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**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

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## 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”*.

## 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*.

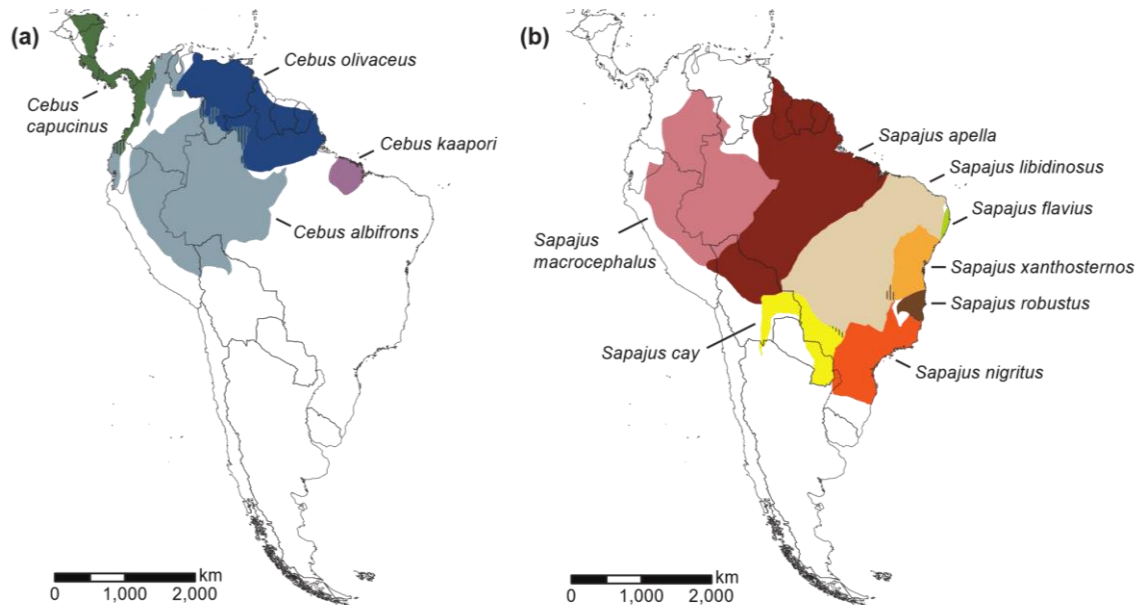
The phylogenetic relationships of *Alouatta* have been poorly investigated and Cortés-Ortiz et al. (2003) were the first to investigate the phylogenetic relationships of *Alouatta*, suggesting that the Central and South American howler monkey species were reciprocally monophyletic groups which diverged 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;

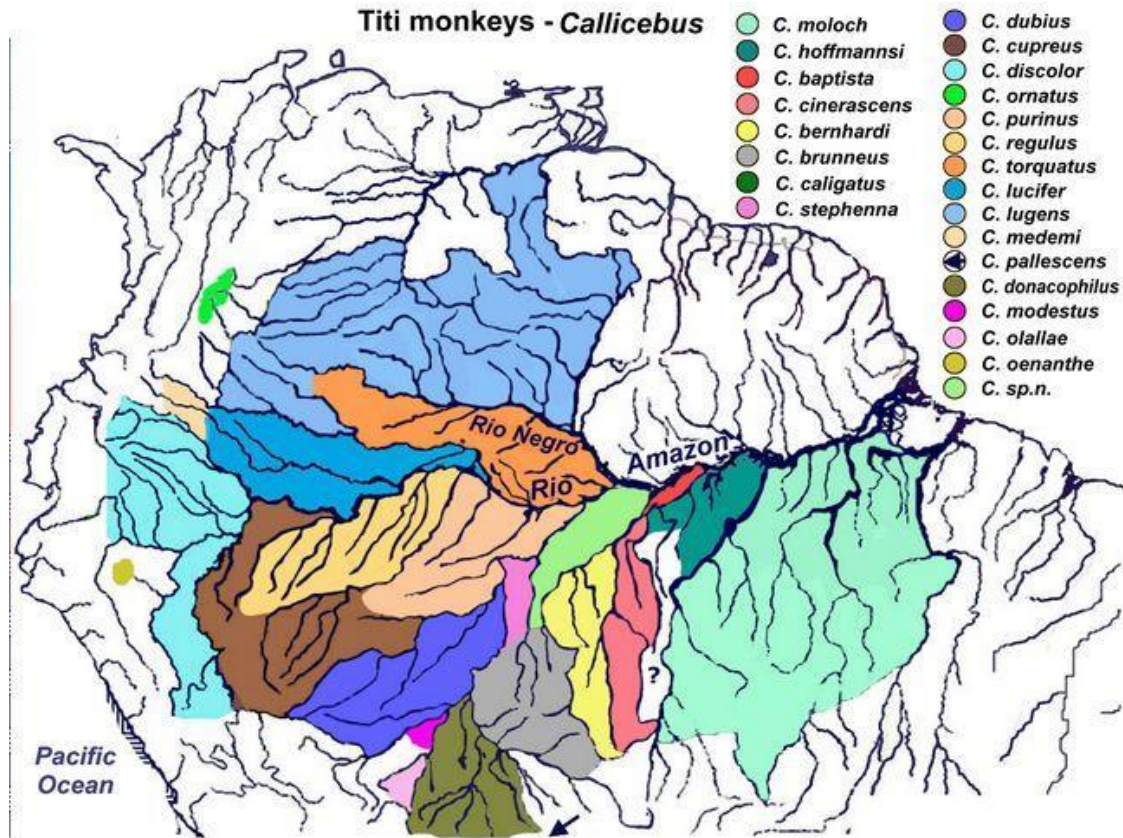
this is the arrangement that I am following at the present contribution.



**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 (Herskovitz, 1988; Herskovitz, 1990; van Roosmalen et al., 2002; Byrne et al., 2016; Byrne et al., 2018) (Figure 5).



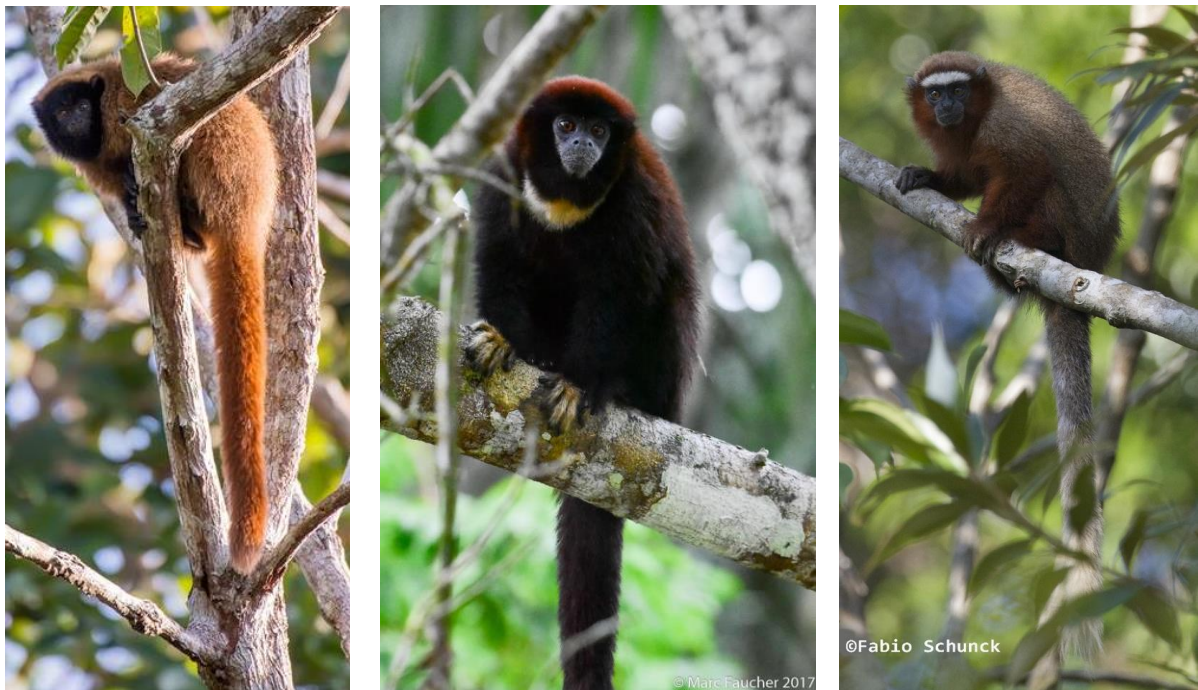


**Figure 5.** Distribution of *Callicebus*' species (after van Roosmalen et al., 2002).

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 (Hershkovitz, 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. Hershkovitz (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.



## 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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