recounts ancient collection expeditions of some naturalists of who collected specimens now held at the MZUSP. Using these corrected and checked localities, I elaborated maps using the ArcGIS 9.3 software and edited with Photoshop CS4 software (Figure 7).

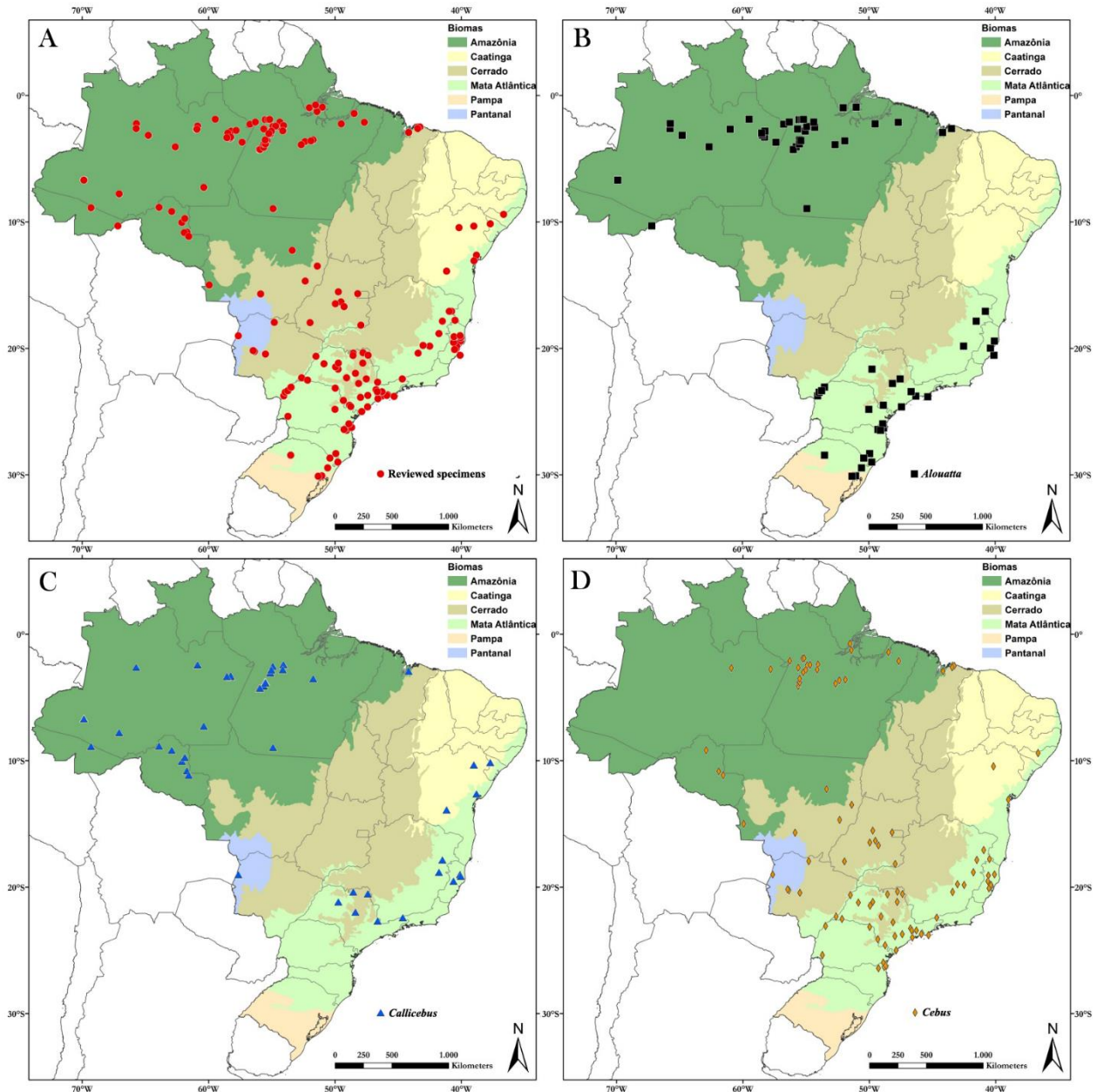


Figure 7. Localities of the reviewed specimens: (A) All the specimens including the three genera; and by genus in (B) *Alouatta*, (C) *Callicebus*, and (D) *Cebus*.

2.4 Phylogenetic data

I obtained the information regarding the phylogenetic relationships of *Alouatta* and *Cebus* from the VertLife portal (<https://vertlife.org/>). This website allows the download of phylogenetic trees elaborate with selected taxa by the user (whenever

available). As a result, a .nex file is generated containing all the elements related to molecular-based trees (e.g. divergence times, distances). In the case of *Callicebus*, I requested this information directly to Hazel Byrne, who has led the most recent studies regarding the systematics and biogeography of *Callicebus* (Byrne et al., 2016; Byrne et al. 2018; Byrne et al., 2021), and kindly provided a pruned tree ready to use. Once the phylogenetic information of all the genera was set up as required by the MorphoJ, I correlated it with the centroid size and Procrustes coordinates (free-allometry shape) information to evaluate if there was a phylogenetic signal influencing on the size and shape of each genus.

2.5 Geometric morphometric analysis

I applied geometric morphometrics (GM) to quantify the intra and interspecific shape variation among the examined taxa. I digitized the 758 skulls (661 of them from subadults and adults) in three different views: dorsal, frontal, and lateral, using a digital photographic camera Canon Rebel T3. I took all the required precautions to avoid possible distortions (e.g. same scale and focal distance, remote shooting, etc.). The photographs were transformed into TPS files using the software TpsUtil 1.60 (Rohlf 2013). Using these TPS files, I digitized 2D landmarks in all views: dorsal (12), frontal (12), and lateral (17) (Figure 8) (see Appendix 2 for the detailed list of landmarks). For this purpose, I used the software TpsDig v.2.26 (Rohlf, 2006; Rohlf and Bookstein, 2003); additionally, I also used this software to generate the outlines which enhance the visualization of the skull variation in my results.

As a first step, I looked for outliers resulting from errors of digitalization of landmarks (e.g. inverted order, missing or exceeding landmarks). I obtained the

Procrustes coordinates by performing a generalized Procrustes Superimposition using the software MorphoJ (Klingenberg, 2011). This 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 (Rohlf and Slice, 1990). I performed a multivariate regression of Procrustes coordinates on centroid size to evaluate possible outliers resultant from scaling problems during the process of digitization. After checking all the specimens, I extracted the information of the centroid size and, using the package Geomorph (Adams, 2004) in the software R, I plotted it into boxplots to compare the differences in size (in terms of centroid size) among sexes and species whenever the number of specimens allowed it (more than 20 specimens).

I used the new Cartesian coordinates (or Procrustes coordinates) obtained after the superimposition 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, although the allometric effect is still influencing the data. After removing this allometric effect by multivariate regressions, I analyzed the shape of the structures independently of size (Klingenberg et al., 2002; Zelditch et al., 2004). As a second checkpoint, I looked for outliers resulting from errors during the digitization process (e.g. inverted order of landmarks) and, after correcting these errors, the data was ready to be analyzed. I prepared sub-datasets containing only adults and subadults individuals and entered the following classifiers: sex, species, locality, and biome. I performed a Principal Component Analysis (PCA) to observe the distribution of the data with no assumption of *a priori* groups.

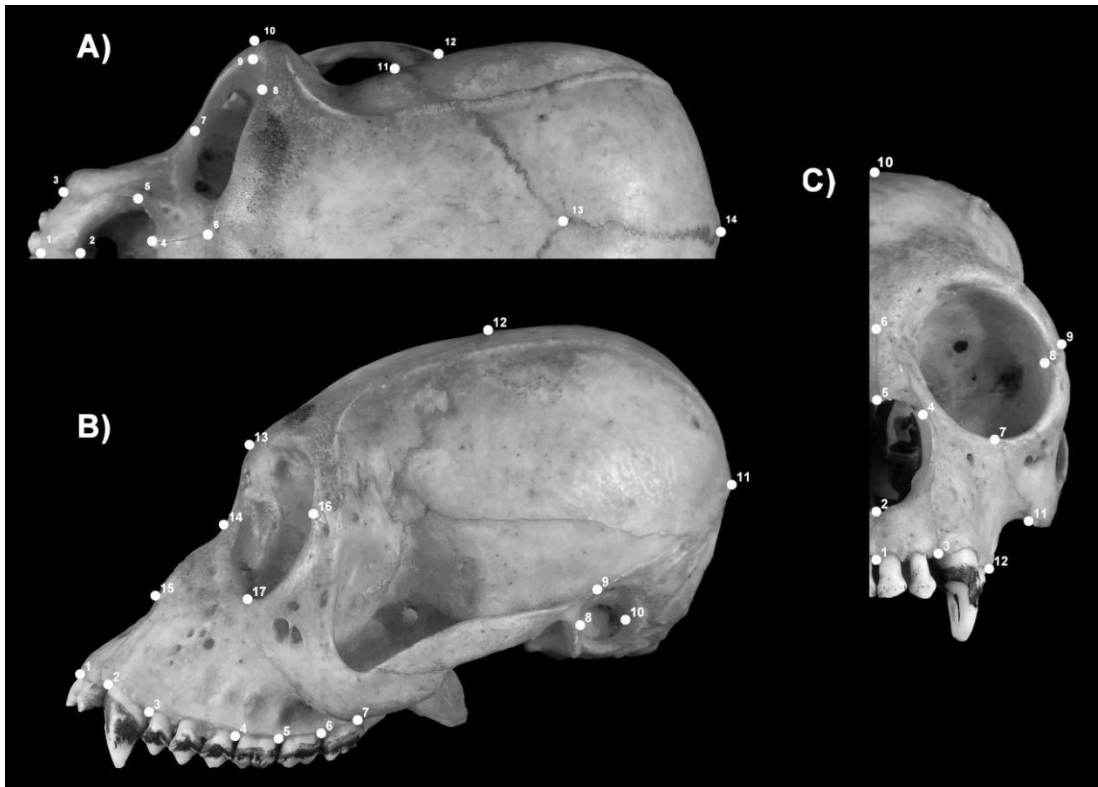


Figure 8. Cranial landmark configuration that will be used in the present study in dorsal (a), lateral (b), and frontal (c) view. Taken from Serrano-Villaviencio (2016).

2.6 Ecomorphological analysis

I added information regarding the latitude and longitude of each specimen's locality. Additionally, I inserted the climatic variables corresponding to each locality, and both geographic and climatic variables were treated as covariates in MorphoJ. Using the Raster package (Hijmans & van Etten, 2012) in R, I downloaded the following climatic variables for each locality:

BIO1 = Annual Mean Temperature

BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))

BIO3 = Isothermality (BIO2/BIO7) (* 100)

BIO4 = Temperature Seasonality (standard deviation *100)

BIO5 = Max Temperature of Warmest Month

BIO6 = Min Temperature of Coldest Month

BIO7 = Temperature Annual Range

BIO8 = Mean Temperature of Wettest Quarter

BIO9 = Mean Temperature of Driest Quarter

BIO10 = Mean Temperature of Warmest Quarter

BIO11 = Mean Temperature of Coldest Quarter

BIO12 = Annual Precipitation

BIO13 = Precipitation of Wettest Month

BIO14 = Precipitation of Driest Month

BIO15 = Precipitation Seasonality (Coefficient of Variation)

BIO16 = Precipitation of Wettest Quarter

BIO17 = Precipitation of Driest Quarter

BIO18 = Precipitation of Warmest Quarter

BIO19 = Precipitation of Coldest Quarter

I employed the climatic variables and latitude and longitude data to perform a Two-block Partial Least Squares analysis (PLS) (Rohlf & Corti, 2000) for separate blocks. PLS identifies the features of shape variation that most co-vary between both blocks indicating the degree of contribution to the total covariation among these blocks (Rohlf and Corti 2000, Klingenberg et al. 2003, Klingenberg 2009). In geometric morphometrics, Partial Least Squares analysis may be used to relate shape data to other types of data (ecological information, experimental conditions, etc.) or to other shape variables. (Klingenberg, 2009). The permutation tests offered in the PLS all concern the null hypothesis of complete independence between the two blocks of variables (in this case

size and shape vs the covariates BIOCLIM and latitude/longitude). Another implementation in this procedure is the RV coefficient which is used as a measure of overall covariation or association among blocks, and it is a multivariate analogue of the squared correlation (Escoufier, 1973). Achieved significance levels are indicated for the RV coefficient, which varies from 0 to 1; 1 indicating a complete correlation between blocks (Klingenberg, 2009).

3. RESULTS

3.1 Skull size

Skull size varied greatly between all three genera. In all views the species of *Alouatta* presented the largest skulls, in terms of centroid size, of all the analyzed genera followed by all the species of *Cebus* and *Callicebus* from the Atlantic Forest. The smallest group were the Amazonian species of *Callicebus* (Figure 9). As expected, this pattern was repeated in all views, and for this reason, I presented only the results of the dorsal view.

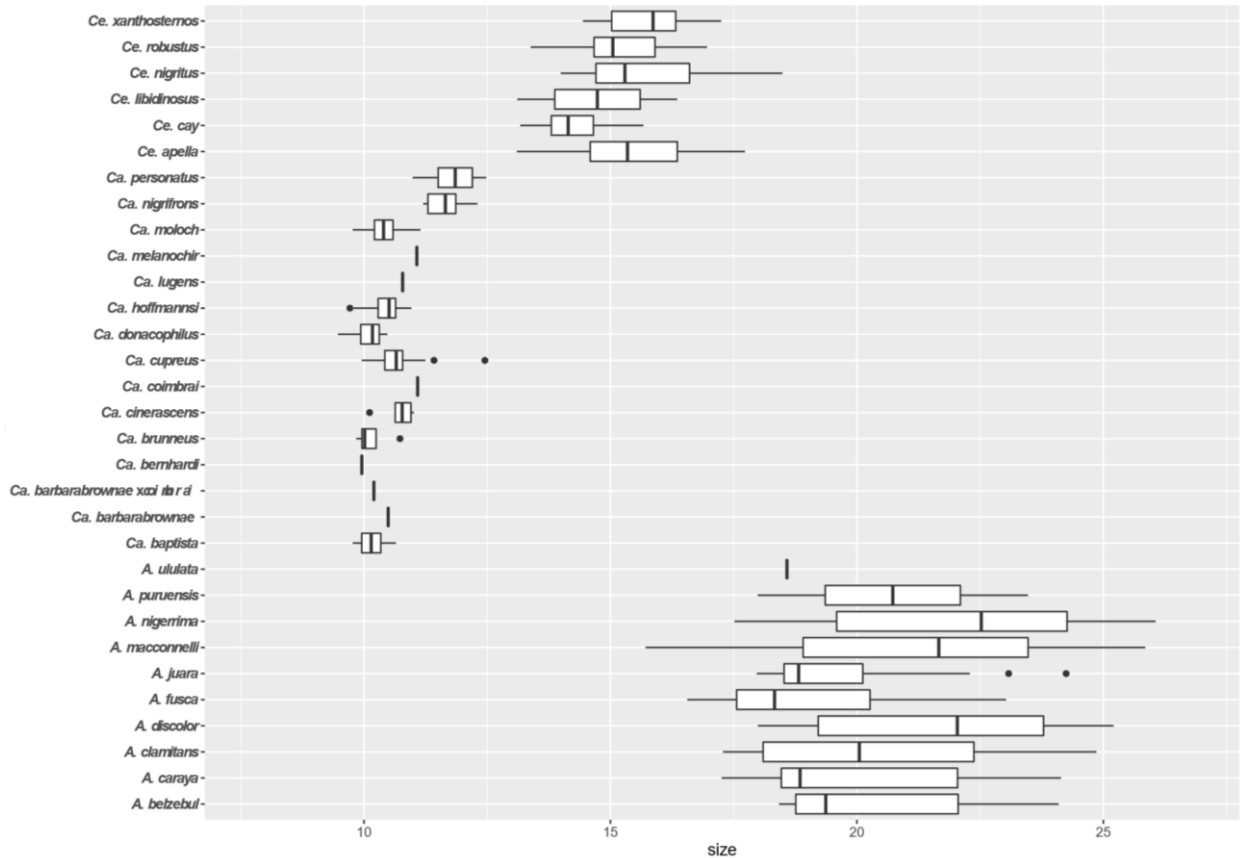


Figure 9. Boxplot of the Centroid size of all the analyzed taxa in this work (Ce = *Cebus*; Ca = *Callicebus*; A = *Alouatta*).

Regarding sexual dimorphism on centroid size, *Alouatta* presented the greatest difference between sexes with males much larger than females in all three views (Figure 10), being an entirely dimorphic genus. Although I detected differences on centroid sizes among males and females of *Cebus* these are not as marked as in *Alouatta* (Figure 10). *Callicebus* was the less dimorphic genus among all the analyzed genera, the centroid size showing no clear differences between sexes (Figure 10).

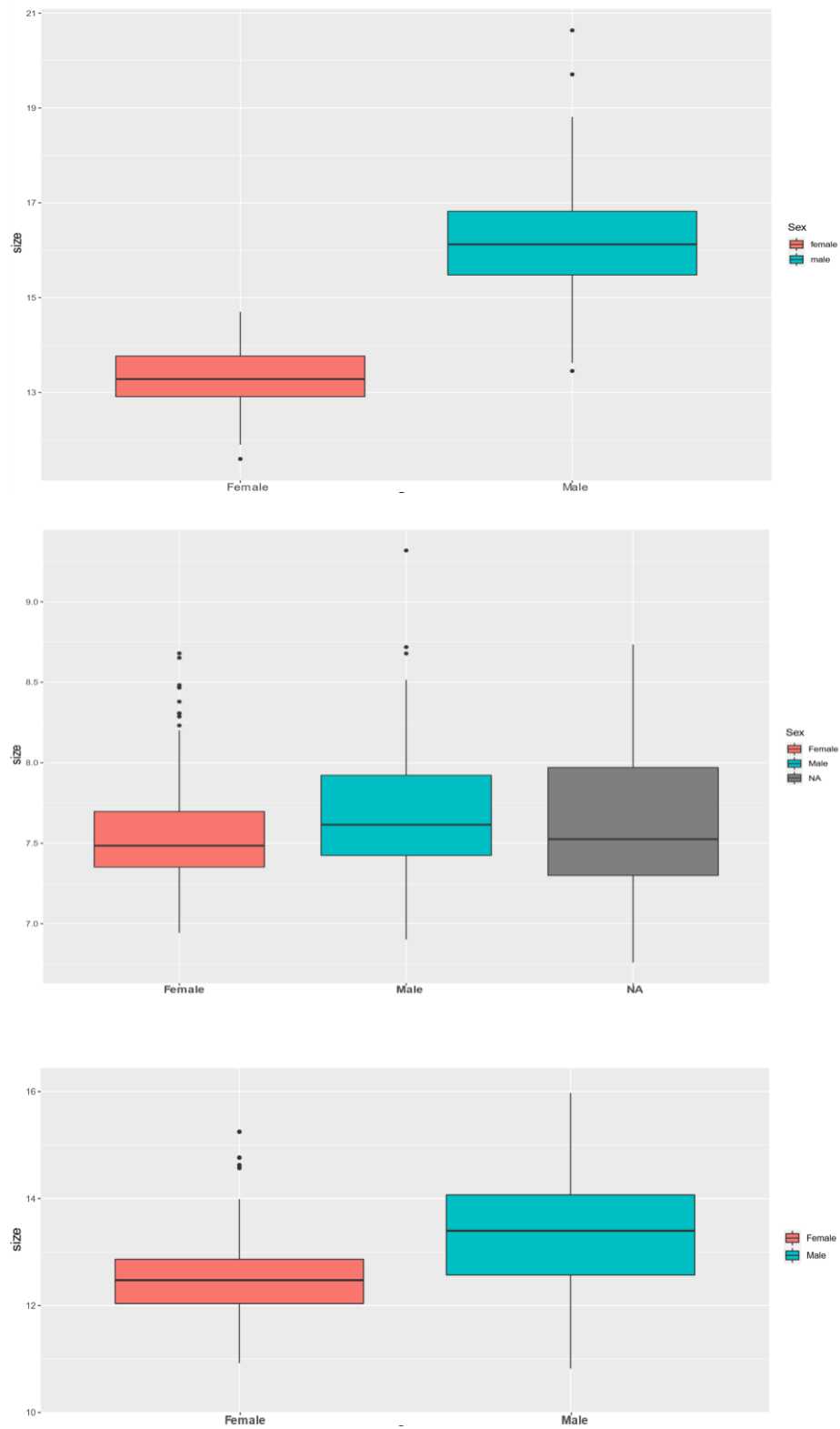


Figure 10. Boxplots comparing the centroid size of females (orange) and males (turquoise) of *Alouatta* (top), *Callicebus* (middle), and *Cebus* (bottom). Points above and below each box represent outlier individual.

To calculate the phylogenetic signal on centroid size, I averaged the data by species and selected those species available on both morphometric and phylogenetic approaches. After this, I mapped the phylogeny into the centroid size information. Finally, I colored the terminals using each biome as a classifier. I performed all these processes in all views for each genus and, to avoid redundancy in the results, I present the results of the dorsal view. In the case of *Alouatta*, the permutation test against the null hypothesis of no phylogenetic signal after 10,000 randomization rounds resulted in a non-significant P-value (0,0860). Therefore, there is no phylogenetic signal influencing centroid size. Additionally, Amazonian species of *Alouatta* presented higher centroid sizes than the one from the Cerrado, *A. caraya* (which partially inhabits the Atlantic Forest) and *A. ululata*, except for *A. juara* and *A. belzebul*, that are Amazonian species. *Alouatta ululata* from the Cerrado, presented the lowest centroid size value; nonetheless, this last result is not conclusive since the sample size of *A. ululata* is one and it is a female adult (Figure 11).

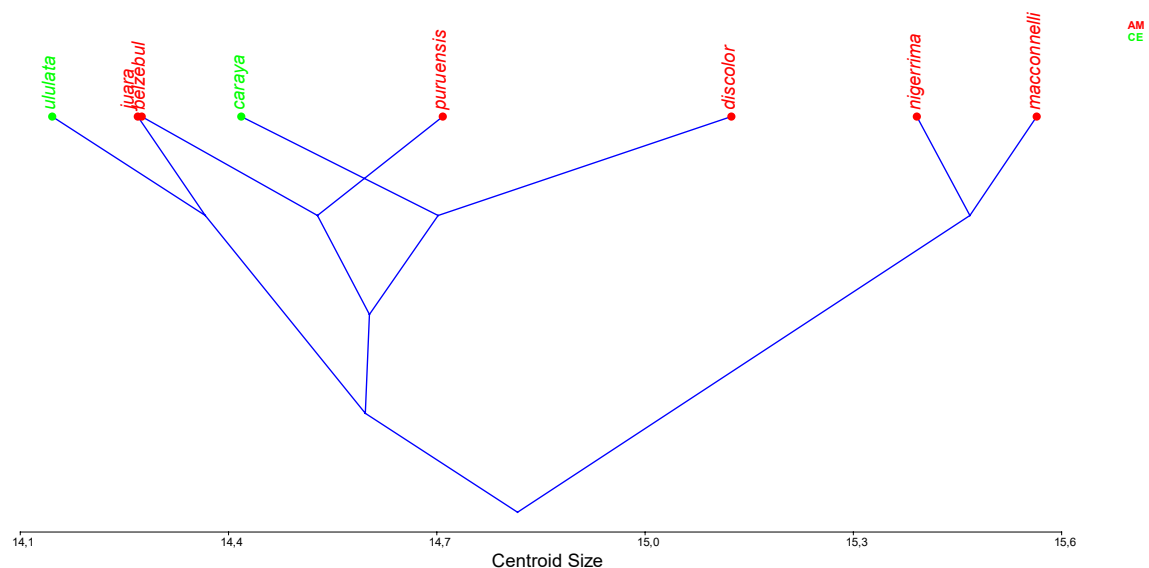


Figure 11. Phylogenetic mapping on centroid size of *Alouatta*. In green are the two species from the Cerrado, *A. caraya* and *A. ululata*; in red the Amazonian *A. juara*, *A. belzebul*, *A. puruensis*, *A. discolor*, *A. nigerrima*, and *A. macconnelli*. Centroid size increases from left to right.

In the case of *Callicebus*, the phylogenetic signal resulting from the permutation test, contrary to *Alouatta*, was significant (P-value = 0,0035), suggesting that centroid size carries a signal determined by the phylogenetic relationships among species of *Callicebus*. The Atlantic Forest species of *Callicebus* presented the highest values of centroid size, although *C. nigrifrons* (the second species with highest centroid size) also comprises another biome, the Cerrado. Amazonian species of *Callicebus* presented the lower centroid sizes with *C. bernhardi* as the smallest one, apart from *C. donacophilus*, which inhabits a different biome, the Pampas. Again, and as in the case of *Alouatta ululata*, the position of *C. donacophilus* could be affected by the sample size (N = 4) (Figure 12).

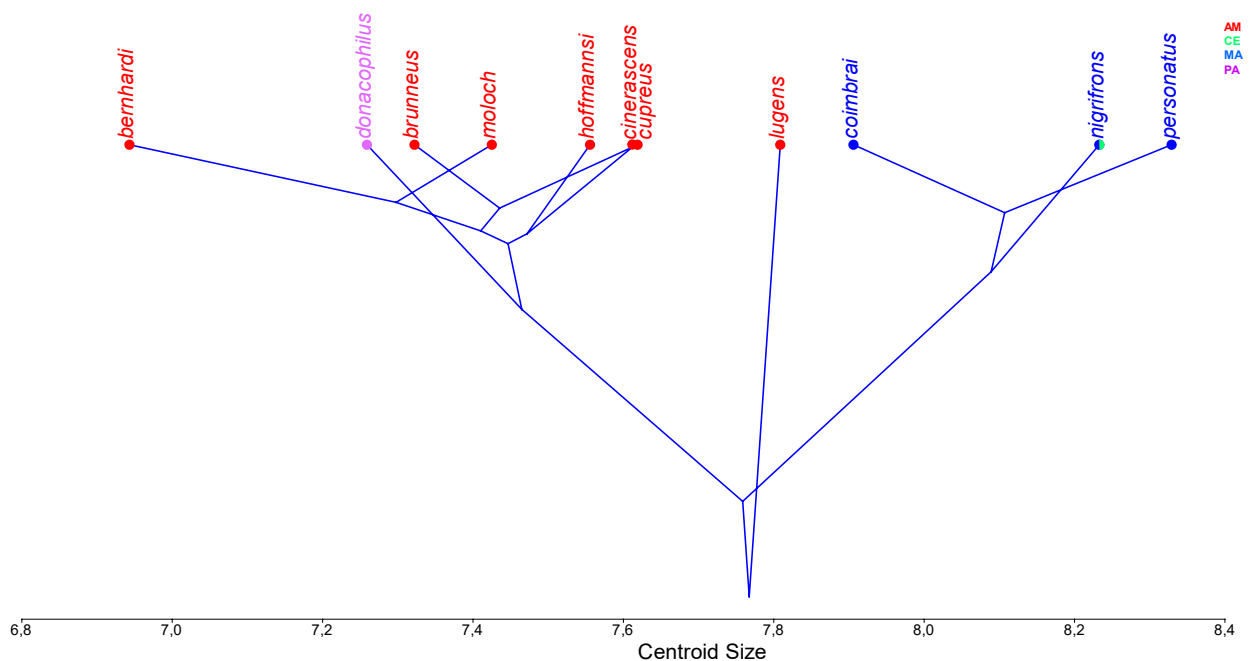


Figure 12. Phylogenetic mapping on centroid size of *Callicebus*. In red the Amazonian species; in purple the only species from the Pampas, *Callicebus donacophilus*; in blue species from the Atlantic Forest, *Ca. nigrifrons* is the only species inhabiting both the Atlantic Forest and the Cerrado. Centroid size increases from left to right.

Cebus presented the same pattern as *Alouatta* with no phylogenetic signal influencing centroid size (P-value = 0,0620). *Cebus olivaceus* presented the highest centroid size among the analyzed species; however, I only had access to two individuals of

C. olivaceus which could be generating biases in the results. Following *C. olivaceus* on centroid size are *C. xanthosternos* (from the Atlantic Forest and the Caatinga), *C. nigrinus* (from the Atlantic Forest and the Cerrado), and *C. robustus* (exclusive from the Atlantic Forest). Lastly, *C. libidinosus* (from the Cerrado, the Atlantic Forest, and the Amazonia), *C. apella* (from the Amazonia and the Cerrado), and *C. cay* (from the Cerrado, the Pampas, and the Amazonia) exhibited the smallest centroid size among all species of *Cebus* (Figure 13).

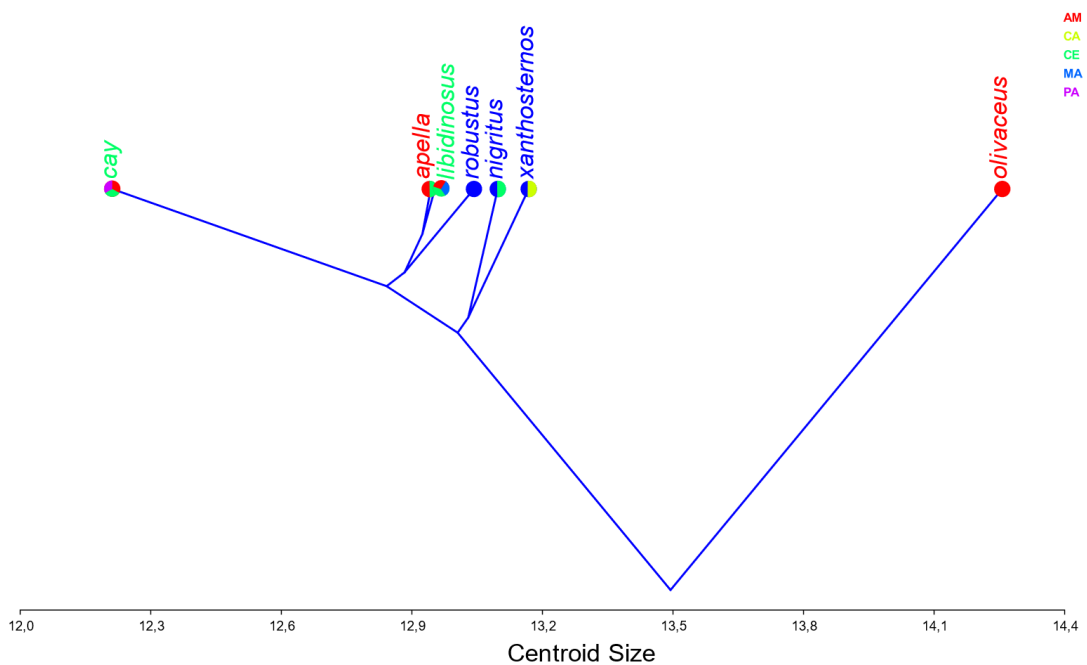


Figure 13. Phylogenetic mapping on centroid size of *Cebus*. *Ce. robustus* (Atlantic Forest) and *Ce. olivaceus* (Amazonia) inhabit exclusively only one biome. Species inhabiting two biomes are *Ce. apella* (Amazonia and Cerrado), *Ce. nigrinus* (Atlantic Forest and Cerrado), and *Ce. xanthosternos* (Atlantic Forest and Caatinga). Two species, *Ce. cay* (Amazonia, Cerrado, and Pampas) and *Ce. libidinosus* (Amazonia, Atlantic Forest, and Cerrado), occupy three biomes. Centroid size increases from left to right.

3.2 Geometric morphometrics

Regarding allometry, the pattern of covariation among measures of size and shape (Klingenberg, 1998), *Alouatta* was the most allometric genus in all three views of the skull

(see Table 2). When this effect is maintained, the difference in shape among sexes in this genus seems to be quite striking. Nonetheless, after removing this allometric effect (size correction), the separation between females and males disappeared (Figure 14). This pattern is also similar in *Cebus*, although that differentiation among females and males is not as marked as in *Alouatta* (Figure 15). Although allometry was statistically significant after the permutation tests in almost all cases (see Table 1), the results of the PCA for *Callicebus* did not change drastically as in the case of *Alouatta* and, moderately, in *Cebus*. *Callicebus* proved to be the less dimorphic genus both in size (in terms of centroid size) and cranial shape (Figure 16).

Table 2. Percentage of allometric effect in dorsal, frontal, and lateral views of *Alouatta*, *Callicebus*, and *Cebus*. Significant values ($P < 0.005$) after permutation test against the null hypothesis of independence (number of randomization rounds = 10,000) are bold.

	Dorsal (%)	Frontal (%)	Lateral (%)
<i>Alouatta</i>	18.22	15.19	35.97
<i>Callicebus</i>	6.44	9.35	6.52
<i>Cebus</i>	12.06	2.07	7.04

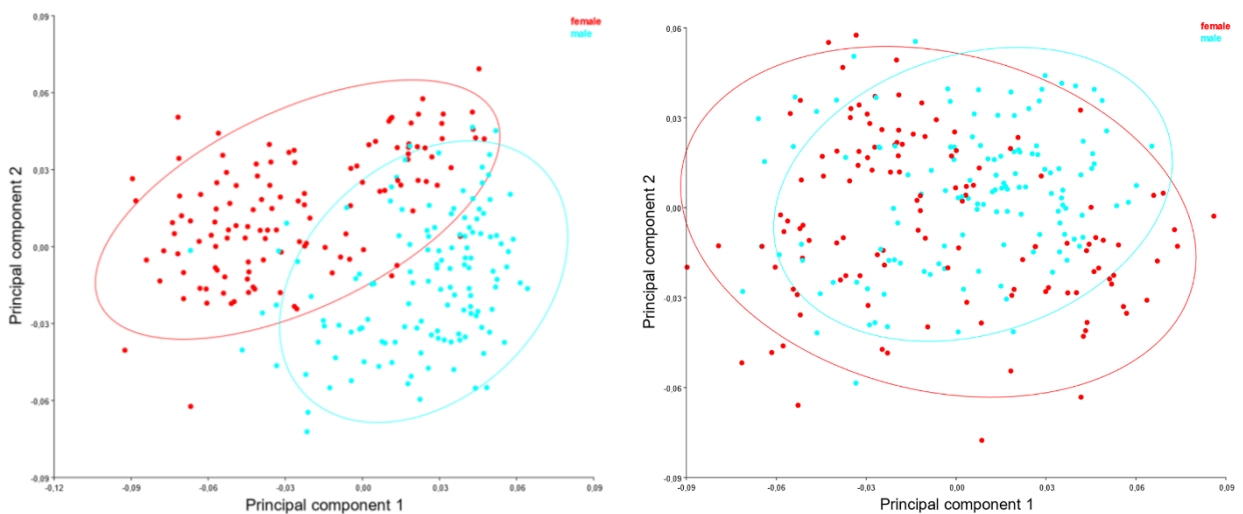


Figure 14. Principal Component analyses (PCA) of *Alouatta* in dorsal view among females and males. Left,

PCA without size correction (allometric effect); right, size corrected PCA.

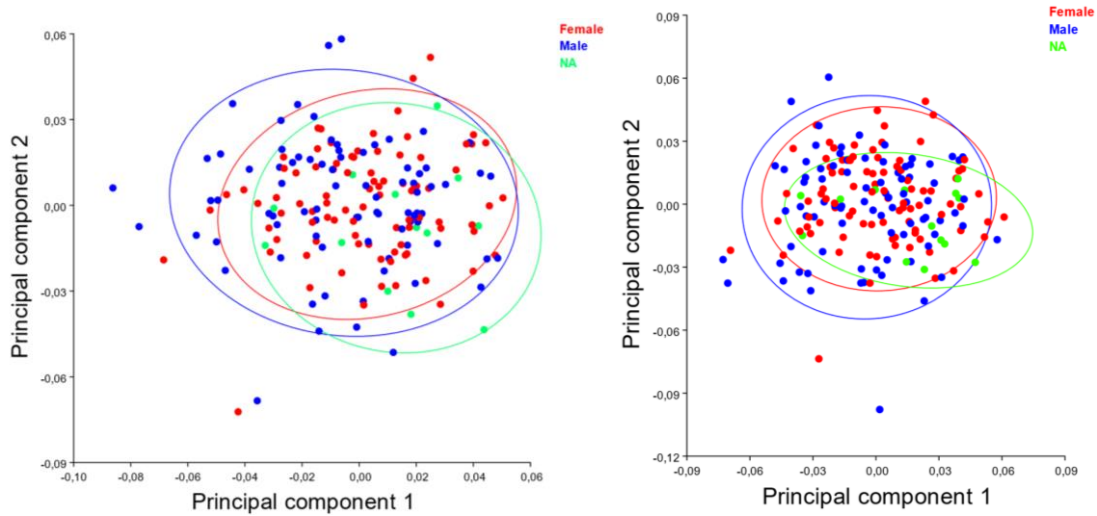


Figure 15. Principal Component analyses (PCA) of *Callicebus* in dorsal view among females and males. Left, PCA without size correction (allometric effect); right, size corrected PCA

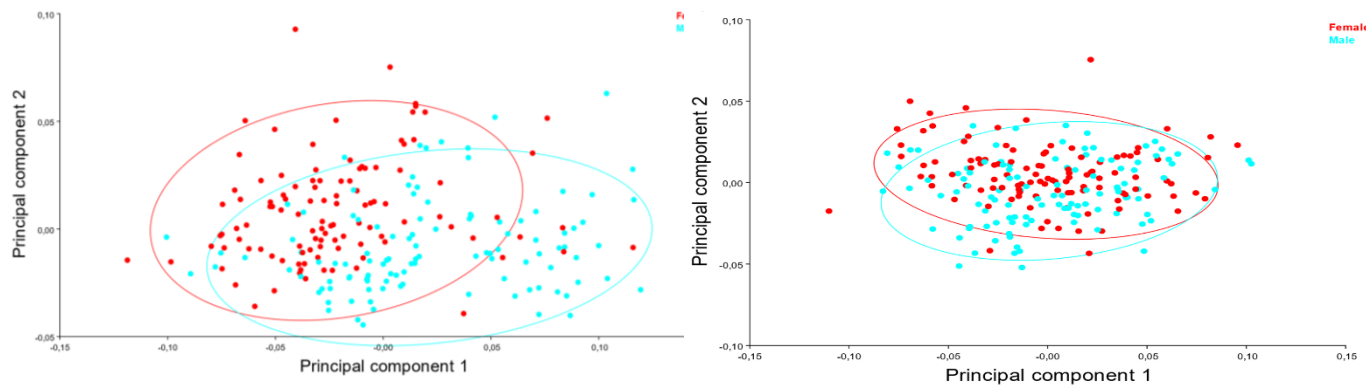


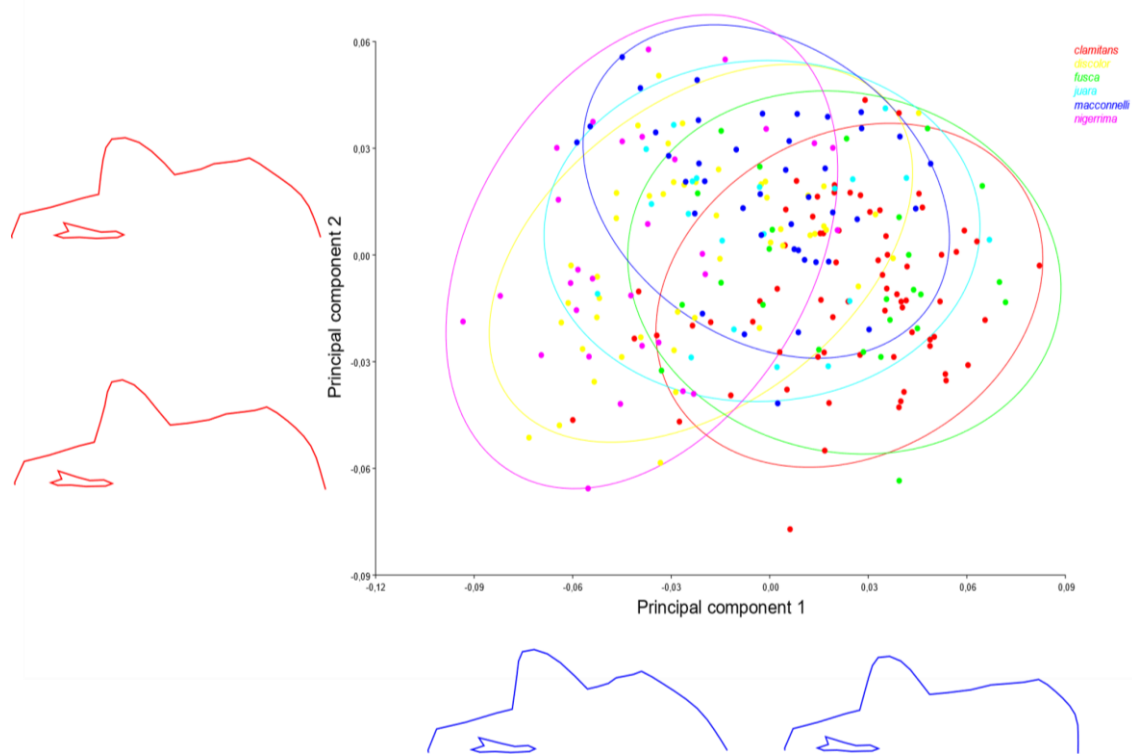
Figure 16. Principal Component analyses (PCA) of *Cebus* in dorsal view among females and males. Left, PCA without size correction (allometric effect); right, size corrected PCA.

3.3 Principal Component Analysis

Dorsal view

After correcting the size by removing the allometric effect, I sorted only species with 20 or more specimens and performed a PCA. The PC1 performed on the skull of species of *Alouatta*, in dorsal view, explained 35.41% of the variance, and did not

discriminate the species, but species as *A. clamitans* was slightly separated from *A. nigerrima*, and at the same time from *A. discolor*. On the other hand, the PC2 explained 19.16% of the variance and did not discriminate among species. Employing “biome” as classifier, groups from the Atlantic Forest and Pampas pooled together and did not show any shape difference. Nonetheless, the only species of the Pampas was *Alouatta clamitans*, which also inhabits the Atlantic Forest. Both groups, Atlantic Forest and Pampas, differ from the Amazon groups mainly in the shape of the zygomatic arch, which could be more robust in Amazonian species; this latter group also possesses shorter parietal and longer occipital bones (Figure 17).



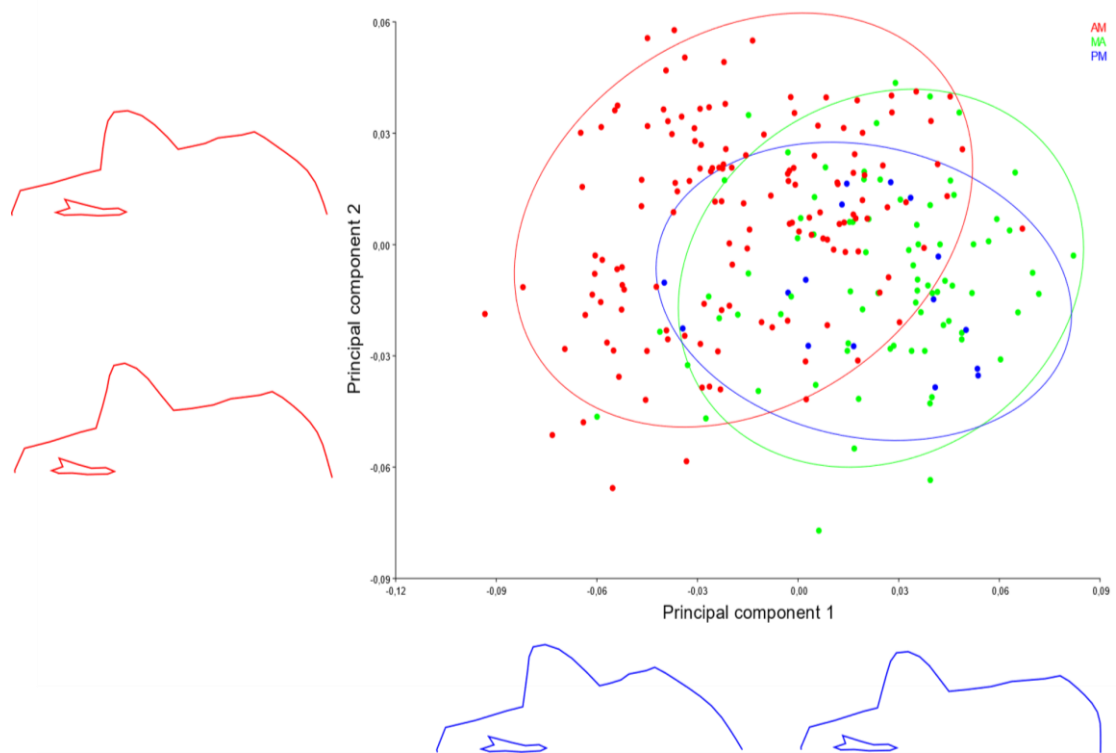


Figure 17. PCA of the dorsal view of *Alouatta* classified by species (upper) and by biome (bottom; AM = Amazonia, MA = Atlantic Forest, PM = Pampas). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.09, +0.09; PC2: -0.06, +0.06).

Regarding *Callicebus*, when classified by species, the PCA showed great overlapping among the taxa. The PC1 explained the 27.09% of the variance, whereas the PC2 the 18.82%. Although this overlap among all the taxa of *Callicebus*, there are some differences: species as *C. nigrifrons* (from the Atlantic Forest), *C. baptista* and *C. hoffmannsi* (both from the Amazon Forest) exhibited a narrow skull, with smaller nasal bones, less projected zygomatic bones, long parietal and rounded occipital bones. When using biome as classifier, specimens from the Cerrado presented the same morphology of the aforementioned species, and Amazon and Atlantic groups exhibited similar morphological variation, being indistinguishable in the shape of the skull (Figure 18).

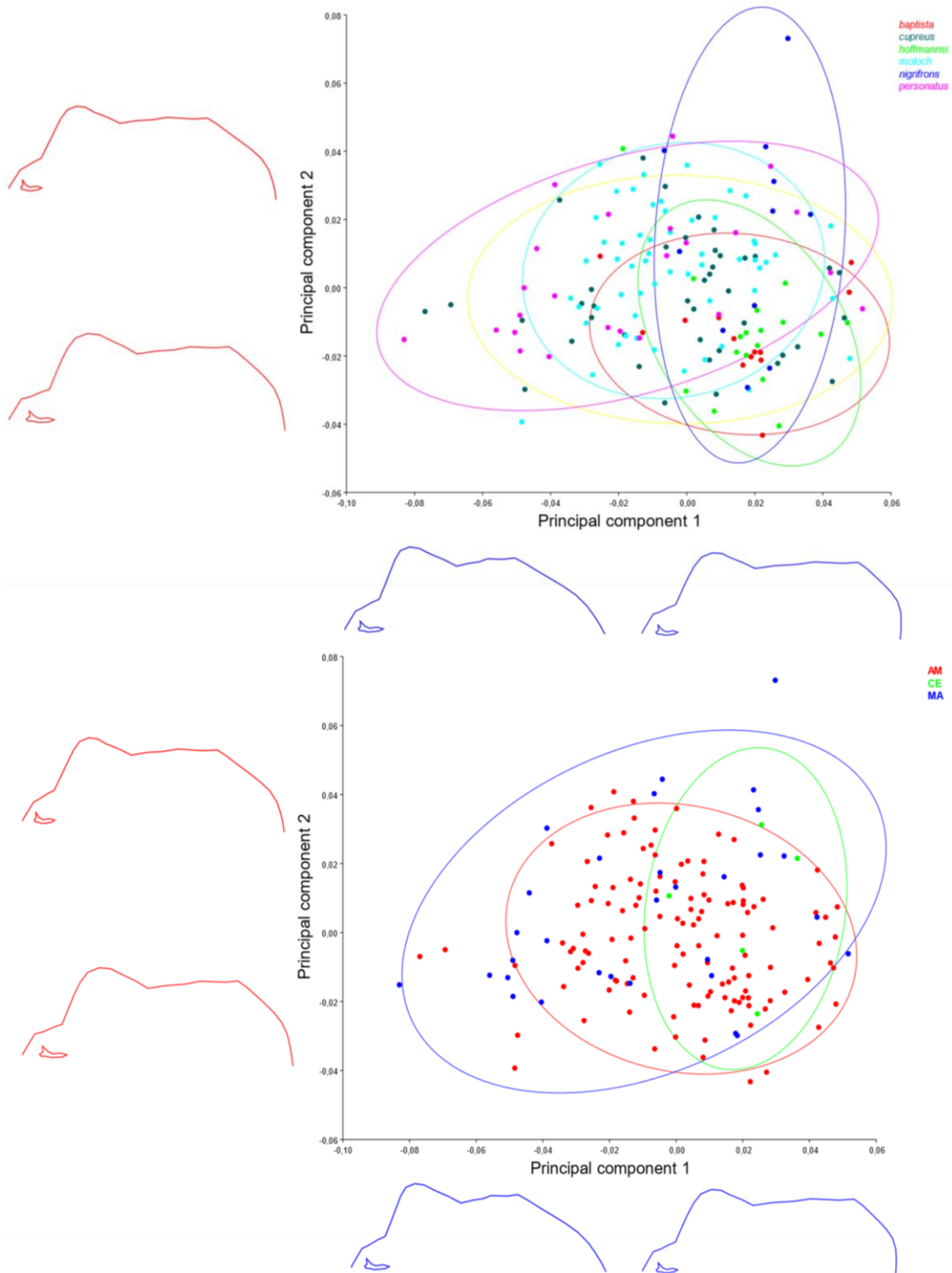
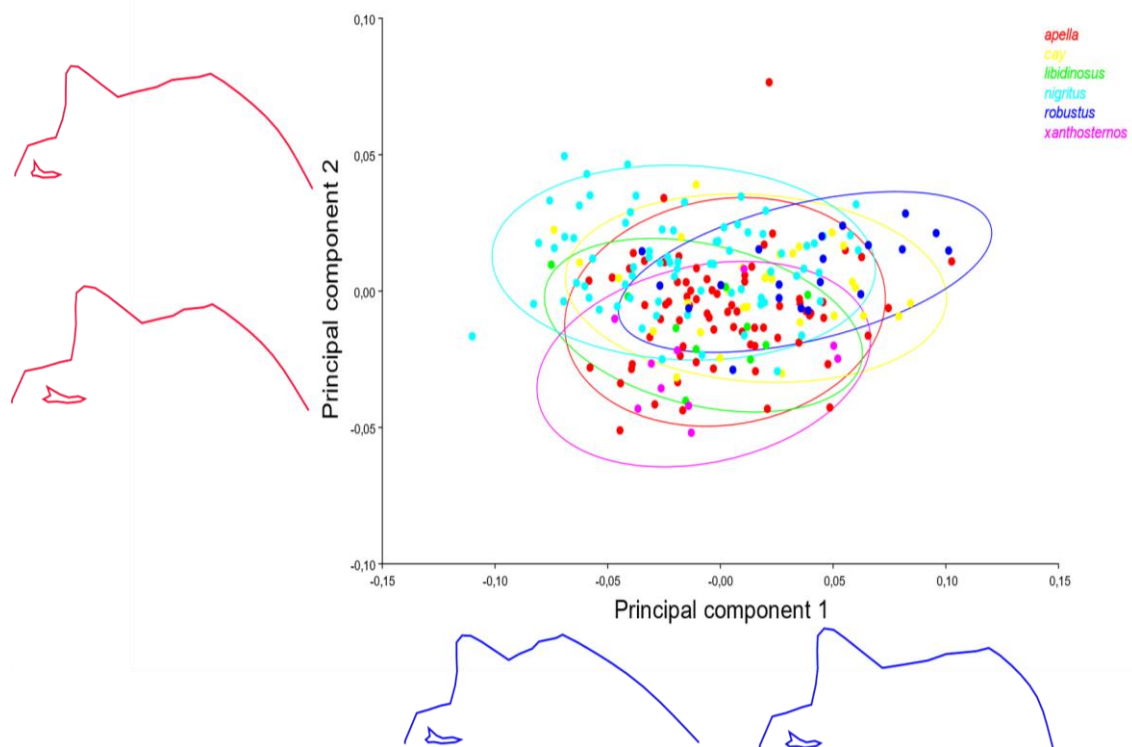


Figure 18. PCA of the dorsal view of *Callicebus* classified by species (upper) and by biome (bottom; AM = Amazonia, CE = Cerrado, MA = Atlantic Forest). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.08, +0.06; PC2: -0.04, +0.06).

In *Cebus* the PC1 explained 55.11% of the variance, whereas the PC2 explained only 12.70%. When classified by species, the PCA showed a slight differentiation among *C. nigritus* and *C. robustus* on the PC1, the latter species with elongated zygomatic arcs and long parietal bones in comparison with the former. The PC2 separated, almost in the same degree that in the first case, *C. xanthosternos* from *C. nigritus* and *C. robustus* mainly related to the length of the parietal bone and the thickness of the zygomatic. Using biome as classifier there is a great overlap among all groups, the only group that had a restricted morphological variation was the Caatinga; however, this group had as limitation the small number of specimens (Figure 19).



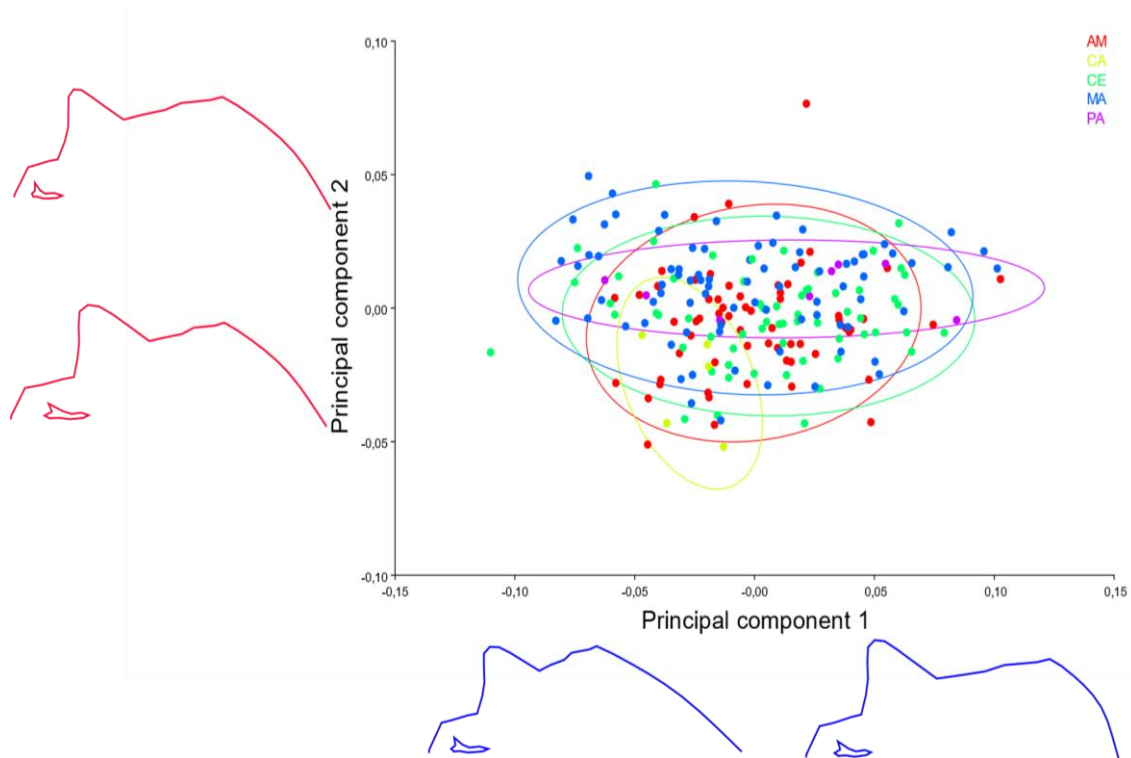


Figure 19. PCA of the dorsal view of *Cebus* classified by species (upper) and by biome (bottom; AM = Amazonia, CA = Caatinga, CE = Cerrado, MA = Atlantic Forest, PA = Pampas). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.1, +0.1; PC2: -0.05, +0.05).

Frontal view

In the PCA of *Alouatta*, the PC1 explained the 29.73% of the variance but did not discriminate the species. Although the PC2 explained the 18.54% of the variance, at least two species, *Alouatta clamitans* (from Atlantic Forest) and *A. macconnelli* (from Amazon), were differentiated in this axis. The main differences between these two species were the long orbits and nasal bone, short frontal bone, and protuberant zygomatic bone in *A. clamitans*. When using “biome” as a classifier, the three groups, Atlantic Forest, Amazonia, and Pampas, did not show any shape differences. The group of *Alouatta* inhabiting the Pampas, although with fewer specimens than the other two groups, presented a more

restricted variation in the PC2 (Figure 20).

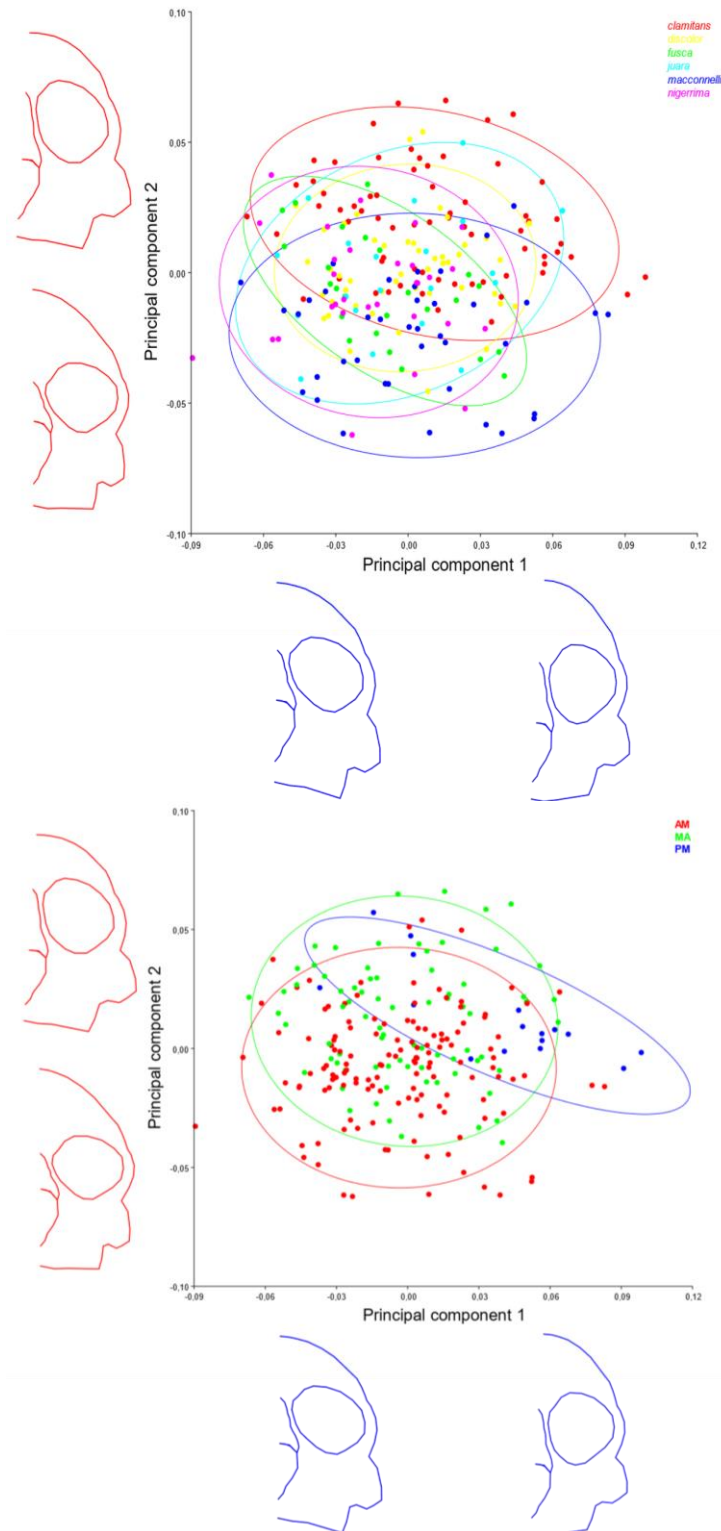


Figure 20. PCA of the frontal view of *Alouatta* classified by species (upper) and by biome (bottom; AM = Amazonia, MA = Atlantic Forest, PA = Pampas). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.06,

+0.09; PC2: -0.05, +0.05).

In *Callicebus*, the PCA showed great overlapping of the individual scores between all the species. The PC1 explained the 22.21% of the variance and in this axis *C. baptista* and *C. personatus* were subtly separated from *C. hoffmannsi*. This latter species possessed more straight parietal bones, more rounded orbitals, shorter nasals, and less projected zygomatic bone than the two former species. The PC2 explained the 17.17% of the variance and discriminated *C. baptista* from both *C. cupreus* and *C. hoffmannsi*. *Callicebus baptista*, in comparison with the two latter species, possesses a more flattened skull, wider orbits, and a short nasal bone. When using “biome” as a classifier, the PC1 separated the Amazonia group from the other two groups, Cerrado and Atlantic Forest. Specimens from the Cerrado and the Atlantic Forest, when compared with those from the Amazonia, presented larger orbits and nasal bone, and flattened premaxillary and maxillary bones. Among the Cerrado and Atlantic Forest groups there were no differences (Figure 21).

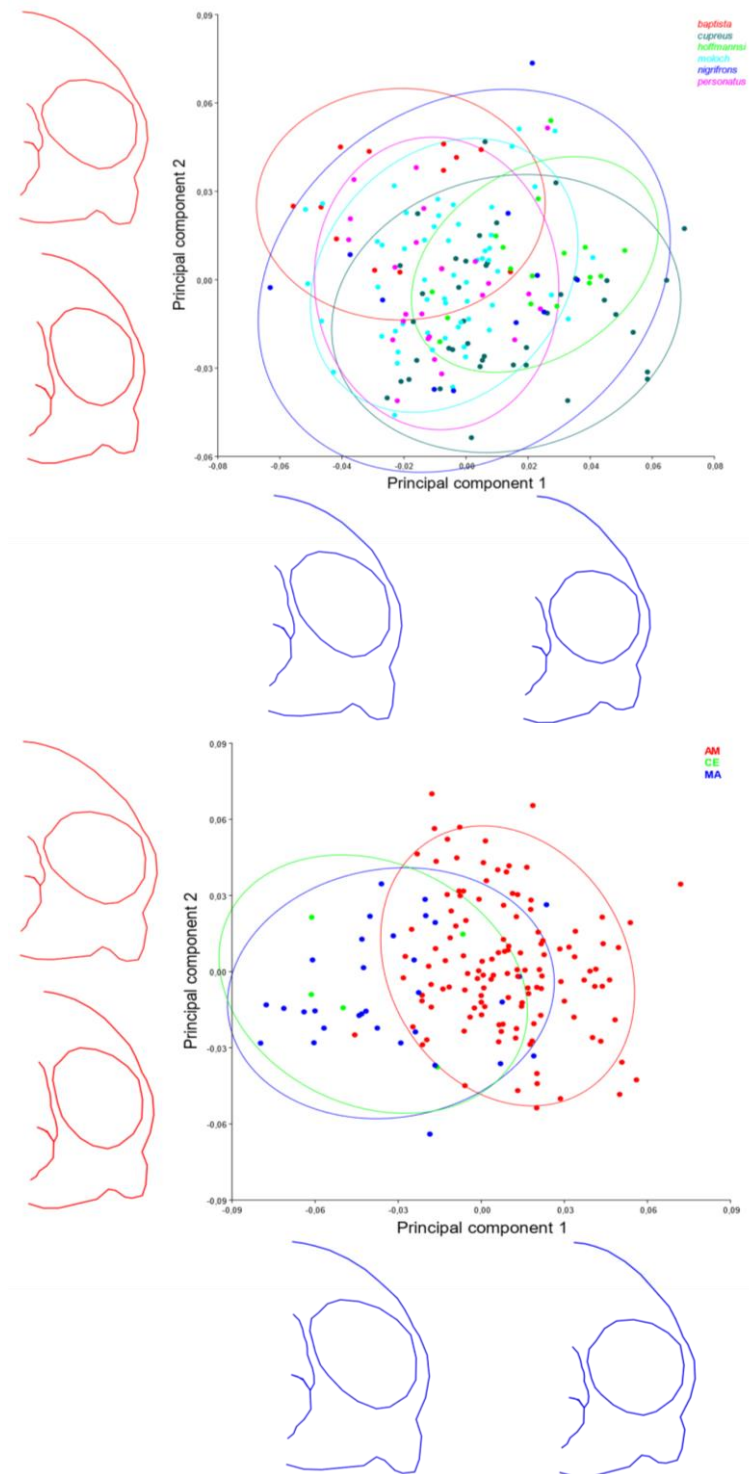


Figure 21. PCA of the frontal view of *Callicebus* classified by species (upper) and by biome (bottom; AM = Amazonia, CE = Cerrado, MA = Atlantic Forest). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.06, +0.06; PC2: -0.06, +0.06).

In *Cebus* the PC1 explained 41.52% of the variance, whereas the PC2 explained the 14.10%. When classified by species, the PC1 showed differences among *Ce. apella* and *C. robustus*, *Ce. nigritus*, and *Ce. libidinosus*. *Cebus apella* presented a more robust and wider skull with large and wide orbits, straight premaxillary and maxillary bones on the PC1, the latter species with elongated zygomatic arcs and long parietal bones in comparison with the former. All species showed great variation along the PC2, but no group was identifiable in this axis. Using biome as a classifier, two main groups were visible along the PC1, the first one consisting of the specimens of the Amazonia and Caatinga and, the second one, formed by those from the Atlantic Forest and the Pampas. The first group distributed in the negative side matches the morphological characters forementioned for *Ce. apella*, while the individuals of the second group possess narrower skulls and orbits, a longer frontal bone and curve maxillary bone. Specimens from the Cerrado presented a high cranial variation (Figure 22), being overlapped to the two previously described groups.

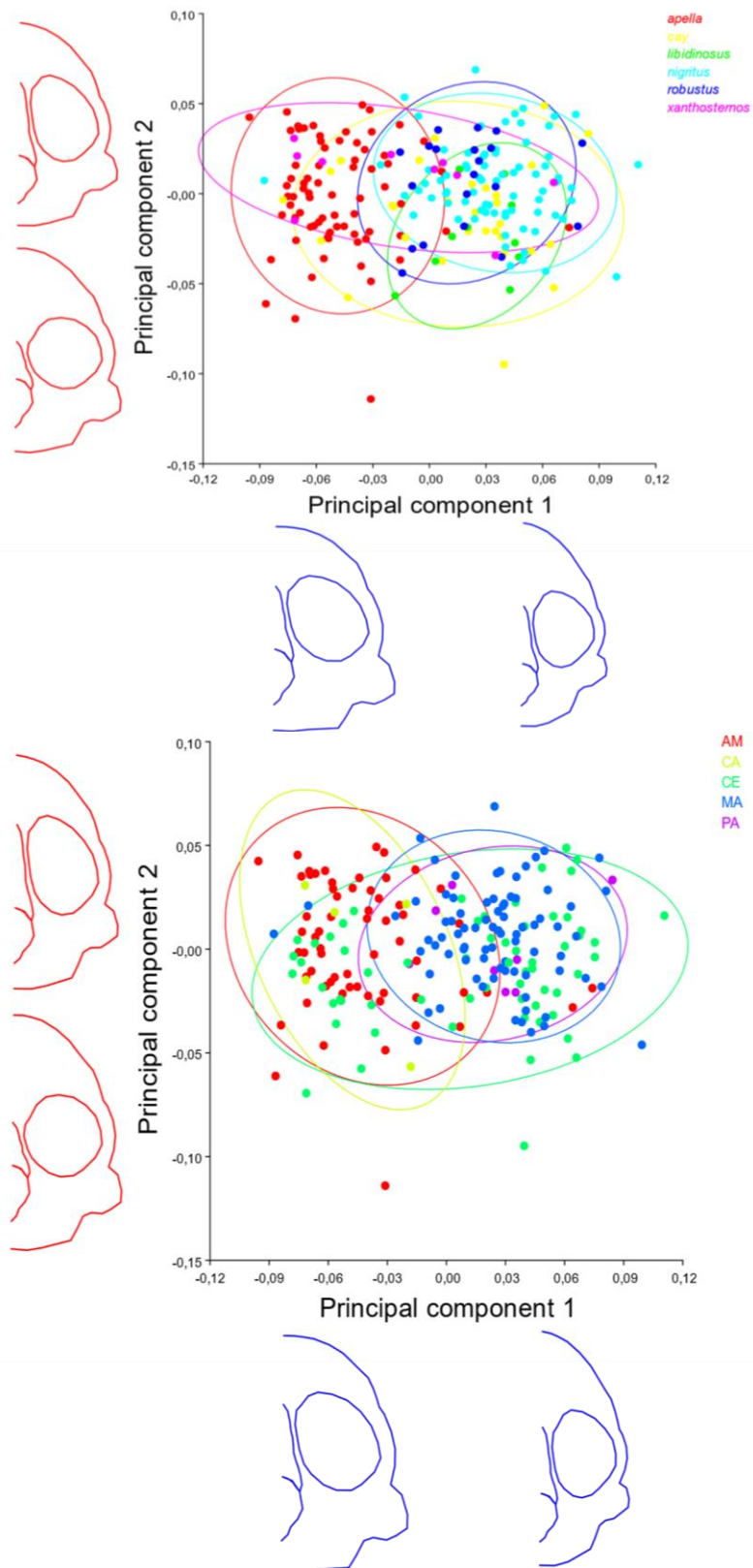
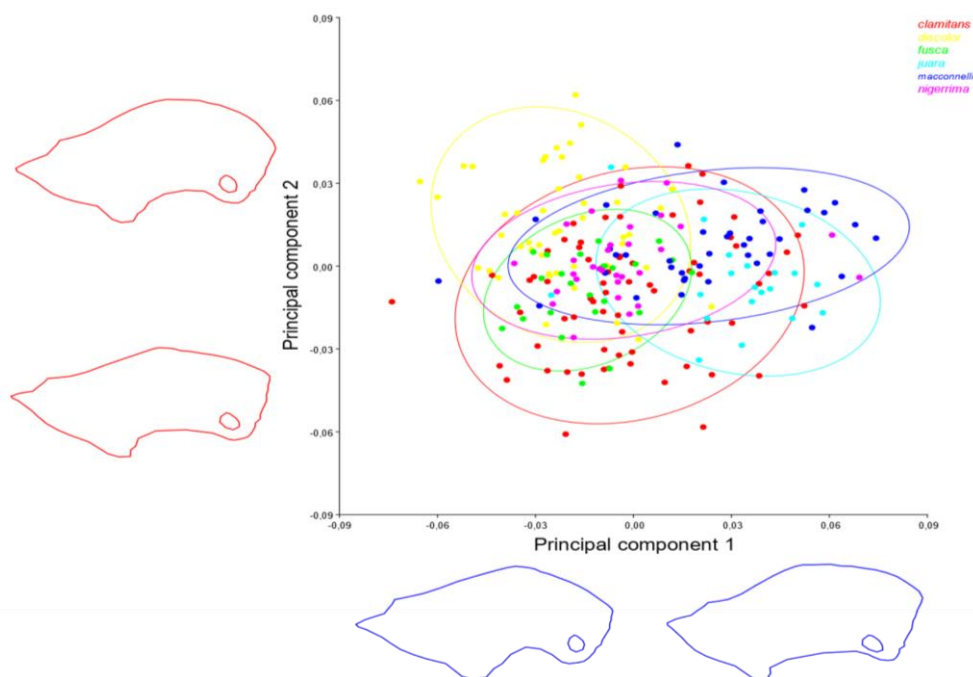


Figure 22. PCA of the frontal view of *Cebus* classified by species (upper) and by biome (bottom, AM = Amazonia, CA = Caatinga, CE = Cerrado, MA = Atlantic Forest, PA = Pampas). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the

graph (Factor scale: PC1: -0.09, +0.09; PC2: -0.09, +0.09).

Lateral view

In the PCA of *Alouatta*, the PC1 explained the 37.45% of the variance and in this axis species as *A. discolor* and *A. fusca* differed from *A. juara* in having shorter and flatter parietal bones and more robust zygomatic bones. The remaining species, *A. clamitans*, *A. macconnelli*, and *A. nigerrima*, presented a broader morphological variation along the PC1. The PC2 explained the 16.70% of the variance, *Alouatta discolor* showed the greatest variation in this axis. This species presented a more rounded skull with long premaxillary bone. Using “biome” as classifier, the three groups, Atlantic Forest, Amazonia, and Pampas did not show any clear differences. Nevertheless, the Amazonia and Atlantic Forest groups presented a noticeable variation along the PC1 not seen in the Pampas group, matching that morphology observed and described above for *A. discolor* (Figure 23).



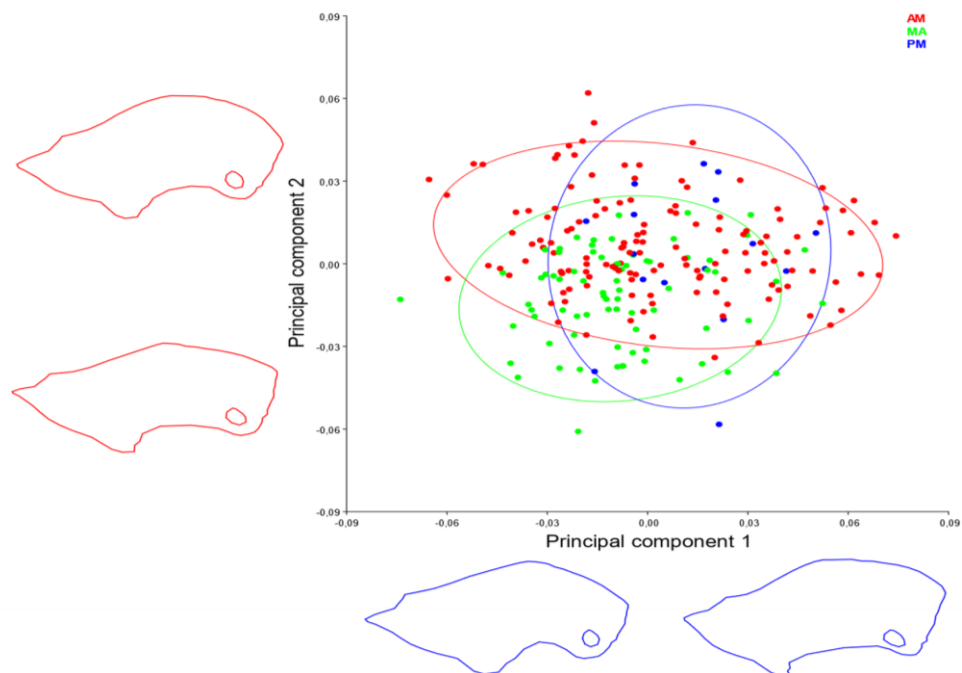


Figure 23. PCA of the frontal view of *Alouatta* classified by species (upper) and by biome (bottom, AM = Amazonia, MA = Atlantic Forest, PA = Pampas). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.06, +0.06; PC2: -0.06, +0.06).

The PCA of *Callicebus* showed, once again, great overlapping among all the species. The PC1 explained the 17.49% of the variance, and *C. cupreus* and *C. nigrifrons* were subtly separated by a longer and more oblique skull in the latter species. The PC2 explained the 13.15% of the variance and did not discriminate any groups when classified by species. When using “biome” as a classifier, all the specimens are grouped together in both PC1 and PC2. Thus, no clear group is identifiable with this classifier (Figure 24).

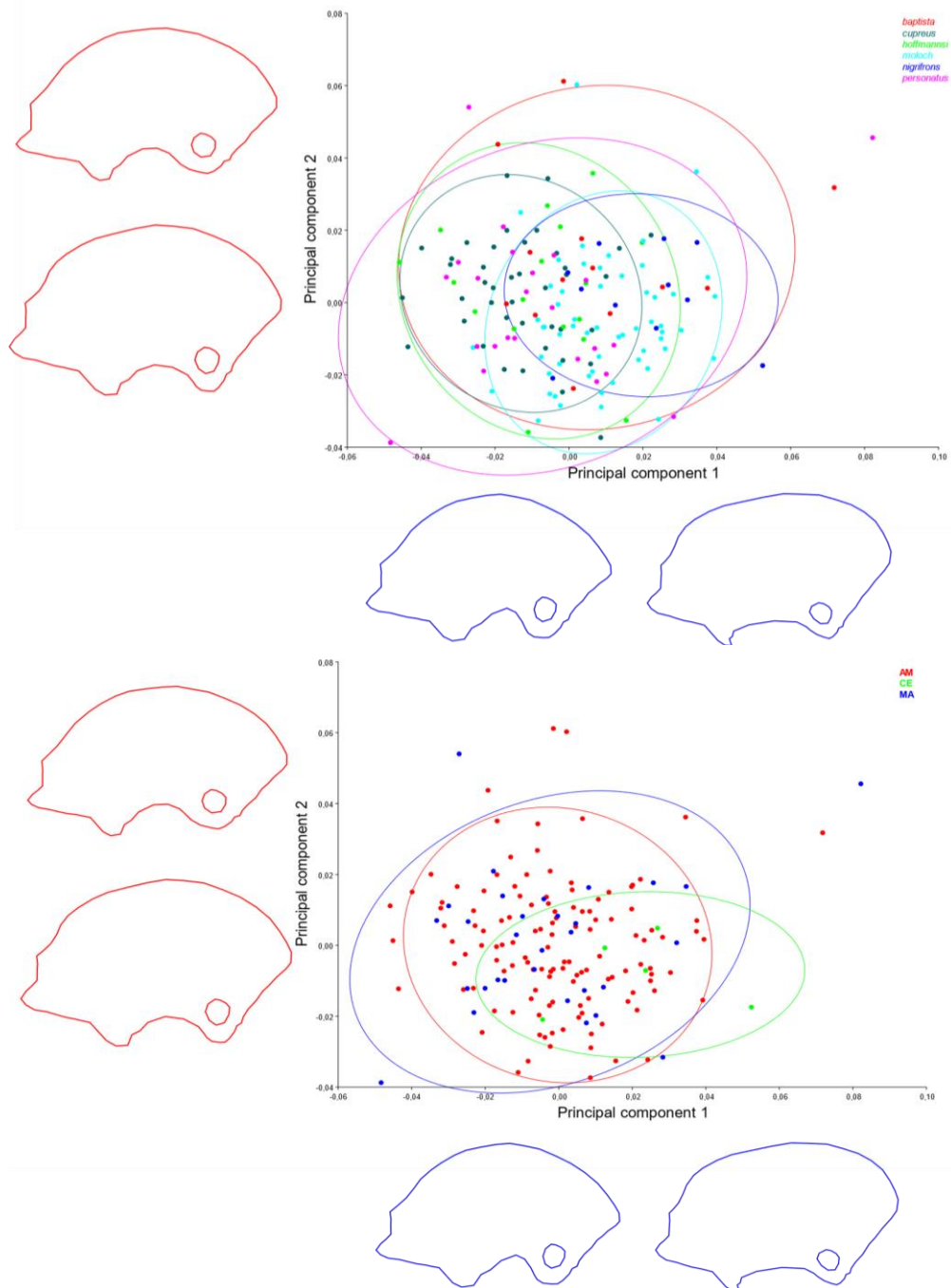
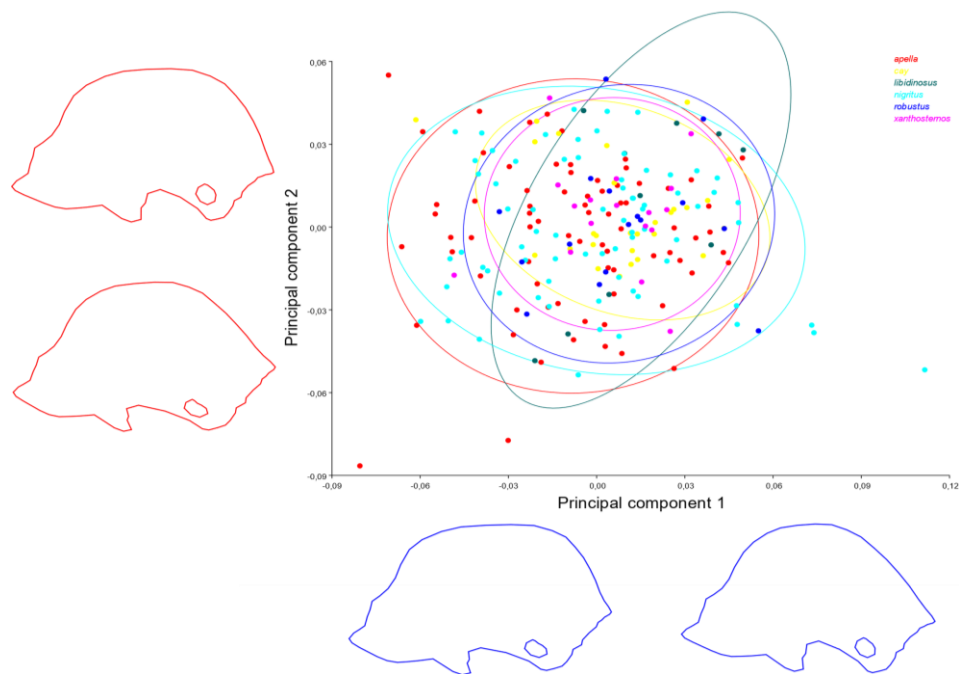


Figure 24. PCA of the frontal view of *Callicebus* classified by species (upper) and by biome (bottom, AM = Amazonia, CE = Cerrado, MA = Atlantic Forest). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.06, +0.06; PC2: -0.04, +0.06).

The lateral view was found to be the least informative in *Cebus*. The PC1 explained 21.83% of the variance, whereas the PC2 explained the 19.74%. When classified by

species, *Ce. nigritus* showed the greatest degree of variation, passing through all morphologies of the PC1. This is a pattern, although to a lesser degree, shared also by *Cebus apella*. As in the case of the PC1, there were no clear groups along the PC2. There is, nonetheless, a great morphological variation in the case of *Ce. libidinosus*, like *Ce. nigritus* and *Ce. apella* in the PC1. When using biome as classifier, all the groups presented high morphological variation among both axes. The only group presenting a narrow variation in the PC1 and PC2 was the Pampas one (Figure 25).



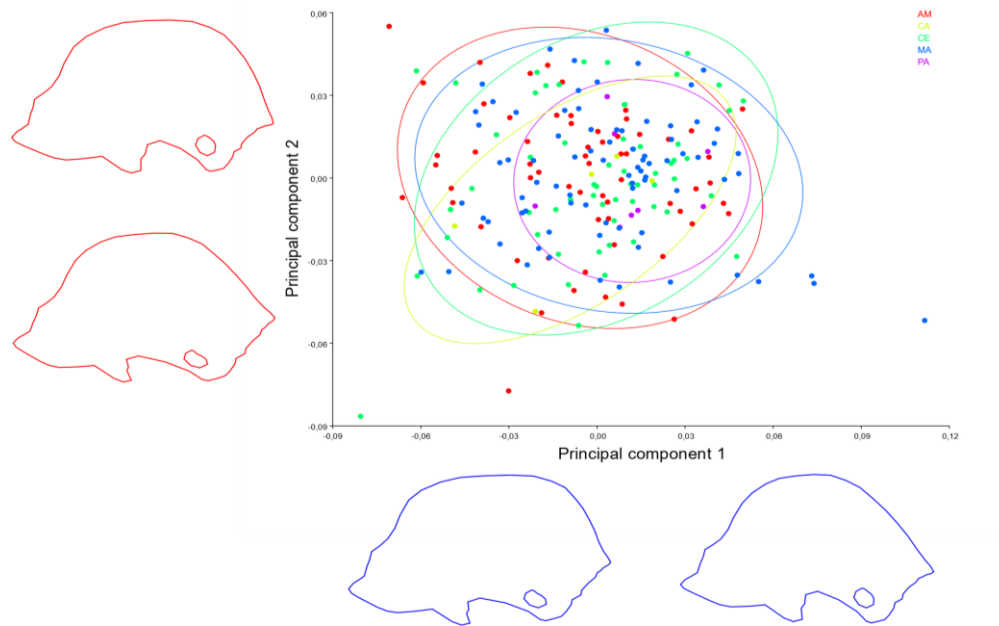


Figure 25. PCA of the lateral view of *Cebus* classified by species (upper) and biome (bottom, AM = Amazonia, CA = Caatinga, CE = Cerrado, MA = Atlantic Forest, PA = Pampas). The view of each landmark configuration at the negative and positive end in both PC1 and PC2 are shown below and beside of the graph (Factor scale: PC1: -0.06, +0.09; PC2: -0.06, +0.06).

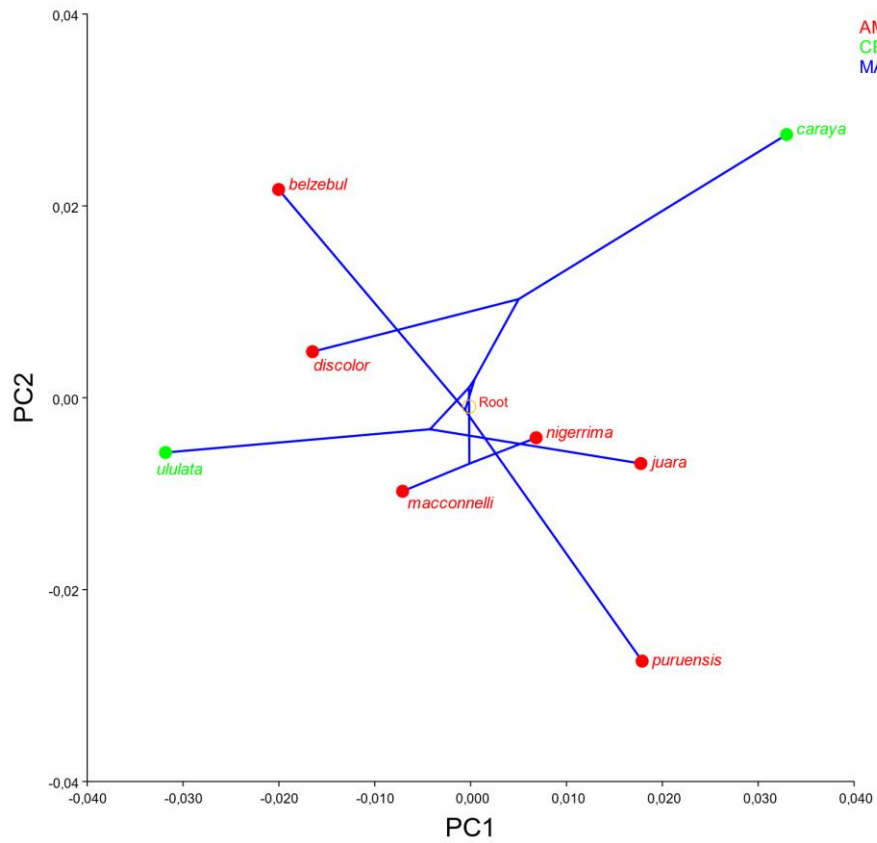
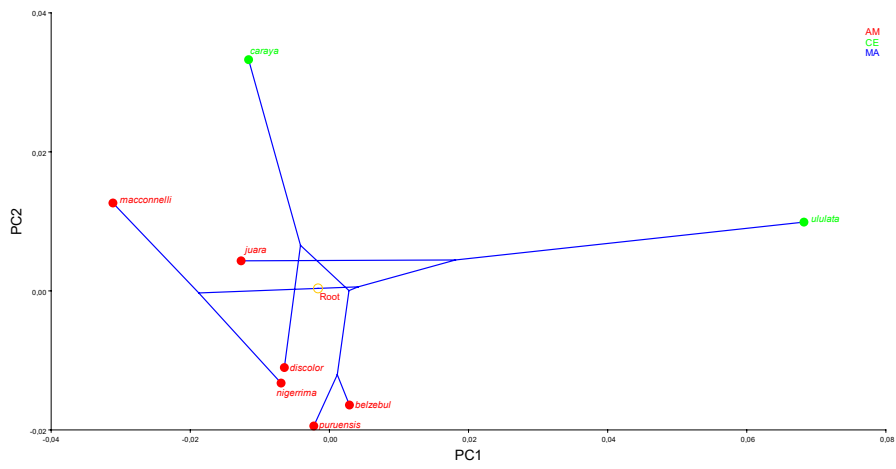
Phylogenetic Principal Component Analysis

To evaluate if there was a phylogenetic signal influencing the shape variation, I firstly averaged the shapes for species and performed a PCA with these new Procrustes coordinates. After this step, I selected the species that were also present in the phylogenetic tree. After uploading the phylogenetic tree into the MorphoJ software, I plotted it into the PCA. I repeated this procedure for each genus in all three views.

In the case of *Alouatta*, in dorsal view, the permutation test against the null hypothesis of no phylogenetic signal, after 10,000 randomization rounds, was not significant (P-value = 0.58). Thus, there is no significant correlation among phylogeny and shape in *Alouatta*. The PC1 explained the 55.67% of the total variance whereas the PC2 the 21.52%. After choosing “biome” as classifier, species from different biomes were

clearly separated; *A. caraya* (Cerrado), although more closely related to *A. discolor* (Amazonia), was placed in the most positive extreme point of the PC2 (+0.03). All species but *A. belzebul* and *A. ululata* were distributed in the negative side of PC1 whereas in the PC2 two main groups were clearly distinguishable, one of them with *A. discolor*, *A. nigerrima*, *A. belzebul*, and *A. puruensis*, all distributed in the negative side of the PC; on the other hand, scores of *A. macconnelli*, *A. juara*, *A. caraya*, and *A. ululata* are distributed along the positive side of this axis. All the Amazonian species remained close phylogenetically; *Alouatta ululata* (Cerrado), a species closely related to *A. juara* (Amazonia), was placed on the most extreme point of the PC1 (+0.07), quite far from all the remaining species. There are, nonetheless, two points to be addressed regarding this result: i) the phylogenetic relationships among the analyzed species, which are clearly influenced by the set of species available; and ii) the small sample size of *A. ululata* (N = 1), suggesting that the position of *A. ululata* in the PCA might be considered as preliminary. In the frontal view, the influence of the phylogenetic signal was not significant (P-value = 0.8120). The percentage of variance explained by the first two Principal Components were 37.91 and 23.72, respectively. Once selected "biome" as a classifier, the pattern of differentiation is like the one of dorsal view, with species grouped by its corresponding biome along the PC1 axis. In the most negative extreme PC1 was *Alouatta ululata* (from the Cerrado), following by the Amazonian species from -0.02 to +0.02 of PC1, and finally *A. caraya* in the positive extreme of the PC1. In lateral view, the phylogenetic signal was also not significant (P-value = 0.5837). The PC1 explained the 53.42% of the variance, whereas the PC2 the 29.73%. In this view, *A. caraya* fell within the Amazonian species in the PC1, near to *A. discolor* and *A. belzebul*; *A. puruensis* and *A.*

ululata fell in the negative and positive extremes of the PC1, respectively (Figure 26).



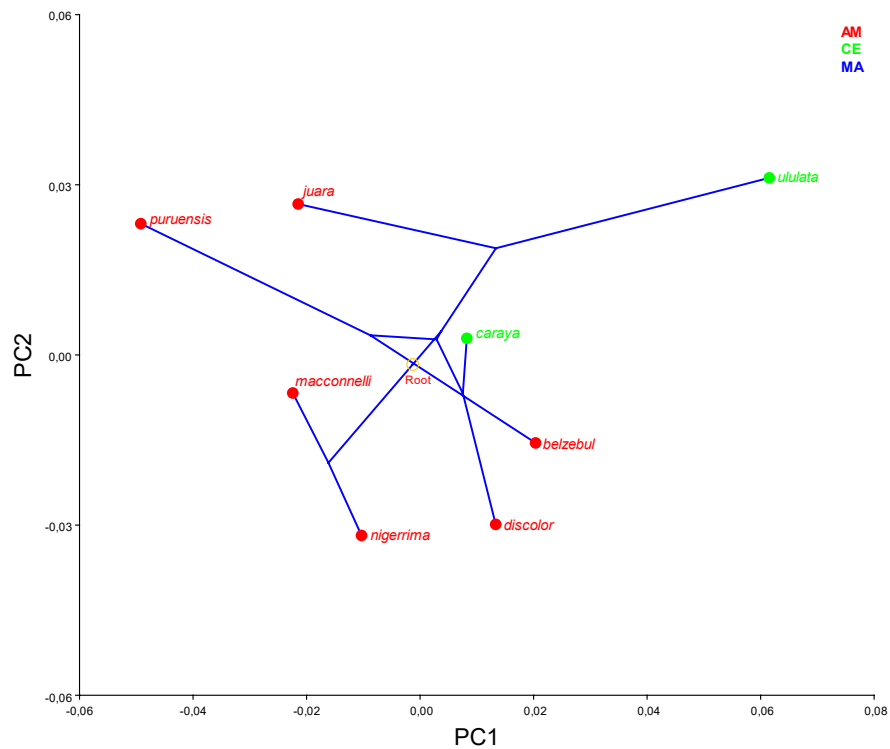
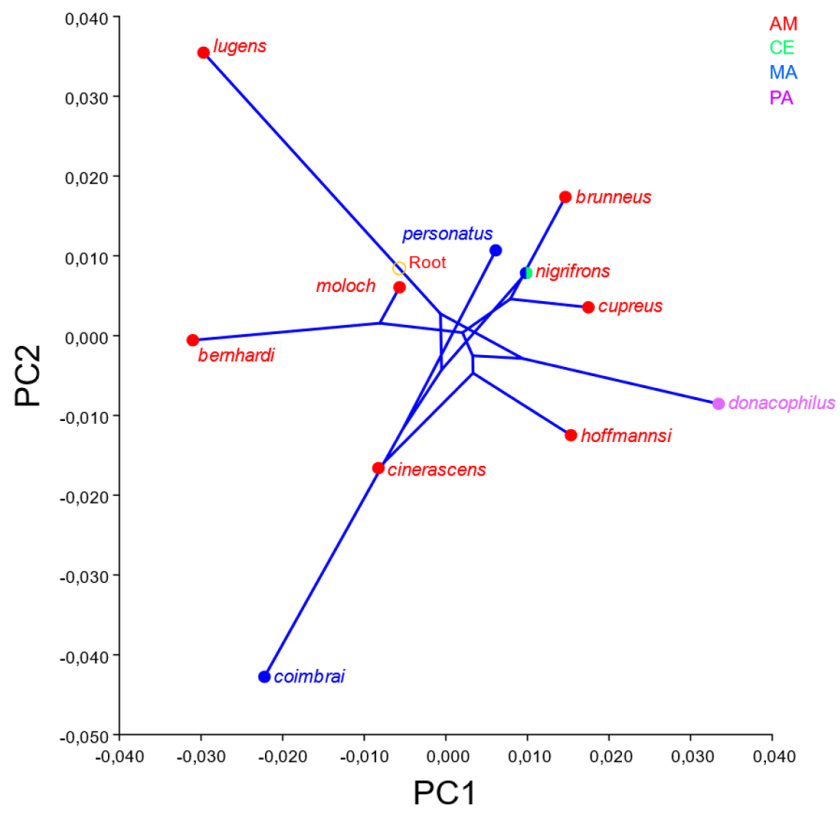
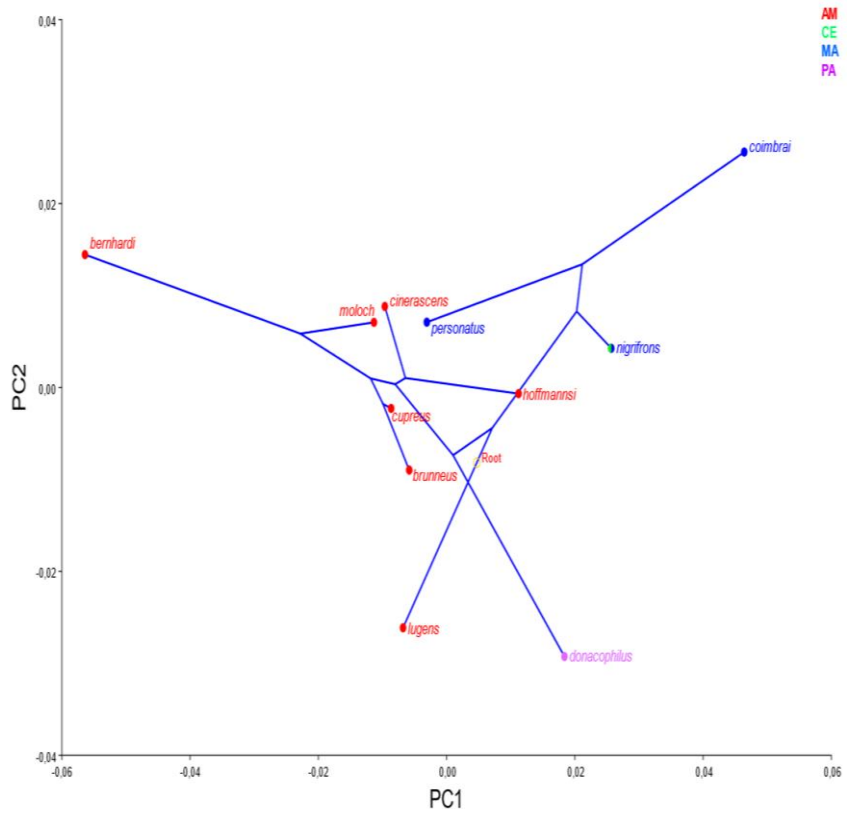


Figure 26. Phylogenetic mapping on PCA Shape of *Alouatta* in dorsal (top) frontal (middle), and lateral (bottom) view. In green are the two species from the Cerrado, *A. caraya* and *A. ululata*; in red the Amazonian *A. juara*, *A. belzebul*, *A. puruensis*, *A. discolor*, *A. nigerrima*, and *A. macconnelli*.

Regarding *Callicebus*, the phylogenetic signal was significant (P-value = 0.0364). The PC1 and the PC2 explained the 52.09% and 20.44% of the variance, respectively. As in the case of *Alouatta*, when classified by “biome”, species of *Callicebus* from Amazonia were closely distributed, but *Ca. personatus*, from the Atlantic Forest and phylogenetically related to *Ca. coimbrai*, was closer in the morphospace to the Amazonian species *Ca. cinerascens* and *Ca. moloch*. The averaged shape of *Ca. bernhardi* (Amazonia) and *Ca. coimbrai* (Atlantic Forest) represented the most extreme variations among the PC1. In the PC2 *Ca. coimbrai* was in the positive extreme of the PC2, whereas *Ca. lugens* and *Ca. donacophilus* fell on the extreme negative side. In frontal view, the phylogenetic signal was not significant (P-value = 0.2239); the PC1 and PC2 explained the 32.31% and 29.94% of the variance, respectively. Using “biome” as classifier no clear

segregation is clear, as Amazonian species are separated in the PC1, in the negative side *Ca. lugens*, *Ca. moloch*, *Ca. bernhardi*, and *Ca. cinerascens* are grouped with *Ca. coimbrai* (Atlantic Forest). The other two species of the Atlantic Forest, *Ca. personatus* and *Ca. nigrifrons* were on the positive side of the PC1 along with the remaining Amazonian species and *Ca. donacophilus* (from the Pampas). As in the previous view, *Ca. bernhardi* and *Ca. donacophilus* represented the most extreme variation in the negative and positive PC1, respectively. In lateral view, there was a significant phylogenetic signal (P-value = 0.0098). The PC1 and PC2 explained the 37.47% and 23.20% of the variance, respectively. At this point it is important to highlight the great disparity among *Ca. bernhardi* and the remaining Amazonian species of *Callicebus* that, although been phenotypically and genetically close to *Ca. moloch*, presented a cranial morphology which in all three views. *Ca. donacophilus* and *Ca. lugens* were also two species well differentiated in all the analyzes of this section (Figure 27).



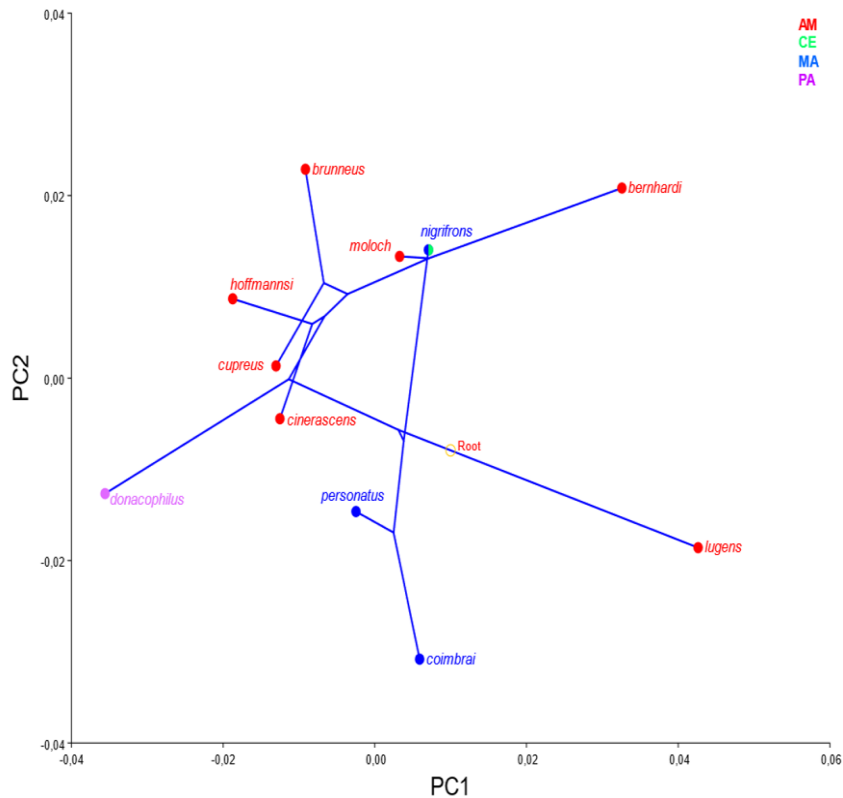
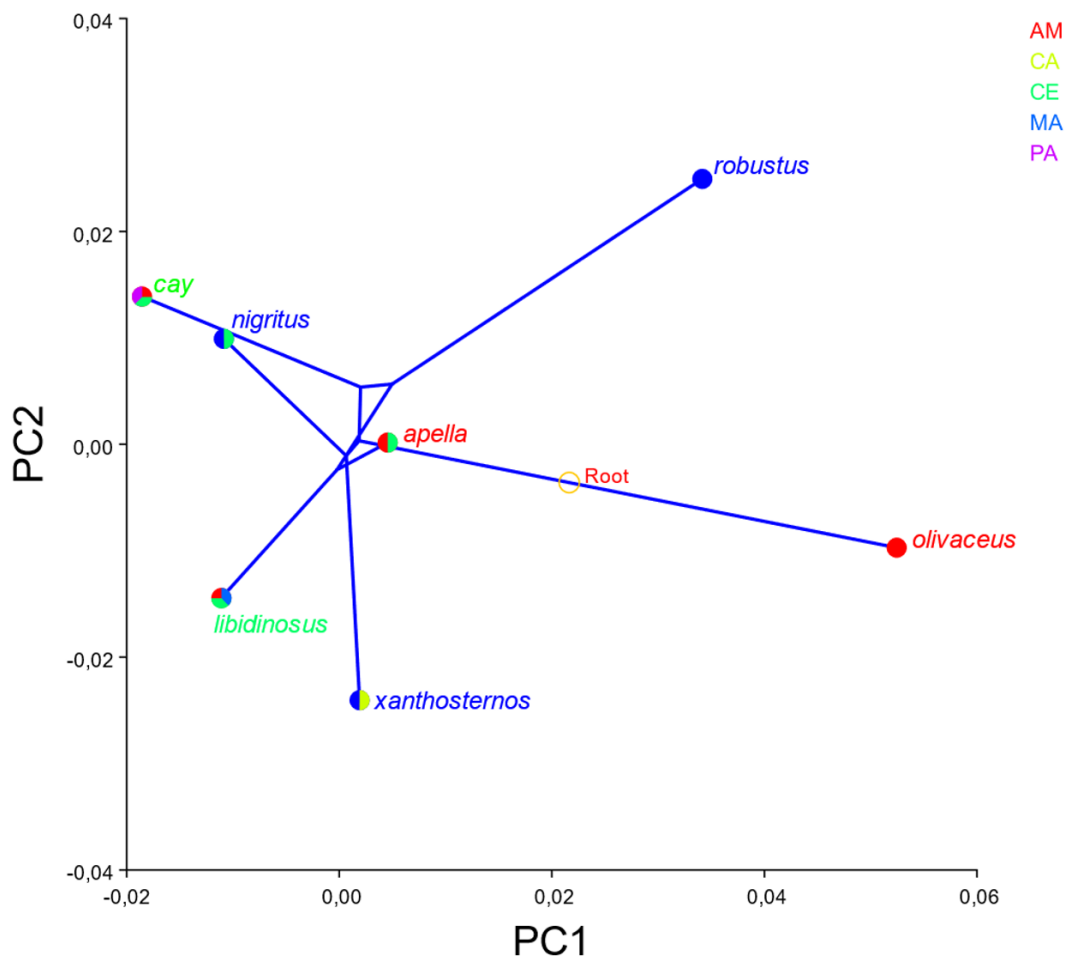


Figure 27. Phylogenetic mapping on shape of *Callicebus* in dorsal (top), frontal (middle), and lateral (bottom) view. In red the Amazonian species; in purple the only species from the Pampas, *Callicebus donacophilus*; in blue species from the Atlantic Forest, *Ca. nigrifrons* is the only species inhabiting both the Atlantic Forest and the Cerrado.

In *Cebus* the phylogenetic signal was also not significant (P-value = 0.4482). The PC1 and the PC2 explained the 51.71% and 26.28% of the variance, respectively. No clear segregation was detected in this genus. Using “biome” as classifier, *Ce. cay*, *Ce. nigritus*, and *Ce libidinosus* fell in the negative portion of the PC1. *Ce. olivaceus* was stand alone in the positive end of PC1. Nonetheless, this species was represented in this analysis by only one individual, which is certainly not showing the morphological variation of this taxon. In the positive PC2, *Ce. cay*, *Ce. nigritus*, and *Ce. robustus* were separated from all other species with the latter in the most extreme point of this axis. There was no significant phylogenetic signal in the frontal view of *Cebus* (P-value = 0.3390). The total variance

explained by the first two Principal Components was of 67.61% and 15.68%, respectively. There was no clear separation when classified the data by “biome”, *Ce. apella* fell at the negative end of the PC1 and *Ce. olivaceus* at the positive one. In lateral view the phylogenetic signal was also not significant (P-value = 0.1107) and the PC1 explained the 80.71% of the variance while the PC2 the 8.31%. Although the PC1 explained a great amount of variance, this seems to be directly influenced by *Ce. olivaceus* which position remains preliminary (Figure 28).



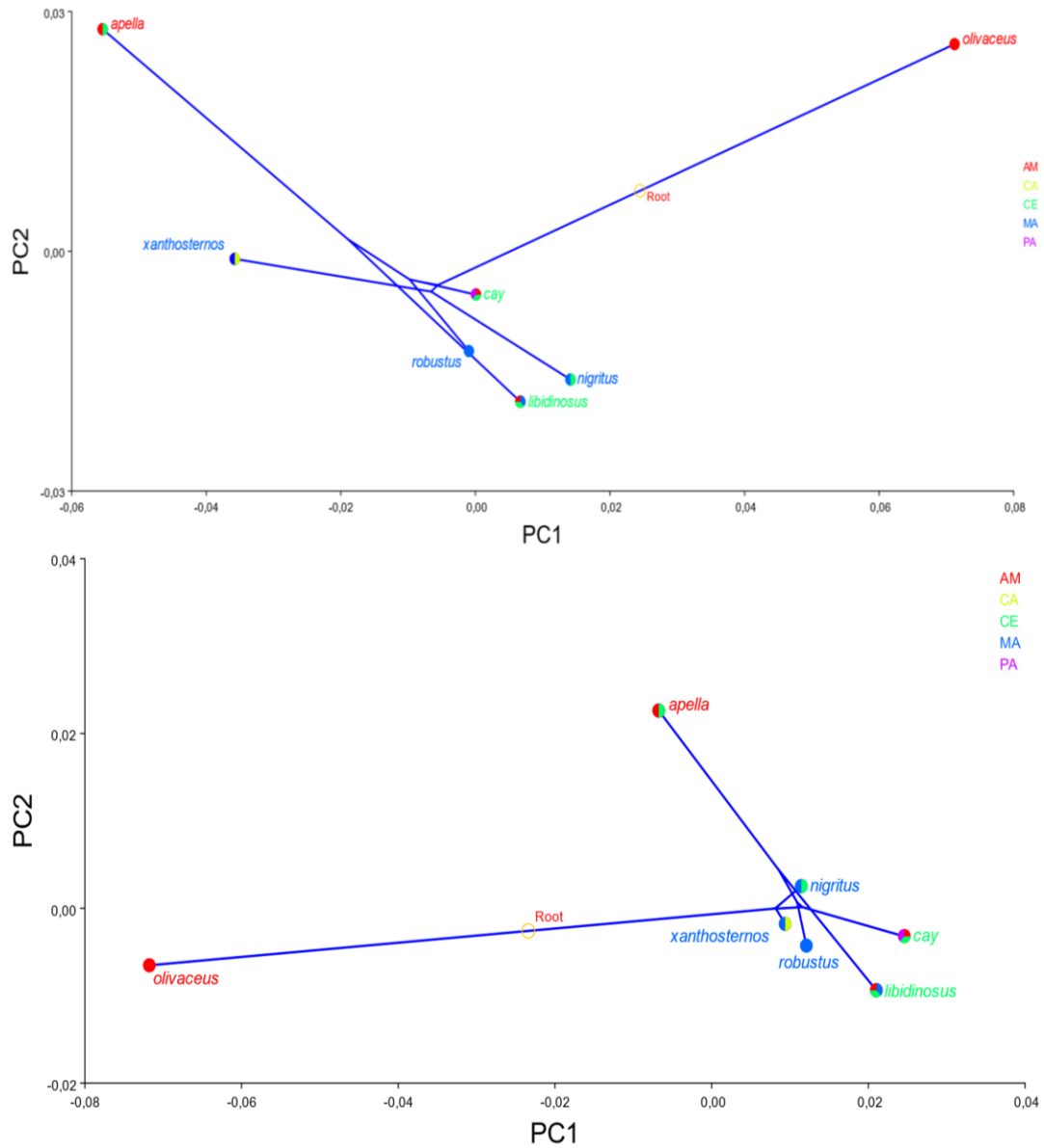


Figure 28. Phylogenetic mapping on shape of *Cebus* in dorsal (top), frontal (middle), and lateral (bottom). *Ce. robustus* (Atlantic Forest) and *Ce. olivaceus* (Amazonia) inhabit exclusively only one biome. Species inhabiting two biomes are *Ce. apella* (Amazonia and Cerrado), *Ce. nigrinus* (Atlantic Forest and Cerrado), and *Ce. xanthosternos* (Atlantic Forest and Caatinga). Two species, *Ce. cay* (Amazonia, Cerrado, and Pampas) and *Ce. libidinosus* (Amazonia, Atlantic Forest, and Cerrado), occupy three biomes.

3.4 Ecomorphology

Size

The PLS between Size (Block 1) and BIOCLIM (Block 2) produced RV coefficients

with a clear pattern in all three views and genera. *Callicebus* presented the highest RV coefficients in dorsal (0.267, $p < 0.0001$), frontal (0.238, $p < 0.0001$), and lateral (0.330, $p < 0.0001$) views, significantly higher than those of *Alouatta* (0.024, $p = 0.015$; 0.085, $p < 0.0001$; 0.046, $p = 0.0001$; respectively) and *Cebus* (0.021, $p = 0.045$; 0.060, $p < 0.0001$; 0.050, $p = 0.0001$; respectively). The same pattern is observed when comparing Size (Block 1) with Latitude/Longitude (Block 2), *Callicebus* (0.334, $p < 0.0001$; 0.326, $p < 0.0001$; 0.399, $p < 0.0001$; in dorsal, frontal, and lateral view, respectively) presented significant highest RV coefficients (0.334, $p < 0.0001$; 0.326, $p < 0.0001$; 0.399, $p < 0.0001$; in dorsal, frontal, and lateral view, respectively) than *Alouatta* (0.038, $p = 0.002$; 0.112, $p < 0.0001$; 0.059, $p < 0.0001$) and *Cebus* (0.011, $p = 0.143$; 0.021, $p < 0.042$; 0.011, $p = 0.148$) (see Table 3). Although all these RV coefficients are weak (< 0.5), the results point out that skull size is more influenced by covariates as bioclimatic factors (BIOLCIM) and Latitude/Longitude in the case of *Callicebus* rather than in *Alouatta* and *Cebus*. Since the Block 1 was represented by the univariate centroid size, I only obtained one singular value (SV) and the percentage of between-block total squared covariance explained by the set of PLS1 was of 100% in all cases.

In the case of the three views (dorsal, frontal, and lateral) of *Alouatta* the PLS plot of Size vs BIOCLIM showed overlapping between Amazonian species (*A. puruensis*, *A. belzebul*, *A. discolor*, *A. macconnelli*, *A. nigerrima*, and *A. ululata*), whereas *A. caraya* (from the Cerrado) fell within the species from the Atlantic Forest, *A. clamitans* and *A. fusca* (Figure 29). The correlations among these two blocks in dorsal, frontal, and lateral view were 0.172 ($p = 0.034$), 0.311 ($p < 0.0001$), and 0.227 ($p = 0.002$), respectively. In the PLS Size vs Latitude/Longitude, there was great gap among the Amazonian species and

the Atlantic Forest and Cerrado species. In the former there was a great overlapping excepting for *A. juara* that remained isolated from other Amazonian species. The correlations among Size Block1 and Latitude/Longitude Block1 in dorsal, frontal, and lateral view were 0.198 ($p=0.003$), 0.339 ($p<0.0001$), and 0.246 ($p=0.0001$), respectively (see Table 4). In both comparisons, Size vs BIOCLIM and Size vs Latitude/Longitude, the correlations were higher in frontal view.

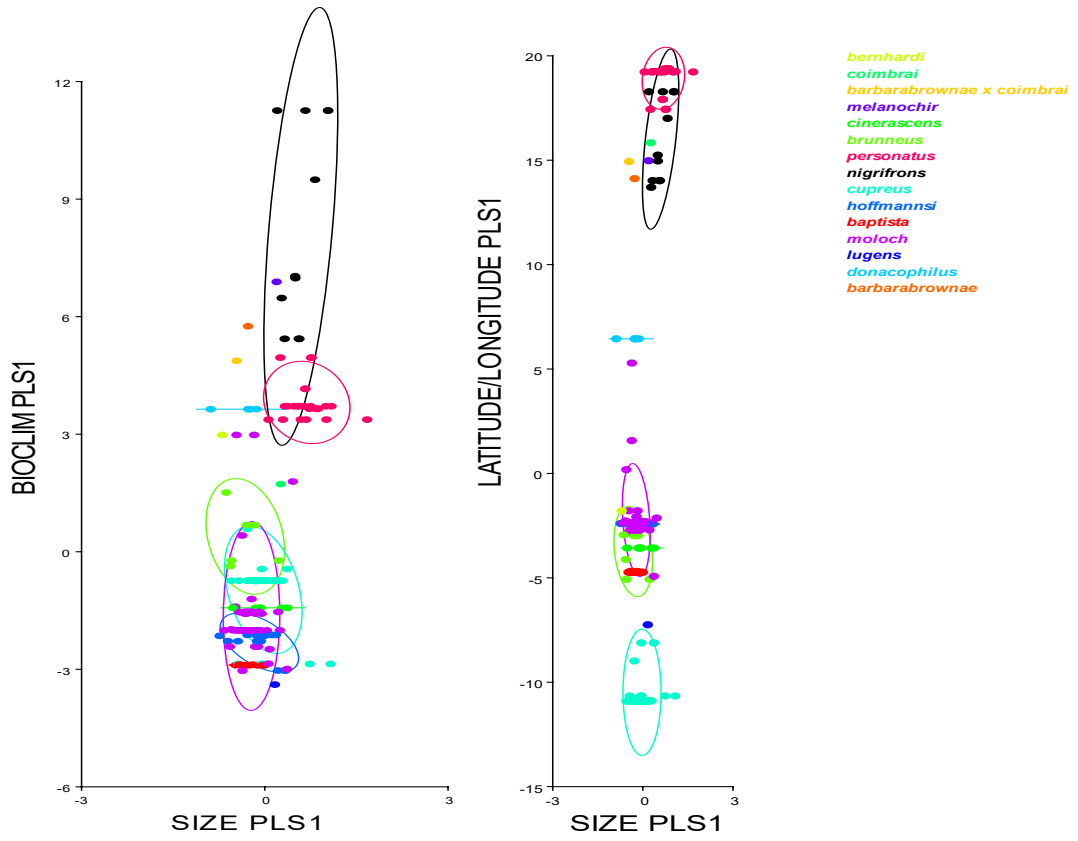
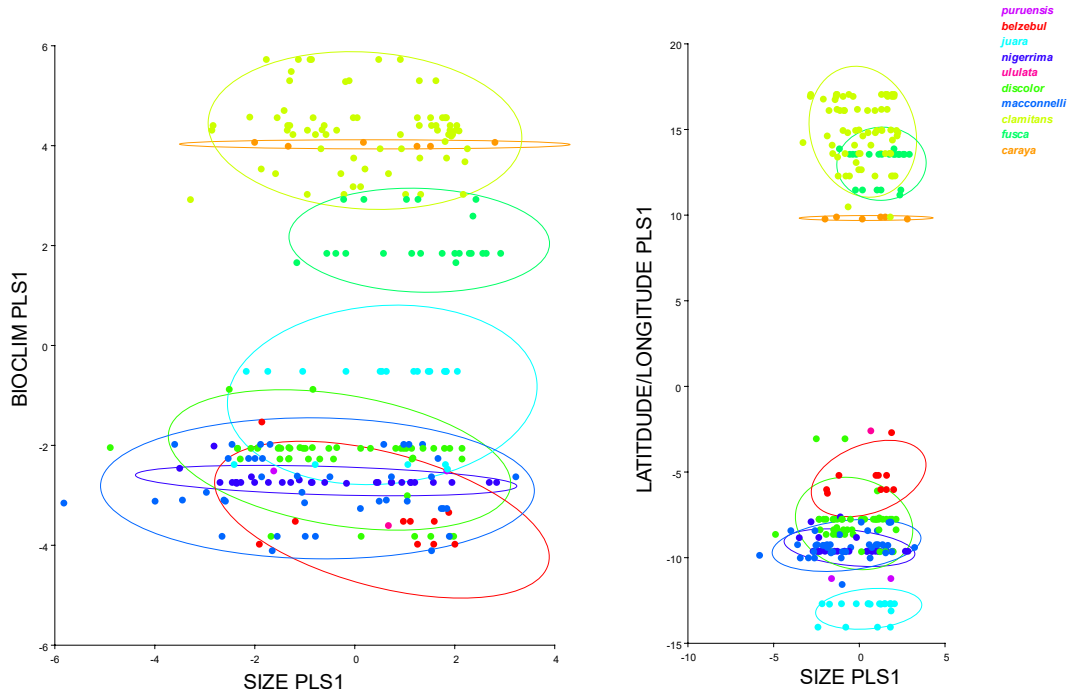
Table 3. Correlation between size and the covariates Climate and Latitude/longitude, as measured by the RV coefficient. The same analysis was performed in each view of the skull for all three genera, *Alouatta*, *Callicebus*, and *Cebus*.

	Size			
	Climate		Latitude/longitude	
	RV	P	RV	P
(A) Dorsal view				
<i>Alouatta</i>	0.024	0.015	0.038	0.002
<i>Callicebus</i>	0.267	<.0001	0.334	<.0001
<i>Cebus</i>	0.021	0.045	0.011	0.143
(B) Frontal view				
<i>Alouatta</i>	0.085	<.0001	0.112	<.0001
<i>Callicebus</i>	0.238	<.0001	0.326	<.0001
<i>Cebus</i>	0.060	<.0001	0.021	0.042
(C) Lateral view				
<i>Alouatta</i>	0.046	0.001	0.059	<.0001
<i>Callicebus</i>	0.330	<.0001	0.399	<.0001
<i>Cebus</i>	0.050	0.000	0.011	0.148

The PLS plot of Size vs BIOCLIM of *Callicebus* showed a great overlapping between Amazonian species (*Ca. lugens*, *Ca. baptista*, *Ca. hoffmannsi*, *Ca. cinerascens*, *Ca. cupreus*, and *Ca. moloch*); nonetheless, part of the Amazonian *Ca. moloch*, *Ca. bernhardi*, and *Ca. donacophilus* (from the Pampas) fell within species from the Atlantic Forest, *Ca. personatus*, *Ca. barbarabrownae*, *Ca. nigrifrons* (which also occurs in the Cerrado) (Figure

29). In the same manner, the Atlantic Forest species *Ca. coimbrai* was closer to Amazonian species. The correlations among these two blocks in dorsal, frontal, and lateral view were 0.557 ($p < 0.0001$), 0.531 ($p < 0.0001$), and 0.613 ($p < 0.0001$), respectively. In the PLS Size vs Latitude/Longitude, Amazonian species and the Atlantic Forest/Cerrado species were far one from another with *Ca. donacophilus* in the middle of both groups (Figure 29). The correlations among Size Block1 and Latitude/Longitude Block1 in dorsal, frontal, and lateral view were 0.6 ($p < 0.0001$), 0.59 ($p < 0.0001$), and 0.654 ($p < 0.0001$), respectively (see Table 4). In both comparisons, Size vs BIOCLIM and Size vs Latitude/Longitude, the correlations were higher in frontal view.

Finally, the PLS plot of Size vs BIOCLIM of *Cebus* showed a great overlapping between all the species. This might be explained by the distributions of some *Cebus* species as *Ce. apella*, *Ce. libidinosus*, or *Ce. cay* that extended through two or more biomes, occupying distinct climatic conditions in each. The correlations among these two blocks in dorsal, frontal, and lateral view were 0.197 ($p = 0.031$), 0.328 ($p < 0.0001$), and 0.360 ($p < 0.0001$), respectively. In the PLS Size vs Latitude/Longitude, *Cebus* was the genus with more overlapping among species when compared with *Alouatta* and *Callicebus* (Figure 29). Nonetheless, it is important to point out that the geographical coverage of *Cebus*' samples was more continuous than in the other two genera. The correlations among Size Block1 and Latitude/Longitude Block1 in dorsal, frontal, and lateral view were low and not significant in all cases (0.122, $p = 0.160$; 0.148, $p = 0.073$; 0.134, $p = 0.109$, respectively (see Table 4).



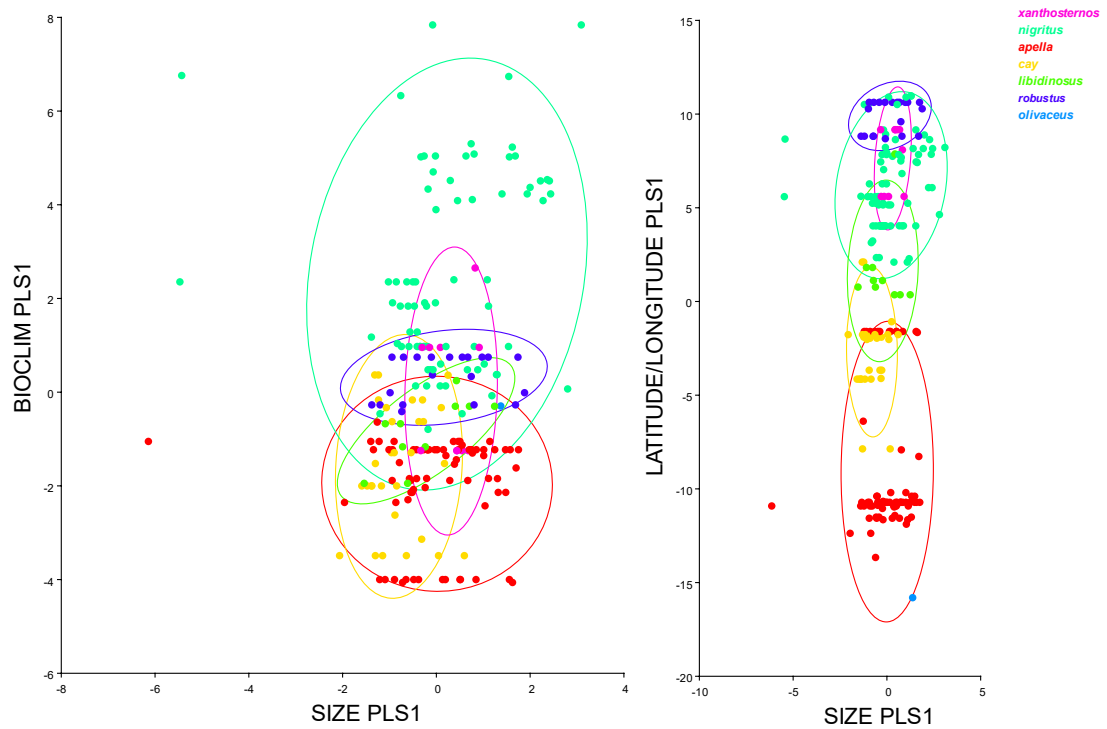


Figure 29. Scatter plot showing the first pair of singular warp axes extracted by two block PLS with skull size as block 1 and bioclimates (left) and latitude/longitude (right) as block 2 in dorsal view of *Alouatta* (top), *Callicebus* (middle), and *Cebus* (bottom) classified by species in all cases.

Table 4. PLS correlation among size covariates Climate and Latitude/longitude as measured by the between-block correlation coefficient of PLS1. The same analysis was performed in each view of the skull for all three genera, *Alouatta*, *Callicebus*, and *Cebus*.

	SIZE									
	PLS1 - Climate					PLS1 - Latitude/Longitude				
	Singular value	P-value (perm.)	% total covar.	Correlation	P-value (perm.)	Singular value	P-value (perm.)	% total covar.	Correlation	P-value (perm.)
Dorsal view										
<i>Alouatta</i>	0.943	0.015	100.00	0.172	0.034	3.904	0.002	100.00	0.198	0.003
<i>Callicebus</i>	0.753	<.0001	100.00	0.557	<.0001	2.527	<.0001	100.00	0.600	<.0001
<i>Cebus</i>	0.580	0.045	100.00	0.197	0.031	1.139	0.143	100.00	0.122	0.160
Frontal view										
<i>Alouatta</i>	1.446	<.0001	100.00	0.311	<.0001	5.515	<.0001	100.00	0.339	<.0001
<i>Callicebus</i>	0.541	<.0001	100.00	0.531	<.0001	1.896	<.0001	100.00	0.590	<.0001
<i>Cebus</i>	0.594	<.0001	100.00	0.328	<.0001	0.926	0.042	100.00	0.148	0.073
Lateral view										
<i>Alouatta</i>	1.773	0.001	100.00	0.227	0.002	6.663	<.0001	100.00	0.246	0.000
<i>Callicebus</i>	1.281	<.0001	100.00	0.613	<.0001	4.231	<.0001	100.00	0.654	<.0001
<i>Cebus</i>	0.896	0.000	100.00	0.360	<.0001	1.121	0.148	100.00	0.134	0.109

Shape

The PLS between Shape (Block 1) and BIOCLIM (Block 2) produced RV coefficients with no clear pattern as the one observed in the previous analysis of size. *Alouatta* presented the highest RVs both in dorsal (0.279, $p < 0.0001$) and lateral (0.177, $p < 0.0001$); *Cebus* presented the highest RV in frontal view (0.395, $p < 0.0001$). *Callicebus* presented the lowest values of RV in two views, dorsal (0.093, $p < 0.0001$) and lateral (0.07, $p < 0.0001$) (see Table 5). The same pattern is observed when comparing Shape (Block 1) with Latitude/Longitude (Block 2), the RV values for each genus were as follow: *Alouatta* (0.271, $p < 0.0001$; 0.116, $p < 0.0001$; 0.182, $p < 0.0001$; in dorsal, frontal, and lateral view, respectively); *Callicebus* (0.095, $p < 0.0001$; 0.237, $p < 0.0001$; 0.072, $p < 0.0001$); and *Cebus* (0.054, $p < 0.0001$; 0.43, $p < 0.0001$; 0.173, $p < 0.0001$). Although all these RV coefficients are also weak (< 0.5) as in the first case with size, the results point out that skull shape is more influenced by covariates as bioclimatic factors (BIOCLIM) and Latitude/Longitude in the case of *Alouatta* and *Cebus* rather than in *Callicebus*, the opposite of what I found in the PLS of size. Since the Block 1 was represented by the univariate centroid size, I only obtained one singular value (SV) and the percentage of between-block total squared covariance explained by the set of PLS1 was of 100% in all cases.

Table 5. Correlation between shape and the covariates Climate and Latitude/longitude under a non-allometric PLS, as measured by the RV coefficient. The same analysis was performed in each view of the skull for all three genera, *Alouatta*, *Callicebus*, and *Cebus*.

	Shape			
	Climate		Latitude/longitude	
	RV	P	RV	P
(A) Dorsal view				
<i>Alouatta</i>	0.279	<.0001	0.271	<.0001
<i>Callicebus</i>	0.093	<.0001	0.095	<.0001
<i>Cebus</i>	0.079	<.0001	0.054	0.001
(B) Frontal view				
<i>Alouatta</i>	0.137	<.0001	0.116	<.0001
<i>Callicebus</i>	0.196	<.0001	0.237	<.0001
<i>Cebus</i>	0.395	<.0001	0.430	<.0001
(C) Lateral view				
<i>Alouatta</i>	0.177	<.0001	0.182	<.0001
<i>Callicebus</i>	0.070	0.000	0.072	0.000
<i>Cebus</i>	0.165	<.0001	0.173	<.0001

In the case of the three views (dorsal, frontal, and lateral) of *Alouatta* the PLS plot of Shape vs BIOCLIM presented similar results that those from the analysis with size, showing overlapping between Amazonian species (*A. puruensis*, *A. belzebul*, *A. discolor*, *A. macconnelli*, *A. nigerrima*, and *A. ululata*), whereas *A. caraya* (from the Cerrado) fell within the species from the Atlantic Forest, *A. clamitans* and *A. fusca* (Figure 30). The correlations among these two blocks in dorsal, frontal, and lateral view were 0.632 ($p < 0.0001$), 0.575 ($p < 0.0001$), and 0.723 ($p = 0.002$), respectively. In the PLS Shape vs Latitude/Longitude, there was great gap among the Amazonian and the Atlantic Forest and Cerrado species. In the former there was a great overlapping excepting for *A. belzebul* which did not overlap with *A. nigerrima* and *A. juara*. The correlations among Shape Block1 and Latitude/Longitude Block1 in dorsal, frontal, and lateral view were 0.617 ($p < 0.0001$), 0.537 ($p < 0.0001$), and 0.711 ($p < 0.0001$), respectively (see Table 6).

Table 6. PLS correlation among shape covariates Climate and Latitude/longitude as measured by the between-block correlation coefficient of PLS1. The same analysis was performed in each view of the skull for all three genera, *Alouatta*, *Callicebus*, and *Cebus*.

	SHAPE									
	PLS1 - Climate					PLS1 - Latitude/Longitude				
	Singular value	P-value (perm.)	% total covar.	Correlation	P-value (perm.)	Singular value	P-value (perm.)	% total covar.	Correlation	P-value (perm.)
Dorsal view										
<i>Alouatta</i>	0.073	<.0001	97.71	0.632	<.0001	0.241	<.0001	98.79	0.617	<.0001
<i>Callicebus</i>	0.029	<.0001	73.57	0.516	<.0001	0.097	<.0001	91.48	0.612	<.0001
<i>Cebus</i>	0.036	<.0001	87.07	0.422	<.0001	0.083	0.001	92.21	0.457	<.0001
Frontal view										
<i>Alouatta</i>	0.049	<.0001	90.34	0.575	<.0001	0.154	<.0001	94.35	0.537	<.0001
<i>Callicebus</i>	0.051	<.0001	87.81	0.615	<.0001	0.170	<.0001	89.90	0.672	<.0001
<i>Cebus</i>	0.106	<.0001	97.76	0.700	<.0001	0.297	<.0001	98.83	0.725	<.0001
Lateral view										
<i>Alouatta</i>	0.044	<.0001	81.55	0.723	<.0001	0.151	<.0001	84.26	0.711	<.0001
<i>Callicebus</i>	0.017	0.045	45.34	0.381	0.003	0.072	0.000	87.72	0.462	<.0001
<i>Cebus</i>	0.048	<.0001	91.47	0.668	<.0001	0.131	<.0001	93.79	0.679	<.0001

The PLS plot of Shape vs BIOCLIM of *Callicebus* presented similar, if not identical, results with those from the Size's PLS with an overlapping between Amazonian species (*Ca. lugens*, *Ca. baptista*, *Ca. hoffmannsi*, *Ca. cinerascens*, *Ca. cupreus*, and *Ca. moloch*); and the Amazonian *Ca. moloch*, *Ca. bernhardi*, and *Ca. donacophilus* (from the Pampas) within species from the Atlantic Forest, *Ca. personatus*, *Ca. barbarabrownae*, and *Ca. nigrifrons* also occurring in the Cerrado) (Figure 30). In the same manner, the Atlantic Forest species *Ca. coimbrai* was closer to Amazonian species. The correlations among these two blocks in dorsal, frontal, and lateral view were 0.516 ($p < 0.0001$), 0.615 ($p < 0.0001$), and 0.381 ($p = 0.003$), respectively. In the PLS Shape vs Latitude/Longitude, there was a gap between Amazonian species and the Atlantic Forest/Cerrado species with *Ca. donacophilus* in the middle of both groups (Figure 30). The correlations among Shape Block1 and Latitude/Longitude Block1 in dorsal, frontal, and lateral view were 0.612 ($p < 0.0001$), 0.672 ($p < 0.0001$), and 0.462 ($p < 0.0001$), respectively (see Table 6).

Finally, the PLS plot of Shape vs BIOCLIM of *Cebus* showed less overlapping among species than in the case of size analysis. Species as *Ce. apella* (Amazonia and Cerrado) and *Ce. olivaceus* (Amazonia) were in the positive end of BIOCLIM PLS1 did not overlap with *Ce. nigritus*, in the negative end of this PLS block, which inhabits the Atlantic Forest and part of the Cerrado. Between these groups, there was an overlap among the remaining species of *Cebus*, *Ce. cay*, *Ce. libidinosus*, *Ce. robustus*, and *Ce. xanthosternos*. The correlations among these two blocks in dorsal, frontal, and lateral view were 0.422 ($p < 0.0001$), 0.7 ($p < 0.0001$), and 0.668 ($p < 0.0001$), respectively. In the PLS Shape vs Latitude/Longitude, presented similar results that those from BIOCLIM comparison. In this case, *Ce. apella* and *Ce. olivaceus* were more distant from other species of *Cebus* which

presented a similar distribution that in the BIOCLIM analysis (Figure 30). The correlations among Shape Block1 and Latitude/Longitude Block1 in dorsal, frontal, and lateral view were high and significant in all cases (0.457, $p < 0.0001$; 0.725, $p < 0.0001$; 0.679, $p < 0.0001$, respectively (see Table 6).

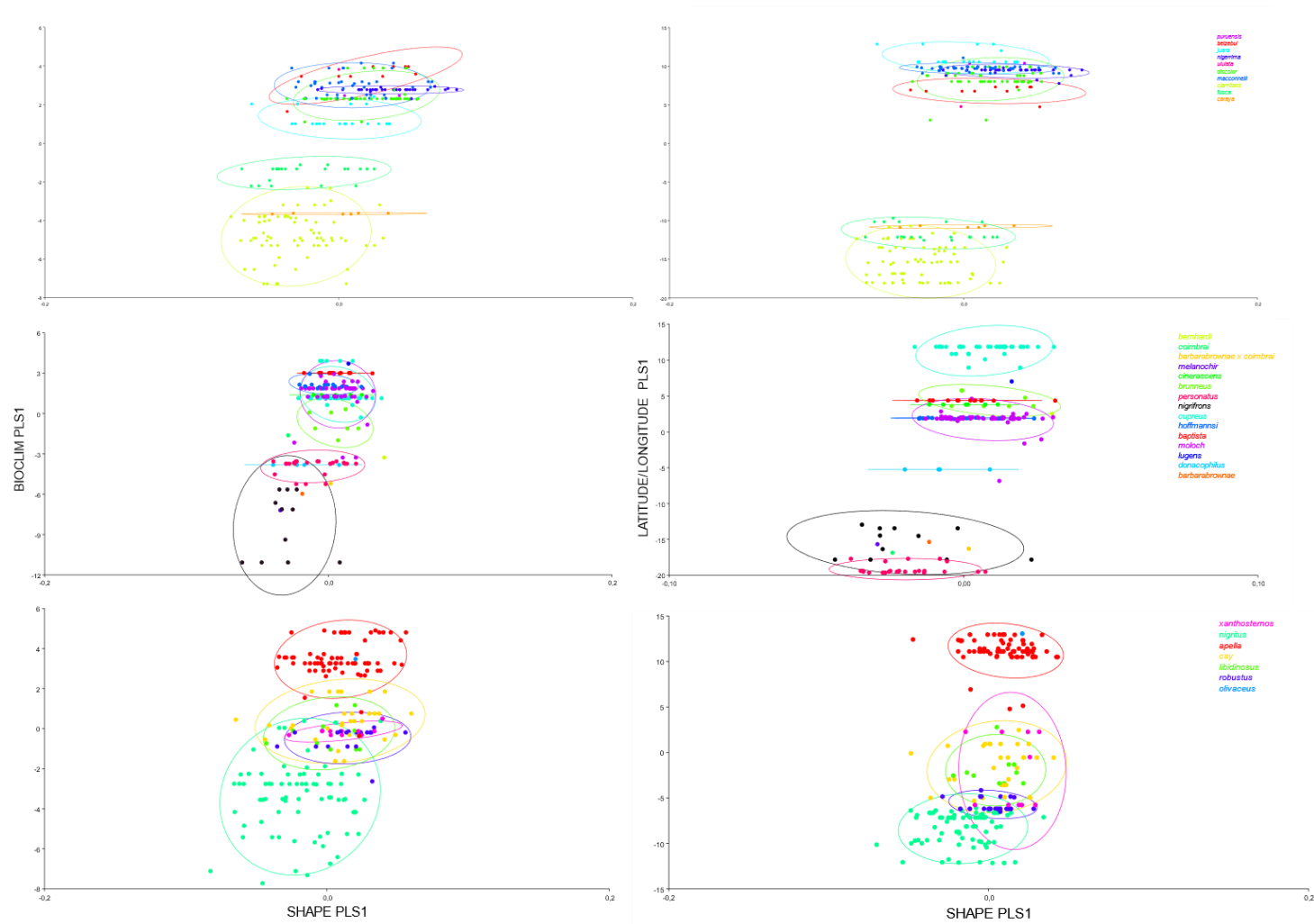


Figure 30. Scatter plot showing the first pair of singular warp axes extracted by two block PLS with skull Size as Block 1 and BIOCLIM as Block 2 (left) and Latitude/Longitude as Block 2 (right) in dorsal view of *Alouatta* (top), *Callicebus* (middle), and *Cebus* (bottom) classified by species in all cases

4. DISCUSSION

Callicebus offered new ways to interpret of what was known for widespread genera besides *Alouatta* and *Cebus* as the colonization of the Atlantic Forest by Amazonian populations of both genera and the posterior occupation of new ecoregions through processes of expansion and contraction of the Amazon and the Atlantic Forest (Lynch Alfaro et al., 2012a,b; Lima et al., 2017; Cortés-Ortiz et al., 2003; Doyle et al., 2021). In this context, titi monkeys presented interesting results that are opposite to those from howler and capuchin monkeys as a strong phylogenetic signal related to size not seen on *Alouatta* nor *Cebus*. Other points related to be addressed when comparing these three genera in terms of size are: 1) differently to *Alouatta* and *Cebus*, species of *Callicebus* from the Atlantic Forest are bigger than the Amazonian ones; 2) *Callicebus* was the least sexually dimorphic genus; and 3) contrary to *Alouatta* and *Cebus*, the allometric effect in *Callicebus* is negligible.

This size-related evidence may be an example of the Bergmann's Rule. This rule postulates a correlation between latitude and body size that predicts that in endotherm species with wide latitudinal distribution, individuals from higher latitudes would exhibit larger sizes (Bergmann, 1848; Meiri, 2011). This rule has been tested and matches in some mammals like the crab-eating fox (genus *Cerdocyon*) only from Southern latitudes to the equator whereas the opposite North to it (Martinez et al., 2013). Nonetheless, there are several examples of a reverse Bergmannian pattern, mainly in small mammals as rodents (Maestri et al., 2016; Medina et al., 2007; Belk and Houston, 2002; Gohli and Voje, 2016). In Neotropical primates this rule has been poorly investigated. Bubadué et al. (2018) tested the Bergmann's Rule, in Cis-Andean South American howler monkeys. Their

results pointed out to a reverse pattern that would be expected for Bergmann's Rule, with Amazonian howler monkeys larger in skull size than those from the Atlantic Forest. More importantly, these authors found that the body size variation in *Alouatta* would be explained by the Rensch's rule, which predicts that sexual dimorphism increases with body size for species whose males are larger than females (Rensch, 1950; Fairbairn, 1997, 2007, 2013; Fairbairn et al., 2007).

According to the results obtained here, species of genus *Cebus* showed, although in a lower degree, the same reversed Bergmann's rule pattern as in *Alouatta*. Moreover, there is statistical evidence to affirm that *Callicebus*' skull size follows Bergmann's rule (see Table 2 and 4). According to my results it might be a positive correlation between allometry and sexual dimorphism in terms of size and, at the same time, these both elements also would be directly linked with the effects of Rensch's rule. Among the three genera analyzed here, *Callicebus* did not present sexual dimorphism neither in size nor shape of the skull and presented the lowest percentages of allometric effect. This is a good starting point to investigate if these two rules, Bergmann's and Rensch's, are mutually exclusive and if the patterns observed here (non-allometric species with wide distributions fulfilling Bergmann's rule and do not the Rensch one and vice versa) might be present in other Neotropical primates.

In regards of ecomorphology, there are important questions to be addressed. Regarding the analysis of PLS of Size vs. Climate and also vs. Latitude/Longitude, species of genus *Callicebus* presented significant values of correlation whereas *Alouatta* and *Cebus* do not (in all the analyzed views). Nonetheless, the correlation of these covariates with shape were much higher in the case of *Alouatta* and *Cebus* than in size. These latter

results agree those of Meloro et al. (2014a), Cáceres et al. (2014), and Meloro et al. (2014b) in which they identified almost identical directions of skull shape changes across biomes and/or bioclimatic variables in *Alouatta* and *Cebus*. However, when introducing *Callicebus* into the analysis, this group presents a completely opposite direction of morphological evolution (See Table 3). This might be related to the phylogenetic relationships and the divergence times between the three genera here assessed. Although belonging to different families, *Alouatta* and *Cebus* are more closely related between them than either of these two taxa to *Callicebus*. The split between Amazonian and Atlantic Forest populations of howler and capuchin monkeys diverged in 1.1 Mya [following a more conservative *Alouatta*'s divergence time as proposed by Cortés-Ortiz et al. (2003)]. In other words, both taxa, *Alouatta* and *Cebus*, had evolved under the same climatic and temporal conditions and there is biogeographical evidence to point out that they both follow similar paths to colonize the ecoregions where are they found in the present (Lynch Alfaro et al., 2015).

This contradictory directions among *Alouatta/Cebus* and *Callicebus* is also reflected in the skull morphology. *Alouatta* for being adapted to eat primarily leaves (but not exclusively) possesses enlarged molars, and narrower incisors, together with a short zygomatic area positioned more posteriorly (Rosenberger 1992; Rosenberger et al. 2011). For having an omnivorous diet, *Cebus* presents a curved rostrum with enlarged incisors and premolars, together with a large zygomatic arch, placed more anteriorly for an efficient bite force (Rosenberger, 1992; Wright 2005; Wright et al. 2009; Rosenberger, 2020); whereas in *Callicebus* there is a loss of prominence of the rostrum which is probably tied to the evolutionary reduction of their snout and a reorganization of their

front teeth for dietary and social reasons (Rosenberger, 2020).

All three genera presented very distinct ecomorphologies, what confirms that although these three groups nowadays inhabit in general the same ecoregions of South America followed different paths at different moments. With more advances in our understanding of historical biogeography and systematics, as well as with more robust analyses, including unanalyzed taxa (such as those groups from the Andean and trans-Andean region), we will be able to complement studies such as the present one and thus better understand the intrinsic forces and extrinsic forces that have shaped the morphology of neotropical primates.

5. CONCLUSIONS

- Regarding size, there is a strong influence of phylogenetic signal in *Callicebus* which is not the case of *Alouatta* and *Cebus*.
- *Callicebus*, the least dimorphic genera analyzed here, followed the Bergmann's Rule presenting bigger species in the Atlantic Forest than in the Amazonia.
- *Alouatta* and *Cebus*, on the other hand, seems to follow the Rensch's rule what explains their morphological differences among sexes.
- In terms of ecomorphology, and although the three genera occupy similar ecoregions in recent times, their evolutionary histories are different creating dissimilar responses to climatic and biogeographical factors.
- The results here obtained are a starting point to continue the study of morphological evolution in other Neotropical primates because we are in an era of constant development of new useful methodologies to elucidate questions related to the evolutionary history of this group of mammals.

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APPENDIX 1 – Biological Material

Alouatta belzebul: BRAZIL. MARANHÃO: Santo Antonio, Rio Tocantins: MZUSP 13483. PARÁ: Cameté: MZUSP 5405, 5407, 5408, 10489; Estrada BR-010, Km 93: MZUSP 8910, 8911, 8937, 8939; Largo do Souza, Rio Iriri: MZUSP 25448.

Alouatta caraya: BRAZIL. PARANÁ: Ilha Sete Quedas: MZUSP 19179; Querência do Norte (Ilha Julião): MZUSP 11155, 11156, 1982; Rio Pacaraí: MZUSP 7707, 7708, 7709.

Alouatta clamitans: BRAZIL. ESPÍRITO SANTO: Pau Gigante: MZUSP 2212. MINAS GERAIS: Rio Matipó: MZUSP 3530, 3531. PARANÁ: Castro: MZUSP 2464; Garuva (Fazenda Rio Turvo): MZUSP 7128, 7131, 7132; Porto Camargo: MZUSP 7711. RIO GRANDE DO SUL: Bom Jesus (Fazenda Monte Alegre): MZUSP 11184, 11185, 19170, 19171, 19175; Guaíba: MZUSP 11111, 11112, 11115, 11116, 11118, 11119, 11121, 11123; Panambi: MZUSP 3189; São Francisco de Paula: MZUSP 19167, 19168; Viamão: MZUSP 11124, 11125, 11126, 11127, 11128, 11130, 11131, 11135, 11136, 19183, 19184. SANTA CATARINA: Corupá: MZUSP 426, 429, 430, 579; Jacinto Machado (Serra de Pedra): MZUSP 11190; Jaraguá do Sul (Ribeirão Luz Vitória): MZUSP 10410, 10411, 10414; Joinville: MZUSP 1669, 1670, 1671, 1672, 1687; São Joaquim: MZUSP 19067, 19068, 19070, 19071, 19073, 19074. SÃO PAULO: Anhembi: MZUSP 8464, 8465, 8466, 8467, 8906, 8907, 8908; Apiaí: MZUSP 2442; Embu: MZUSP 19532; Lins (Fazenda Varjão): MZUSP 5899; Paranapiacaba: MZUSP 407, 408, 412; São Paulo: MZUSP 314, 317, 2344, 2345, 2346, 6737; São Paulo (Horto Florestal): MZUSP 10365; São Paulo (Serra da Cantareira): MZUSP 5864, 5868, 6487; São Sebastião: MZUSP 97.

Alouatta discolor: BRAZIL. AMAZONAS: Fordlandia: MZUSP 18966, 18967, 18968, 18969, 18970, 18971, 18975, 18976, 18977, 18978, 18980, 18982, 18983, 18984, 18985, 18986, 18987, 18989, 18991, 18993, 18994, 18995, 18999. PARÁ: Barreira: MZUSP 18972; Boca do Bacajá: MZUSP 25450; Bom Jardim, Rio Amazonas: MZUSP 5409, 5410, 5573, 5747, 7110, 18996, 24833; Cachimbo: MZUSP 8066, 8067; Caxiricatuba, Rio Tapajós: MZUSP 5328, 5565, 5566, 5567, 5570, 6022, 10565, 19118; Piquiatuba: MZUSP 5329, 5330, 5333, 5574, 10495; Rio Tapajós: MZUSP 3644, 24256; Taperinha: MZUSP 18935.

***Alouatta fusca*: BRAZIL. ESPÍRITO SANTO: Pau Gigante: MZUSP 2205, 2209; Rio Doce: MZUSP 2201, 2206, 2207, 2208, 2211, 2399, 2401, 2402, 2403, 2404, 2406, 2407, 2408, 2414, 19124; Santa Leopoldina, Rio Santa Maria: MZUSP 6202, 11183, 19185. MINAS GERAIS: Machacalis: MZUSP 7876, 7877, 7878; Teófilo Otoni: MZUSP 2734, 2735, 2736, 2737, 2738.**

***Alouatta juara*: BRAZIL. AMAZONAS: Eirunepé: MZUSP 5099, 7114, 10562, 18940; Lago Mamirauá, Fóz do Japurá: MZUSP 19026; Lago Tracajá, Rio Japurá: MZUSP 17540, 17541; Rio Juruá: MZUSP 766, 769, 772, 773; Santa Cruz, Rio Eiru: MZUSP 5102, 5103, 5105, 5107, 5108, 7109, 7111, 10576, 18942, 19080, 19081.**

***Alouatta macconnelli*: BRAZIL. AMAPÁ: Vila Terezinha, Serra do Navio: MZUSP 19159, 19160, 19164, 19166. AMAZONAS: Balbina: MZUSP 22909, 22913, 23171, 23762, 23763, 23765, 24796; Faro: MZUSP 9955, 9956; Igarapé Anibá: MZUSP 5092, 5098, 10573; Itacoatiara: MZUSP 10572; Rio Macujaí, Fazenda Capitão Ene: MZUSP 9672; Silves: MZUSP 10575, 19078. PARÁ: Boiuçu: MZUSP 5095, 5096, 5473, 5474, 19088; Bravo: MZUSP 5094, 5470, 5471, 5478, 5480, 5481, 7113, 19123; Jaquara: MZUSP 19121; Óbidos: MZUSP 3637, 3638, 3639, 3640, 19086, 19087; Paissandú (Igarapé Bom Jardim): MZUSP 9951, 9952, 9953, 9954, 9957, 19085; Posto do DNER, Rio Tracajatuba: MZUSP 19154, 19155, 19156, 19157, 19158, 19161, 19162.**

***Alouatta nigerrima*: BRAZIL. AMAZONAS: Lago do Baptista: MZUSP 4815, 4816, 5289, 5290, 5291, 5293, 5294, 5295, 5296, 5297, 5298, 5396, 5399, 5400, 5401, 5404, 10490, 10492, 10493, 10494, 10564, 10566, 10570, 10574, 18965; Parque Nacional do Tapajós: MZUSP 19119, 24603; Urucurituba, Rio Tapajós: MZUSP 19002. PARÁ: Aruam (Aruá), Rio Arapiuns: MZUSP 5397; Itaituba: MZUSP 3646; Óbidos: MZUSP 3643; Sumaúma: MZUSP 19003.**

***Alouatta puruensis*: BRAZIL. ACRE: Plácido de Castro: MZUSP 7334; AMAZONAS: Redenção, Rio Purus: MZUSP 10559, 10569.**

***Alouatta ululata*: BRAZIL. MARANHÃO: Miritiba: MZUSP 2750.**

***Callicebus baptista*: BRAZIL. AMAZONAS: Lago do Baptista: MZUSP 4957, 5145, 5161,**

5162, 5163, 5164, 5168, 7168, 7169, 7173, 7174; **Lago Tapaiúna:** MZUSP 7166, 7167, 7171.

Callicebus barbarabrownae: BRAZIL. BAHIA: 18.3 Km ao N de Euclides da Cunha: MZUSP 35259.

Callicebus barbarabrownae x coimbrai: BRAZIL. SERGIPE: Fazenda Venturosa: MZUSP 35257.

Callicebus bernhardi: BRAZIL. RONDÔNIA: Nova Brasília: MZUSP 20053.

Callicebus brunneus: BRAZIL. RONDÔNIA: Cachoeira de Nazaré, Rio Machado: MZUSP 20432, 20434, 20435; **Pedra Branca:** MZUSP 22897; **Porto Velho:** MZUSP 7798, 7799; **Santa Barbara:** MZUSP 20141.

Callicebus cinerascens: BRAZIL. AMAZONAS: Prainha, Rio Aripuanã: MZUSP 11807, 11808, 11809, 11810, 11811, 11812.

Callicebus coimbrai: BRAZIL. BAHIA: Fazenda Engenho Campina: MZUSP 35262.

Callicebus cupreus: BRAZIL. ACRE: Manoel Urbano: MZUSP 11237; **AMAZONAS:** **Eirunepé:** MZUSP 5055, 5058, 5059, 5060, 5061, 5063, 5065, 5074, 5078, 5079, 11534; **Pauini:** MZUSP 11831, 11832; **Rio Juruá:** MZUSP 725, 729, 730, 910, 911; **Santa Cruz, Rio Eiru:** MZUSP 5054, 5057, 5062, 5064, 5066, 5067, 5068, 5069, 5070, 5071, 5072, 5073, 5076, 5077, 5081, 5082, 5086, 5088, 5089, 5090; **Santo Antonio, Rio Eiru:** MZUSP 4798. **PARÁ:** Caxiricatuba, Rio Tapajós: MZUSP 5154.

Callicebus donacophilus: BRAZIL. MATO GROSSO DO SUL: Corumbá: MZUSP 3355, 3356, 3358, 3359.

Callicebus hoffmannsi: BRAZIL. AMAZONAS: Fordlandia: MZUSP 11731, 11839; **Urucurituba, Rio Tapajós:** MZUSP 10155, 11743, 11815, 11833, 19534. **PARÁ:** **Itaituba:** MZUSP 3574, 3575, 3576; **Santa Rosa, Ilha de Urucurituba, Rio Tapajós:** MZUSP 11834, 11835, 11836; **Sumaúma, Rio Tapajós:** MZUSP 11741. **RONDÔNIA:** **Brasília Legal:** MZUSP 11715, 11721, 11726.

***Callicebus lugens*: BRAZIL. AMAZONAS: Lago da Cobra, margem direita do Rio Mucajaí: MZUSP 9689.**

***Callicebus melanochir*: BRAZIL. BAHIA: Fazenda Corcovado: MZUSP 35263.**

***Callicebus moloch*: BRAZIL. AMAZONAS: Fordlandia: MZUSP 10151, 11716, 11717, 11718, 11719, 11723, 11724, 11725, 11727, 11729, 11730, 11733, 11734, 11735, 11737, 11738, 11739, 11740, 11744, 11813, 11814, 11816, 11838, 11840, 19364, 19690; Itacoatiara: MZUSP 19549. MARANHÃO: Santo Antonio, Rio Tocantins: MZUSP 13472. PARÁ: Boca do Bacajá: MZUSP 25444; Bom Jardim, Rio Amazonas: MZUSP 5200; Cachimbo: MZUSP 8062; Caxiricatuba, Rio Tapajós: MZUSP 5143, 5144, 5147, 5149, 5150, 5151, 5152, 5159, 5165, 5166, 5167, 5196, 24735; Foz do Curuá: MZUSP 5197; Itaituba: MZUSP 3566; Monte Cristo, Rio Tapajós: MZUSP 3567, 3569, 11817; Piquiatuba, Rio Tapajós: MZUSP 5142, 5156, 5158, 5160; Santarém, Fazenda Marucá: MZUSP 3572. RONDÔNIA: Nova Brasília: MZUSP 20055, 20058; Nova Colina: MZUSP 18956.**

***Callicebus nigrifrons*: BRAZIL. MATO GROSSO: Barretos: MZUSP 1419, 1420, 1421. RIO DE JANEIRO: Itatiaia, Maromba: MZUSP 7427, 7428, 7429, 19548. SÃO PAULO: Boa Esperança do Sul, Fazenda Itaquerê: MZUSP 9812, 9813; Franca: MZUSP 1077; Lins, Rio Tietê (margem direita): MZUSP 5901; Visconde de Soutelo: MZUSP 6562.**

***Callicebus personatus*: BRAZIL. ESPÍRITO SANTO: Colatina: MZUSP 2220, 2221, 2222, 2223, 2225, 2227; Rio Doce, Reserva Natural do Rio Doce em Linhares: MZUSP 2409, 2411, 2412, 2413; Sooterama: MZUSP 11142, 11148, 11152, 11164, 11711, 11712, 11713, 11804, 11805. MINAS GERAIS: Rio Doce, Baixo Rio Suaçuí: MZUSP 5931, 5932; Teófilo Otoni: MZUSP 2712, 2713, 2714.**

***Cebus apella*: BRAZIL. Fordlandia: MZUSP 19564, 19565, 19566, 19568, 19569, 19570, 19571, 19572, 19573, 19574, 19575, 19576, 19577, 19579, 19580, 19581, 19583, 19585, 19589, 19590, 19591, 19592, 19593, 19594, 19595, 19596, 19597, 19598, 19599; Santa Rosa, Ilha de Urucurituba, Rio Tapajós: MZUSP 19602, 19603. MARANHÃO: Miritiba: MZUSP 2577, 2741, 2742, 2743, 2744, 2745, 2746, 2882, 2883, 2884, 2885, 2886, 2887;**

Primeira Cruz: MZUSP 2381, 2386; **Santo Antonio, Rio Tocantins;** MZUSP 13480. **PARÁ:** **Aruã, Rio Arapiuns:** MZUSP 5133, 5674, 5675; **Belém, Utinga:** MZUSP 24250; **Boca do Bacajá:** MZUSP 25452; **Boim:** MZUSP 4291; **Boiuçu:** MZUSP 5126, 5134; **Bom Jardim, Rio Amazonas:** MZUSP 5128, 5132; **Bravo:** MZUSP 5115, 5116, 5117, 10546; **Cachoeira do Espelho, Rio Xingu:** MZUSP 21325; **Caxiricatuba, Rio Tapajós:** MZUSP 5118; **Curral Grande:** MZUSP 3636; **Estrada BR-010, Km 93:** MZUSP 8920; **Foz do Curuá:** MZUSP 5129, 5130, 10499, 10536, 10538, 10544; **Largo do Souza, Rio Iri:** MZUSP 25453; **Monte Cristo, Rio Tapajós:** MZUSP 19563; **Paissandú, Paraná do Bom Jardim:** MZUSP 8956, 8957, 8958, 8959; **Piquiatuba:** MZUSP 10503; **Rio Pucuruí, afl. Tocantins:** MZUSP 13482; **Urucurituba:** MZUSP 19601, 19604, 19605, 19606, 19608, 19609, 19610, 19611, 19612, 19613, 19616. **RONDONIA:** **Brasília Legal:** MZUSP 19561; **Cachoeira de Nazaré, Rio Machado:** MZUSP 20436; **Nova Brasília:** MZUSP 20057, 20059; **Santa Barbara:** MZUSP 20140. **SANTA CATARINA:** **Corupá:** MZUSP 432, 434, 868, 19640; **Joinville:** MZUSP 1667; **São Francisco do Sul, Figueira:** MZUSP 19635, 19638, 19639, 19641.

Cebus cay: BRAZIL. **BRASÍLIA:** **Brasilândia, Fazenda Barma:** MZUSP 28539, 28540. **MATO GROSSO:** **Lagoa Ipavu, Parque Indígena do Xingu:** MZUSP 10716; **Porto Guaporé, Rio:** MZUSP 6961, 6968; **Rio Aricá, Fazenda Aricá:** 6318, 6319, 6320, 6321, 6322, 6325; **São Domingos, Rio das Mortes:** MZUSP 6960, 6963, 6964, 6965, 6969, 6971; **Xavantina:** MZUSP 6713. **MATO GROSSO DO SUL:** **Corumbá:** MZUSP 3361, 3362, 3363, 4317; **Coxim:** MZUSP 3770, 19697; **Miranda:** MZUSP 3773, 3774, 3775; **Palmeiras:** MZUSP 6323; **Rio Piqueri:** MZUSP 19696; **Salobra:** MZUSP 4299, 5788.

Cebus libidinosus: BRAZIL. **ALAGOAS:** **Palmeira dos Indios:** MZUSP 9999; **GOIÁS:** **Anicuns, Fazenda Água Clara:** MZUSP 11095, 11096; **Fazenda Esperança, Rio Araguaia:** MZUSP 2364, 2365; **Goiânia:** MZUSP 10642, 19618, 19619; **Inhumas:** MZUSP 3937; **Jataí:** MZUSP 7905, 7906, 7907; **Ponte Ipê Arcado:** MZUSP 1430. **MARANHÃO:** **Boa Vista:** MZUSP 2488, 2493. **MINAS GERAIS:** **Mariana:** MZUSP 294.

Cebus nigrurus: BRAZIL. **ESPÍRITO SANTO:** **Colatina:** MZUSP 2213, 2217; **Ibiraçu:** MZUSP 2218; **Pau Gigante:** MZUSP 2215, 2216; **Santa Leopoldina, Rio Santa Maria:** MZUSP 11103, 11105. **MINAS GERAIS:** **Rio Matipó:** MZUSP 3532. **PARANÁ:** **Garuva, Fazenda Rio**

Turvo: MZUSP 7133; **Jacarézinho:** MZUSP 421; **Parque Nacional Foz do Iguaçu:** MZUSP 19630, 19631; **Querência do Norte, Porto Natal:** MZUSP 19629, 19642, 19643. **RIO DE JANEIRO:** **Itatiaia, Maromba:** MZUSP 7056; **Parque Nacional do Itatiaia:** MZUSP 7055. **SANTA CATARINA:** **Corupá:** MZUSP 432, 434, 868, 19640; **Joinville:** MZUSP 1667; **São Francisco do Sul, Figueira:** MZUSP 19635, 19638, 19639, 19641. **SÃO PAULO:** **Anhembi, Fazenda Barreiro Rico:** MZUSP 10341, 10342, 10349; **Avanhandava:** MZUSP 2849, 2850, 2852, 2853, 2855, 2856, 2857, 2859, 2860, 2863, 2864, 19652; **Bauru:** MZUSP 466, 489, 490, 491, 2858; **Boraceia:** MZUSP 6887; **Cananéia:** MZUSP 3909; **Capivari, Alto da Serra:** MZUSP 397, 398, 400; **Engenheiro Ferraz:** MZUSP 19620, 19622; **Franca:** MZUSP 790, 794, 815, 828, 831, 832, 833, 2926; **Francisco Morato:** MZUSP 2440; **Itapura:** MZUSP 1934; **Itararé:** MZUSP 1155, 1156, 1157; **Ituverava:** MZUSP 3003, 3004, 3005, 3006; **Lajeado:** MZUSP 2851; **Lins, Rio Tietê (margem direita):** MZUSP 5903, 5904, 5905, 5906, 5907, 6165; **Morro do Diabo:** MZUSP 8493; **Piedade:** MZUSP 6733; **Porto Cabral, Rio Paraná:** MZUSP 6013, 6014, 6015, 6016, 6017; **Ribeirão Preto:** MZUSP 7134; **Rio Grande, Mato Grosso de Barretos:** MZUSP 1418; **São Miguel Arcanjo:** MZUSP 3813; **São Paulo:** MZUSP 2350; **São Paulo, Ipiranga:** MZUSP 6638; **São Paulo, Serra da Cantareira:** MZUSP 6483; **São Sebastião:** MZUSP 98; **Teodoro Sampaio:** MZUSP 8905; **Valparaíso:** MZUSP 3812; **Varjão do Guaratuba:** MZUSP 9640, 9641, 9642.

***Cebus olivaceus:* BRAZIL. AMAZONAS:** **Fazenda Poção, Rio Mucajaí:** MZUSP 9678; **PARÁ:** **Rio Amapari:** MZUSP 9960.

***Cebus robustus:* BRAZIL. ESPÍRITO SANTO:** **Rio São José:** MZUSP 6200, 6201; **Sooterama:** MZUSP 11141, 11143, 11144, 11145, 11146, 11147, 11149, 11151, 11163, 11165, 11166, 11168, 11169, 11170, 11173, 11176, 11179, 11187, 11188, 11189. **MINAS GERAIS:** **Machacalis:** MZUSP 7879; **Mairinque:** MZUSP 2716; **São José da Lagoa, Fazenda Boa Esperança:** MZUSP 5921; **Teófilo Otoni:** MZUSP 2715, 2717, 2718, 2719, 2720.

***Cebus xanthosternos:* BRAZIL. BAHIA:** **Aratuípe:** MZUSP 3857, 3859, 3860, 3861; **Senhor do Bonfim:** MZUSP 2582, 2583, 2584, 2585, 2586, 2587. **MINAS GERAIS:** **Rio Doce, Baixo Rio Suaçuí:** MZUSP 5914, 5915, 5916, 5917, 5918, 5920.

APPENDIX 2 – 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. Frontomalare orbitale: where frontozygomatic suture crosses inner orbital rim.
9. Frontomalare 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. Frontomalare orbitale: where frontozygomatic suture crosses inner orbital rim.
17. Zygo-max superior: antero-superior point of zygomaticomaxillary suture taken at orbit rim.